The Southern Pine Beetle

United States
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Expanded Southern Pine Beetle
Research and Applications Program

Forest Service
Science and Education Administration
Technical Bulletin 1631

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U.S. Department of Agriculture

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Preface

In 1973, two chronic forest insect problems, the gypsy moth in the Northeast and the southern pine beetle in the South, were severe. The tussock moth outbreak in the Pacific Northwest was climaxing that year as well. The extensive damage caused by these three insects caused national concern. In August 1973, the Assistant Secretary for Conservation, Research, and Education, U.S. Department of Agriculture, requested that four agricultural agencies—the Agricultural Research Service (ARS), the Animal and Plant Health Inspection Service (APHIS), the Cooperative State Research Service (CSRS), and the Forest Service (FS)—develop coordinated short-term programs to reduce damage caused by the three pests. The appropriation bill was signed by the President in August 1974. The heads of these four agencies plus four knowledgable administrators from research and user groups made up the program board, which participated in the planning and reviewed annual plans of work and budgets. The three-pest program—termed USDA combined Forest Pest Research and Development Program (CFPP)—was coordinated from the Office of the Secretary.

The transfer of technological information acquired during the three CFPP programs was of major concern to this office. Program managers were directed to plan for the most effective means of communicating this knowledge to the planners and managers who needed it. This compendium is one method chosen to accomplish this task; it is the result of the efforts of many scientists from the Department of Agriculture, universities, and State agencies. Although it does not contain all the answers to the southern pine beetle problem, it does explain known methods of control. Equally important, this work defines continuing research and development needs essential to improve further the methods of coping with this periodically destructive insect. The quality and amount of sound and useful information presented in this compendium demonstrate the value of cooperative research by Federal, State, and university scientists and forest pest managers representing a variety of disciplines and experience. Such research must continue if we are ultimately to provide truly effective protection to our forest resources.

Ned D Bayley

Ned Bayley
Acting Assistant Secretary for
Conservation, Research, and Education

Acknowledgements

Jack Coster and Gerry Hertel guided and coordinated the planning and preparation of this book. Each chapter was outlined by a principal author (multiple authors for Chapter 12), these outlines were reviewed and revised by Program management, and the first and final drafts were prepared by the authors for peer review and submission to the Program. The book would not have been completed had it not been for the dedication, patience, and technical skills of all concerned. I am especially grateful to T. L. Payne, Chapter 2; C. W. Berisford, Chapter 3; R. R. Hicks, Jr., Chapter 4; R. N. Coulson, Chapter 5; F. P. Hain, Chapter 6; W. A. Leuschner, Chapter 7; P. L. Lorio, Jr., Chapter 8; R. P. Belanger, Chapter 9; R. F. Billings, Chapter 10; J. E. Coster, Chapter 11; and G. D. Hertel, Chapter 12.

We are appreciative of the intensive reviews by Ron Stark, University of Idaho, Moscow, Idaho; and Fred M. Stephen, University of Arkansas, Fayetteville, Arkansas. Their suggestions contributed to improving several sections of the book.

I wish to commend and extend my heartfelt appreciation to the editor of this entire book, Janet Searcy. The multitude of details and the special problems and frustrations encountered along the way required a great deal of effort and considerable sacrifice on her part. Those who benefit from this publication owe her lasting gratitude, as I do.

Many people from State and Federal government, universities and colleges, various associations and organizations, industry, and the general public participated in or otherwise contributed to the implementation and completion of the Southern Pine Beetle Research and Applications Program. At various times, over 100 investigators and students were involved in the Program. Organizations included 14 universities, 2 State forest services (commissions), 3 forest experiment stations, and one Area of the USDA Forest Service. A number of other State forestry commissions, extension services, forestry associations, military installations, and individual forestry organizations contributed in an informal way to the accomplishment of Program goals.

I hope that we have provided the kind of results that were expected from the Program. To all who contributed in any way, my sincere thanks and appreciation.

R. C. Thatcher

R. C. Thatcher,
Program Manager

Introduction

R. C. Thatcher[1]

1

Because of favorable growing conditions in the South, this part of the country is expected to provide an increasing share of the world's supply of wood and related resources. To do so will require more intensive management and more practical means for dealing with pest outbreaks.

The southern pine beetle (SPB) is a native pest whose existence has been documented since the 1750's. Even though virgin forests were completely cut over by the 1920's and 1930's, the SPB continued to damage the new, second-growth forests.

In the last 100 years, numerous beetle outbreaks have occurred in the 13 Southeastern States (Price and Doggett 1978). At times, outbreaks have erupted simultaneously in several States, causing widespread, often spectacular tree mortality for periods of 2 or more years. Such losses have upset management plans, reduced potential yields from managed forests, and devastated the forest holdings of many small, private, nonindustrial landowners — the principal owners of commercial forest land in the South. In peak SPB years, the glut of beetle-killed timber has temporarily exceeded the capacity of local mills. Because many infestations are small and scattered, salvaging has been impractical and less than 50 percent of the total loss is recovered for use.

SPB Research in the South

Interest in the southern pine beetle usually fluctuates with the occurrence of outbreaks. Research, generally limited to a few university and Forest Service locations, has not been coordinated among organizations and ranges from basic to applied studies. Between epidemics, there is little support for intensive research. And researchers do not adequately address many of the basic needs dealing with the detection, evaluation, suppression, and prevention of outbreaks. Rather than recognizing that the problem is basically a forest management problem, the *symptoms* of which are SPB outbreaks, the forestry community deals with beetle damage only after it has reached a crisis state.

When beetle populations began to cause severe damage in 10 States in the early 1970's, there was a great demand for new or improved ways to deal with the problem. With the approval and funding of the Expanded Southern Pine Beetle Research and Applications Program (ESPBRAP) in 1974, the Federal government made available almost $12 million for a 6-year accelerated research and development effort. The accelerated program filled many gaps in our knowledge about the SPB, such as determining the economic impact of infestations on multiple forest resources, developing sampling techniques and spot growth models, determining the characteristics of susceptible stands, and developing preventive and remedial controls. ESPBRAP was one of three regional, accelerated pest management R&D programs, in the U.S. Department of Agriculture's Combined Forest Pest Program (CFPP) (Ketcham and Shea 1977).

The Expanded Program greatly augmented research, development, and applications efforts throughout the South. Besides bringing together all that was known about the beetle early in the Program, investigators and experts in many disciplines worked on a variety of related tasks. We have benefited from past research and have built a stronger base of knowledge that can be used to manage the SPB and its forest environment. Continuing work is needed to test results under a variety of forest conditions and management objectives and to package and disseminate results in ways useful to resource managers. Soon, we expect to be able to predict future outbreaks and initiate management practices to prevent or reduce potential losses.

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ESPBRAP Planning, Organization, and Management

The 93rd Congress, in its amendment to the budget dated June 11, 1974, stated that the CFPP will

- Implement available technological developments for reduction of losses from the insects (Douglas-fir tussock moth, gypsy moth, southern pine beetle).
- Develop and evaluate new short- and long-term forest pest management systems that will effectively suppress or prevent infestations.

Goals for the Southern Pine Beetle Program were as follows:

- Establish demonstration areas Southwide to illustrate available techniques for reducing beetle damage.
- Develop and pilot test an integrative model for predicting impacts, population levels, and forest susceptibility.
- Complete field and safety tests, formulation studies, and use patterns for pheromones and other behavioral chemicals used for survey and suppression.
- Complete field and safety tests on new or improved toxicant formulations and methods of application.
- Complete studies on natural enemies as potential control agents.
- Develop optimal forest and pest management systems using the above information.

Subsequent deliberations narrowed the list of tasks to be accomplished. Setting up demonstration areas and studying biological control agents that might regulate beetle population numbers were two topics left for later investigation. However, if Program management decided that biological agents were critical to understanding SPB population dynamics or predicting population trends, then funds from the Program budget could be shifted to support work on selected biological agents or organisms (e.g., insect parasites, predators, and diseases). Ultimately, these subjects did receive attention during the Program.

With specific tasks in mind, the principal line officers of the Southern Pine Beetle Program – the Program manager, a research coordinator, and an applications coordinator – were recruited and a 5-year activity schedule was prepared. Management identified three major jobs:

(1) Develop technology to predict damage and population trends.

(2) Develop methods for managing beetle populations and forest stands to minimize damage.

(3) Integrate technology on prediction of damage and beetle population trends, manipulative methods, and cost/benefit data to develop pest and forest management systems.

Next, management developed a plan of work and budget for fiscal year 1975 and submitted it to the *ad hoc* CFPP Program Board for review and approval.

A solicitation package was developed by Program management and sent out to Forest Service units, State agricultural experiment stations, State forestry organizations, and universities in the Southern States. An eight-member *ad hoc* Technical Review Panel was formed to review proposals and recommend actions to Program management.

The research activities needed to achieve Program objectives fell into seven subject areas: social, economic, and environmental impacts; insect sampling and population dynamics; mortality and competition factors; site/stand characteristics of susceptible forests; stand manipulative practices; behavioral chemicals; and toxicants. For each area, management identified a working group consisting of a subject area coordinator and funded investigators working on related projects. Working groups interacted as needed to discuss approaches, share results, review progress, identify additional needs, and recommend needed changes to Program management. When new research and applications projects were suggested, the *ad hoc* Technical Review Panel reviewed them prior to acceptance and funding. In the final 2 years of the Program, when management had identified particular lines of work requiring special skills, specific proposals were solicited from selected individuals and organizations.

In deciding which proposals to fund, management put the projects on a fully competitive basis. Previous performance of proposed principal investigators, the facilities of the performing organization, and the relevance of proposals to achieving Program objectives were three paramount considerations. Management also considered the state of the art and the feasibility of accomplishing proposed work within the time frame and monetary contraints of the ESPBRAP.

After projects were funded, the Program staff interacted with working group leaders, investigators, organizational administrators, and business office personnel throughout the Program. This provided the opportunity for coordination, communication, and monitoring of results, and assured a continuing focus on Program and project objectives.

The activities schedule was revised several times during the Program to reflect attainment of goals earlier than anticipated, the realization that certain tasks could not be achieved on schedule, the identification of unproductive or duplicative work, the need to follow up on promising leads, and the adoption of improved approaches resulting from other research.

Accomplishment reports prepared by investigators were used in planning and managing the Southern Pine Beetle Program. These were submitted twice yearly – a detailed technical report in midwinter, a concise update in midsummer. Management also required plans of work and budget each year to support new or continuing work.

Except for a few cases where formal data-sharing agreements were necessary, scientists freely exchanged data with the understanding that suitable credit would be given for use of such information in publications. No centralized data management system was set up, although final copies of certain data sets were ultimately stored in Forest Service computers in Atlanta and Fort Collins for possible future use.

Technology Transfer and Postprogram Needs

Two major responsibilities of the Southern Pine Beetle Program were to (1) make new technology available to users (technology transfer), and (2) identify additional research and application needs. To accomplish this, many of the procedures developed by the Program must be validated or tested under other outbreak and/or forest conditions. Likewise, many of the results of the Program must be "translated" from highly technical terms to more easily understood language, reduced to simplest terms, or tested under operational conditions involving the usual management constraints. In many cases, training aids, management guidelines, users' guides, training sessions, and workshops and/or symposia are needed to communicate findings more effectively to users.

The responsibility for technology transfer and much of the followup in completing unfinished research and applications work is not vested solely in the Program. Research (Federal and State), State and Private Forestry, State forestry organizations, Cooperative Extension Service, and other professional organizations also have a role to play, as do the land managers themselves. To help accomplish these tasks, Program management prepared and released a report entitled "Communicating Research Results to Practitioners – A Technology Transfer Plan" (1978). The report recommended that technology transfer teams be formed for major subject areas. Each team was to be made up of representatives from research and various Federal, State, and industrial user organizations.

Working with the Southeastern Area of State and Private Forestry, ESPBRAP management organized a Southern Pine Beetle Technology Transfer Task Force to review research findings, to assess needs and priorities for passing these results on to users, and to recommend means for accomplishing technology transfer and evaluating its effectiveness. Their report (U.S. Department of Agriculture Forest Service 1979) recommended, among other things, that the technology transfer teams continue work in eight applications areas: (1) silvicultural practices and stand-rating systems, (2) guidelines for utilizing beetle-killed timber, (3) socioeconomic guidelines, (4) new insecticides and improved spray systems, (5) sampling methods and predictive models, (6) aerial survey and navigation systems, (7) behavioral chemicals, and (8) integrated management strategies. Each team was asked to review research in its respective area, to identify additional research and/or applications studies needed to facilitate implementation, to identify opportunities for demonstrations and implementation of research findings, and to document recommended followup actions. A special report, "Southern Pine Beetle Research, Applications, and Implementation Activities for the Southern Forest Community" (Belanger et al. 1979a), summarized the activities needed to set the stage for completing work and implementing ESPBRAP results.

Program management has also met with Forest Service research representatives from the Washington Office and the Southeastern and Southern Forest Experiment Stations to identify research needs. A number of basic and applied research tasks constitute opportunities for followup which will lead to the filling of important voids or capitalizing on earlier research findings. If resources are available, the southern Federal research community has indicated that they will consider this "unfinished business," either through in-house or extramural efforts during the next 5 years.

In addition to technical and semipopular articles in refereed journals, the Program put out a newsletter ("Southern Pine Beetle News"), a series of How-To handbooks, technical bulletins, symposium proceedings, a number of southern pine beetle fact sheet Technology Updates (through the Southeastern Area), and a variety of feature articles and special reports. State and Private Forestry, Extension, and State forestry organizations also released some of the Program's results in other forms suited to the needs of their clientele. These and other activities will continue for several years to assure that the technology from the Southern Pine Beetle Program is fully utilized.

A Word About This Book

The compendium is intended to accomplish three purposes: first, to present a synthesis of the knowledge on the southern pine beetle with emphasis on the accomplishments of the Expanded Southern Pine Beetle Program; second, to present to all users a summary of what we know about the beetle problem and how to deal with it; and third, to define continuing research and development needs for the future.

The chapters were prepared, for the most part, by single authors and reviewed by people knowledgable in the respective fields. The early chapters are concerned with basic scientific information needed to understand and formulate forest or integrated pest management approaches. Later chapters deal with management practices and materials – the alternative control tactics. These subjects are followed by a discussion of how integrated pest management strategies are being developed for the SPB. Finally, we present the research and development needs identified by the technology transfer teams. Here, we recognize that continuing research and development and the implementation of Program findings will rest on the adequacy of future funding in the USDA Forest Service, State Agricultural Experiment Stations, State forestry commissions, and universities. Regulation of southern pine beetle outbreaks in the future will be possible only if a continuous program of monitoring, research, applications, and implementation is undertaken.

Life History and Habits

Thomas L. Payne[1]

2

Introduction

The southern pine beetle (SPB) – *Dendroctonus frontalis* Zimmermann (Coleoptera: Scolytidae) – is the most destructive insect pest of pine forests in 13 Southeastern States and in parts of Mexico and Central America. This is a well-worn statement but nonetheless richly deserved and quite accurate. The beetle ideally represents the definition of its genus – killer of trees.

The southern pine beetle is one of more than 12 American species of *Dendroctonus.* It is a primary bark beetle pest, attacking several coniferous species throughout its range. The SPB is an aggressive tree killer that can attack and overcome healthy, vigorous trees when its populations are large (epidemic). But its success is somewhat limited when its populations are quite low (endemic) and attacks are confined to weakened or dying trees, host material attacked by other insects, particularly the omnipresent *Ips* species, or even downed timber.

Most outbreaks are of relatively short duration (e.g., 2 to 3 years). This fact has led to the belief that the beetle is cyclical in nature, particularly since major epidemics seem to occur about every 10 years. In fact, a feature that differentiates SPB somewhat from other species of *Dendroctonus* is its decided periodicity in the level of activity where outbreaks have recurred over the years. MacAndrews (1926 unpublished) summed up the situation aptly: "It is either abundant, killing up to 50 percent of the stands of pine over large areas and killing out groups of pine here and there throughout the country, *or* so rare during the intervening years that it is difficult even to make collections."

Somewhere within the beetle's range, epidemic populations may be found almost every year. And beetle activity fluctuates significantly in local areas and across the range of the insect (fig. 2-1). In Texas, for example, infestation levels have fluctuated dramatically over the last 20 years but not necessarily on a typical 10-year cycle (fig. 2-2).

Adult SPB attack the living host tree by boring through the bark and feeding upon the phloem tissue, where they also oviposit for the next generation. Their ability to overtake host trees is due, in part, to their mass attack on trees over a relatively short period of time. At times, such behavior makes it possible for them to overcome even the most resistant host. Also, the beetle produces multiple overlapping generations each year throughout its range – a fact that adds to its effectiveness as a destructive pest.

Long before formal records of its damage were kept, accounts suggest that the southern pine beetle plagued virgin southern yellow pine forests over large areas in the late 1700's and early 1800's. Price and Doggett (1978) found accounts, from Moravian settlers and others dating back to 1750, describing the destruction of vast amounts of pine timber due to the "mischief" of what appears to have been bark beetles. Oldtimers in east Texas report that early in this century settlers used beetle infestations to clear the land for pasture. First they hit the trees with the back of an ax and then leaned infested "sticks" against them (J. P. Vité personal communication).

No doubt some of the earliest accounts reported damage due to more than one species of bark beetle: pre-nineteenth century observers did not have the benefit of Dr. Charles Zimmermann's initial description of the species (1868). However, it is most probable that SPB were involved in many of these outbreaks.

Early accounts of tree mortality caused by the southern pine beetle are fragmentary, but one can still determine its general impact. For example, St. George and Beal (1929) reported that in a single outbreak, timber valued at $2 million was destroyed and that timber killed by SPB from 1891 to 1929 had a value of at least $50 million. Records compiled from sketchy data by Price and Doggett (1978) for 1882 to 1960 showed that the SPB was responsible for killing over 200,000 cords and 500 million board feet of timber.

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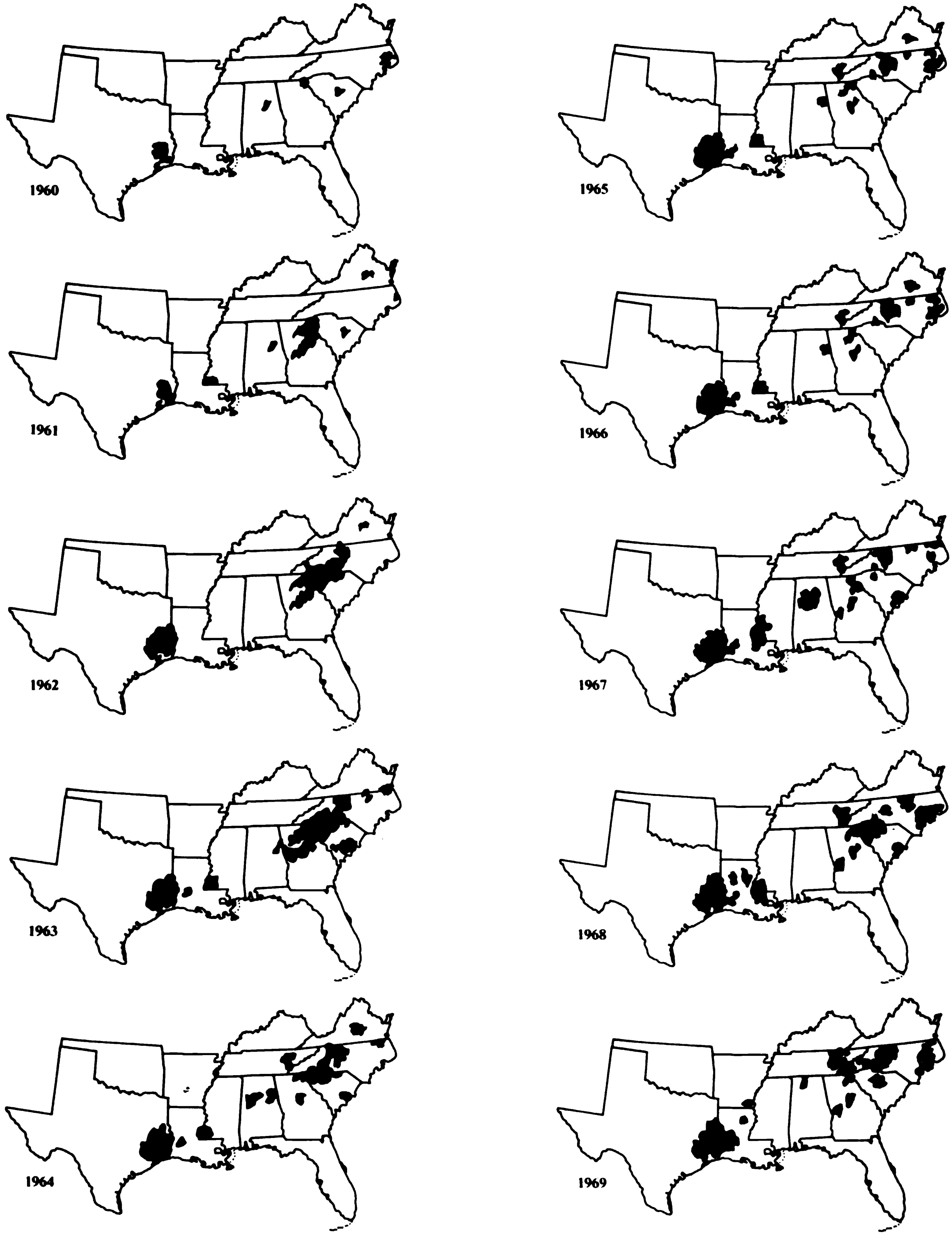
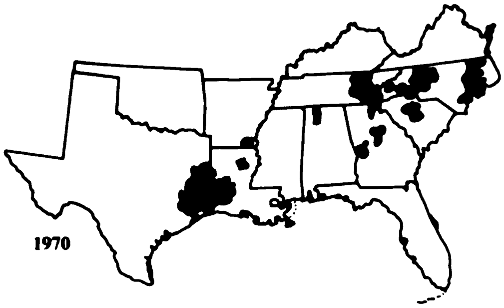
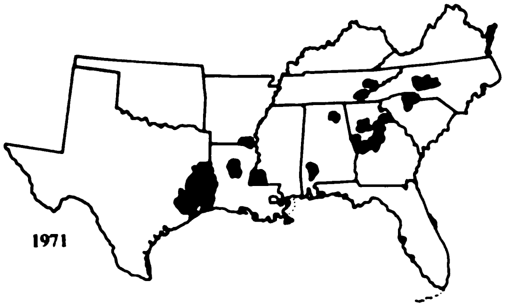
Figure 2-1 – Distribution of southern pine beetle infestations in the United States from 1960 through 1979 (after Price and Doggett 1978).

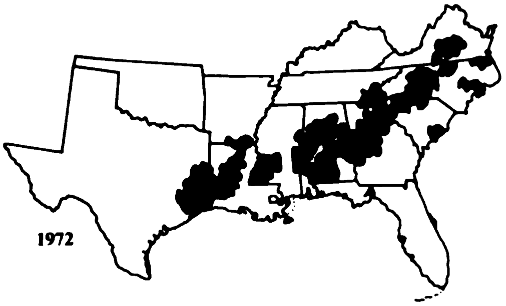




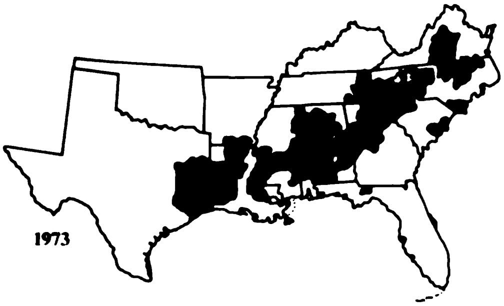
1970



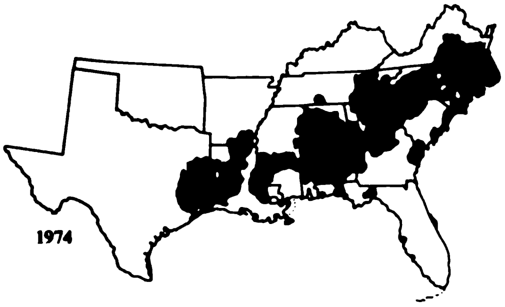
1971



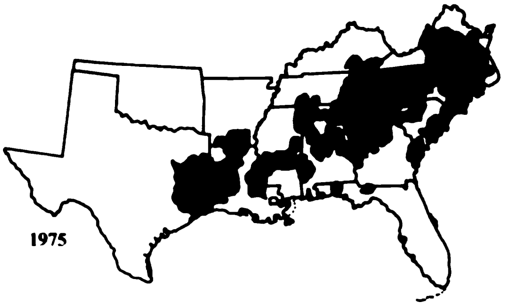
1972



1973

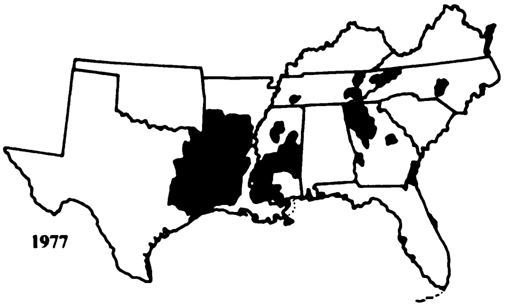


1974

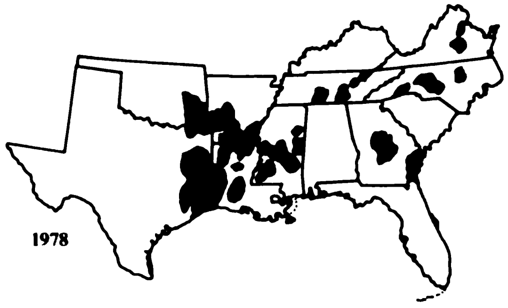


1975

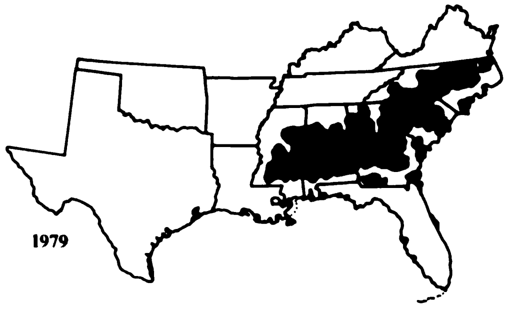
1976



1977



1978



1979

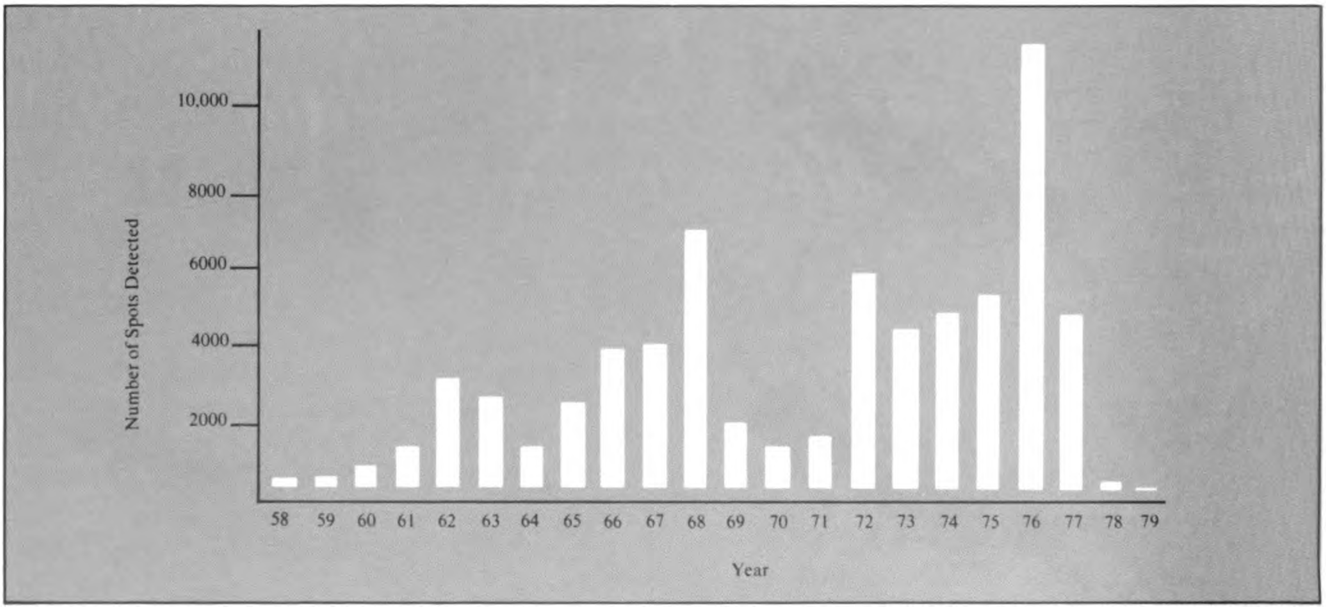
Since 1960, more accurate records have been kept on the damage caused by the beetle in the Southeast. Data compiled from 1960 to 1978 for 12 States (Alabama, Arkansas, Florida, Georgia, Kentucky, Louisiana, Mississippi, North and South Carolina, Tennessee, Texas, and Virginia) show an estimated total volume of timber killed of nearly 9 million cords and 3 billion board feet. This loss has been valued at more than $225 million. Fluctuations in the size of infested areas and volume killed each year over that time period have been quite striking.

Considerable destruction by the beetle has also occurred in Mexico and Honduras; however, documentation of losses in these countries is much less complete than in the United States. Fox et al. (1964) reported that an infestation in Honduras extended over 4.9 million acres (2 million ha) from 1962 through 1964. Devastation of pine forests in Mexico and Central America by the SPB is undoubtedly much more extensive than available records indicate.

As would be expected, the significance of the southern pine beetle as a forest pest has stimulated much concern and numerous investigations. Hopkins (1909b) carried out a monumental study to describe aspects of the biology and behavior of the beetle. Since that time, other studies have examined the problem from all angles (*see* reviews by Thatcher 1960, Dixon and Osgood 1961, Coulson et al. 1972b).

Although we have learned a lot about the pest, its host, and associates, we have not come up with effective means for dealing with the beetle on a long-term basis. It is not surprising, then, that our need for an integrated pest management system – a system that would incorporate detailed knowledge of the pest, its host, and the environment as a functional component of overall forest management – became apparent in the early 1970's. At that time a massive outbreak occurred in 10 Southeastern States. Under the USDA Expanded Southern Pine Beetle Research and Applications Program (ESPBRAP), knowledge of the life history and habits of the SPB has been greatly expanded. This chapter, a blend of previous and new knowledge, explains our current understanding of the life history and habits of the southern pine beetle.

Figure 2-2. – Number of southern pine beetle infestations detected in Texas, 1958 - 1979 (after Texas Forest Service 1978).



Taxonomy

Zimmermann originally described the southern pine beetle in 1868, placing it in the family Hylurgidae under the tribe Hylurgi. He synonymized it with *Bostrichus frontalis* Fabr. in his description. This was later corrected by Le Conte (1876). SPB was placed in the family Scolytidae. In 1963, Stephen Wood synonymized *Dendroctonus arizonicus* Hopkins, which occurred in Arizona and New Mexico, and *Dendroctonus mexicanus* Hopkins, which occurred in Mexico, with *Dendroctonus frontalis* Zimmermann. Later Rose (1966 unpublished) suggested distinct differences between *D. frontalis* and *D. mexicanus* based to a large extend on host preferences, and recommended that further investigations be undertaken.

After years of controversy about the beetle's taxonomy, Vité et al. (1974) provided conclusive evidence, based upon biological and biochemical studies, that *D. frontalis* and *D. mexicanus* are two separate species. They found that beetles from Texas, Virginia, and Arizona differed significantly from the Mexican species in aspects of external morphology, gallery construction, host species preferences, structure of the male seminal rod, and in pheromone production. In addition, the Texas beetles failed to breed with the Mexican beetles. Their findings prompted Wood (1974) to reinstate *D. mexicanus* as a valid species. Furthermore, their findings have been cor-

Figure 2-3. – Present known distribution of the southern pine beetle (after Hendrichs 1977 unpublished).

roborated by subsequent efforts. Lanier (1977 unpublished) showed through breeding experiments and karyotype analyses that *D. frontalis* from the southeastern United States, Arizona, and Mexico are conspecific; whereas *D. mexicanus* is chromosomally distinct and reproductively isolated from them. He confirmed the seminal rod differences between the species and that where *D. frontalis* occurs in Mexico, it is found on host species different from *D. mexicanus.* This finding was also reported by Hendrichs (1977 unpublished).

Geographical Distribution and Hosts

There has been confusion as to the distribution of the southern pine beetle in the United States (i.e., was it in Arizona?) and Central America (i.e., was it in Mexico, or was the beetle *D. mexicanus*?). The studies of Vité et al. (1974, 1975) and the revision by Wood (1974), coupled with the surveys of Lanier (1977 unpublished) and Hendrichs (1977 unpublished), have provided an accurate account of the present distribution of the beetle (fig. 2-3).

The southern pine beetle occurs in North America south of a line from New Jersey to central Arizona, south in Central America to northern Nicaragua. It has also been reported in Delaware, Pennsylvania, Ohio, New Jersey, Indiana, Illinois, and Missouri (St. George and Beal 1929). Vité (1974) noted that under the present concept of the geographical distribution of the beetle, two large areas are involved – the southern and southeastern United States, where the distribution is continuous and roughly coincides with the distribution of loblolly pine (*Pinus taeda* L.), and an area ranging from Arizona to Honduras, where the populations are not so continuous, being interrupted by the Isthmus of Tehuantepec and Guatemala.

Anderson, Berisford, and Kimmich (1979) found significant differences in the electrophoretic analyses of six genes in beetles from Texas, Georgia, Virginia, Arizona, and Mexico. Although *D. frontalis* populations occur in Arizona and Mexico, they appear to have become genetically differentiated from each other. Genetic evidence supports the possibility that the disjunct Mexican and Arizonan populations of the beetle diverged from the main body of the species in the southern and southeastern United States.

The southern pine beetle has been reported to attack and kill all pine species in its range (Hopkins 1909b, St. George and Beal 1929, Dixon and Osgood 1961). In the Southeastern States it prefers loblolly and shortleaf pine (*P. echinata* Mill.) but has successfully colonized pitch pine (*P. rigida* Mill.), Virginia pine (*P. virginiana* Mill.), table-mountain pine (*P. pungens* Lamb.), eastern white pine (*P. strobus* L.), longleaf pine (*P. palustris* Mill.), spruce pine (*P. glabra* Walt.), slash pine (*P. elliotti* Engel.), as well as red spruce (*Picea rubens* Sarg.) and Norway spruce (*P. abies* L.). SPB have also attacked and killed Japanese red pine (*P. densiflora* Sieb. and Zucc.), red pine (*P. resinosa* Ait.), and pond pine (*P. serotina* Michx.). In Arizona and New Mexico, the SPB has been reported only from ponderosa pine (*P. ponderosae* Laws.) (Hopkins 1909b, Wood 1963). However, more recent investigations revealed that its attacks are limited to Apache pine (*P. engelmannii* Carr.) (Vité et al. 1974, 1975; Lanier 1977 unpublished; Hendrichs 1977 unpublished). Exceptional hosts (e.g., *P. strobus* or *Picea* spp.) are occasionally attacked in a "spill over" during an epidemic in the preferred host types. Such exotic species do not support epidemics, though (J. P. Vité personal communication).

In the northeastern part of its range in Mexico, the southern pine beetle attacks *P. teocote* Schiede and Deppe on the gulf side of the Sierra Madre Orientale in Nuevo León (Vité et al. 1974, Lanier 1977 unpublished, Hendrichs 1977 unpublished). In southern Mexico, it is found at lower elevations coinciding with the range of *P. oocarpa* Schiede, on the gulf side of the Sierra Madre Orientale and the plateaus of Chiapas, as well as the Pacific slopes of Chiapas, the Sierra Madres del Sur, and the Sierra Madre Occidentale (Lanier 1977 unpublished and Hendrichs 1977 unpublished). SPB has also been found in Pringle pine (*P. pringlei* Shaw), in Guerrero on the Pacific coast (Hendrichs 1977 unpublished).

In Honduras the SPB occurs at lower elevations coincident with *P. oocarpa* but has also been reported in *P. pseudostrobus* Lindl. (Vité et al. 1974, 1975; Hendrichs 1977 unpublished). It has been found only in *P. oocarpa* in Nicaragua (Vité et al. 1974, 1975). The beetle has been reported from El Salvador, but the host species was not given (Hendrichs 1977 unpublished). The presence of the beetle in *P. oocarpa* along the Guatemalan border of Mexico and in Honduras and Nicaragua suggests its presence in Guatemala, since the host is abundant; however, the SPB has yet to be reported from that country.

Life Stages

The southern pine beetle is a multivoltine species with a complete metamorphosis consisting of the egg, larval, pupal, and adult stages. Detailed descriptions of the life stages were presented by Hopkins (1909b), and have been subsequently added to by others (references in Thatcher 1960 and Dixon and Osgood 1961).

Egg

The egg is slightly oblong to oval with rounded ends (fig. 2-4A). It is opaque, pearly white, and shiny, measuring about 1.5 mm long by 1 mm wide. The egg stage lasts from 3 to 11 days, at a temperature range of 30° to 15° C and as long as 34 days at temperatures as low as 10° C (Gagne 1980 unpublished).

Larva

The larva is a subcylindrical, wrinkled, legless grub with 3 thoracic and 10 abdominal segments (fig. 2-4B). It is yellowish white in color. Upon emergence from the egg, the larva is curved and approximately 2 mm long. Its head is prominent, having well-developed mouthparts with the mandibles stout and dark. In fact, the mandibles begin to show through the egg covering approximately 1 day before eclosion. The head and last abdominal segment are clothed with a few long, white hairs. The mature larva is 5 to 7 mm long. Its body is essentially straight, with the head a reddish color, and with frontal

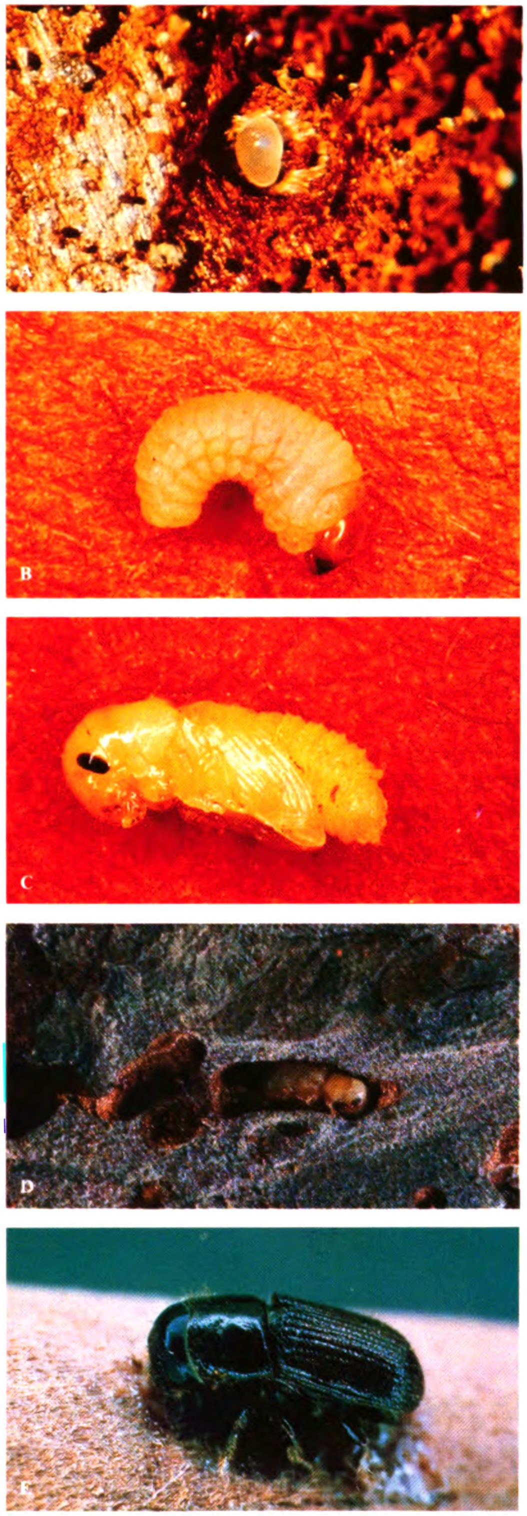


Figure 2-4. – Life stages of the southern pine beetle: A – egg; B – larva; C – pupa; D – callow adult; E – mature adult.

elevations or tubercles and a few long hairs. The mandibles are reddish black with obscure antennae situated in depressions just above the bases of the mandibles.

Fronk (1947) investigated the larval instars using head capsule measurements and Dyar's Law, and determined that the SPB has four instars with the following ranges in head width: 1st instar – 0.294 - 0.336 mm; 2nd instar – 0.378 - 0.504 mm; 3rd instar – 0.547 - 0.672 mm; 4th instar – 0.756 - 0.960 mm. Fronk pointed out that the largest individuals of one instar may be larger than the smallest individuals of the next larger instar. Goldman and Franklin (1977) and Mizell and Nebeker (1979) also found four larval instars in their investigations. Fronk's ratio of increase for instar growth (1.39) fell within the range found by Mizell and Nebeker (1.34 - 1.44). The overall larval stage lasts from 15 to 40 days, over a temperature range of 25° to 15° C (Gagne 1980 unpublished). Individual larval stages have durations ranging from 7 to 13 days (Fronk 1947).

Pupa

The pupa has the general color of the larva (yellowish white) and is fragile. It has the form of the adult, but with the wing pads and legs folded beneath and the abdominal segments exposed (fig. 2-4C). Fleshy tubercles and spines are present on the posterior edges of its second and seventh abdominal segments. The front of the head has a groove. Pupae range in size from 3 to 4 mm in length. The pupal stage lasts 5 to 17 days, over a temperature range of 30° to 15° C (Gagne 1980 unpublished).

Adult

New callow adults are yellowish white (fig. 2-4D). They change from this color to yellowish brown to reddish brown, finally becoming dark brown approximately 1 week before the adult is ready to emerge from the host tree. This stage lasts from 6 to 14 days, over a temperature range of 30° to 15° C (Gagne 1980 unpublished).

The adult SPB is cylindrical and somewhat stout to elongated (fig. 2-4E). It is 2 to 4 mm in length and brownish to black in color. The head is broad and prominent, with well-developed chewing mouthparts and median elevations forming a distinct frontal groove. The front of the head is coarsely punctured and channeled in both sexes. The elevations, or tubercles, are rougher and more acute on the male, while the middle front of the female's head is more convex and shiny. The back of the head is thickly covered with very fine punctures.

The eyes are compound, round to oval and are situated behind the base of each antenna. The antennae are seven-segmented, consisting of the basal pedicel, elongated scape, four-segmented funicle, and an enlarged club.

The prothorax is shiny and slightly narrowed toward the head. Its surface is thinly covered with different-sized punctures and a relatively smooth, distinct dorsal line. The elytra have fine to coarse rubosites between rows of obscure to distinct punctures. The elytral declivity is convex. Females are distinguished from males by the presence of a transverse, rather broad elevated ridge, called a mycangium, on the anterior pronotum. Males lack the mycangium but have a distinct frontal groove, and elevations or tubercles on the head are more distinct.

Generations

The duration from egg to adult ranges from 26 to 54 days, depending upon the season (Thatcher 1960, 1967). The beetle may have as few as three generations per year in the northern part of its range (North Carolina, Virginia) and as many as seven to nine generations per year in the southern parts of its range (Texas, Honduras) (Thatcher 1960). However, the subject of discrete generations in the higher numbers has been questioned, due to the overlapping of successive generations (*see* Chapter 5).

MacAndrews (1926 unpublished) presented the following early predictive model by which to determine the time of successive generations: "The emergence of the first generation was correlated with the opening of the blossoms of the flame-colored azalea (*Rhododendron calendulaceum*). That of the second with the opening of mountain laurel (*Kalmia latifolia*) blossoms. The third with sourwood (*Oxydendrum aboreum*) blossoms."

Factors Influencing Development

There are several abiotic and biotic factors that influence the development of the beetle through its life stages. Temperature probably represents the greatest single abiotic influence and generally affects the developmental rates of the various stages as well as their behavior (Fronk 1947, Bremer 1967 unpublished, White and Franklin 1976, Gagne 1980 unpublished; *see* Chapter 5). Parasites and predators of the various life stages, as well as competitors for the beetle's food supply, have significant effects on the life stages of the beetle (Dixon and Payne 1979b, Birch et al. 1980, T. D. Paine personal communication; *see* Chapters 3 and 5). These probably represent the more important biotic influences, along with tree physiology and site and stand parameters, which affect host susceptibility (Hodges et al. 1979; *see* Chapter 6).

Life Cycle and Behavior

The life cycle of the southern pine beetle can be characterized as a sequence of behavior components that culminate in propagation of the species. The sequence begins with the emergence of brood adults from their host trees. They fly from the host tree where they developed to a new host tree, where they bore through the bark and start constructing galleries in the phloem-cambium tissues. Just prior to or at the onset of the boring activity, the adults release pheromones (secondary attractants). Perception of the pheromones, as well as host odors released from the freshly wounded tree, stimulates aggregation on the tree by other SPB in the area. As these beetles attack the tree, they also release pheromones, which, along with host odors, attract more beetles. As a result of this aggregation behavior, the tree is successfully attacked, mating takes place, egg galleries are constructed, eggs are deposited, broods develop, and adults emerge to attack new host trees.

Although biological systems generally defy precise behavioral classifications, the activities of the SPB can be broadly classified in terms of host selection, aggregation, colonization, reemergence and emergence, dispersal, and overwintering (Wood 1972, Vité and Francke 1976).

Host Selection

Initial Attacks

Conceptually, host selection has been attributed to the efforts of beetles that initially attack susceptible host trees. They are commonly referred to as "pioneer" beetles (Borden 1974). Pioneers are essential, for they must successfully establish a focal point for the next generation. For the SPB, females are responsible for host selection. The females must locate suitable host trees without the aid of secondary attractants and thus are the first to become established in new host trees. Male SPB enter the picture only after the females have selected and successfully attacked a host and secondary attraction has been initiated.

Seasonal Behavior

Several investigators have indicated that beetle populations behave differently in the winter, spring, summer, and fall (Thatcher and Pickard 1967, Franklin 1970a, Hedden and Billings 1977, Billings 1979; *see* Chapter 5). This is consistent with the seasonal behavior of other organisms. SPB disperse in the fall, so that by winter the populations are often scattered throughout the forest in single trees and small infestations. Some beetles may also remain in small groups of infested trees in larger spots. These populations remain dispersed until spring, and development proceeds at a slow rate. Some infestations are associated with lightning-struck trees (Hodges and Pickard 1971). In general, overwintering spots seem insignificant because of their small size and widespread distribution, the lack of spot growth, and very slow crown discoloration. However, with the arrival of warm spring weather, the picture often changes dramatically. During March through May, the emergence and flight of brood adults lead to the initiation and growth of larger infestations. During the summer months, infested trees deteriorate more rapidly, brood development accelerates, and the beetles remain within the infestations, contributing to spot growth.

Fall- and spring-dispersing SPB are likely to be true pioneer beetles in that they select suitable host trees in the uninfested surrounding forest without the benefit of secondary attractants. By comparison, summer-emerging beetles are likely to be continually affected by the presence of secondary attractants coming from newly attacked trees at the edges of active infestations. Host selection might seldom occur during the summer, when continued emergence and reemergence prevents the collapse of aggregation within existing spots (Gara 1967). These SPB can overcome tree resistance and continually attack new trees over time. The beetles generally attack new host trees near the old ones.

Overwintering beetles generally do not develop at a rate that would provide massive populations to attack large numbers of new host trees. Furthermore, colder temperatures greatly reduce emergence and any subsequent flight. Because of prolonged development times and the absence of favorable weather conditions through the winter, secondary attractants are less likely to be available near suitable host trees. Beetles emerging during winter and early spring would have trouble finding newly attacked trees. As a result, they would be stimulated to disperse and engage in host selection rather than attack trees within the infestation areas where they developed (Gara 1967). When temperatures are low, beetles may not fly but simply migrate to and attack unattacked portions of the same trees in which they developed (Thatcher and Pickard 1964).

Fat content. – The fat content of emerging beetles may be an important factor in the seasonal behavior of SPB. Fat content is commonly used as a measure of the energy available for flight and subsequent colonization.

Spring- and fall-emerging beetles in Texas have significantly more fat than those emerging in the summer and winter, and thus are better equipped for dispersal. Female beetles have a higher fat content than males (Hedden and Billings 1977). This should be expected, however, since females are responsible for host selection, aggregation, and reproduction.

Pheromones.—Pheromone content and perception also show seasonal differences that are likely to influence SPB behavior. The pheromone content of the beetles reaches its peak in the fall, when the beetles are less aggregated and when any communication via pheromones would likely require greater amounts of the chemicals than in the summer (fig. 2-5) (C. W. Berisford personal communication). At the same time, sensitivity at the olfactory receptor level appears to increase toward the fall (Dickens 1977 unpublished). Behaviorally, the beetles are less responsive to pheromones (based on laboratory tests) in the summer, when infestations expand and pheromone content and olfactory sensitivity are lower, than in the fall (fig. 2-6).

Primary Attraction or Random Landing?

There are two main hypotheses about how beetles locate and select hosts. Some investigators have proposed primary attraction via olfactory stimuli as the means by which the beetle accomplishes host selection. "Primary" is used to reflect that the phenomenon takes place as a result of some stimulus released from the host tree before any beetle visits it. That is, the host tree does not provide a source of "secondary attraction" via beetle-produced volatiles. It has been hypothesized that pioneer beetles are attracted to susceptible hosts by changes in the volatile compounds resulting from deterioration of the plant tissues (Person 1931, Heikkenen 1977). This phenomenon has been shown for species of ambrosia beetle (e.g., Moeck 1970); however, definitive experiments have not been carried out that confirm the primary attraction phenomenon for SPB.

Random landing by dispersing beetles has been proposed as another means the SPB uses to locate and select its host, guided only by its strong preference to land on vertical objects (Gara, Vité, and Cramer 1965). Hypothetically, beetles land at random on both host and nonhost trees. Once on a host tree, female beetles bite the outer bark in response to chemical stimuli there (Thomas, Richmond, and Bradley 1979). If the SPB female identifies a suitable host, she initiates boring activity, and the aggregation phase of the beetle's life cycle begins. If the host is unsuitable, she flies on to another tree.

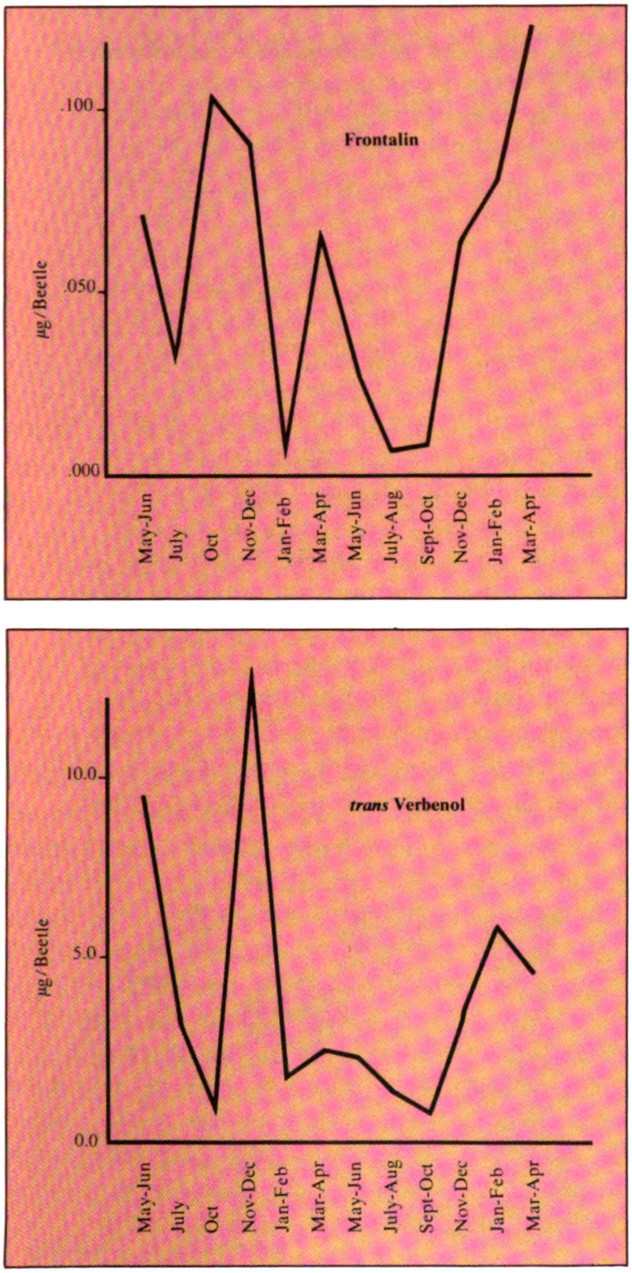


Figure 2-5—Seasonal variation in pheromone content of the female southern pine beetle.

Aggregation

Once a few beetles have selected a susceptible host tree, secondary attraction begins. As a result, other beetles begin to aggregate on the tree. This phase of the beetle's life cycle is critical: it enables the insects to arrive on the host tree in sufficient numbers and over a short enough period of time to overcome the natural resistance of the tree. It is unlikely that a single beetle could successfully colonize a tree since the resin pressure would usually pitch it out. With multiple attacks, however, the tree becomes weakened, and continuing attacks result in successful colonization.

We do not know how many successful attacks it takes to initiate aggregation behavior. Theoretically, one beetle could initiate secondary

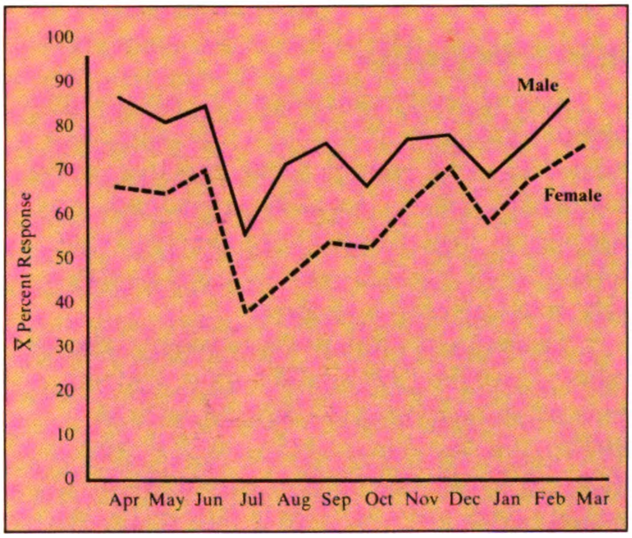


Figure 2-6—Seasonal variation in response to an attractant (frontalin, verbenone, and turpentine) by southern pine beetles in the laboratory (1975-1977).

attraction. We do know, however, that the process is heavily dependent upon the perception of both beetle- and host-tree-produced volatiles and their effects on the flying beetles (Payne 1979).

Olfactory Perception

In general, the olfactory organs of insects are located on the antennae; this is the case with SPB. It is possible to investigate the beetle's olfactory sense at the single-cell and whole antenna (electroantennogram) levels (fig. 2-7).

All of the structures (sensilla) that perceive odor are found on the distal segment of the antenna – the club (Dickens and Payne 1978a). The location and arrangement of the olfactory sensilla on the club are well adapted for the beetle's needs. Most sensilla are located within the sensory bands, which encircle the club. Each club has hundreds of olfactory sensilla, and the cuticle of each individual sensillum is perforated with thousands of pores that collect the important airborne molecules of pheromone and host odor from the environment surrounding the beetle. Ultimately the molecule-bound information is transfered through the central nervous system of the beetle and changed into a behavioral response.

Behavioral Chemicals

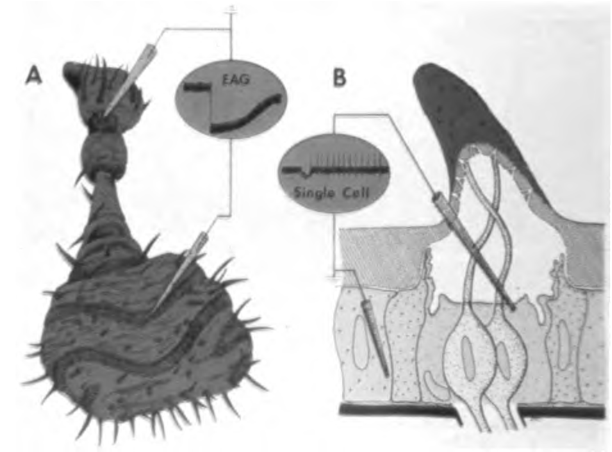
Several compounds have been isolated and identified from the beetle, host tree, associated microorganisms, and the beetle-host tree system (Appendix, table 1). All of the compounds have not been evaluated, but a few have significant effects on the beetle and are believed to play a role in its aggregation behavior.

Frontalin. – Frontalin is considered the primary aggregation pheromone of the southern pine beetle (Kinzer et al. 1969, Payne et al. 1978a). It is found in the hindguts of newly emerged female beetles (Coster and Vité 1972) and probably is released when they make contact with suitable host trees (Renwick and Vité 1969). In fact, by the time the female has fed, the level of frontalin has declined significantly (Coster and Vité 1972).

The pheromone is naturally synthesized in a ratio of 15 percent positive to 85 percent negative of its enantiomeric forms (Stewart et al. 1977). The beetle responds significantly more to the negative than the positive form; however, it responds as well to the racemic mixture of the two forms as to the negative form (Payne et al., unpublished).

By itself, frontalin attracts flying beetles of both sexes (Payne et al. 1978a). But in the presence of host odor, its effect is greatly enhanced (Kinzer et al. 1969; Payne et al. 1978a). About three times as many males are attracted to the pheromone as females. This predominatly male response may be due to testing procedures and the tendency of males to orient closer to the pheromone source than females (Hughes 1976). However, the entire pheromone complement of the beetle-tree system, including frontalin, causes male and female beetles to aggregate on host trees in a nearly 1:1 ratio (Coster et al. 1977a).

It is likely that frontalin functions primarily in close-range communication to keep individual SPB close together so they are present in sufficient numbers to overcome the resistance of host trees. Frontalin probably does not function over long distances (Payne et al. 1978b, Johnson and Coster 1978). Along with *trans*-verbenol and host odor (i.e., α-pinene), frontalin may promote



Fugure 2-7—Schematic of olfactory sensillum and whole antenna showing sensilla distribution (A) electroantennogram (EAG), and (B) single-cell recording techniques (after Payne 1979).

close-range communication on the surface of the host tree, since in closely related species it has been shown to stimulate male beetles to produce an "attractant chirp" known to occur when the male is near the entrance hole of a female (Rudinsky 1973, Rudinsky et al. 1974).

Alpha-pinene. —*Alpha*-pinene has been singled out as the most significant host tree odor in the behavioral chemical complex of the SPB (Renwick and Vité 1969). By itself, the terpene is not attractive to field populations, nor is any other host tree odor. However, it does synergize the attractiveness of frontalin in aggregating beetles on host trees (Kinzer et al. 1969). The SPB probably does not rely on this terpene alone as its input from the host tree. In fact, turpentine tends to be a more effective synergist (Payne et al. 1978a), a fact suggesting that the host tree signal is not embodied in one compound. Although α-pinene does not attract flying beetles, it is arrestive to walking beetles (McCarty et al. 1980). In combination with frontalin, it may serve to aid beetles in orientation on the surface of the host.

Alpha-pinene has been proposed to function as an arrestant in combination with frontalin (Renwick and Vité 1970, Payne 1973). That is, the pheromone attracts beetles to the tree, and the host tree odor arrests their flight so they land. The terpene has been shown to arrest beetles on nonsticky traps baited with frontalin, whereas beetles that responded to frontalin alone did not remain on the trap (J.A.A. Renwick and J. P. Vité personal communication).

***Trans*-verbenol.** — Female beetles produce *trans*-verbenol (Renwick 1967). It is naturally synthesized in a ratio of 60 percent positive and 40 percent negative of its enantiomeric forms (Plummer et al. 1976). However, the behavioral effects of the enantiomers have not been determined. *Trans*-verbenol can synergize the attractiveness of frontalin (Kinzer et al. 1969, Payne et al. 1978a) and has been proposed as a substitute for host odors as resin exudation ceases (Renwick and Vité 1969). *Trans*-verbenol may also have an arresting effect on beetle flight (Dickens and Payne 1978b). On the host tree, it probably aids in close-range communication between the sexes, since in combination with frontalin and α-pinene it was shown to elicit the attractant chirp from males (Rudinsky 1973; Rudinsky et al. 1974).

The compound is found in the hindgut (Renwick 1967), frass, and volatiles from SPB-infested host material (R. M. Silverstein and J. R. West personal communication). The level of *trans*-verbenol in the hindgut is influenced by exposure of the beetle to vapors of α-pinene (Hughes 1973; Renwick, Hughes, and Ty 1973). The biological significance of this apparent chemostimulated synthesis is unknown since newly emerged, unfed females contain up to 75 percent more *trans*-verbenol in their hindguts than do females that have entered the host, fed, and thus become greatly exposed to resin vapors (Coster and Vité 1972). Exposure of males to α-pinene stimulated synthesis of *trans*-verbenol, which under other circumstances is not synthesized in that sex (Renwick et al. 1973).

Verbenone. — Verbenone is produced essentially by males and is found in the hindgut (Renwick 1967), as well as in the frass and volatiles from SPB-infested host material (R. M. Silverstein and J. R. West personal communication). The pheromone is also found in female beetles but in very small amounts.

Verbenone is believed to affect beetle behavior in several ways (Rudinsky 1973). At lower concentrations it affects beetles attracted to host trees by reducing the number of males and thereby balancing the sex ratio more toward 1:1 (Renwick and Vité 1969, Payne et al. 1978a). In higher amounts it tends to inhibit the aggregation of both males and females on host trees. In contrast, when released in very small amounts by the female, verbenone is believed to synergize the attractant pheromone mixture (frontalin, *trans*-verbenol, and host odor) in close-range orientation of males to the entrance holes of females (Rudinsky 1973). Experimentally, low concentrations of the pheromone have elicited attractant chirps from males. At higher concentrations, those believed to be principally associated with the male, verbenone elicits "rivalry chirps" from males.

***Endo*-brevicomin.** – *Endo*-brevicomin is produced, in very small amounts, in the hindgut of the male beetle only (Pitman et al. 1969) throughout most of its range. However, in Arizona-Honduras beetles, *endo*-brevicomin is found in greater amounts (Vité et al. 1974). It inhibits the response of both male and female SPB to attractive host trees and thus facilitates attacks on other new trees (Vité and Renwick 1971, Payne et al. 1978a). The pheromone may also contribute to male competition on the host tree since it has been shown to elicit rivalry chirps (Rudinsky et al. 1974).

Myrtenol. – Myrtenol is produced by both male and female beetles and is found in their hindguts (Hughes 1973, Renwick et al. 1973). In laboratory tests, it synergized the attractant mixture of frontalin and *trans*-verbenol, causing males to stop near the source of the pheromones (Rudinsky et al. 1974). When released by the female, myrtenol may have a similar function as that proposed for verbenone in helping males find the entrance holes of females.

Role of microorganisms. – The microorganisms associated with the southern pine beetle may be responsible in part for the ultimate composition of the behavioral chemical system that regulates its behavior. Mycangial fungi in female beetles, for example, are capable of oxidizing *trans*-verbenol to verbenone (Brand et al. 1976). The significance of this phenomenon in the behavior of the beetle is not known; however, both of the pheromones are important. A basidiomycete in the mycangium produces the compounds isoamyl alcohol, 6-methyl-5-hepten-2-one and 6-methyl-5-hepten-2-ol (Brand and Barras 1977). The behavioral significance of these compounds has not been determined; however, isoamyl alcohol does enhance the attractiveness of a pheromone mixture in laboratory bioassays. In fact, isoamyl acetate, 2-phenyl-ethanol, and 2-phenylethyl acetate – metabolites of three yeasts isolated from the beetle – are highly effective in synergizing unattractive concentrations of the attractant mixture of frontalin, *trans*-verbenol, and host odor (Brand et al. 1977). By themselves, the metabolites are unattractive. The metabolites are not attractive to field populations either, suggesting that they may function in close-range olfactory behavior of the beetle on the host tree.

It is unlikely that the behavioral chemical system of the southern pine beetle has been completely described. Many compounds have been isolated from the SPB and the beetle-host tree system, but few have been identified. All remain to be evaluated for their roles in the life cycle of the beetle.

Olfactory Receptor System

The beetle's antennal olfactory receptor system uses available sense cells efficiently, in that several of the behavioral chemicals interact on some of the same receptors (Dickens and Payne 1977). At first it may appear that such a situation would prevent the beetle from determining if it should respond to an attractant or to an inhibitor if both stimulate the same receptor. But the beetle's olfactory sense is quite sophisticated and can readily sense the difference.

The ability of the beetle to decipher the complex olfactory messages in its environment depends on the number and specificity of the receptors it has for various behavioral chemicals. Whether or not a pheromone will elicit a behavioral response is in part dependent upon the number of receptors stimulated. The apparent differences that exist in the number of receptors for the different compounds provide the beetle with the flexibility and versatility to perceive the chemicals and translate the information into behavioral reponses. In addition, the rate at which the receptors recover from stimulation adds to the SPB's versatility in perceiving the behavioral chemicals and the messages they carry.

From a simplistic view, the olfactory receptor system segregates the behavioral chemicals as attractants, inhibitors, and synergists. Although both male and female beetles respond to the same compound, their receptor systems differ (Dickens and Payne 1977). The attractants, inhibitors, and synergists form three discrete groups in the female receptor system (fig. 2-8). Receptors for frontalin form an all-inclusive group, while verbenone and *endo*-brevicomin form a second mutually exclusive group, which occupies 85 percent of the receptors for frontalin. Receptors for the synergists α-pinene and *trans*-verbenol form a third group, which occupies between 33 and 48 percent of the frontalin receptors.

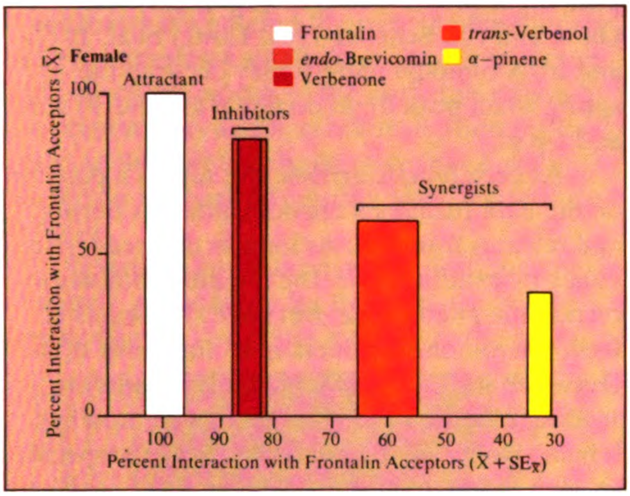


Figure 2-8–Female southern pine beetle olfactory receptor system. Mean percent interaction of pheromones and host terpenes with frontalin acceptors. Width of columns represents X̄ ± SE for each compound with the exception of frontalin (Dickens and Payne 1977).

The olfactory receptor system of the male beetle differs considerably from that of the female (fig. 2-9). The inhibitors occupy 66 to 76 percent of the receptors for frontalin. The synergists occupy 44 to 68 percent of the receptors. The overlap of verbenone with both the synergist and inhibitor groups may have implications in the multifunctional characteristics of the pheromone (Rudinsky 1973, Rudinsky et al. 1974).

Southern pine beetles have the largest number of receptors for the attractant frontalin; all of the other compounds, both pheromones and host odors, share them, although not all of them. For example, the inhibitors *endo*-brevicomin and verbenone can stimulate 66 to 85 percent of the receptors, depending on whether the beetle is male or female. The synergists *trans*-verbenol and α-pinene, on the other hand, can react with 33 to 68 percent of the receptors. This does not mean that when a beetle is smelling frontalin it cannot also smell another compound. Certainly not, or how could α-pinene, or *trans*-verbenol for that matter, synergize the effect of frontalin?

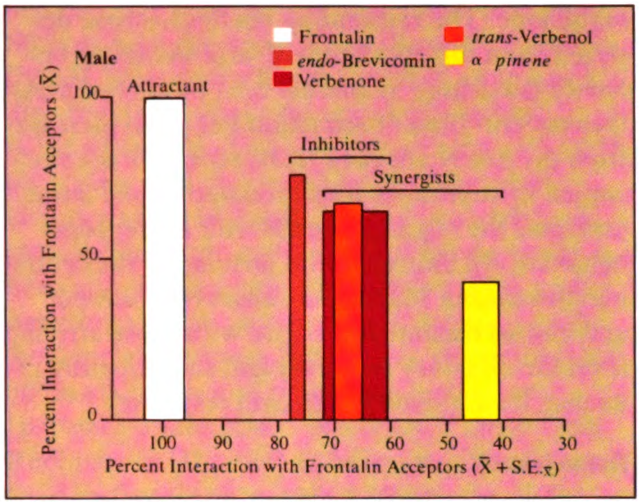


Figure 2-9.– Male southern pine beetle olfactory receptor system.

In nature the beetle is not likely to come in contact with such a concentration of any one compound (except possibly a host odor) that all of the receptors for the material would be occupied at the same time. More likely, the beetle has many receptors constantly receiving olfactory signals from different odors, such that the resulting behavior comes from an integration in the central nervous system of all of the information from those receptors (Payne 1979). Therefore, when the beetle's receptors are receiving primarily frontalin and synergist stimulation, the pattern of signals arriving in the central nervous system elicits aggregation behavior. This phenomenon is continuous, and as the qualitative and quantitative characteristics of the odor stimuli change, different behaviors result.

As the concentration of attractant decreases and the concentration of inhibitors increases, changes occur in the pattern of the incoming signals to the central nervous system and in the resulting behavior. Receptors once stimulated by frontalin, or possibly a synergist, now become increasingly stimulated by *endo*-brevicomin and verbenone. The responding beetles become deterred from the attacked tree, and switching behavior (switching to another host tree) results. As the concentration of attractant begins to increase from the newly attacked trees, receptors once occupied by inhibitors are stimulated by the attractants and the beetle responds with aggregation behavior. All along, stimuli arriving in the central nervous system from other senses (e.g., sound and vision) become integrated with those arriving from the olfactory receptors and subsequently influence the ultimate behavioral response.

Behavioral Events

Our current understanding of the sequence of events in the aggregation phase of the SPB's life cycle leaves us with an incomplete picture. But despite this fact, we can still begin to understand the events taking place in the interactions of the beetle and the host tree.

After selecting and attacking a suitable host tree, a female immediately begins to release the aggregation pheromone frontalin (Kinzer et al. 1969; Renwick and Vité 1969, 1970). Frontalin, along with host tree odors, attracts large numbers of male and female beetles to the tree. Males predominate. The initial attack and aggregation occur on the midbole of the tree (fig. 2-10) (Coster et al. 1977a, Fargo et al. 1979). As more females arrive, more pheromone is released and more beetles are subsequently attracted. Attacks then begin to spread from the midbole to the upper and lower areas of the bole (fig. 2-10). During the winter, however, additional attacks may be limited more to the upper bole of the tree (Thatcher and Pickard 1964). Aggregation behavior follows a diurnal pattern in summer, with peak flight activity at 5 p.m. (fig. 2-11) (Vité, Gara, and von Scheller 1964; Coster et al. 1977a and b). A bimodal pattern may occur in the spring when peak flight occurs at around 10 a.m. and 5 p.m.

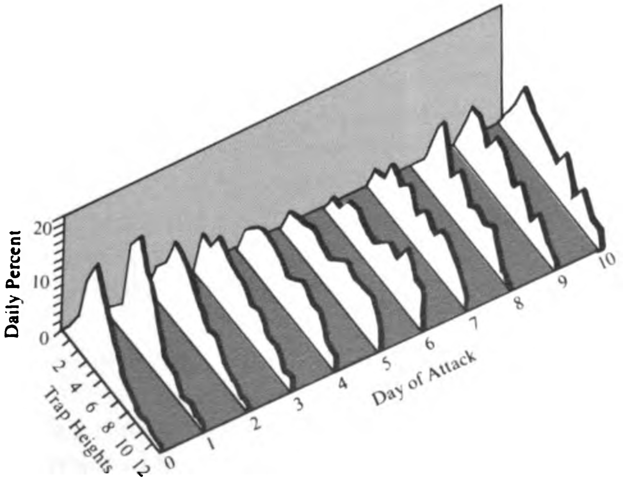


Figure 2-10.—Height distribution of southern pine beetles on host trees during the aggregation phase (after Coster et al. 1977a).

As each female arrives, she selects a position on the bark (usually a crevice), initiates boring, and releases frontalin. As long as the tree resists attack by exuding resin, the female continues to release the pheromone. But once she begins to feed, pheromone production declines and stops. During this activity the female may stridulate, sending off a series of chips when near another female. Such signaling may have an intraspecific spacing function during the selection of entrance sites and may be caused by a chemostimulus (Rudinsky and Michael 1973).

Generally, at the point where each female enters the tree, a characteristic pitch tube forms as a result of the severing of resin ducts by the boring beetle (fig. 2-12). Pitch tube formation depends upon what condition the host tree is in and whether pitch flow has ceased as a result of other earlier attacks. Those beetles arriving late in the

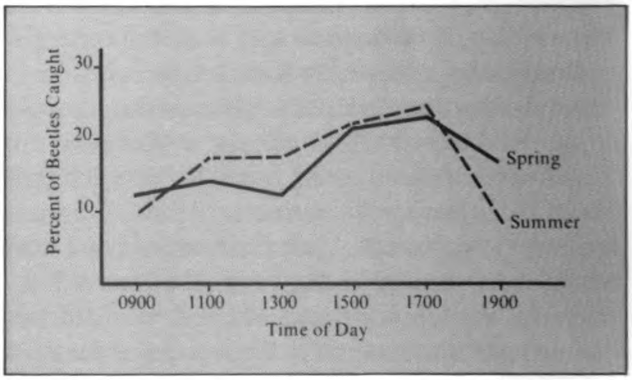


Figure 2-11.— Diurnal distribution of southern pine beetles on host trees during the aggregation phase (after Coster et al. 1977b).

aggregation phase are less likely to stimulate pitch tube formation since the resin pressure in the tree has been reduced by beetles that attacked earlier.

Besides frontalin, the females also release *trans*-verbenol immediately upon landing on the host (Renwick and Vité 1969, 1970). *Trans*-verbenol enhances the aggregating effect of frontalin (Renwick and Vité 1969, Payne et al. 1978a). Once they have entered the tree, the females are believed to release small amounts of verbenone. This substance enhances the attractive effects of the pheromones and host odors in orienting males to the entrance holes once they have landed on the bark (Rudinsky 1973, Rudinsky et al. 1974).

When the males land on the host, they begin to search, presumably for the entrance hole of a female beetle. The males move over the bark, investigating crevices, entrance holes, and pitch tubes as they encounter them (Bunt 1979 unpublished). Most of the males search in an upward direction from where they land on the bark. Some males orient directly to an entrance hole or pitch tube, and thus exhibit chemoklinotaxis. Others search randomly. Upon contact with an entrance hole, the male circles the hole, pokes it head and thorax inside, clears away frass, and sometimes swims in the resin, if there is any. In the female's entrance hole, males frequently give off an audible sound or attractant chirp as a "presence-announcing" stridulation (Barr 1969, Rudinsky 1973), which is believed to be stimulated by female pheromones (Rudinsky 1973, Rudinsky et al. 1974).

Figure 2-12. – Characteristic pitch tubes on host tree mass attacked by the southern pine beetle.

In some cases, the male encounters another male while searching the bark for a female's entrance hole (Bunt 1979 unpublished). Then the males may simply resume searching or drop from the host; however, direct combat can occur. Fighting most frequently takes place when confrontation occurs at a female's entrance hole. Males may give off a "rivalry chirp." In any event, when combat ensues the males butt heads and generally the larger of the two drives the other away to search for another female.

When the male finally locates and enters the female's entrance hole, he begins to release verbenone, which balances the sex ratio of responding beetles by reducing the response of males to females (Renwick 1969, 1970; Payne et al. 1978a). As higher amounts of verbenone are released, the response of both sexes is inhibited. In addition to verbenone, the males also release *endo*-brevicomin, which reduces the attraction of both males and females to the host tree (Vité and Renwick 1971, Payne et al. 1978a). As the population of males on the tree increases, so does the amount of verbenone and *endo*-brevicomin being released. As a result more and more males and females are deterred from the host, and the phenomenon of "switching" takes place (Gara and Coster 1968). The focus of aggregation and attack by the beetles is switched to an adjacent host tree, and the dynamic process begins all over.

Generally, only those trees within a critical distance of the attacked host are likely to come under attack by switching populations (Gara and Coster 1968). In large spots the shifting of attack can take place rapidly; and under the local influence of the aggregation pheromones, beetle attack may occur on more than one tree before the mass attack is complete on an individual tree. However, in small spots the pheromones are less profuse, and the attack remains focused on a single tree at a time. As the level of attraction increases on an adjacent tree, so does the focus of flight, landing, and boring activity. The success of the switching activity is to some extent dependent upon the proximity of adjacent host trees. The closer trees are to one another, the likelier it is that switching will take place and adjacent trees will be colonized (Gara and Coster 1968, Johnson and Coster 1978). (*See* Chapter 5 for a detailed discussion of infestation growth and proliferation.)

The aggregation phase is by far the most dynamic aspect of the life cycle of the beetle. During the warmer months of the year, when beetle populations are most active, the entire aggregation phase – including initial attack, mass attack, and switching – may be completed within 10 days (fig. 2-13) (Coster et al. 1977a, Fargo et al. 1979). In fact, in most cases a host tree can be completely mass attacked within 3 to 5 days after the first pioneer female lands on its bark. The rapid increase in beetle numbers aggregating on and mass attacking a tree, following by an equally rapid decline, can be attributed for the most part to the relative amounts of behavioral chemicals present over the aggregation and attacking period.

Colonization

Once the male joins the female on the host tree, mating occurs and the colonization phase of the beetle's life cycle begins.

Mating

The southern pine beetle is monogamous, and copulation takes place in the nuptial chamber formed in the inner bark by the female once

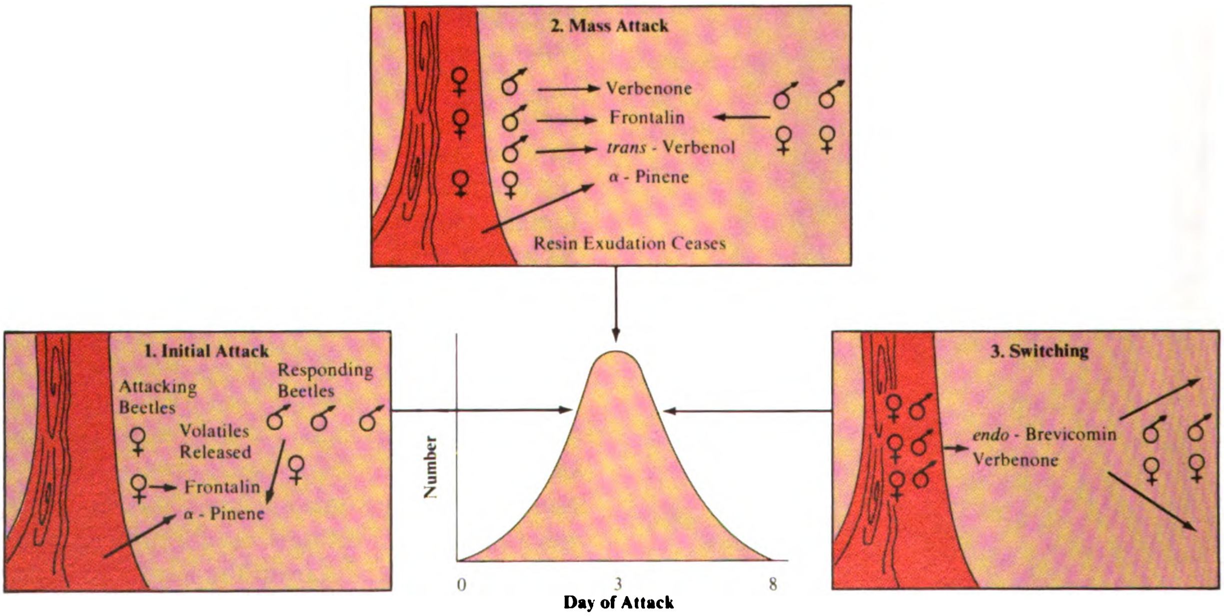


Figure 2-13. – Simplistic model of role of behavioral chemicals during the aggregation phase (revised after Renwick and Vité 1969, Coster et al. 1977a).

resin flow has stopped (fig. 2-14) (Hopkins 1909b, Thatcher 1960). The nuptial chamber is somewhat shoe shaped and is formed directly opposite the entrance from the outer bark (MacAndrews 1926 unpublished).

Often, when resin flow is profuse, both the female and male work for some time in order to excavate an entrance hole and keep it open (Hopkins 1899). In some cases, they fail and become entombed in a resin-filled entrance hole or initial egg gallery. When the resin flow is persistent, the female may excavate a preliminary gallery that proceeds upward and laterally, often for some distance, in the outer area of the inner bark before the inner bark is completely penetrated. Generally these galleries have a short, curved form, lack beetles, and are packed with frass and hardened resin.

The southern pine beetle's mating behavior has been observed under laboratory conditions (Yu and Tsao 1967). When the male reaches the female in the gallery, he moves to her posterior end and begins to remove the frass she has made. When that job is completed, he backs out of the gallery entirely or to a widened area of the gallery, turns around and backs in. When he meets the female, he mates with her end to end. In laboratory experiments, a single female mated with up to six different males when they were presented separately at the entrance hole. This suggests that although the SPB is monogamous and generally only one male and one female are found in a gallery, a given female could mate with more than one male.

Egg Laying

Once the female has mated, she begins to construct an S-shaped or serpentine egg gallery (fig. 2-14) (Hopkins 1899, MacAndrews 1926 unpublished, Thatcher 1960). As debris (frass) accumulates in the gallery, the female pushes it back with her legs and packs it, using her abdomen like a scoop. The male follows the female and helps her remove boring particles from the area of current activity. However, the male contributes little to the female's activities if she was previously mated (Yu and Tsao 1967). The female moves back and forth, packing pieces of bark down with her head and putting fallen pieces in place with her mouthparts. She keeps a space of approximately 15 to 25 mm clear of frass (Hopkins 1899).

The gallery is mined in the cambium diagonally across the grain of the wood and sometimes lightly scores the sapwood. It is always continuous, never branches, and forms a long, winding track such that as the host tree becomes heavily infested, individual galleries crisscross each other. Widened areas may be formed in the gallery wall to afford space for beetles to turn around (T. L. Wagner personal communication). Single galleries range from 10 to 24 cm in length.

When the egg gallery is approximately 2 to 3 cm long, the female begins to cut individual egg niches in the walls of the gallery. An egg is deposited in each niche and held in place by a thin wall of fine, tightly packed borings (Fronk 1947). Eggs are deposited at irregular intervals along the gallery at a rate of up to 30 per gallery (Lashomb and Nebeker 1979, T. L. Wagner personal communication).

Reemergence

Parent adults begin to emerge 1 to 3 days after mass attack, mating, and egg deposition (fig. 2-14) (Coulson et al. 1978). The scattered holes that appear on the bark surface at this stage were thought to be ventilation holes, before the extent of reemergence was recognized (T. L. Wagner personal communication). Depending on when a given adult entered the host during the aggregation phase, reemergence continues for 16 to 20 days. Once the parent adults have left a host, their role in colonization of that tree is over. But they continue to play a vital role in the dynamics of the infestation, because they remain capable of receiving olfactory signals, attacking new hosts, producing pheromones, mating, and laying eggs (Franklin 1970a, Coulson et al. 1978, Telfer 1979 unpublished, Cooper and Stephen 1979. *See* Chapter 5 for details.).

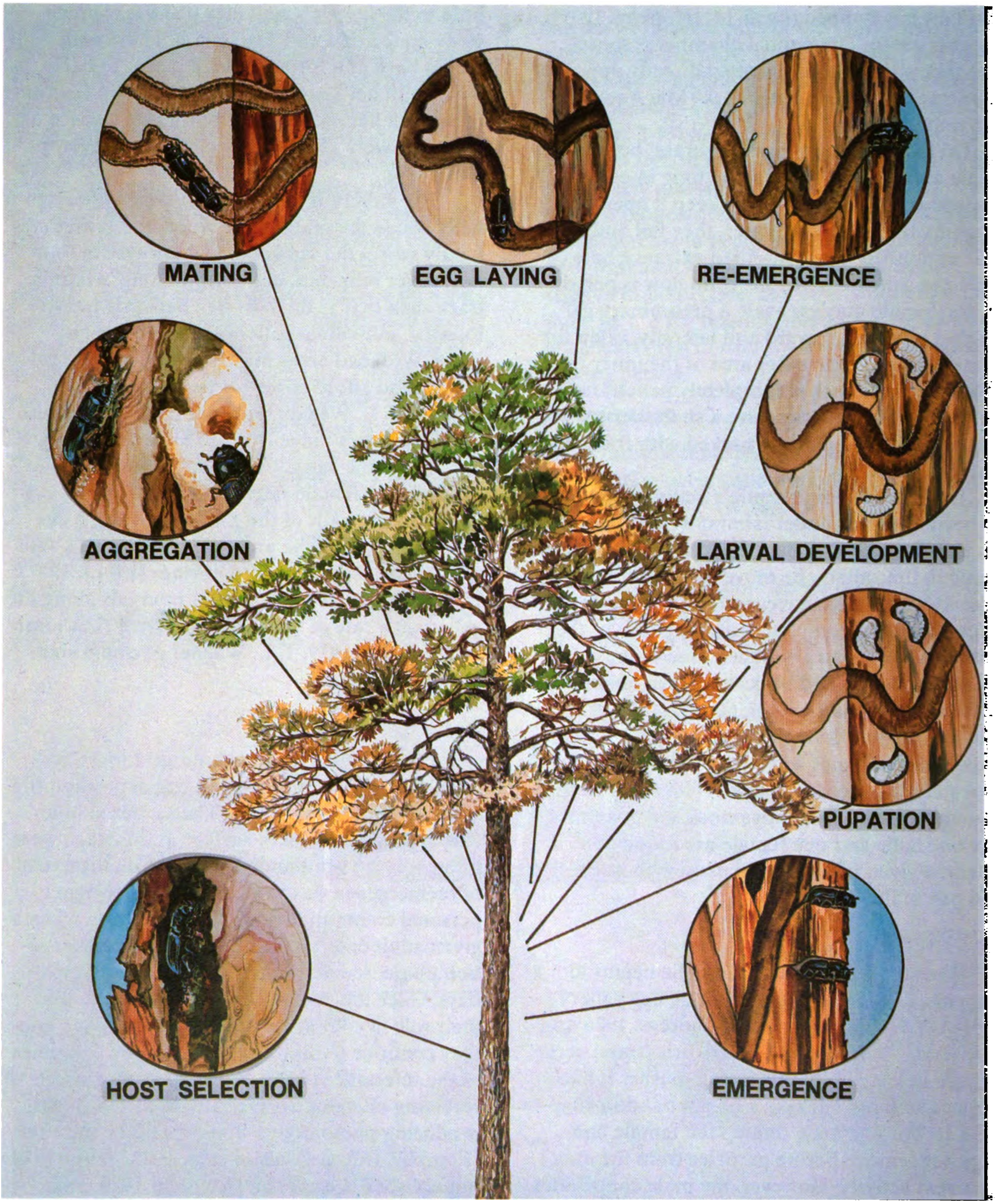


Figure 2-14. – Stages of host tree colonization by the southern pine beetle.

Larval Development

The eggs hatch in 2 to 9 days after being laid (Fronk 1947, Gagne 1980 unpublished). The emerging first-instar larva begins to bite and subsequently enters the cambium layer of the host. Initially it makes a fine, threadlike, gently winding gallery a few centimeters long in the cambium and perpendicular to the adult gallery. Then it enters the inner bark, where it spends most of its larval period. As the larva molts to each successive stage, the gallery enlarges (fig. 2-14). Some initial galleries are completely hidden in the phloem tissue. Others are exposed early or late in larval development. When nearly mature, the larva bores to the outer area of the inner bark; and in the fourth instar it bores to the outer, dead bark (Goldman and Franklin 1977).

Pupation

Upon reaching the outer bark, the fully mature larva forms an oblong pupal cell (fig. 2-14). Occasionally, pupal cells are formed in a widened area of the larval mine within the inner bark, but normally they occur in the outer bark. Once the cell is formed, the mature larva transforms into the pupal stage.

Adult Development

The mature pupa transforms into a callow adult and remains in the pupal cell as the hardening and darkening process of the cuticle takes place. During this time, the adult changes from yellowish tan to reddish brown to its final color of black-brown (fig. 2-14).

Emergence, Dispersal, and Overwintering

Once the adult southern pine beetle has fully developed, it constructs an exit hole from the pupal cell by boring directly through the outer bark, leaving a clear-cut, open hole behind (fig. 2-14). If conditions are not correct, however, the adult may remain under the bark for some time. Generally this delay in emergence is associated with colder air temperatures (Kinn 1978).

Emergence does not take place all at once. A few beetles emerge initially, followed by a larger number, and then a declining number over an extended period of time (*see* Chapter 5).

Environmental conditions affect beetle dispersal. During the winter, emerging beetles may not disperse, but instead reattack the same tree (Thatcher and Pickard 1964). Generally, though, emerged beetles leave the host tree and, depending upon the time of the year, either aggregate on adjacent trees under attack or leave the previously established center of attraction and find a suitable new host tree elsewhere (*see* Chapter 5).

The southern pine beetle overwinters in all life stages (MacAndrews 1926 unpublished). Mature larvae, pupae, and adults overwinter in the corky outer bark, while young larvae and eggs are found in the inner bark. The beetle does not go through a diapause. Development of all stages continues throughout the year, slowing considerably in the winter and accelerating in the spring and summer (Thatcher 1967).

Conclusion

Our knowledge of the life history and habits of the southern pine beetle has increased tremendously since the mid-1700's, when the Moravians were remarking on its "mischief." The extensive works of Hopkins, MacAndrews, St. George and Beal, Fronk, and others in the early 1900's have provided us with a good basic understanding of the general biology of the beetle, from which more detailed studies have been launched.

In the ensuing years, detailed studies have been carried out at both the basic and applied levels. Information has been gathered on the beetle's biology and physiology, its interaction with the host, the influence of pathogens, parasites, predators, and associates on its populations, silvicultural influences, and chemical control. Since the late 1950's, significant advances have been made in our understanding of the behavior of the beetle. Valuable insights were gained on the aggregation behavior of the beetle and the role of behavioral chemicals.

All of these efforts paved the way for much of the progress made in the Expanded Southern Pine Beetle Research and Applications Program in increasing our understanding of the beetle's behavior and in our efforts to develop behavioral chemicals for use in pest management. Through the Program, information has continued to be collected and synthesized to provide us with a fuller understanding of the life history and habits of the beetle and insights into how we might manipulate its populations as part of forest management.

Acknowledgments

The author wishes to thank Dr. J.P. Vité Direktor, Forstzoologisches Institut, Universitat Freiburg, West Germany, for his critical review of the chapter, and Mrs. P. D. Billings for assistance in constructing the table.

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Natural Enemies and Associated Organisms

C. Wayne Berisford[1]

3

The southern pine beetle is intimately associated with a large number of other organisms. They directly or indirectly affect its development and survival through parasitism, predation, competition, and symbiosis. These associates include other insects, mites, birds, fungi, nematodes, and various insect and plant disease oranisms.

Since the beetle is difficult and expensive to control with current technology, and some of its associates obviously can influence SPB population growth, the ESPBRAP supported studies seeking to better understand the roles of many associates. If we are to develop integrated suppression tactics, we must understand the life processes of the beetle *and* its associates.

Studies prior to ESPBRAP dealt primarily with compiling lists of SPB associates. Most of the attention was focused on other insects, mites, and nematodes. The known or suspected roles for the parasites, predators, and scavengers were indicated (Thatcher 1960, Dixon and Osgood 1961, Moser and Roton 1971, Moore 1972, Coulson et al. 1972a, Overgaard 1968). However, the impacts and interactions of these associates were unknown. Studies supported by ESPBRAP were oriented toward determining the specific roles and impacts of associates, particularly parasitoids and predators. We need this type of information to develop realistic SPB population models that can detect and/or forecast population trends, and to implement control strategies which can capitalize on SPB population suppression by natural enemies.

Arthropod Enemies of SPB

Insects and mites are among the principal natural enemies of the southern pine beetle. Recent research has identified these mortality agents and described their seasonal, geographic, and within-tree distribution, and general biology. Some reports concentrate on one or a few species (Lenhard and Goyer 1979, Hain 1978 unpublished, Dixon and Payne 1979a, Gargiullo and Berisford 1980).

Dixon and Payne (1979b) have provided information on SPB associates attracted to infested trees and include data on numbers and temporal and spatial distribution of the associates.

An illustrated guide to insect associates of the SPB has been developed (Goyer et al. 1980). The guide includes color photographs and distinguishing characteristics of each insect. Using this manual, workers with minimal training in entomology can easily identify the associates.

Stephen and Taha (1976) have developed a sampling system for estimating numbers of natural enemies in Arkansas. The system describes a sampling protocol and presents curves for number of samples *v.* sample unit sizes needed to obtain 90 percent statistical confidence (fig. 3-1; *see also* fig. 6-8).

Predators

A number of arthropods, primarily insects, prey on the SPB (Appendix, table 2). Predators may attack SPB adults during tree colonization and/or prey on the egg and larval stages during

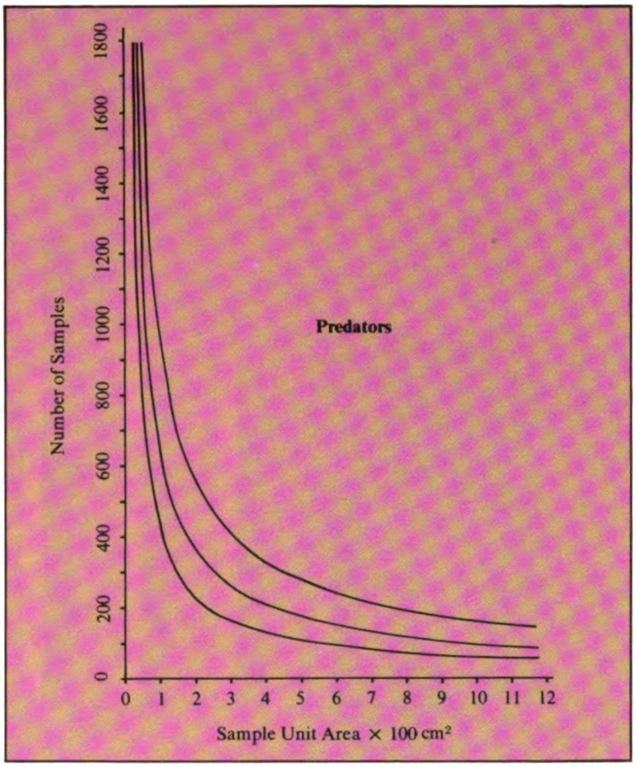

Figure 3-1. – Relationships between number of samples needed and size of the sample unit to estimate the density of predators. The 90 percent confidence limits are included. (Redrawn from Stephen and Taha 1976.)

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brood establishment and development. Generally, predators are not closely associated with their prey for a long period of time. Each prey usually constitutes a single meal, and each predator may consume several prey during its lifetime. With the exception of predaceous mites, most predators of SPB are larger than their host(s).

Checkered Beetles

The most common, colorful insect predator of SPB is the checkered or clerid beetle, ***Thanasimus dubius*** (F.) (Coleoptera:Cleridae). Clerid adults eat attacking SPB adults, and clerid larvae attack SPB larvae. This predator responds to SPB attractants and aggregates on trees undergoing mass attack by the beetle (Vité and Williamson 1970).

Hopkins (1899) first recognized *T. **dubius*** as a potentially important natural enemy of pine bark beetles. Several subsequent studies examined its biology, behavior, and impact on the SPB. Dixon and Payne (1979a) described the temporal and spatial distribution of *T. **dubius*** on SPB trees under mass attack in Texas. They reported peak numbers of clerids 1 day after peak SPB attack (fig. 3-2). Clerids were most abundant 4 days after initial SPB attack. Attacks by both SPB and the clerids lasted up to 11 days. Highest numbers of both were trapped early and late in the day in Texas and in Georgia (Dix and Franklin 1977). About 64 percent of both species were trapped on the lower half of the infested bole (Dixon and Payne 1979a).

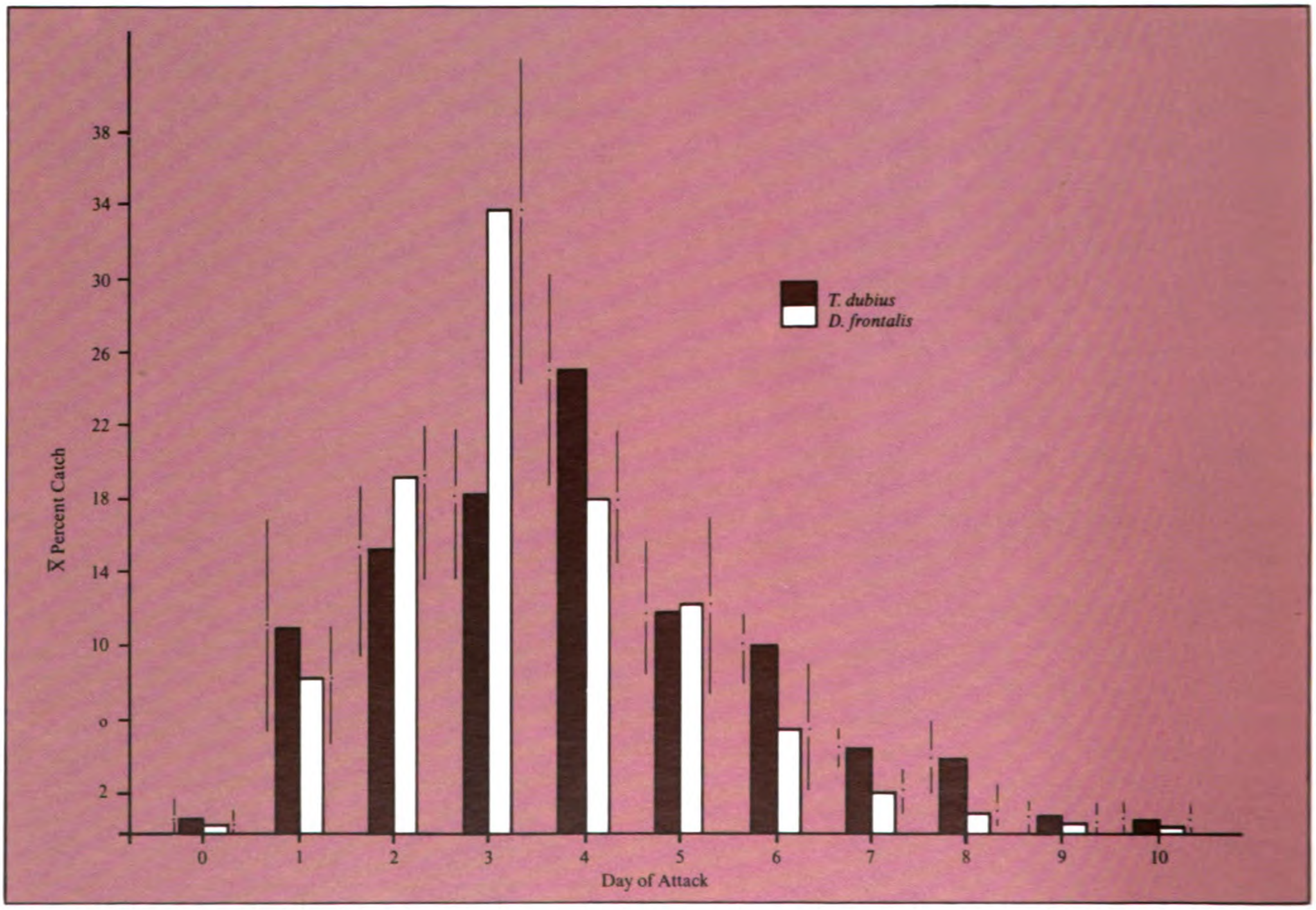

Figure 3-2. – Sequence of arrival of *T. **dubius*** and southern pine beetles on trees under mass attack by SPB. Vertical bars = ± $SE_{\bar{x}}$. Based on 7 trees, 3,173 *T. dubius*, and 29,896 SPB. (From Dixon and Payne 1979a.)

Lenhard and Goyer (1980) reared *T. dubius* from log bolts taken during 1975 through 1977 in Louisiana. SPB activity was very high during this period. Clerids were found to be most active during spring and winter. Clerid densities did not strongly correlate with either SPB egg gallery length or bark thickness.

Frazier et al. (1980) described in detail the predatory behavior of adult *T. dubius.* They found that both sexes go through six typical behavioral acts as they prey on SPB (figs. 3-3 and 3-4). Frazier's team determined the average time invested in each act and calculated the predator's efficiency.

Studies of developmental rates of *T. dubius* revealed that immature stages developed more rapidly as temperatures increased from 12.5° C to 27° C (Nebeker and Purser 1980). Total developmental time (egg to adult) was the same whether clerid larvae were fed small or large SPB larvae or large pupae. But the prepupal and pupal periods were longer for clerids that had been fed on large SPB larvae and pupae.

Corticeus Predators

Beetles in the genus *Corticeus* (Coleoptera: Tenebrionidae) are very abundant and are commonly observed on SPB-infested trees (fig. 3-5).

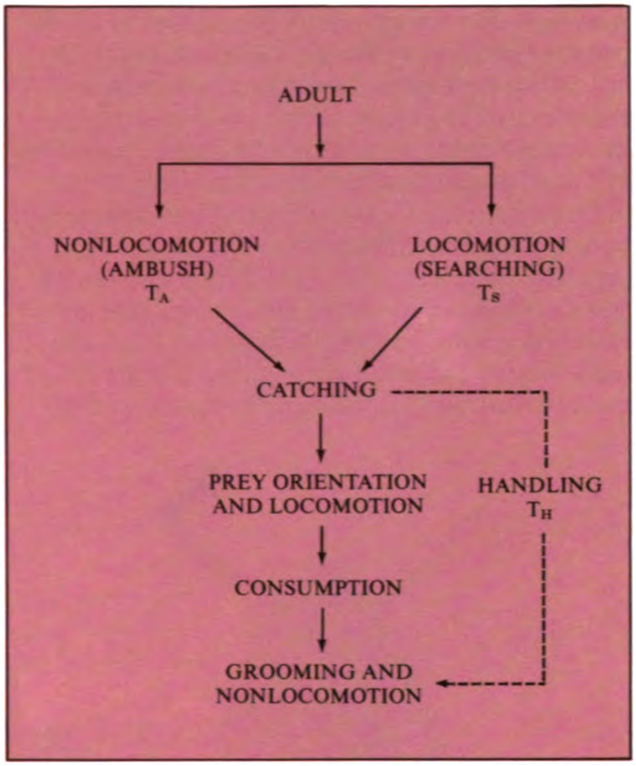

Figure 3-3. – The behavioral sequence of events in predation by *Thanasimus dubius* adults. (From Frazier et al. 1980.)

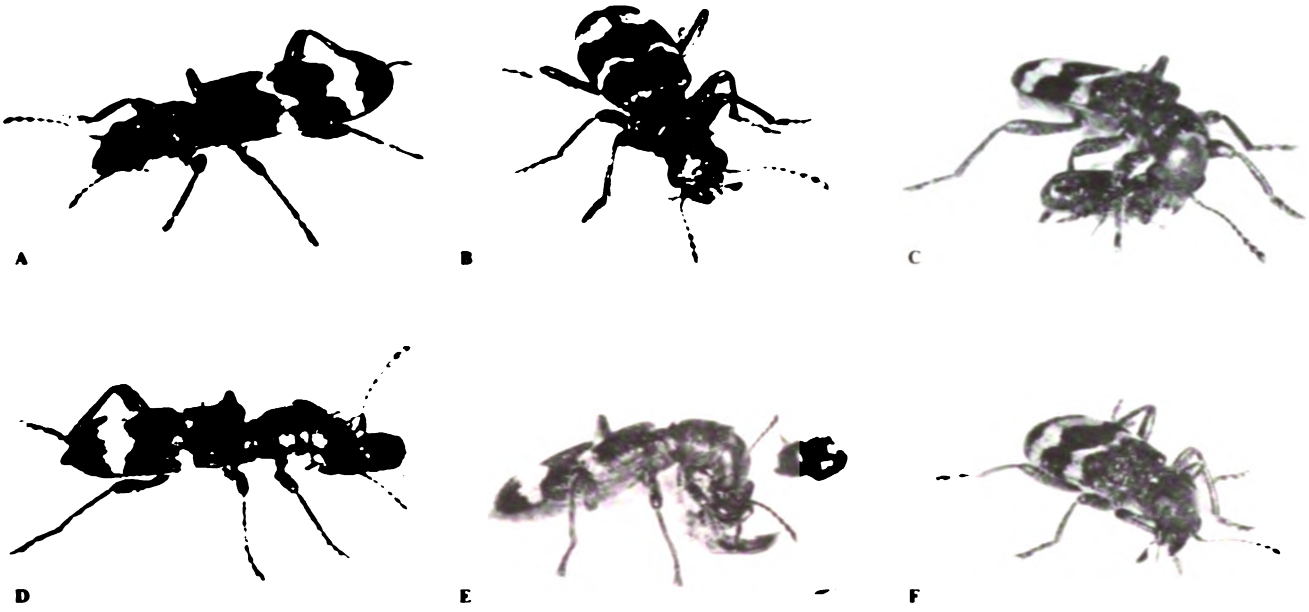

Figure 3-4. – Predatory behavior of adult *Thanasimus dubius. A* = ambush, *B* = searching, *C* = catching, *D* = prey orientation and locomotion, *E* = prey consumption, and *F* = grooming and nonlocomotion. (From Frazier et al. 1980.)

Although they are generally considered to be facultative predators (Moser, Thatcher, and Pickard 1971), their sheer abundance has attracted considerable attention. Smith (1978) described the immature stages of *C. glaber* and *C. parallelus* and determined that they both have five larval instars. Controlled laboratory studies showed that both species complete their development from eggs to adults in 30 to 41 days. Observers found that *Corticeus* adults enter SPB entrance or reemergence holes and egg galleries by removing frass (waste products and sawdust). Adults frequently feed on SPB frass and blue-stain fungi (*Ceratocystis minor* Hedgecock) prior to mating and oviposition. Gut analyses of adult *Corticeus* spp. (Smith 1978) revealed that 80 percent of the beetles had consumed SPB frass and/or blue-stain fungi. Stomachs of the remaining beetles contained fatty material, possibly some SPB life stage. *Corticeus* females oviposit in SPB egg galleries, laying single or small groups of eggs.

Figure 3-5. – Adult of the tenebrionid beetle *Corticeus glaber*. Photo by R. A. Goyer.

Laboratory experiments (Smith 1978) confirmed that *Corticeus* spp. adults were facultative predators and fed on SPB eggs, first- and second-instar larvae, as well as SPB frass and blue-stain fungus.

In Louisiana, *C. glaber* is almost four times more abundant than *C. parallelus* (Smith and Goyer 1980). *Corticeus* spp. arrive at SPB-infested trees for up to 14 days after SPB mass attack. *C. glaber* is most abundant in March–April and October–November, while *C. parallelus* is more abundant from February through June. The predators are more abundant in the lower parts of SPB-infested trees.

Miscellaneous Predators

Lenhard and Goyer (1980) (table 3-1, figs. 3-6 and 3-7) found that in Louisiana the most frequently encountered predators included *Corticeus* spp., *Scoloposcelis mississippensis* (Hemiptera:Anthocoridae), *Aulonium ferrugineum* (Coleoptera:Colydiidae), and *Medetera bistriata* (Diptera:Dolichopodidae). Numbers of predators were generally poorly correlated with SPB egg gallery length and bark thickness.

When the impact of individual predaceous species is known, we can contribute to models to evaluate the efficacy of the predator complex under different conditions.

Parasitoids

Parasitoids differ from predators in that parasitoids are more intimately associated with their host. Whereas predators feed as adults and/or larvae on several hosts, parasitoids usually develop from egg to adult on a single host. Parasitoids known to attack SPB are listed in the Appendix, table 2.

Some parasitoids are host specific: they attack only one host species or a group of closely related species with similar habits. Only a few host-specific parasitoids are known for the SPB.

Table 3-1. – Mean number of predators per 100 cm² and percent of total predators considered.

	Mean number per 100 cm²	Percent of total predators
Hemiptera		
Anthocoridae		
Lyctocoris elongatus (Reuter)	.072	1.4
Scoloposcelis mississippensis (Drake and Harris)	.470	8.9
Coleoptera		
Histeridae		
Platysoma cylindrica (Paykull)	.069	1.3
Platysoma parallelum Say	.057	1.1
Plegaderus spp.	.244	4.6
Cleridae		
Thanasimus dubius (F.)	.378	7.2
Tenebrionidae		
Corticeus spp.	2.899	55.2
Colydiidae		
Aulonium ferrugineum (Zimmermann)	.458	8.7
Aulonium tuberculatum LeConte	.170	3.2
Diptera		
Dolichopodidae		
Medetera bistriata Parent	.439	8.4
TOTAL	5.255	100

Most SPB parasitoids are common on, or will accept, other bark beetle or ambrosia beetle hosts (Dixon and Osgood 1961, Thatcher 1960, Bushing 1965). Many parasitoids of SPB also attack one or more species of *Ips* bark beetles (Berisford, Kulman, and Pienkowski 1970; Berisford et al. 1971; Berisford 1974a; Kudon and Berisford 1980b). Parasitism of more than one bark beetle species is not surprising since one or more *Ips* spp. often occur in the same parts of the same trees attacked by SPB.

Identification of Parasitoids

All of the more common parasites are illustrated in the SPB associates identification guide by Goyer et al. (1980).

Until recently, no single source existed for identifying immature parasitoids of southern pine bark beetles. Finger and Goyer (1978) have published descriptions of the mature larvae of the most common hymenopterous parasitoids of the SPB. Their article includes a key for identifying late-stage larvae and adults (Appendix, table 3). This will help investigators considerably in determining the identities, biologies, roles, and interactions of individual parasitic species.

Parasitoid Attack Behavior

Adult parasitoids apparently respond to insect- and host-produced odors to locate trees infested with advanced SPB brood stages (Camors and Payne 1973). How female parasitoids locate potential hosts beneath the bark is unknown. Some experimental evidence from studies of other bark beetles suggests that they orient to sound (Ryan and Rudinsky 1962) or heat (Richerson and Borden 1972). Female parasitoids generally oviposit through the bark onto third- or fourth-instar larvae (Berisford 1976 unpublished). Most parasitoids apparently sting the host to immobilize it before depositing their eggs. But one of the most common SPB parasitoids, *Roptrocerus xylophagorum* Ratzeburg, enters the bark through SPB entrance and air holes

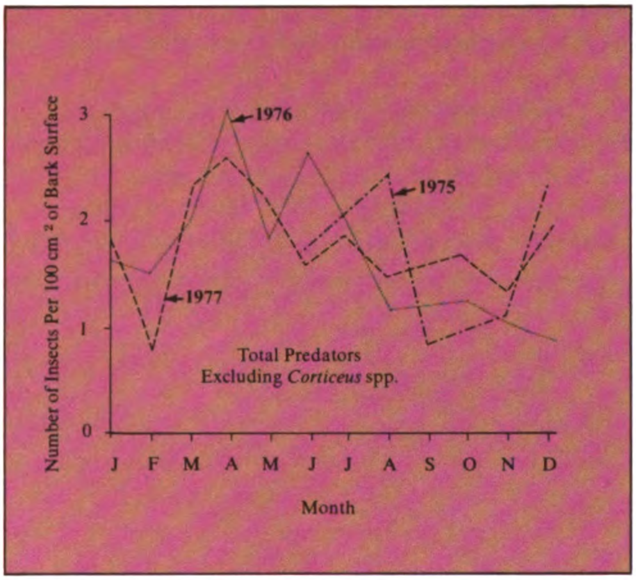

Figure 3-6. – Estimated numbers of SPB predators except *Corticeus* spp., 1975–1977. (From Lenhard and Goyer 1980.)

and oviposits in the SPB egg galleries. Another parasitoid, *Heydenia unica* Cook and Davis, arrives during the beetle's attack stage, possibly to mate, since no SPB larvae are available to parasitize (Camors and Payne 1971, Dixon and Payne 1979b).

Most of the parasitoids associated with SPB arrive at infested trees when large numbers of acceptable hosts are available (Camors and Payne 1973, Dixon and Payne 1979b.) Figure 3-8 shows arrival patterns of some common parasitoids relative to SPB brood development.

Factors Influencing Parasitoid Populations

Numbers of parasitoids in SPB-infested trees may be strongly influenced by beetle brood density and bark thickness (Goyer and Finger 1980, Gargiullo and Berisford 1980). Regressions of numbers of parasitoids against SPB brood density for different bark thickness categories revealed the relative effect of each factor on individual parasitic species. Figure 3-9 shows regressions calculated for two common SPB parasitoids, *Spathius pallidus* and *Coeloides pissodis.*

Bark thickness. – Most of the parasitoids – *Heydenia unica* Cook and Davis, *Cecidostiba dendroctoni* Ashmead, *Dendrosoter sulcatus* Musebeck, *Coeloides pissodis* Ashmead, *Eurytoma* spp., *Rhopalicus* spp., *Spathius pallidus* Ashmead – increased in number as the bark became thinner. *Roptrocerus xylophagorum* was strongly affected by bark thickness even though it enters the SPB galleries to lay its eggs. Most of the parasitoid species reached maximum numbers at intermediate host densities, with the exception of *Eurytoma* spp. *Spathius pallidus* was apparently unaffected by host density, and *R. xylophagorum* became increasingly abundant as host density increased and bark became thinner. It was the only parasitoid that showed a significant interaction between bark thickness and host density.

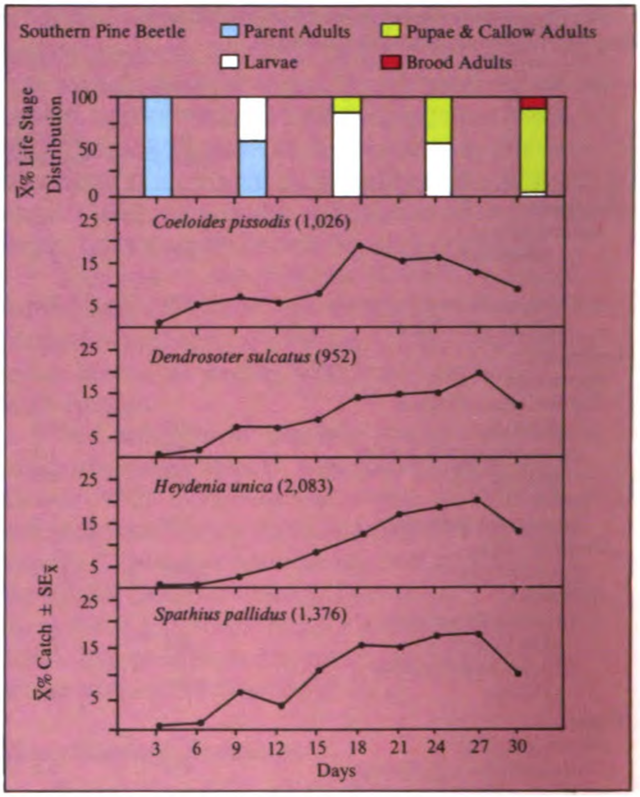

Figure 3-8. – Sequence of arrival of the SPB parasitoids *Coeloides pissodis, Dendrosoter sulcatus, Heydenia unica,* and *Spathius pallidus,* in relation to SPB brood development. Numbers trapped are shown in parentheses. Totals were from seven trees. (From Dixon and Payne 1979b.)

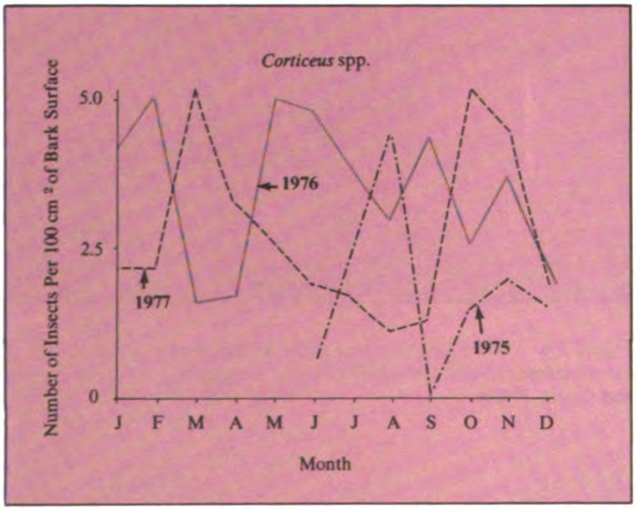

Figure 3-7. – Numbers of *Corticeus* spp. associated with SPB, 1975-1977. (From Lenhard and Goyer 1980.)

Parasitoid population differences. – Hain (1978 unpublished) reported quantitative and qualitative differences in natural enemy populations at three locations in North Carolina. But differences were not as well correlated with SPB brood adult densities as in Louisiana (fig. 3-10). In Louisiana highest numbers of parasitoids occurred during April–June, with a second peak in August. Lowest parasitoid populations were found in the fall and winter, when SPB populations were also low (fig. 3-11). Similar seasonal patterns were observed in Texas (Stein and Coster 1977) and Arkansas (Stephen 1980).

Parasitoid Responses to Behavioral Chemicals

The response of parasitoids to beetle- and/or tree-produced compounds released from SPB-infested trees has received only limited attention. Camors and Payne (1971) showed that one parasitoid, *Heydenia unica,* responds to host tree terpenes and a component of the SPB attractant chemical, or pheromone. Dixon and Payne (1980) caught four species of SPB parasitoids in

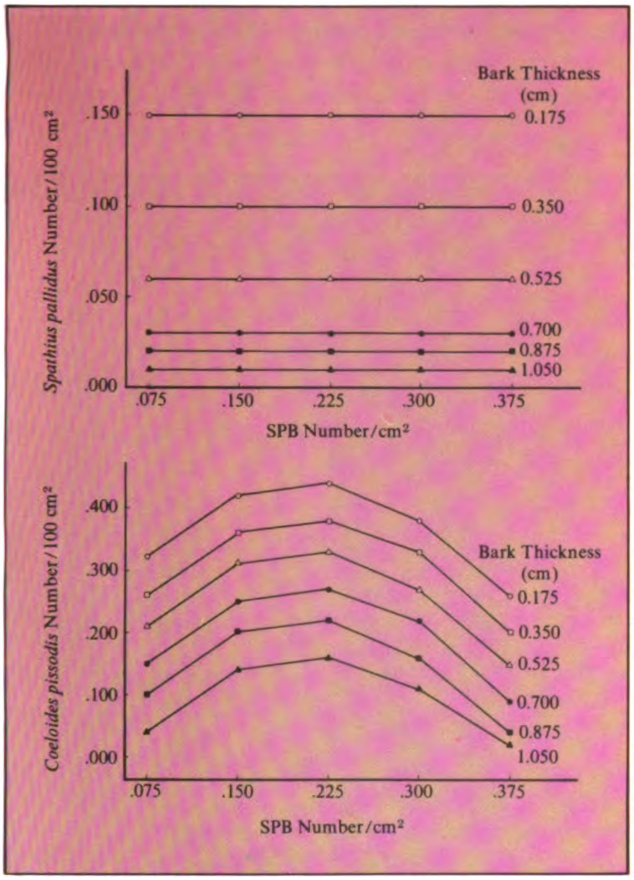

Figure 3-9. – Numbers of the parasitoids *Spathius pallidus* (A) and *Coeloides pissodis* (B) relative to numbers of SPB at different bark thicknesses. (From Gargiullo and Berisford 1980.)

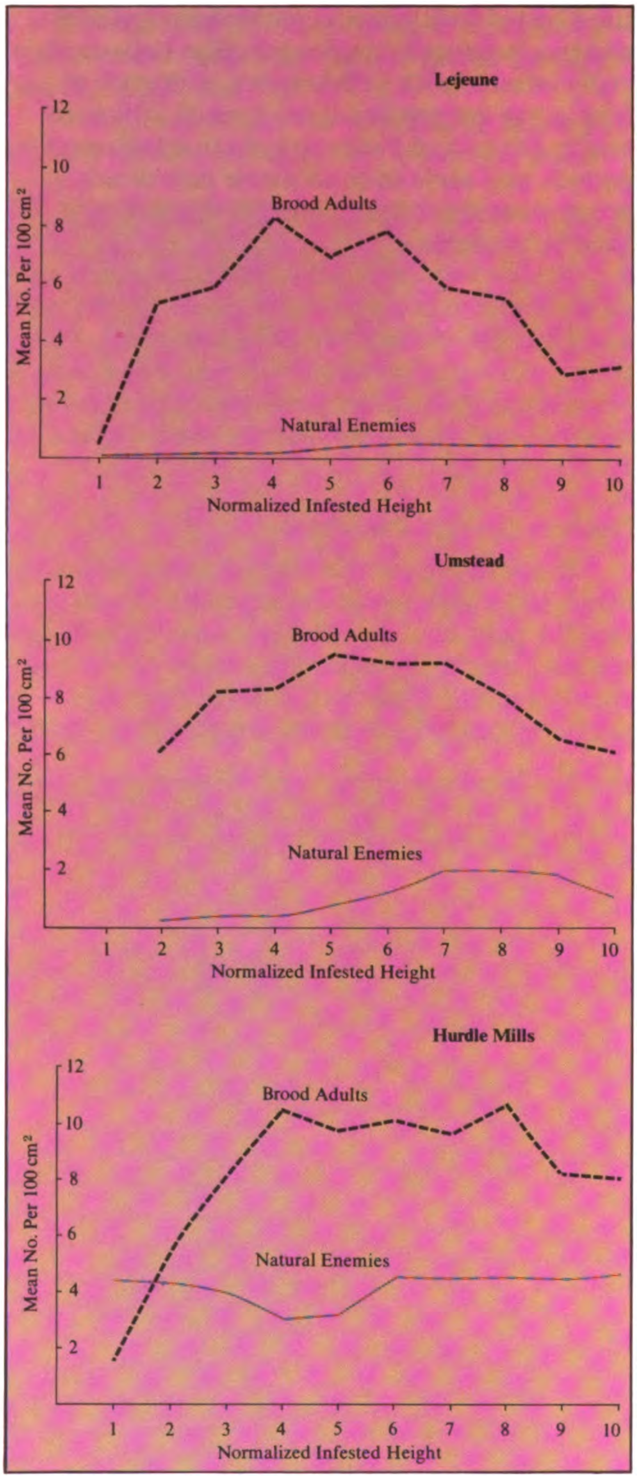

Figure 3-10. – Numbers of natural enemies, including parasitoids relative to numbers of SPB brood adults at three locations in North Carolina. (From Hain 1978 unpublished.)

traps baited with various combinations of SPB- and tree-produced compounds, plus bolts artificially infested with SPB females. Although no host larvae are present at the time of SPB mass attack, Dixon and Payne suggest that the compounds may serve to concentrate parasitoids in areas where hosts in suitable life stages would soon be available.

Kudon and Berisford (1980a) developed an olfactometer to evaluate the response of SPB parasitoids to insect- and tree-produced odors. This device will aid in preliminary screening of compounds that may attract parasitoids. Final determinations of attractancy must be made in the field, however.

Nonhost-Specific Parasitoids

Many of the parasitoids that attack SPB also attack other bark beetles, as noted previously. In fact, the parasitoid complexes associated with *Ips avulsus* Eichoff, *I. grandicollis* Eichoff, *I. calligraphus* (Germar), *I. pini* Say, and the eastern juniper bark beetle (*Phloeosinus dentatus* [Say]) share with the SPB three of the most common species – *Roptrocerus xylophagorum* (= *eccoptogastri*), *Heydenia unica*, and *Coeloides pissodis* (Berisford et al. 1970 and 1971, Berisford and Franklin 1971, Berisford 1974a and b).

It has been generally assumed that the SPB parasitoids which were not host-specific would utilize the most abundant acceptable hosts available and that other bark beetles (e.g., *Ips* spp.) would serve as reservoir hosts when SPB populations were low. However, Berisford (1974a) found that when both SPB and *Ips* spp. were available, parasitism did not readily shift from one species to the other. This fact suggests that some parasitoids may prefer a particular host, if they are not host specific.

Kudon and Berisford (1980b) showed that when adult parasitoids were reared from SPB-infested logs in field cages and given simultaneous choices between different logs containing late-instar larvae of SPB and *Ips* or SPB and *P. dentatus*, a high percentage of the parasitoids se-

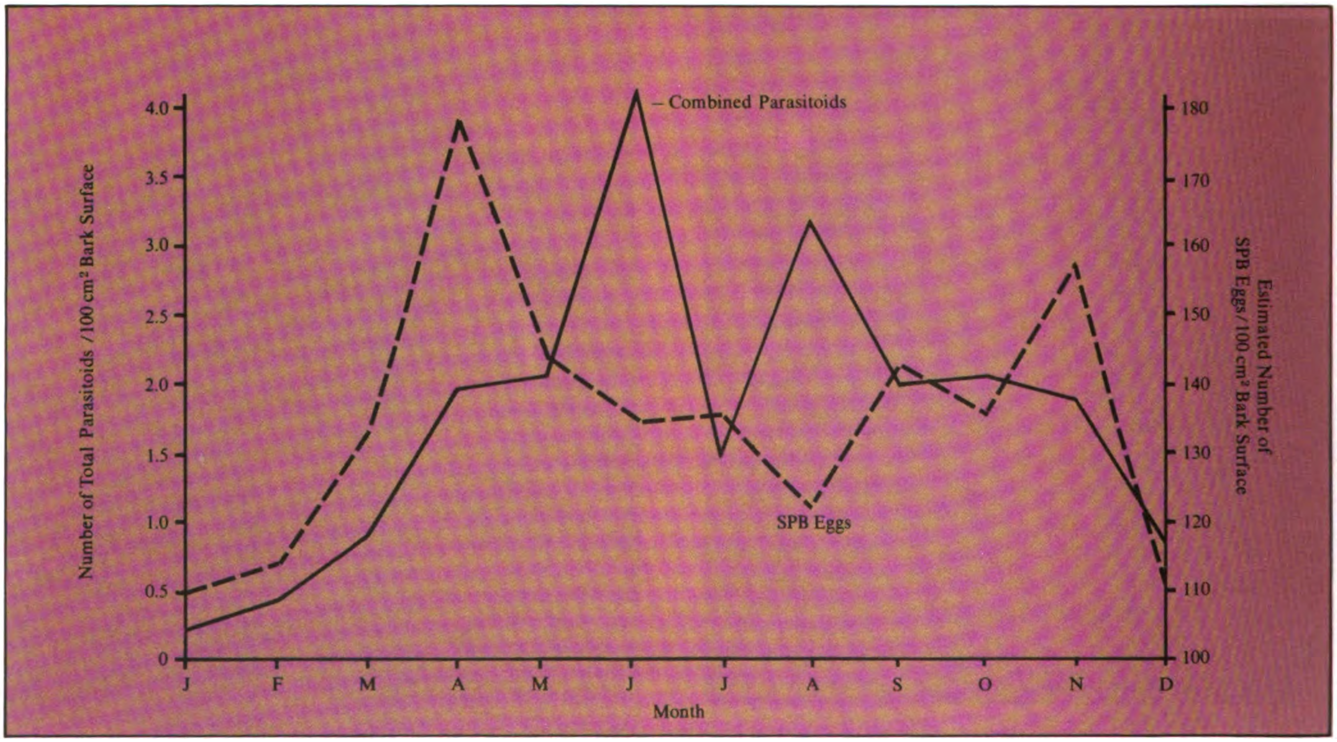

Figure 3-11. – Seasonal abundance of parasitoids relative to numbers of SPB eggs in SPB-infested trees in Louisiana. (From Goyer and Finger 1980.)

lected logs with SPB (fig. 3-12A and B). When parasitoids were reared from *Ips* or *P. dentatus,* the parasitoids reversed their preferences. The preferences were even greater when the parasitoids could select between both beetle hosts (SPB *v. P. dentatus*) and tree hosts (pine *v.* cedar) instead of beetle hosts only (SPB *v. Ips*) in loblolly pine (fig. 3-12C and D).

Thus, it seems that the parasitoids, although not host-specific, are entrained to initially select

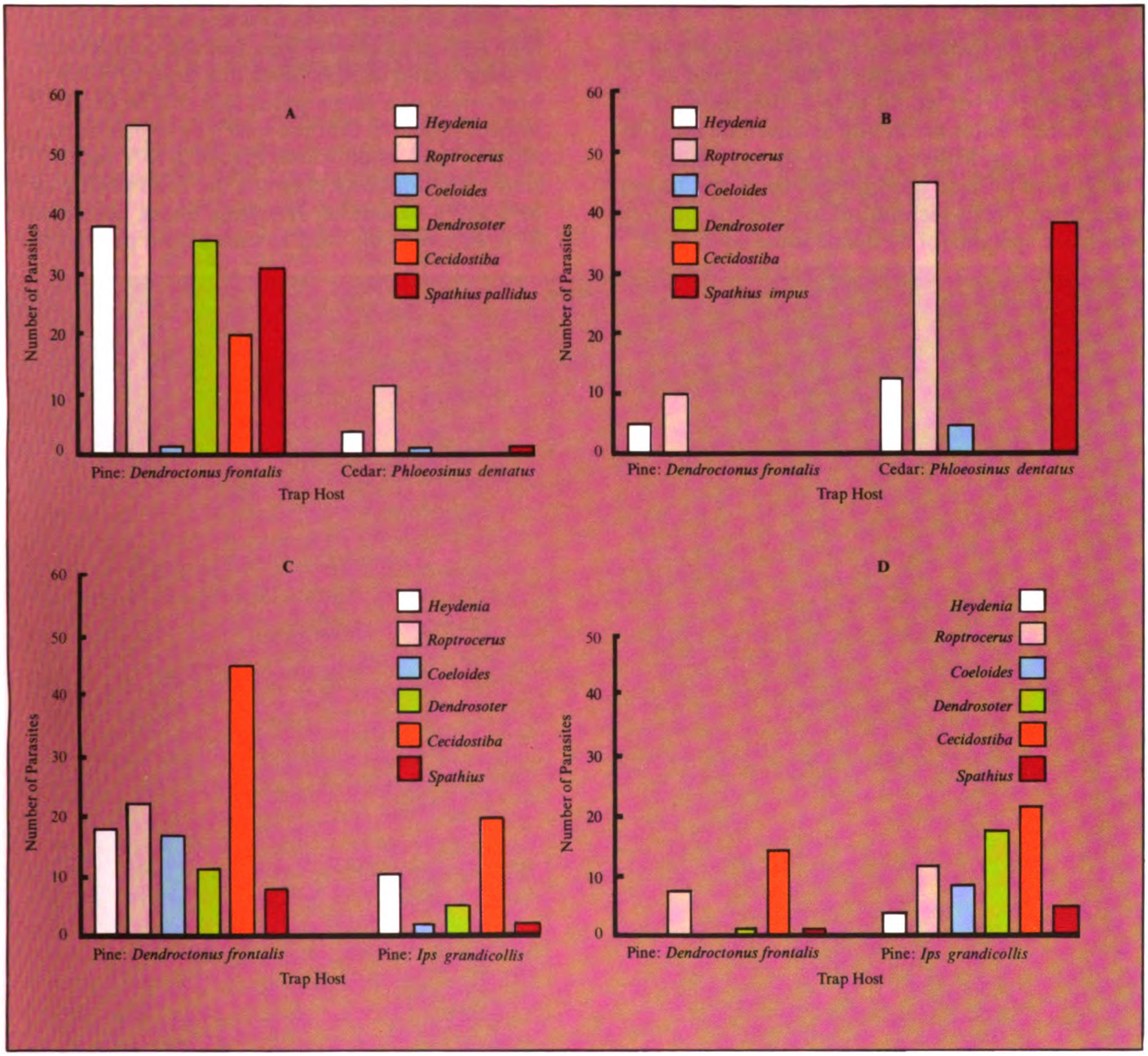

Figure 3-12. – Parasitoids reared from SPB (A) and *Phloeosinus dentatus* (B) presented with simultaneous choices of logs infested with SPB or *Phloeosinus dentatus.* Parasitoids reared from SPB (C) and *Ips grandicollis* (D) presented with simultaneous choices of logs infested with SPB or *Ips grandicollis.* (From Kudon and Berisford 1980b.)

the host on which they were reared. This phenomenon appears to be the first documented manifestation of Hopkins' (1916) Host-Selection Principle among insects that prey on other insects.

Identification of Previous Hosts of Predators and Parasitoids

Knowing the identity of previous hosts of adult parasitoids or predators that respond to SPB-infested trees would help to determine if other bark beetles are acting as alternate and/or reservoir hosts. Miller et al. (1979) and Miller (1979) have utilized immunodiffusion and immunoelectrophoresis techniques to produce antisera which are specific for SPB and some of its bark beetle associates (*Ips* spp. and black turpentine beetle). These techniques may be used to help determine the prey of SPB predators such as *Thanasimus dubius* and may help estimate the number of prey consumed. Kudon and Berisford (1980c) found that the fatty acid composition of parasitoids reared from SPB and some of its common associates closely matched the composition of their beetle host(s). With this discovery the host origin of a single parasitoid can be determined, provided that the host's lipid profile has already been established. Figure 3-13A and B shows the similarity between the lipid profile of SPB and a parasitoid, *Heydenia unica,* reared on SPB. Figure 3-13C and D shows lipid profiles for

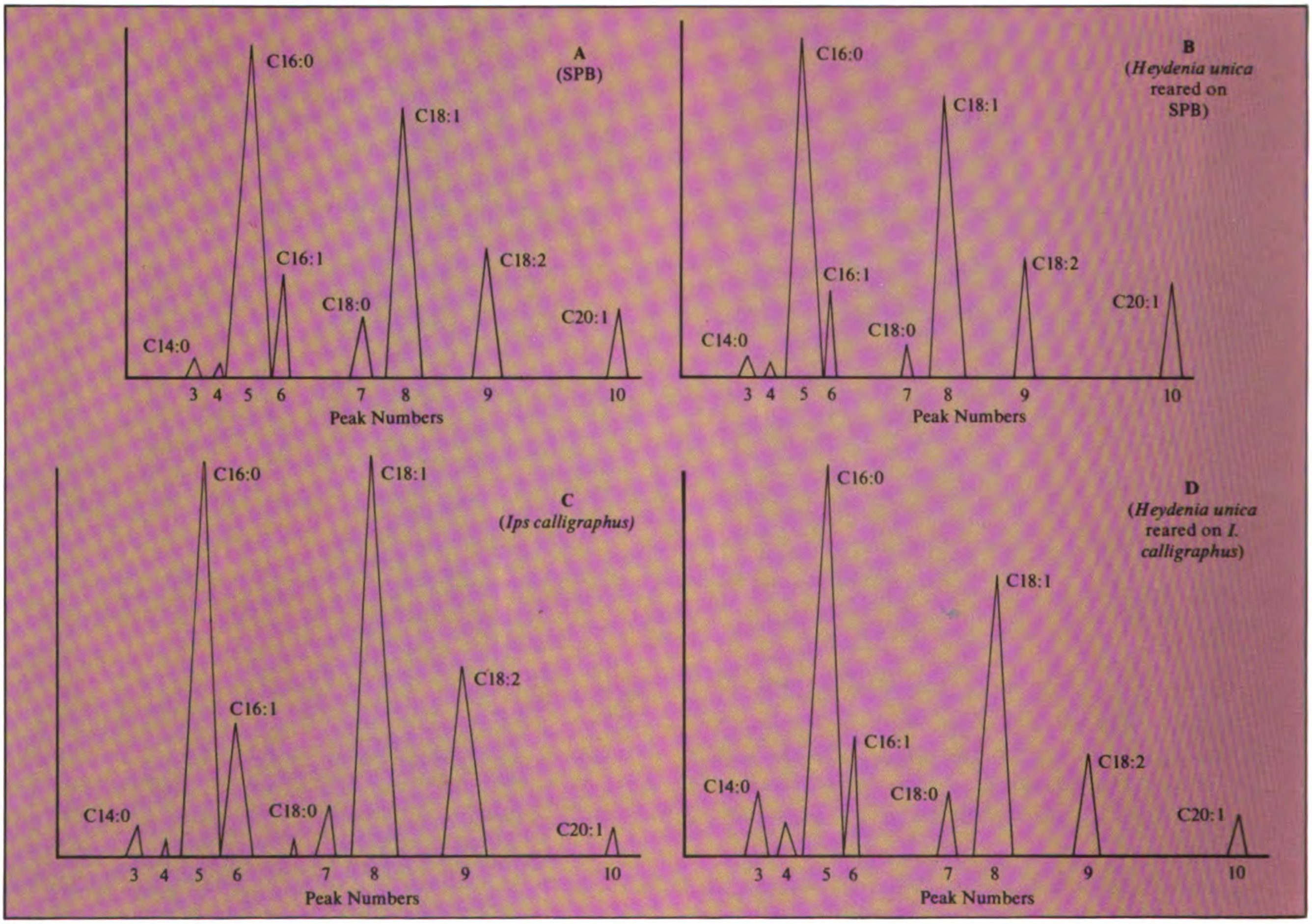

Figure 3-13. – Lipid profile of SPB (A) and a parasitoid, *Heydenia unica* (B), that had been reared on SPB. Lipid profile of *Ips calligraphus* (C) and the same *Heydenia unica* (D) which had been reared on *I. calligraphus.* (From Kudon and Berisford 1980c.)

I. calligraphus and *H. unica* reared on *I. calligraphus*. The technique of comparing lipid profiles may also help to determine predator hosts if they feed on a single prey species. The clerid *Thanasimus dubius* was fed on SPB and the cowpea weevil (*Callosobruchus maculatus*). The profile of *T. dubius* reared on SPB matches the host profile well. But the profile of those reared on the weevil — an unnatural host — differs from that of clerids fed on the SPB.

The host-induced preferences of parasitoids may be a factor affecting the impact of the parasitoid complex on SPB populations. Although the relatively high populations of *Ips* spp. usually present in logging slash, damaged trees, lightning strikes, etc., can support substantial parasitoid populations, *Ips* may not be a reservoir for SPB parasitoids, due to their host preferences. On the other hand, the parasitoids seem able to attack other hosts if the preferred host is not readily available. This adaptability may be a survival-enhancing mechanism.

At this point we do not understand the mechanism of parasitoid switching from one host to another. If we assume that the preferences will create a lag in acceptance of nonpreferred hosts, this may reduce potential parasitism in at least one generation of hosts. A theoretical conceptual model of parasitoid-host interactions among SPB, *Ips*, and their common parasitoid complex has been proposed (Berisford and Kudon unpublished). The model is based on a relatively stable *Ips* population *v.* fluctuating SPB populations. It describes the shifts of parasitoids between the beetle hosts as each host becomes more or less abundant relative to the other host over time. During SPB epidemics, *Ips* populations will also increase since *Ips* spp. normally attack SPB-infested trees. The relative populations, however, still fit the hypothesis of the model, i.e., that the relatively scarce host loses parasitoids to the relatively abundant one regardless of absolute populations.

Figure 3-14 illustrates the theoretical parasitoid-host relationships of SPB populations for a full cycle from endemic to epidemic to endemic states. At endemic SPB levels, *Ips* populations in logging slash, damaged trees, etc., are relatively large compared to SPB, and most parasitoids would go from *Ips*- to *Ips*-infested material since they developed on this host. As SPB populations begin to expand, parasitoids find SPB increasingly easier to locate relative to *Ips* and they begin to shift from *Ips*- to SPB-infested trees. As SPB reaches epidemic levels, the shift to SPB becomes very pronounced. There is no tendency to select the now relatively low populations of *Ips* beetles. As SPB populations decline, the parasitoids switch back to the relatively more abundant *Ips* as the preferred host (SPB) becomes less available.

The same phenomenon may occur within individual trees. During SPB epidemics, a high percentage of an infested tree bole is occupied by

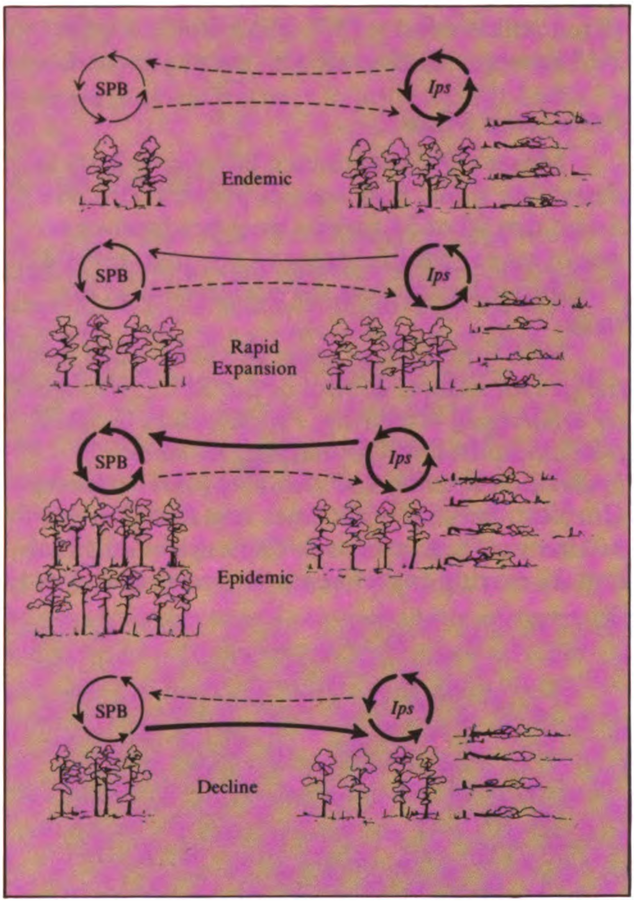

Figure 3-14. — Theoretical stand model of parasitoid shifts from the relatively scarce hosts to the more abundant host bark beetles (*Ips* spp. and SPB) during the buildup of SPB from endemic to epidemic levels and the subsequent decline to endemic populations. (From Berisford and Kudon 1979 unpublished.)

SPB. Any shift of parasitoids is most likely to be from *Ips* to SPB since searching adult parasitoids would frequently encounter SPB. When SPB is at endemic levels, though, it frequently occupies only a small part of a tree; the remainder is occupied by *Ips*. The parasitoids will cycle from *Ips* to *Ips* and have reduced impact on the less abundant SPB.

Mites

A large number of phoretic mites are associated with the southern pine beetle (Moser and Roton 1971, Moser 1975). Several species prey on SPB. Some indirectly affect SPB by reducing flight and mobility, while others indirectly benefit the beetle by preying on parasitic nematodes (Kinn and Witcosky 1977, Kinn 1980). Figure 3-15 shows an SPB adult with mites attached.

Predaceous Mites

Moser (1975) conducted laboratory tests to determine which mite species prey on SPB. He found that 32 of 51 species were predaceous on one or more SPB life stages (Appendix, table 4). First-instar larvae were the preferred host life stage.

Four mite species appeared to be good candidates for natural control of the SPB: *Histiogaster arborsignis* Woodring, *Proctolaelaps dendroctoni* Lindquist and Hunter, *Macrocheles boudreauxi* Krantz, and *Dendrolaelaps neodisetus* Hurlbutt. Subsequent studies revealed that *M. boudreauxi* feeds primarily on nematodes. In laboratory rearing experiments, its presence did not affect SPB egg hatch or brood production (Kinn and Witcosky 1977). Four other species – *Eugamasus lyriformis* McGraw and Farrier, *Dendrolaelaps neocornutus* Hurlbutt, *D. isodentatus* Hurlbutt, and *Proctolaelaps fiseri* Samsinak – were suggested as secondary choices for control of SPB in the field.

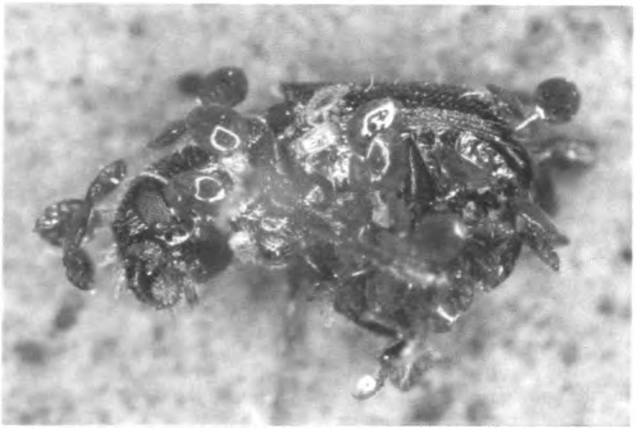

Figure 3-15. – An SPB adult with phoretic mites attached. Photo by J. C. Moser.

Dendrolaelaps neodisetus apparently has a mutualistic relationship with the SPB (Kinn 1980). In this study progeny production by the SPB was not different in broods reared from adult beetles with and without *D. neodisetus*. However, emerging brood adults had a significantly lower incidence of parasitism by the nematode *Contortylenchus brevicomi* if *D. neodisetus* mites were present on the parent SPB. In field-collected samples from SPB-infested trees, there was a strong negative correlation between numbers of the nematode *C. brevicomi* and presence of *D. neodisetus*. Therefore, SPB populations with only a few of the phoretic *D. neodisetus* would be more likely to have a higher incidence of parasitism by *C. brevicomi*. The mutual benefits to SPB and *D. neodisetus* are obvious. The SPB provides a mechanism for the flightless mites to move to new beetle infestations, and the SPB benefits by having a reduced chance of nematode parasitism because the mites feed on the free-living stages of *C. brevicomi*.

Mite Associates Key

Kinn (1976) published a key that identifies 15 species of phoretic mites most commonly associated with SPB (Appendix, table 5). The key is written with minimal acarology jargon so that researchers and students untrained in mite taxonomy can use it efficiently. It also contains instructions for mounting mites on slides for identification.

Phoretic Mites

A nondestructive SPB trap (Moser and Browne 1978) has been used to evaluate the effect of phoretic mites on the flight of SPB adults (Kinn and Witcosky 1978). The researchers found that 36 percent of SPB adults trapped (primarily males) carried uropodid mites or their attachment pedicels. It was also found the the color of mite pedicels indicated the relative age of SPB to which they were attached. Callow SPB adults or other newly emerged adults have white pedicels; reemergent parent adults have amber or black pedicels.

Under forest conditions at least one-third of the SPB carry mites (Moser 1976a). Further, beetles attacking lower portions of trees have more attached mites than those attacking upper stems. Flying SPB can carry at least 20 percent of their weight in mites (Moser 1976b). These and results from other investigators (Dixon and Osgood 1961) indicate that mites may have a significant effect on flight dispersal.

Although many of the mites are usually regarded as phoretic on the SPB alone, many species also ride on other bark beetles and associated species to get to other host material (Moser 1976a). Therefore, mites associated with SPB-infested trees may have gotten there on a variety of insects.

Profile of Mite Associates

Stephen and Kinn (1980) reported the distribution, seasonal fluctuation, and relative diversity of mites associated with SPB. More mite species are found in the upper boles of SPB-infested trees than in the lower boles, due to higher numbers of other bark beetles in that portion of the bole and larger numbers of a few mite species in the lower bole. The distribution of *Tarsonemus krantzi* Smiley and Moser was somewhat uniform over the entire bole. *Trichouropoda australis* Hirschmann and *Dendrolaelaps neodisetus* were more abundant in the lower bole. *Pygmephorellus bennetti* (Cross and Moser) and *Tarsonemus ips* Lindquist were most abundant in the upper bole.

Seasonal distribution. – The relative abundance of the common mite associates varied seasonally. *Proctolaelaps dendroctoni, Longoseius cuniculus* Chant, and *Macrocheles boudreauxi* were most common in early summer. During midsummer, *D. neodisetus, Eugamasus lyriformis,* and *Trichouropoda australis* were most abundant. *Tarsonemus krantzi* and *T. ips* increased in numbers from midsummer through early fall. *Anoetus varia* Woodring and Moser and *Histiogaster arborsignis* were most abundant during the fall. One species, *Ereynetoides scutulis* Hunter, showed little change in seasonal abundance (D. N. Kinn personal communication).

Sampling methods. – Sampling for mites phoretic on SPB and other bark beetles is best accomplished with emergence traps (Kinn 1979). The traps described by McClelland et al. (1978) give reliable estimates because they minimize losses due to rearing, dessication, and transporting samples. Also, fewer nonphoretic stages accumulate in the collecting medium.

The various species of mites associated with SPB perform different functions. Some are predators, while others are scavengers, facultative predators, predators of other natural enemies, or even mechanical barriers to normal SPB flight.

Avian Predators

Birds, especially woodpeckers, have been credited as important natural enemies of the SPB since the earliest beetle studies (Hopkins 1899 and 1909a, St. George 1931). But despite their apparent importance in regulating beetle populations, there have been few attempts to quantify the role of woodpeckers or to describe the forest conditions under which such predation is most effective. Dixon and Osgood (1961) reported higher mortality of SPB from low temperatures in trees where bark had been partially removed by woodpeckers than in trees with no evidence of foraging. In fact, woodpeckers feeding on SPB trees often remove most of the bark (fig. 3-16). Overgaard (1970) reported a 24 percent reduction in SPB populations by woodpeckers. Moore (1972) concluded that woodpeckers were very effective SPB predators.

In a comprehensive study, Kroll and Fleet (1979) studied four species of woodpeckers (downy, hairy, pileated, and red-bellied) (fig. 3-17A-C) to determine their role in SPB population dynamics in Texas. They found that all of the woodpecker species studied preyed heavily on SPB. During a period of rapid SPB buildup in

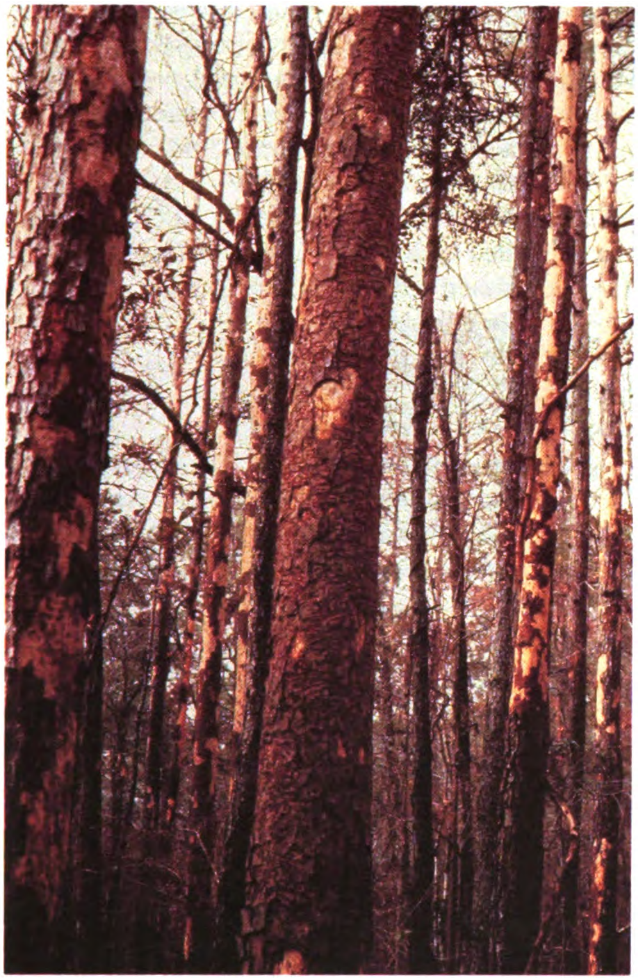

Figure 3-16. – A tree that has been heavily foraged by woodpeckers and contains SPB brood. (From Kroll et al. 1980.)

Texas (1966–76), woodpecker censuses showed a strong correlation between numbers of birds and numbers of SPB spots. Woodpeckers were found to feed heavily on SPB when they were very abundant and on soft mast when beetle populations were low.

Highest numbers of woodpeckers were found in SPB spots during late summer and lowest numbers in late winter (fig. 3-18). Woodpeckers were up to 50 times more numerous in stands infested with SPB than in neighboring, noninfested stands. All four woodpecker species showed some ability to shift from uninfested to infested stands. Downy and hairy woodpeckers accounted for most of the predation on SPB by

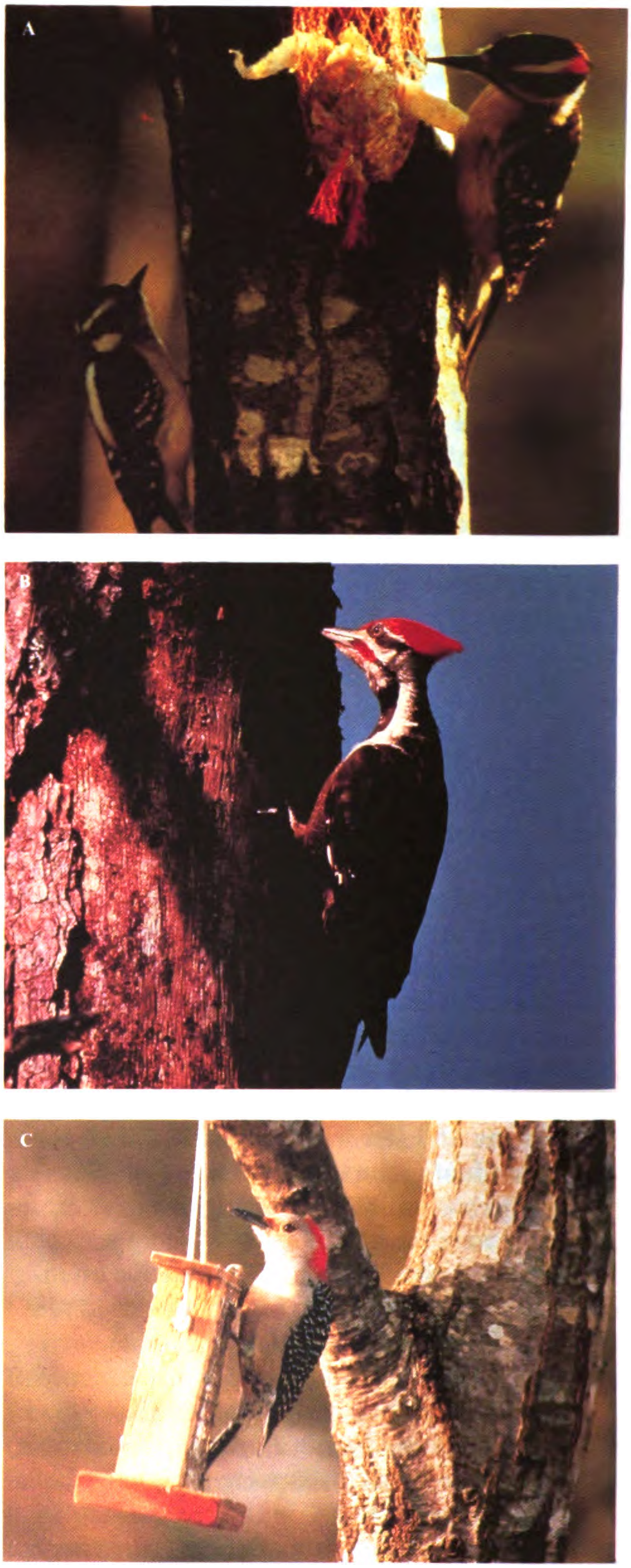

Figure 3-17. – *A:* Adult downy (below left) and hairy (above right) woodpeckers. *B:* Pileated woodpecker. *C:* Red-bellied woodpecker. (From Kroll et al. 1980.)

birds. In uninfested stands, mixed pine-hardwoods generally had higher densities of woodpeckers than pure pine stands, probably because there were more nesting sites and other food sources (e.g., mast).

In SPB-infested trees, woodpecker activity was greatest in the midbole—where the beetles congregate. Predation was greatest during fall and summer and least during spring (when SPB spots begin to become active and proliferate) (fig. 3-19).

Woodpeckers preyed mainly on SPB brood adults (64 percent) and least often on eggs (4 percent). Foraging was almost twice as great on shortleaf as on loblolly pine, probably because the woodpeckers could flake off the thinner bark of shortleaf pines more easily to get at the SPB.

The seasonal impact of woodpeckers on the SPB and some of its associates was evaluated by protecting portions of SPB-infested trees from woodpeckering as SPB broods matured. Beetle mortality was highest during the winter (36 to 63 percent) and lowest in summer (12 to 30 percent.) Figure 3-20 illustrates survival of SPB in screened and unscreened sections of trees. The portions of trees from which woodpeckers were excluded had substantially higher beetle survival than unscreened parts of the same trees.

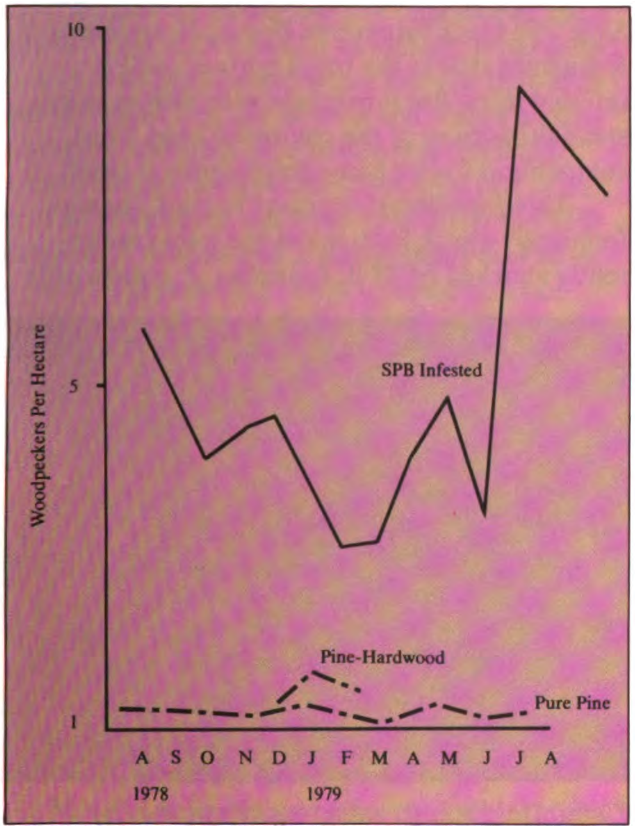

Figure 3-18. – Densities of woodpeckers in SPB spots at different times of the year. (From Kroll 1979 unpublished.)

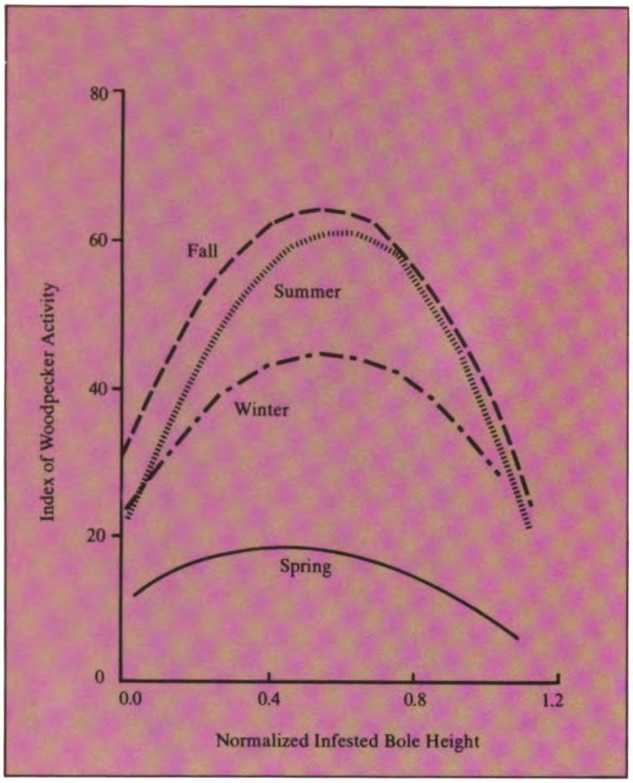

Figure 3-19. – Distribution of woodpecker feeding activity on the boles of SPB-infested trees during different seasons. (From Kroll 1979 unpublished.)

Kroll, Conner, and Fleet (1980) proposed the adoption of timber management practices to increase the number of woodpeckers and their impact on SPB. They advocate maintaining mixed pine-hardwood stands and promoting shortleaf and longleaf pine stands where suitable. Other woodpecker-enhancing tactics include providing more nesting sites for woodpeckers and modifying current cut-and-leave suppression tactics to leave standing those trees already vacated by SPB broods for woodpecker nesting sites.

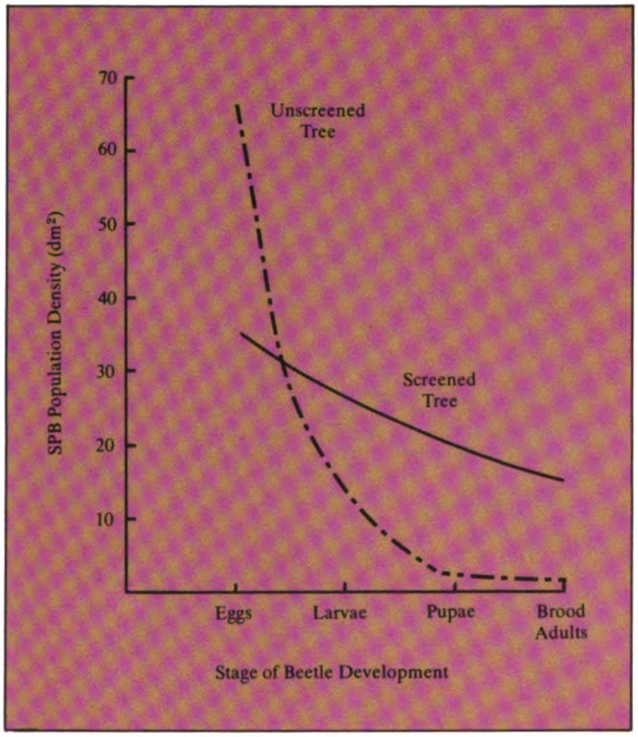

Figure 3-20. – Survival of SPB in trees which were screened to prevent woodpecker predation and survival in unscreened trees. (From Kroll 1979 unpublished.)

Competitors

The southern pine beetle competes with other insects for the same food supply during a part of its developmental period. This competition for available food and/or space may significantly reduce SPB survival.

Southern Pine Sawyer

Although this associate has been known for some time, the first comprehensive study of its role as an SPB competitor was conducted only recently (Coulson et al. 1976b). Results confirmed that foraging by larvae of the southern pine sawyer (fig. 3-21), *Monochamus titillator* (Fab.) (Coleoptera: Cerambycidae), significantly reduced SPB survival. The distribution of *M. titillator* over the bole of infested trees has been described and mathematical models have been developed to account for SPB mortality caused by sawyer larvae. Figure 3-22 shows the impact of cerambycid foraging when observed and expected numbers of SPB were compared in areas foraged by *M. titillator.*

Procedures have been developed for predicting SPB mortality based on *M. titillator* activity. Coulson et al. (1980a) showed that the sawyer foraged up to 20 percent of the inner bark/outer wood surface area of SPB-infested trees, killing about 14 percent of the SPB per tree. However, SPB mortality in foraged areas ranged up to 70 percent. Sawyer feeding was greater in larger trees. Foraging and subsequent SPB mortality increased from the base to the top of the infested trees.

Bark Beetle Associates

Four other bark beetles – *Dendroctonus terebrans* (Olivier), *Ips avulsus, I. grandicollis, I. calligraphus* – are commonly associated with the SPB. The black turpentine beetle, *D. terebrans,* frequently attacks the basal portion of SPB-infested trees. But it overlaps with SPB in only a small proportion of the colonized bole. Thus competition for the same food supply is small.

Three species of engraver beetles, *Ips* spp., frequently attack portions of the trees concurrently attacked by SPB. *I. avulsus, I. grandicollis,*

Figure 3-21. – The southern pine sawyer, *Monochamus titillator.* (From Goyer et al. 1980.)

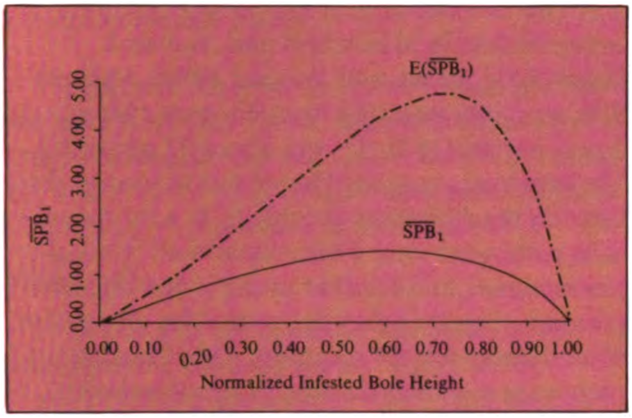

Figure 3-22. – Impact of foraging by pine sawyer larvae on SPB broods. Curves show differences between expected numbers of SPB and those actually observed. (From Coulson et al. 1980a.)

and *I. calligraphus* may compete with SPB for the same food supply and space.

Birch and Svihra (1979) studied the competitive interactions among the five bark beetle species in Texas. Examination of loblolly pines felled shortly after bark beetle attack showed that SPB and the associated *Ips* all attacked within a short timespan. Southern pine beetle was the first to initiate attacks in most cases, but only two of 28 trees were attacked solely by SPB. After the SPB attacked, *I. avulsus* and *I. calligraphus* moved in quickly. *I. grandicollis* rarely infested boles of standing trees but was frequently found in branches. The portions of the main bole occupied by the various species of bark beetles are shown in figure 3-23.

Paine, Birch, and Svihra (1980) determined how much of the tree was occupied by SPB and four species of competitors and how much overlap occurred among them. *I. avulsus* occupied the greatest length of bole and *I. grandicollis* the shortest length. The upper parts of infested trees were dominated by *I. avulsus,* while the lower parts were dominated by SPB. *I. avulsus* thus overlapped only slightly with SPB. *I. calligraphus* showed considerable overlap with SPB.

More bark beetle species occupied the mid-bole area than any other part of the tree. Fewer species overlapped with each other at the extremes of the infested area.

Pheromones

The southern pine beetle and its associated bark beetle competitors all produce aggregation pheromones (Birch 1978). Some bark beetles may use pheromones as species isolation mechanisms (Wood 1970, Lanier and Wood 1975). Birch and Wood (1965) and Byers and Wood (1980) demonstrated that two closely associated bark beetles

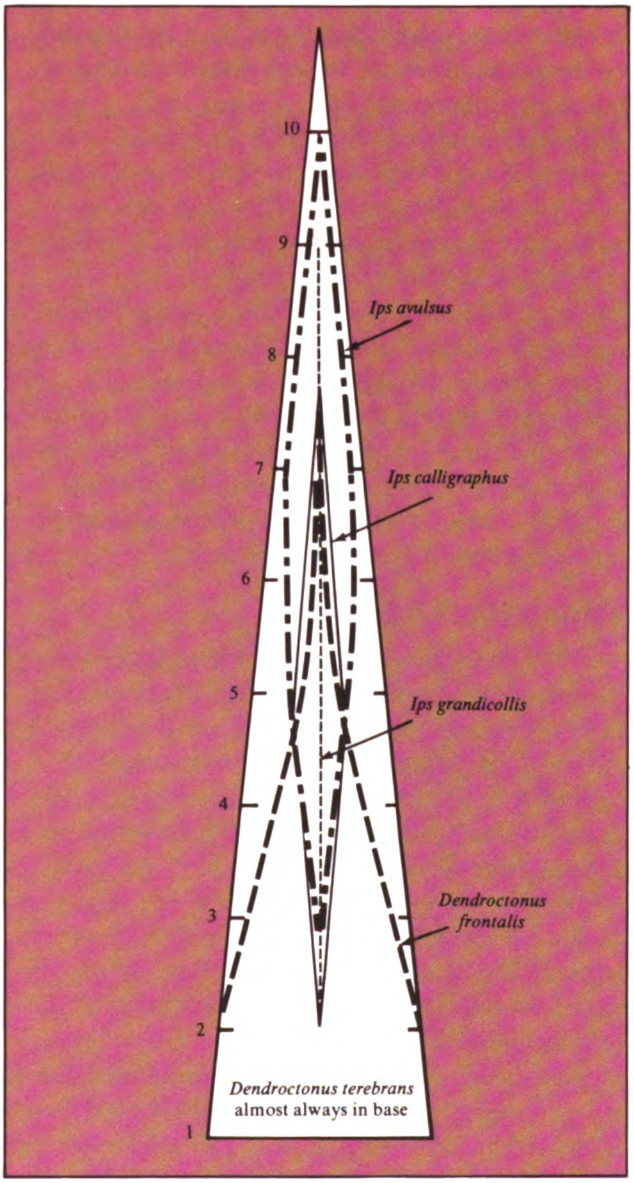

Figure 3-23. – Area of the main bole of loblolly pine occupied by each of five species of bark beetles. (From Birch and Svihra 1979.)

may utilize reciprocal inhibition to avoid competing for the same food. These species may colonize the same tree but occupy different parts due to inhibition of attacks by species that follow the primary attacker.

Birch et al. (1980) determined the response of different beetles to logs infested with various combinations of SPB, *I. avulsus, I. grandicollis,* and *I. calligraphus.* The first beetles to arrive were generally SPB if SPB females were present in experimental logs. Southern pine beetles did not respond, however, to logs infested with any *Ips* species. Response by *I. avulsus* and *I. grandicollis* was enhanced when SPB and males of either of the *Ips* spp. were present. The response of *I. avulsus* to its own attractant was also enhanced by the presence of *I. grandicollis.* This phenomenon was previously reported by Hedden, Vité, and Mori (1976). *I. calligraphus* was inhibited by *I. avulsus.* Conversely, *I. avulsus* response was enhanced by the presence of *I. calligraphus.* Reciprocal inhibition occurred between SPB and *I. grandicollis.* The olfactory interactions during attack on new host material resulted in rapid colonization of trees and minimal competition between the species.

Pathogenic Organisms

The southern pine beetle is attacked by a variety of organisms that may kill the beetle outright or reduce its egg production and survival. Although occasional references to diseases of SPB may be found, serious attempts to identify these disease organisms and determine their roles in regulating beetle populations have received little attention in the past. Moore (1971) found that fungi and bacteria caused an average SPB mortality of 22 percent in North Carolina. Mortality varied with the stage of beetle development, season, location on trees, and species of host trees. Diseases were more common in spring and winter, and higher percentages of infected SPB were found in the midbole region of infected trees. In North Carolina, disease incidence was higher in Virginia pine than in loblolly or shortleaf pines.

The diseases of SPB have also been intensively studied in Mississippi and Alabama (Sikorowski, Pabst, and Tomson 1979). Average SPB mortality resulting from diseases over a 2-year period (1975–77) was about 22 percent. The organisms responsible for this mortality are listed in the Appendix at table 6. The most common pathogens were a microsporidian, *Unikaryon minutum,* and another unidentified microsporidian. Together they accounted for 30 percent of all disease-related mortality. Other important pathogens included the fungi *Paecilomyces* sp. and *P. viridis,* and two parasitic nematodes, *Contortylenchus* sp. and *C. brevicomi.*

Infectivity tests in the laboratory showed that SPB larvae were most susceptible to the fungi *Metarhizium anisophilae* and *P. viridis.* The infection rate was 50 percent.

Different pathogens were more prevalent at different times of the year (fig. 3-24). Fungi and bacteria were common during cool weather, while protozoans were prevalent during hot weather. Overall mortality was also highest during low-temperature periods (fig. 3-25). There was no apparent correlation of diseases with rainfall.

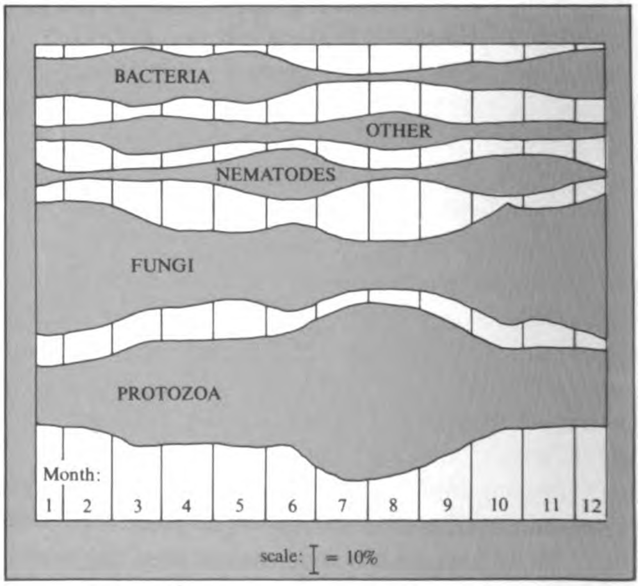

Figure 3-24. – Relative seasonal abundance of SPB pathogens in Mississippi and Alabama 1975–1977. (From Sikorowski et al. 1979.)

Entomophagous Fungi

Pabst and Sikorowski (1980) found that under laboratory conditions, three entomophagous fungi—*Beauvaria bassiana, Metarhizium anisophilae,* and *Paecilomyces viridis*—were pathogenic to SPB larvae. *B. bassiana* was most virulent.

Nematodes

Nematodes are common associates of the southern pine beetle (Joye and Perry 1976). Massey (1974) extensively reviewed the biology and taxonomy of nematode parasites and associates of bark beetles in the United States.

Recent studies by MacGuidwin (1979) showed that SPB females infected with the nematode *Contortylenchus brevicomi* produced fewer eggs and constructed shorter galleries than healthy females during the 3-week period after attack. No differences were evident during the first week. Parasitism of either male or female SPB by *C. brevicomi* did not affect survival of progeny, even though number of eggs was reduced.

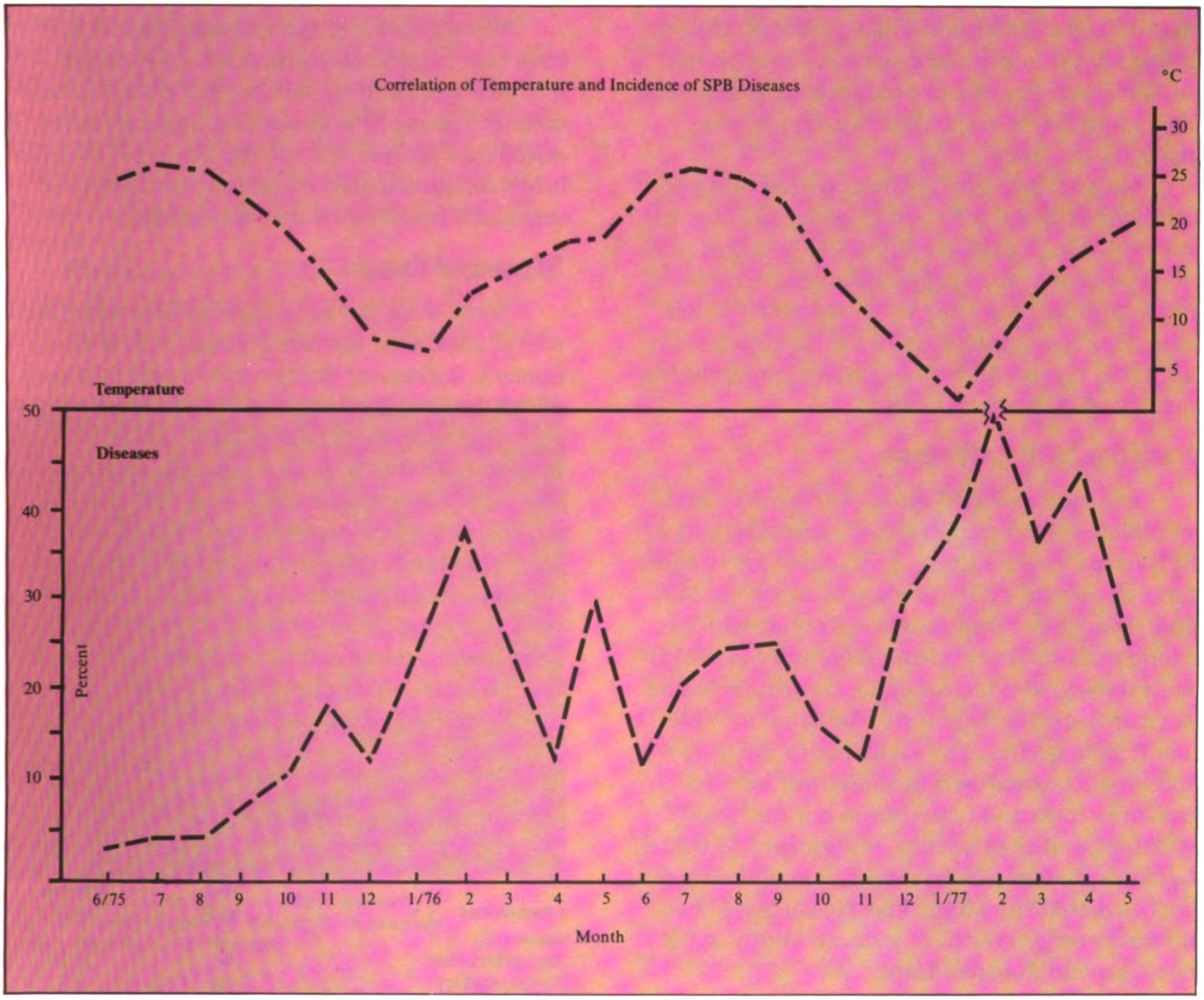

Figure 3-25. — Incidence of SPB disease and yearly temperature. (From Sikorowski et al. 1979.)

SPB emerging from the lower and middle portions of tree boles have a higher incidence of endoparasitism by *C. brevicomi* than those emerging from the upper part of the tree (Kinn and Stephen 1980). However, these investigators found no differences in infection among attacking beetles flying at different heights as they arrived at the trees. Females emerging from trees were more heavily infected by *C. brevicomi* than males, but more males were infected among the beetles flying to new host trees. These findings may be due to more pronounced effects of the endoparasitism on the females, especially reduced flight capabilities. The number of SPB infected with *C. brevicomi* decreased through the summer, perhaps due to predation on the free-living forms of the nematode by the phoretic mites (Kinn 1980).

MacGuidwin (1979) also reported that a recently described microsporidian parasite, *Unikaryon minutum* (Knell and Allen 1978), was present in 65 percent of the beetles examined. However, microsporidian infection in female SPB—either alone or in combination with the nematode—did not affect egg production or gallery length during the 3-week period after attack.

Sampling SPB Pathogens

Atkinson and Wilkinson (1979) developed a frontalure-baited trap to secure large numbers of SPB for pathogen studies. It permits SPB to enter but excludes the clerid predator *Thanasimus dubius.* Though the trap caught only male SPB in Florida studies, results from laboratory investigations showed that the incidence of nematode and microsporidian infection was the same for male and female beetles. The incidence of the microsporidian *U. minutum* was similar for beetles caught in traps and reared from bolts infested with field-collected beetles. But trapped SPB had significantly fewer *C. brevicomi* nematodes than beetles reared from logs. This fact suggests that infested beetles may have reduced ability to fly, or to respond to baited traps.

Symbiotic Organisms

Among SPB associates, there are several organisms that benefit the beetle and also receive some benefits in return. These symbiotic organisms, primarily fungi and bacteria, may alter the phloem (inner bark) of pines under SPB attack, making nutrients more readily available to the beetles. Other symbiotic organisms may be involved in the production or enhancement of aggregating pheromones (Brand et al. 1976 and 1977).

Several bark beetles, including the SPB, have specialized body structures – mycangia – in which symbiotic organisms, mainly fungi, are carried. During SPB attack the fungi are introduced into the tree. Barras and Perry (1975) published an annotated bibliography on symbiotic organisms associated with bark beetles.

Mycangial Fungi

Some work has been done to determine the role of associated microorganisms in SPB development. Barras and Bridges (1976 unpublished) found that in the laboratory, SPB without mycangial fungi were more successful in initiating attacks in bolts, but their egg galleries averaged only a little over half as long as galleries cut by beetles with mycangial fungi (table 3-2). The difference in production of progeny was even more striking. Beetles with fungi produced 36 progeny per gallery and those without fungi, only 2. The same pattern continued through a second generation, suggesting that populations of SPB without mycangial fungi cannot survive for long.

Table 3-2. – Progeny (F_1) produced by southern pine beetle adults with and without mycangial fungi. (From Barras and Bridges 1976 unpublished.)

	Parents	
Observations	**With fungi**	**Without fungi**
Success (%)	14	42
Avg. gallery (cm)	44	25.24
Progeny/gallery	36	1.7
Ratio of increase	18	0.8

Phloem lipids were analyzed to help explain why SPB brood development was inhibited in the absence of mycangial fungi. Results showed that lipids in phloem lacking mycangial fungi decreased over time, while lipids increased in phloem colonized by the fungi.

The blue-stain fungus *Ceratocystis minor* (fig. 3-26), which is always associated with the SPB, was included in inoculations along with two mycangial fungi. *C. minor* is not always carried in the mycangium of SPB but can be carried on the outer surface of the body (Barras and Perry 1975). Inner bark colonized with the blue-stain fungus had the highest amounts of total lipids. But earlier findings have shown that SPB broods fail to develop in phloem infected with the fungus (Barras 1970, Franklin 1970b). Therefore, at this time the exact relationship between *C. minor* and the SPB appears contradictory if lipids are critical to the development and survival of SPB broods.

Brown and Michael (1978 unpublished) suggested that beetle attacks favor successful invasion of the wood by the blue-stain fungus. Moist inner bark/outer wood conditions associated with newly excavated egg galleries probably allow the fungus to become well established before invading the wood. Brown and Michael concluded that blue-stain fungi are the primary cause of tree death since water stress results from the rapid drying of infected xylem associated with blockage of the water-conducting tracheids by fungal hyphae.

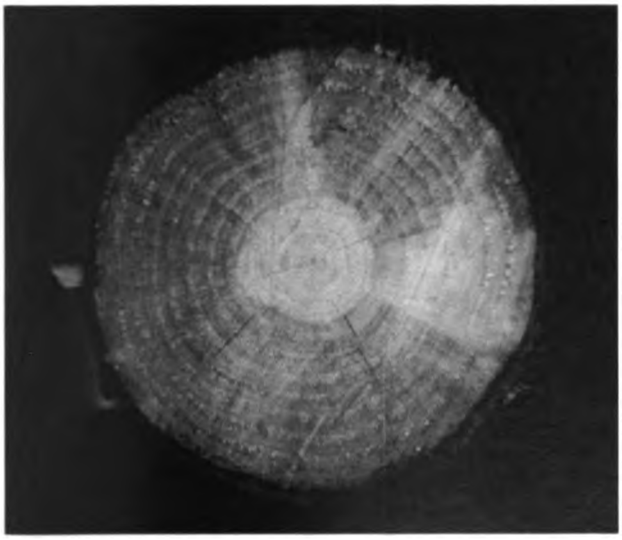

Figure 3-26. – Cross section of a tree attacked by SPB which shows extensive staining by *Ceratocystis minor*. Photo by C. W. Berisford.

Natural Enemies' Impact

Sufficient information has been accumulated that we can begin to evaluate the impact of a complex of natural enemies on the southern pine beetle.

SPB Brood Mortality

Mortality of SPB broods caused by parasitoids and predators was determined by excluding them from SPB-infested trees during specific periods of SPB brood development (Linit and Stephen 1980). More than half of the total numbers of these natural enemies, mostly predators, arrived during the first week of SPB development. Since predators were thought to consume more than one host, highest SPB mortality probably occurred due to their activities. Total mortality caused by parasitoids and predators during SPB brood development was estimated to be about 15 percent. Obviously, studies on SPB population dynamics should consider the role and impact of parasitoids and predators.

Stephen (1980) has developed SPB population dynamics models that allow testing of the role of natural enemies in the regulation of SPB populations. These models make it possible to simulate the impact of natural enemies on SPB population growth as affected by factors such as host tree species and season of the year. Figure 3-27A and B shows a simulation of SPB population growth in loblolly and shortleaf pine stands. The growth of SPB populations in the absence of natural enemies is rapid with either tree host but is substantially faster in shortleaf pine.

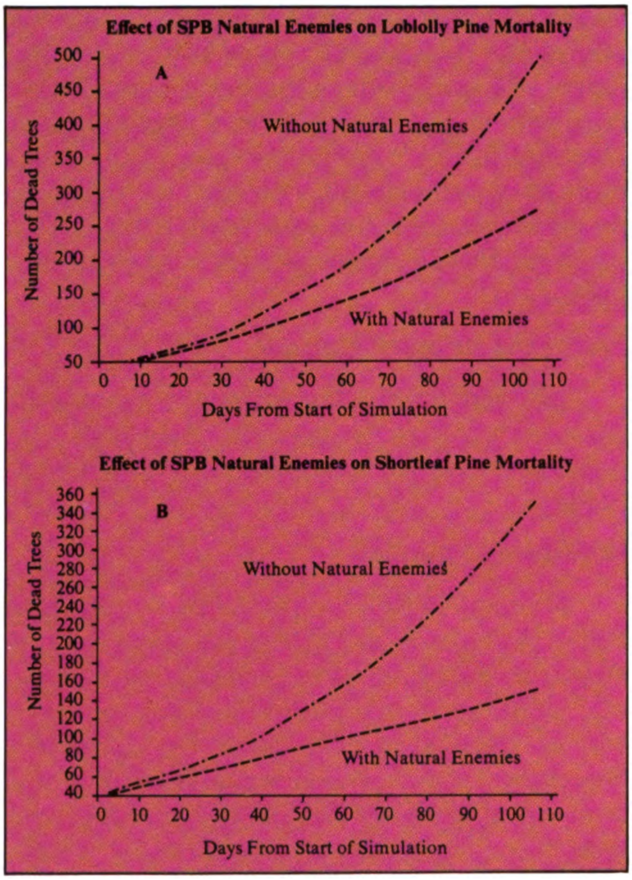

Figure 3-27. – The effect of SPB natural enemies on loblolly (A) and shortleaf (B) pine mortality.

Impact on SPB Spot Growth

Simulations of SPB spot growth, starting at different times of the year, show that natural enemies are important in regulating SPB spot growth in early summer (June) (fig. 3-28). Natural enemies appear to be less significant in late summer and early fall, when spot trend is similar with or without natural enemies.

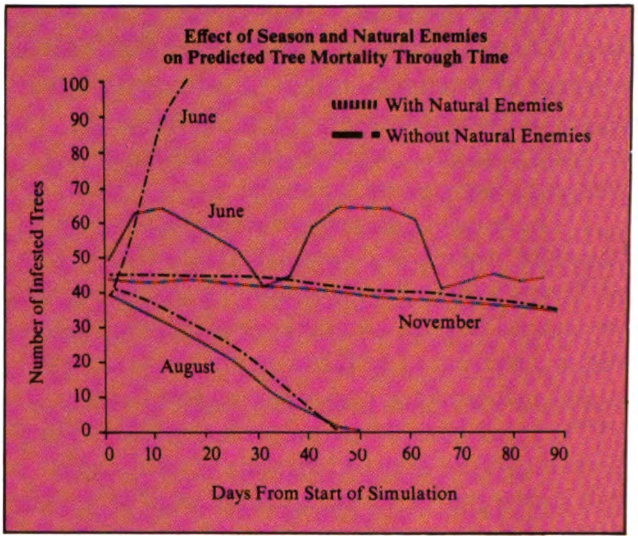

Figure 3-28. – The effect of season and natural enemies on predicted tree mortality through time.

Contributions of ESPBRAP Research

Program-supported studies have substantially increased our understanding of southern pine beetle associates. We can, for the first time, easily identify many associates using new keys and identification guides, quantify the impacts of some natural enemies, and determine how some associates work together to regulate SPB populations.

Research in ESPBRAP has provided a cornerstone for further investigations into the complex interactions among the southern pine beetle and its associates. Future studies will ultimately generate the data required for development and implementation of SPB management plans that recognize and/or augment existing control by natural enemies.

Climatic, Site, and Stand Factors

Ray R. Hicks, Jr.[1]

4

Introduction

Host-pest relationships are complex ecological phenomena that, in undisturbed systems, ultimately achieve a balance. The pest must be able to thrive and reproduce; but, equally important, it must permit some members of the host species to survive. This relationship is especially important when a highly specific association exists, such as that between the southern pine beetle and four or five species of southern pines.

The stands of pines that grow in the South today probably bear little resemblance to the natural forests that existed throughout most of the coevolution of southern pines and the SPB. During recent decades, SPB populations have fluctuated erratically, with an apparent trend toward increasing severity of damage (Hedden 1978b). The magnitude of fluctuations suggests that the system is in a state of imbalance, perhaps due to the abundance of host species. Given time and no interference from people, the system would reestablish an equilibrium through reduction in the pine component of forests. But this process would be counter to the goals of forest managers, many of whom want to achieve maximum productivity of softwood timber from southern forests. Three immediate questions arise: (1) Are there quantifiable causes responsible for the increase in SPB activity? (2) Can we manipulate these factors to achieve the goal of increased forest productivity by reducing SPB-induced losses? (3) Is it economically feasible to perform such manipulations? The site-stand-climatic investigators funded by the Expanded Southern Pine Beetle Research and Applications Program (ESP-BRAP) have tried to answer the first question. Their results and those of other relevant studies are summarized here.

Researchers from Virginia to Texas took measurements on environmental factors affecting beetle-attacked and nonattacked (baseline) stands to determine what, if any, differences existed. These factors ranged from measures of tree competition and vigor to soil and site factors, including several climatic and disturbance characteristics. Prior research dealing with host-tree susceptibility to bark beetles had elucidated numerous relationships; on this foundation ESP-BRAP initiated its research.

Site and stand factors affect several forest insect pests. For example, attacks by western spruce budworm *(Choristoneura fumiferana* Clem.) are found to be associated with high stand densities in some years but not in others (Fellin 1976). Research indicates that physiographic location, tree diameter, stand basal area, and species composition all play a role in susceptibility to spruce beetle, *D. rufipennis* (Kirby) (Schmid and Frye 1976). Logging residues apparently serve as reservoirs for spruce beetle brood (Schmid 1977), and logging practices that remove these residues lead to reduced infestation of residual stands (Beckwith, Wolff, and Zasada 1977).

For fir engraver, *Scolytus ventralis* Lec., competition among trees has been implicated as a prime factor in susceptibility (Schenk et al. 1977), as well as species diversity. In another study concerning susceptibility of white fir *(Abies concolor* [Gord. and Glend.] Lindl.) to fir engraver, induced water stress in trees permitted the beetles to enter more easily. Nonstressed trees were able to "pitch out" the beetles (Ferrell 1978).

Mountain pine beetle *(D. ponderosae* Hopkins), a species related to the southern pine beetle, has been the subject of numerous investigations on host susceptibility. Susceptibility of lodgepole pine *(P. contorta* var. *latifolia* Engelm.) to this beetle is largely a function of tree age, diameter, and phloem thickness. Beetles prefer larger, older trees with thick phloem (Amman and Pace 1976, Amman et al. 1977, Berryman 1976, Cole and Cahill 1976). Mountain pine beetle also attacks ponderosa pine *(P. ponderosa),* and its susceptibility to this insect is related to excessive intertree competition. Investigators recommend thinning of overstocked stands as a means of reducing susceptibility (Sartwell 1971, Sartwell and Stevens 1975, Sartwell and Dolph 1976). These host and stand variables are pro-

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posed as important components of an integrated pest management system for mountain pine beetle (Stage and Long 1977).

Recent research has shown that many of the same site and stand factors affect susceptibility of southern pines to SPB. High stand density characterizes many infestations (Lorio and Bennett 1974), and this overstocking apparently leads to reduced radial growth (Bennett 1971; Coulson, Hain, and Payne 1974). Trees growing on wetter sites seem to be more susceptible due to declining vigor (Bennett 1968, Lorio 1968). Stand disturbances such as lightning can trigger SPB infestations (Hodges and Pickard 1971, Lorio and Yandle 1978).

Obviously site, stand, and climatic factors play a significant role in the SPB-host relationship. Therefore, researchers in the ESPBRAP site-stand area have tried to quantify that relationship so that another piece of the complex model can be put into place and a truly integrated protection program for SPB can be developed, as Coster (1977) suggests. To do this, investigators established plots throughout the Southeast and took data on site, stand, and climatic variables. For comparison, most projects collected data on uninfested plots, which were located in an unbiased manner. The bulk of data was from the West Gulf Coastal Plain, with fewer plots from the Piedmont, North Georgia Mountains, and Atlantic Coastal Plain.

In an effort to summarize the contributions of this ESPBRAP coordinated regional project, and to incorporate appropriate background literature, this chapter discusses the effects of climatic, site, and stand factors on host susceptibility to SPB. ESPBRAP has also issued a Technical Bulletin to preserve basic statistics from the coordinated regional site-stand project (Coster and Searcy 1980).

Climatic Factors

Rainfall

The amount and timing of rainfall probably affect southern pine beetle activity, but we do not know how. For instance, moisture could directly affect the survival and vigor of adult or brood beetles, or it could indirectly affect beetle populations by altering host tree resistance. Several studies have investigated the relationships of tree water balance to successful beetle attack. Others have dealt with the relationship of rainfall to areawide fluctuations in SPB populations (Craighead 1925). The implication is that rainfall affects tree water stress, which in turn affects resistance to attack; the latter affects the population of beetles. Unfortunately, experimental data concerning this chain of events is lacking.

Studies dealing specifically with internal tree water balance and southern pine beetle attack have produced interesting results. Lorio and Hodges (1968) found that oleoresin exudation pressure of large loblolly pines was reduced during periods of drought-induced moisture stress. They contend that the beetles are more successful in attacking trees with lower oleoresin exudation pressures since the beetles are less likely to be pitched out of such trees. Indeed, they found that artificially stressed trees succumbed to induced beetle attack more readily than nonstressed trees (Lorio and Hodges 1977).

Obviously, a relationship exists between host tree resistance and oleoresin exudation pressure as affected by internal water balance. This relationship may in part account for SPB population fluctuations ostensibly related to rainfall. Several workers have investigated the relationship between rainfall and changes in SPB population. The number of beetle spots in an area correlates to some degree with rainfall in previous months. In east Texas, rainfall for the previous summer, fall, and spring was associated with the number of beetle spots in the following summer (Kroll and Reeves 1978). Abundant rain in the previous summer was conducive to more spots in the following year, while previous fall and spring precipitation was negatively correlated with current year infestations. This procedure needs additional refinement before being used. The Texas Forest Service (1978) reported a similar finding regarding previous summer rainfall. However, these data do not substantiate the hypothesis that lowered host resistance due to water stress causes SPB population increases. On the contrary, one would expect low rainfall during the summer growing season to be associated with reduced host resistance and greater beetle activity. Since stress-related host susceptibility would operate for short periods of time during droughts, it may be difficult to show water stress relationships where historical weather records reporting monthly averages are used to predict current or future trends in beetle activity.

At Virginia Polytechnic Institute and State University, researchers studied the associations between several climatic variables and monthly SPB spots per 1,000 acres in Arkansas and North Carolina. They found that precipitation 2 and 4 months prior to the month in question was weakly associated with SPB activity. But in both cases, lower precipitation was associated with higher beetle activity. Since these researchers were predicting SPB activity for the summer months, their lagged precipitation data would be mostly for the winter and spring months and therefore consistent with the negative relationship for spring rainfall found by Kroll and Reeves (1978).

Rainfall almost certainly has an effect on host resistance. But quantifying this effect is difficult because of continuous variations in the host, the beetle, and the weather. These variations account in part for the yearly and regional differences reported concerning the effect of rainfall on SPB populations. For example, King (1972) compared epidemic and nonepidemic years and found low summer rainfall in Georgia, high winter rainfall in Texas, and high spring coupled with low early summer rainfall in the Carolinas to be associated with epidemic years. Hansen, Baker, and Barry (1973) found that outbreaks in the Atlantic Coastal Plain of Delaware, Maryland, and Virginia are associated with extended drought periods. Conversely, Kalkstein (1974) found that SPB activity in Texas and Louisiana was associated with increased late winter moisture.

Although these results are somewhat confusing, it seems that infestations in the Western Gulf Coastal Plain are frequently associated with prior periods of abundant or superabundant rainfall. Infestations along the Atlantic Coastal Plains, however, are frequently associated with prior periods of drought. The Western Gulf relationship seems consistent with findings of Lorio (1968) and studies in Texas and Louisiana, where infestations are frequently found on low-lying or wet sites. On such sites, excessive rainfall tends to accentuate the poor drainage problem. In the Atlantic Coastal Plain, beetle attacks may be more often related to drought stress, as evidenced by their occurrence following dry years.

Temperature

The primary effect of temperature seems directly related to insect survival, but a potential effect on host resistance is related to tree water balance. Kalkstein (1976) found that potential evapotranspiration of trees was a useful variable in predicting beetle population trends in Louisiana and Texas. Evapotranspiration potential relates to several environmental variables, including moisture supply and temperature. This evidence for the involvement of temperature on host resistance is circumstantial at best. Campbell and Smith (1978) did not detect a similar relationship of potential evapotranspiration in an Arkansas study.

Weather-Related Stand Disturbances

Previous research had elucidated the associations of several stand disturbances with initiation of southern pine beetle infestations (Lorio and Bennett 1974, Lorio and Yandle 1978, Hodges and Pickard 1971). Several of these are weather related (e.g., lightning strikes and wind, ice, and hail damage). Investigators in the ESPBRAP site-stand group also recorded the occurrence of these disturbances and others at each site visited. ESPBRAP data for weather-related disturbances generally show a marked association of certain disturbances with SPB occurrence (table 4-1). Most notable is the occurrence of lightning strikes on beetle-infested plots, where 10 to 40 percent were found to have this disturbance, in comparison to less than 1 percent for randomly located, nonattacked (baseline) plots.

Apparently these stand disturbances, which weaken trees, favor initial beetle attack. Such trees form epicenters for beetle spots, and the infestation may enlarge depending on the availability of SPB populations and other environmental conditions prevailing at the time of attack. For example, beetles attacking a lone lightning-struck tree may not successfully initiate an active spot if the surrounding trees are vigorous and not stressed. Overstocking of pine stands seems to be a prime factor in promoting such spot growth (Hedden and Billings 1979).

Site Factors

Landform

Investigators in the site-stand group classified sites according to landform categories outlined in the U.S. Forest Service's *Soils Resource Guide: Southern Region* (U.S. Department of Agriculture Forest Service 1972a). Most of the data were from the Coastal Plain from Mississippi to Texas (Rowell 1978 unpublished). Here a greater-than-expected frequency of infestations was found on low-lying landforms such as swamps, flood plains, stream terraces, bays, and lower slopes. SPB infestations occurred on 27.6 percent of these landforms but on only 17.6 percent of the baseline plots. The most common landform for both infested and baseline plots was upland flat (45.2 percent and 39.6 percent, respectively), and the data indicate that beetles were slightly more frequent on upland flat sites. Likewise, beetles seemed to prefer trees growing on ridge sites (14 percent infested *v.* 5.7 percent baseline). The only sites showing a lower-than-expected frequency of attack were side slopes and steep side slopes (13.2 percent attacked *v.* 37.4 percent baseline).

Stress seems to be the key to the beetles' preference for attacking trees on the higher upland and lowland landform categories. That is, excessive moisture in low-lying areas can induce root damage and stress, while trees growing on ridge tops are prone to drought stress during dry periods. Trees growing on sloping sites (where attacks were less frequent than expected) likely avoid either of these extremes.

Limited data were collected for the Georgia Piedmont and Mountains (Belanger, Hatchell, and Moore 1977; Belanger, Osgood, and Hatchell 1979b). Both differed considerably from the Gulf Coastal Plain in the relationships of landform to beetle attack preference. In the Piedmont, steep side slopes accounted for 60.7 percent of the infestations but only 38.6 percent of the baseline plots. Conversely, ridge sites had a 32 percent attack frequency, compared to almost 50 percent of the baseline plots in this category. Beetles do not prefer trees on low-lying sites in the Piedmont. Apparently, susceptibility of trees to SPB in the Piedmont is not associated with water relations as suggested for the Coastal Plains.

Table 4-1. — Summary of weather-related stand disturbances in infested (attacked) and baseline (nonattacked) plots in the Gulf Coastal Plain.

Disturbance	**Study Area**							
	Arkansas		**Louisiana**		**Texas**		**Georgia**	
	Attacked (%)	Non-attacked (%)	Attacked (%)	Non-attacked (%)	Attacked (%)	Non-attacked (%)	Attacked (%)	Non-attacked (%)
Severe ice or hail (>50% stems affected)	4.0	4.0	0.0	–	0.0	0.0	1.0	0.0
Light ice or hail (<50% stems affected)	20.0	20.0	0.0	–	0.2	0.7	5.0	4.0
Lightning	39.0	0.4	10.2	–	31.6	0.9	23.0	1.0
Wind	1.0	0.4	4.0	–	4.6	0.0	2.0	1.0

In the North Georgia Mountains, a totally different set of landform categories was used; therefore, these results are not directly comparable with those from other physiographic provinces. Infestations in the Mountains occurred more frequently on south-facing slopes, but this is the slope face where most of the pines grow in the southern Appalachians (Belanger et al. 1979b).

Water Regime

Previous discussions of the relationship between landform and occurrence of beetle infestations in the Coastal Plains imply that soil moisture may directly influence beetle susceptibility since infestations occurred more often than expected on low-lying areas and ridge tops. Both Lorio (1968) and Bennett (1968) pointed out that infestations in Texas and Louisiana were common on wet sites and that damage by root-rotting fungi may cause reduced vigor of trees on these sites and predispose them to beetle attack. Hicks et al. (1978) noted differences in radial growth rates of trees in infested *v.* baseline plots on wet and waterlogged sites in Texas. On such sites, trees in beetle infestations were growing comparatively slower than those on other water regimes. But trees in ***baseline*** plots on wet and waterlogged sites were growing faster than on other water regimes. The researchers also noted a greater-than-expected frequency of occurrence of beetle spots on wet and waterlogged sites and a lower-than-expected frequency of occurrence on dry sites in Texas. In the Coastal Plain of North Carolina (Belanger et al. 1977), all infestations visited were classified as being on either moist or wet sites. None were found on dry sites.

Although the evidence is circumstantial, it does appear that at least some of the association between landform and SPB activity in the Coastal Plain is due to differences in moisture regime, with infestations being more frequent on wetter sites. It should be noted that these data were collected during a period when rainfall was adequate. The results might be different during drier periods.

Soil Texture

Considerable regional variation was found in soil texture both within and between the two major physiographic provinces (Piedmont and Coastal Plain). Piedmont infestations uniformly occurred on fairly heavy clay soils; sandy or loamy soils characterized Coastal Plain infestations (tables 4-2 and 4-3).

In the Gulf Coastal Plain, infested and baseline plots were very similar in soil particle size distribution, although a considerable degree of variation existed across geographic areas within the province. For example, in east Texas surface soil sand content was about 70 percent; another project dealing principally with industrial landholdings in Louisiana, Mississippi, and Texas reported an average sand content of only about 50 percent (table 4-2). Clay contents were relatively similar across areas; the variation in sand was thus compensated for by variations in silt content (table 4-2). These variations reflect real differences in soil texture across the Gulf Coastal Plain, with a trend toward sandier soils from northeast to southwest. But they do not imply any selectivity on the part of the SPB based on soil texture.

Table 4-2. – Particle size distribution of soils from beetle-infested plots in the Gulf Coastal Plain.

Geographic area	Surface soil			Subsoil		
	% sand	% silt	% clay	% sand	% silt	% clay
Arkansas	53.8	36.1	10.1	44.6	33.7	21.7
Louisiana	58.9	31.2	9.9	42.9	31.3	25.8
Louisiana, Mississippi, Texas	49.6	39.3	11.1	42.2	35.6	22.2
Texas	68.7	22.4	8.8	50.9	21.5	27.6

Table 4-3. – Particle size distribution of soils from beetle-infested plots in the Piedmont.

Geographic area	Surface soil			Subsoil		
	% sand	% silt	% clay	% sand	% silt	% clay
Georgia	56.4	18.9	24.2	40.7	17.1	42.1
Virginia	37.8	36.5	25.3	28.5	34.8	36.2
North Carolina	54.5	32.2	14.3	35.5	30.6	33.9

In the Piedmont, quite a different situation exists regarding soil texture. First, the soils are much higher in clay content than those of the Coastal Plain. Here, however, a relationship of surface soil clay content with the presence of beetle infestations is apparent. The average surface soil clay content for all Piedmont infested plots is about 21 percent (table 4-3), while the baseline plots had only 18 percent. Conversely, the surface sand content was 55 and 59 percent, respectively, for infested and baseline plots. In the Georgia Piedmont, the situation was even more dramatic. Surface soil clay content for Georgia infested plots was 25 percent, as compared to only 19 percent for baseline plots. Belanger, et al. (1977) reported that both high clay content and abundance of shortleaf pine were associated with beetle infestations in their Georgia Piedmont study. Both these conditions also favor the development of littleleaf disease *(Phytophthora cinnamoni* Rand.), a particular problem on the eroded clay soil of the lower Piedmont. Belanger's team believes that many infestations in the Piedmont may result from "locus" points of low-vigor trees associated with littleleaf sites. Such a hypothesis is consistent with the notion that beetles gain easier access to trees growing under stressful conditions, as proposed by Lorio and Hodges (1968b).

Soil Chemical Properties

Relationship of soil chemical properties to southern pine beetle occurrence has had little prior study. One Program-supported project at Stephen F. Austin State University undertook the quantitative measurement of mineral nutrients in soils of beetle-infested and noninfested plots in Texas. Researchers conducted laboratory analyses for organic matter; phosphorus, calcium, magnesium, potassium, zinc, sodium, and manganese; percent base saturation; and cation exchange capacity.

In the surface soil, several minerals differed significantly between infested and baseline plots: potassium, sodium, calcium, and zinc. Infested plots had lower levels of all these except for sodium, which was elevated in infested plots. In the subsoil, only zinc showed a significant difference, occurring at a lower level in infested plots. The hypothesis generated from these data is that nutrient deficiencies were responsible, in part, for infestations in east Texas. All the elements present at significantly lower amounts in infested plots contribute either directly or indirectly to soil fertility. In the case of sodium, higher amounts characteristic of infested plots could contribute to moisture stress and therefore to increased beetle susceptibility.

These data consist of averages from many plots, some of which were surely susceptible to southern pine beetle attack for reasons other than soil fertility. But even when plots found to have predisposing stand disturbances (e.g., lightning and recent logging damage) were eliminated from the analysis, all elements but potassium still differed significantly among infested and baseline plots. It seems logical that at least *some* stands were susceptible due to nutrient deficiencies and imbalances in the soil.

Attempts to evaluate the effect of fertilization on SPB resistance have, however, met with little success. Haines, Haines, and Liles (1976) recorded SPB occurrence in 176 Southwide fertilization plots and in adjacent unfertilized stands. Only 4 percent of the fertilized stands had SPB, and even fewer of the unfertilized stands were attacked. The Haines team felt that most of the infestations resulted from stand disturbances that happened during thinning some of the treated stands and had little to do with fertilizer treatment. Since the level of SPB activity was very low in both fertilized and unfertilized stands, we cannot draw broad conclusions from these observations. In another study, Moore and Layman (1978) applied 10-10-10 fertilizer to the fringe of active SPB spots. They reported that this practice did not significantly increase resistance of 9- to 11-year-old loblolly pines.

Site Index

A weak but significant positive correlation existed between loblolly pine site index and SPB activity in the Gulf Coastal Plain (Rowell 1978 unpublished). Figure 4-1 shows that infestations developed more frequently in stands with higher site index classes.

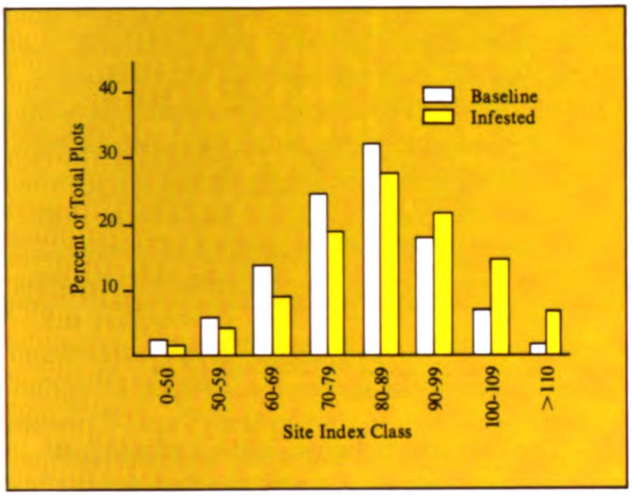

Figure 4-1. – Distribution of infested and baseline plots by site index class for the Gulf Coastal Plain (after Rowell 1978 unpublished).

Some regional deviations were apparent from the different projects. For example, in the upper Coastal Plain of Arkansas, little difference in site index existed between baseline and infested plots. In the other projects located along the lower Gulf Coastal Plain, higher site index was associated with infested plots. Two other facts seem pertinent here. First, shortleaf pine – the most abundant species – was the preferred host species in the Arkansas study, whereas loblolly pine was the preferred host in the other West Gulf studies. Second, neither wet sites nor low-lying landforms were associated with SPB outbreaks in Arkansas as they were in Louisiana and Texas. It is a widely recognized fact that loblolly pine is more abundant than shortleaf pine on moister sites and usually occurs in stands having a higher site index than shortleaf pine (Zahner 1954). Apparently then, the regional differences seen within the West Gulf Coastal Plain relate to differences in species preferred by the beetle and a complex of contributory factors.

Soil Depth, pH, Modifiers, and Accessory Characteristics

Shallow topsoil depth was associated with infestation in the Georgia Piedmont. As previously discussed, this trait is often characteristic of sites prone to littleleaf disease of shortleaf pine, further substantiating the role of this disease in SPB susceptibility in this region. Soil depth was not associated with SPB occurrence elsewhere in the Gulf Coastal Plain (Rowell 1978 unpublished).

Neither soil pH, modifiers, nor accessory characteristics as defined in the *Soil Resources Guide: Southern Region* (U.S. Department of Agriculture Forest Service 1972a) were found to be associated with SPB activity.

Stand Factors

Stand Density

High stand density (fig. 4-2) has long been implicated as a causal factor of southern pine beetle infestations (Bennett 1968, Leuschner et al. 1976, Lorio and Bennett 1974). The rationale is that overstocking causes reduced vigor of trees and therefore predisposes them to SPB attack (Bennett 1971). This hypothesis was borne out, particularly on wet sites in east Texas, where Hicks et al. (1978) noted that low tree vigor was indeed correlated with stand density and that

Figure 4-2. – A high-BA stand of pines that have been attacked by the beetle.

low-vigor stands were markedly more susceptible to beetle attack.

Program-supported studies used two measures of stand density – trees per acre and basal area (BA) per acre. The former was not very useful relative to SPB incidence, since trees per acre are dramatically affected by tree diameter. Also, with the exception of Arkansas, where infested plots had significantly more trees per acre, this variable was not found to be associated with SPB attack. However, spatial arrangement of trees, reflected by trees per acre, may be associated with the rate of growth of active SPB spots. Basal area, on the other hand, was found to be quite highly associated with SPB occurrence. BA was tallied for pines and hardwoods separately; in most cases, it was the pine component that showed the highest degree of association with SPB.

In the Gulf Coastal Plain studies, beetle occurrence was strongly associated with high stand BA. Rowell (1978 unpublished) reported that the average pine BA for 2,021 infested plots in the Gulf Coastal Plain was 114.4 ft^2/acre, as compared with 72.5 ft^2/acre for 1,396 uninfested plots from the same region. Hardwood BA showed a similar trend, with infested plots having 36.7 ft^2/acre, compared to 26.4 for uninfested plots. Hardwood BA was not as consistent as pine BA across projects; i.e., Arkansas data showed little difference for this variable between infested and baseline plots.

Averages for total BA (combining pine and hardwood) were 140.7 and 109.2 ft^2/acre for infested and uninfested plots, respectively, in the Gulf Coastal Plain. Figure 4-3 illustrates the distributions of total BA for infested and uninfested plots. These data leave no doubt that stand density is indeed important in determining susceptibility of stands to SPB attack in the Gulf Coastal Plain. In Arkansas, where site factors assumed less importance than in other parts of the Gulf Coastal Plain, high pine BA was associated with infestation. Thus, it appears that for the Gulf Coastal Plain this is a variable consistently associated with SPB activity and is potentially useful in identifying stands that are more likely to be attacked.

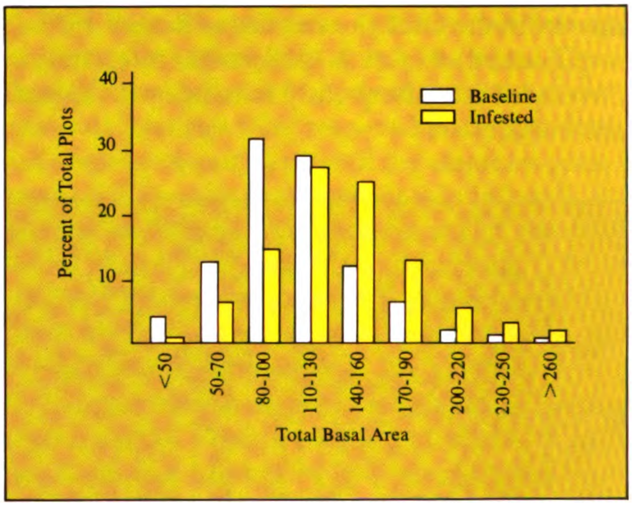

Figure 4-3. – Distribution of baseline and infested plots by basal area classes for the Gulf Coastal Plain (after Rowell 1978 unpublished).

The correlation between BA and southern pine beetle occurrence seems to relate to competition and its effect on tree vigor. This hypothesis is further supported by the fact that higher hardwood BA is associated with beetle attack. Since hardwoods are nonhosts, their effect must be related to their competition with the host pines and resulting loss of vigor.

Studies in the Piedmont regions of Georgia and North Carolina did not find similar relationships between BA and beetle infestation. In Georgia, as previously discussed, site factors, littleleaf disease, and host species (shortleaf pine) were related to SPB occurrence. In the North Carolina study, data were collected primarily on trees within the fluctuating water line of Kerr Reservoir. Here, flooding and related root damage were associated with the infestations (Maki 1978 unpublished).

In the North Georgia Mountains, as in the Coastal Plain, higher pine and hardwood BA were associated with SPB attack (Belanger et al. 1979b).

Radial Growth

Bennett (1968, 1971) suggested that poor tree vigor, expressed as reduced radial growth, was consistently associated with southern pine beetle infestations. Data of Coulson et al. (1974) further substantiated this observation in east Texas.

Data collected on more than 3,000 infested and noninfested plots in the Gulf Coastal Plain during 1975–1979 have verified and quantified the relationship of reduced growth rate with SPB attack. Investigators collected data from three to five dominant or codominant trees within each plot and measured the width of the most recent five annual rings and the preceding five rings. Current 5-year increment for infested plots in the Gulf Coastal Plain was 15.03 mm, compared to 18.02 mm for uninfested plots (Rowell 1978 unpublished). Respective data for the preceding 5-year period were 16.23 mm and 19.51 mm. These results were consistent for all projects in the Gulf Coastal Plain region, although data for current 5-year radial growth in east Texas showed the most marked difference between infested and baseline plots.

In the Piedmont studies a similar association of reduced radial growth with beetle attack was found, but the degree of difference was less than for the Coastal Plain. Table 4-4 shows the results for the Coastal Plain and the Piedmont studies. Although infested plots were consistently slower growing than their noninfested complements, considerable variation existed between regions and among projects within regions. Generally, growth was slower for Piedmont plots compared to the Gulf Coastal Plain. Within the Coastal Plain, Texas and Louisiana trees grew more slowly than those in Arkansas. The Arkansas plots were generally in younger, smaller-diameter stands, which would be expected to grow more rapidly than older, larger trees.

Presumably, radial growth is a reflection of many factors affecting tree vigor. Perhaps this is why radial growth is consistently associated with SPB attack throughout the South. Within the Coastal Plain, it appears that overstocking and wet site conditions – either alone or in combination – contribute to reduced vigor, hence reduced radial growth. In the Georgia Piedmont, the cause of reduced radial growth is more commonly associated with site factors that predispose shortleaf pines to littleleaf disease. The growth reduction reflects the poor vigor of littleleaf trees. In the North Carolina study, periodic flooding along Kerr Reservoir seems to bring about the same effect – reduced vigor of trees. Therefore, radial growth may indeed be a consistent variable that can be used as a Southwide index to SPB susceptibility. To apply such an index, however, researchers need good baseline data for each region or subregion. Some means for adjusting radial growth data for tree or stand age will most likely be needed in order to make comparisons across different age classes (Hicks et al. 1978).

Workers in the site-stand group of the ESP-BRAP measured bark thickness at the fissures and ridges of three to five trees per plot using a standard bark gage. Results were confusing: Southwide, investigators found no distinct differences between baseline and infested plots. This discovery may reflect two facts: data were combined for several pine species, and different species were preferred hosts in the various study areas. Certainly, it is well known that shortleaf has thinner bark than loblolly pine.

Table 4-4. – Radial growth data for infested and baseline plots in the Gulf Coastal Plain and Piedmont.

	Gulf Coastal Plain								Piedmont			
	AR		LA		LA, MS, TX		TX		GA		NC	
	Inf.	Base.	Inf.	Base.	Inf.	Base.	Inf.	Base.	Inf.	Base.	Inf.	Base.
Recent 5 years (mm)	17.9	19.2	14.6	–	16.5	19.3	13.9	17.6	11.5	14.1	8.6	9.1
Previous 5 years (mm)	19.2	21.0	15.3	–	18.0	20.6	15.9	18.7	15.1	18.0	10.2	10.4

In the Coastal Plain, trees in infested plots had significantly thicker bark than their uninfested counterparts. Fissure values were 0.28 inches *v.* 0.27 inches and ridge values of 0.92 inches *v.* 0.83 inches for infested and baseline plots, respectively (Rowell 1978 unpublished).

Certain projects found very strong associations of bark thickness with infestation. For example, in east Texas, fissure bark thickness for infested trees averaged 0.23 inches in comparison to 0.15 for baseline trees. Researchers in this study found that fissure bark thickness was the best single variable to distinguish infested from baseline plots. Another Coastal Plain study dealing with industry-owned lands in Louisiana, Texas, and Mississippi also noted that thicker bark in fissures was associated with SPB attack but had much higher values (0.44 inches *v.* 0.39 inches). These project-related differences could be due to variations in measurement methods.

In Arkansas, researchers found almost no difference between infested and baseline trees relative to bark thickness. In this study, it should be emphasized that shortleaf pine was the preferred host while loblolly pine was the preferred host for other Coastal Plain studies. In the Georgia Piedmont, where again shortleaf pine was the preferred host, no apparent relationship between attack and bark thickness was evident.

Apparently, bark thickness is related to beetle attack in loblolly pine but perhaps not in shortleaf pine, or at least for the latter species the data are obscured by other factors. The exact cause-and-effect relationship between bark thickness and SPB infestation, if one exists, is not immediately obvious. Perhaps beetles are capable of producing more and healthier brood to reinfest adjacent trees when feeding on trees with thicker bark. Such is the case with mountain pine beetle in lodgepole pine (Amman and Pace 1976). In any event, bark thickness is somewhat difficult to measure, owing to within- and between-tree variability and the limitations of currently available measurement devices.

Species Composition

Species of southern pines differ in their susceptibility to the beetle. Longleaf and slash pines are fairly resistant, a phenomenon that has been attributed to their ability to "pitch out" attacking beetles in resinous exudations. However, Program-sponsored studies have found that, even among so-called susceptible host species such as loblolly and shortleaf pines, preferential attack can occur and preferences vary by regions. For example, in east Texas, loblolly pine constituted approximately 30 percent of the species mix, but about 50 percent of the infested trees were loblollies. This species was also found to be the most frequently attacked in other lower Coastal Plain studies. But in the upper Coastal Plain of Arkansas and the Piedmont of Georgia, shortleaf pine was more frequently attacked. These differences probably relate to the unique factors within the various provinces that predispose trees to beetle attack. In the lower Coastal Plain, many infestations occur in overstocked stands on wet sites. Loblolly pine – a more hydric species – is more frequent than shortleaf pine on such sites and thus becomes the preferred host under these conditions.

In the upper Coastal Plain of Arkansas, wet site conditions do not seem to predispose trees to southern pine beetle attack. Except for the extreme southern counties of Arkansas, along the Red River, shortleaf pine is the most abundant species. The greater abundance of shortleaf pine therefore accounts for its higher frequency of attack.

In the Georgia Piedmont the previously noted soil conditions that influence the susceptibility of shortleaf pine to littleleaf disease also seem to be the major predisposing factors to SPB attack. Loblolly pine is less frequently infested with littleleaf and is not the preferred host species in the Piedmont.

In the North Georgia Mountains, shortleaf, pitch, and loblolly pines were found to be more susceptible to SPB than Virginia pine or eastern white pine (Belanger et al. 1979b). These authors recommended species selection as a means to reducing losses from SPB.

Average Stand Age, Height, and Diameter

These highly correlated characteristics were infrequently associated with SPB infestation across the South. Rowell (1978 unpublished) reported that average stand age of infested plots in the Gulf Coastal Plain is about 40 years for both infested and uninfested plots. Considerable regional variation in average stand age, height, and diameter was reported. At the project level, some investigators found them to be associated with SPB occurrence.

Part of the variation in projects is due to differences in ownership and management objectives. For example, a Louisiana study dealing specifically with the Kisatchie National Forest reported the largest and oldest trees of any Gulf Coastal Plain study. Trees in infested stands averaged 44 years of age, 12.2 inches in d.b.h., and 67 ft in height. Trees in National Forests are generally larger than trees on adjoining ownerships. But even so, beetles apparently selected the older and larger trees within the National Forest for attack (fig. 4-4). Examining only infestations on the Davy Crockett National Forest in Texas, Leuschner et al. (1976) also found that infestations occurred more often in larger-diameter trees.

A study dealing with industrial landholdings in Louisiana, Texas, and Mississippi reported the second-oldest and -largest trees in the Coastal Plain, with an average age of 41 years and d.b.h. of 11.2 inches. No differences in age and size between infested and uninfested stands were detected.

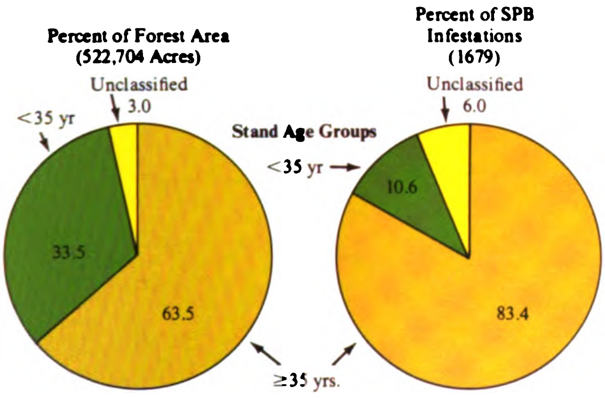

Figure 4-4. – Percentages of SPB infestations and general forest area by stand age classes in the Kisatchie National Forest, Louisiana (from Lorio, *in* Coster and Searcy 1979).

Projects in Arkansas and east Texas reported the smallest trees in the Gulf Coastal Plain. In both areas, plots were selected in an unbiased manner and without regard for landowner. Tree diameters in these studies averaged about 24.5 cm and average heights varied between 17.1 and 19.2 m. In Arkansas younger, smaller-diameter trees were infested more frequently than older, larger ones. This relationship was amplified when plots with stand disturbances were excluded from the analysis (Ku, Sweeney, and Shelburne 1976 and 1977): In east Texas, infestation incidence was not related to age of d.b.h., but infested trees tended to be somewhat taller (fig. 4-5). This observation could relate to the fact that this lower Coastal Plain study found a high proportion of infestations on wet sites, which have a higher site index for loblolly pine, the preferred host species.

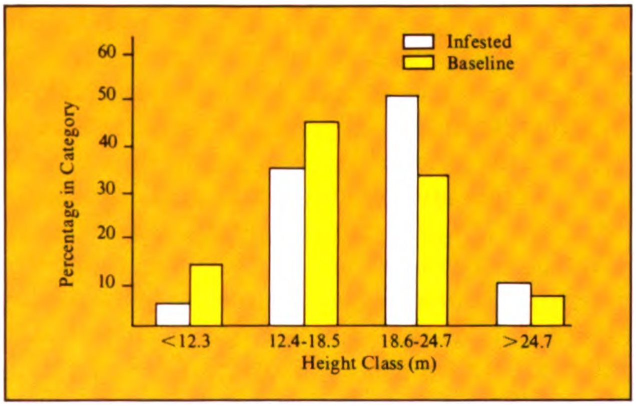

Figure 4-5. – Distribution of baseline and infested plots by total tree height classes for east Texas.

In the Georgia Piedmont, infested pines were much smaller than in the Gulf Coastal Plain (8.5 inches d.b.h., 52 ft tall), but their age (39 years) was about the same (Belanger et al. 1977). Reduced size for age may, in part, be related to the fact that shortleaf pine was the preferred host and many infestations occurred on sites conducive to littleleaf disease. On such sites, stunted growth is common for shortleaf pine.

In the North Georgia Mountains, infested pines were considerably older than elsewhere (Belanger et al. 1979b), but trees were only slightly larger (11.6 inches d.b.h., 67 ft tall). The inherently slower growth of the species attacked and the harsher growing conditions encountered probably account for the reduced size of these older trees.

Diseases and Other Insects

Several other diseases and insects are known to reduce vigor of southern pine and therefore they may predispose trees to attack by the beetle. One such disease is annosus root rot (*Heterobasidion annosum*). This disease is a particular problem in thinned plantations and especially on sandy soils. Under such conditions the disease causes outright death of trees, often spreading in a radiating fashion from an infection point, such as a cut stump. A more subtle condition is the endemic infection of annosus root rot that affects varying proportions of otherwise living pine roots and causes reduced tree growth (Bradford and Skelly 1976). Further, Skelly (1976) noted that approximately 30 percent of the roots of SPB-attacked trees were infected with annosus root rot, compared with 20 percent for unattacked trees on the same site.

Virginia investigators established a series of of plots in Virginia, Georgia, and Texas on high-hazard annosus sites (> 70 percent sand in topsoil). They excavated tree root systems in beetle infestations and adjacent noninfested stands. All trees showed some sign of annosus root rot, but infection was more severe in plantations than in natural stands and on SPB-infested than noninfested plots. These results suggest that under certain conditions annosus root rot is an important predisposing agent for SPB attack.

In another study in the Georgia Piedmont, littleleaf disease of shortleaf pine has also been implicated as a predisposing agent of beetle attack (Belanger et al. 1977). Several facts support this conclusion. First, shortleaf pine, the host of littleleaf disease, is also the preferred SPB host species in the Georgia Piedmont. It constitutes roughly 45 percent of the pine component in the region, and 69 percent of the beetle infestations occur in shortleaf pine. And conditions favoring the development of littleleaf disease (eroded heavy clay soils) are also associated with SPB infestation. It appears that in the Piedmont, littleleaf disease causes reduced growth and vigor of shortleaf pine and this, in turn, predisposes trees to SPB attack.

Other bark beetles, such as black turpentine beetle and *Ips,* are known to weaken trees and lead to infestations of SPB. Preliminary attacks by other bark beetles are often associated with stand disturbances such as logging, lightning, or wind damage (fig. 4-6). Their effect is similar to that of other causal agents in reducing the vigor of the host tree and hence its ability to resist SPB attack.

Figure 4-6. – Pitch tubes signify the attack of black turpentine beetle after this tree was damaged by logging equipment.

Summary and Conclusions

Coastal Plain

Infestations studied in all Coastal Plain projects typically occurred in overstocked stands of slower-than-normal growth. In the lower Coastal Plain of Mississippi, Louisiana, and Texas, a higher-than-expected frequency of infestations occurred on wet or low-lying sites of higher site index. Loblolly pine was the preferred host species. In Coastal Plain stands, increased beetle activity on wet sites often follows periods of abnormally high rainfall. Pines in beetle-infested stands in this region have thicker bark than those in uninfested plots. Infestations in the Kisatchie National Forest of Louisiana occur in stands of older and larger pines. But the age and size of infested pines varies on other ownerships in the lower Coastal Plain, where timber harvesting has eliminated many of the mature and overmature stands.

In the upper Coastal Plain of Arkansas, shortleaf pine was the preferred host species. Overstocking and reduced radial growth were associated with SPB attack, as in the lower Coastal Plain. But trees on low-lying landforms were not preferentially attacked (shortleaf pine is seldom found on these sites). Beetles tended to prefer younger, smaller trees in Arkansas – a reversal of the trend in the Kisatchie National Forest of Louisiana.

A few plots were established in the Atlantic Coastal Plain from Virginia to Georgia. Although inconclusive, the results are generally similar to those of the Gulf Coastal Plain in that overstocked stands of loblolly pine with reduced radial growth growing on wet sites are most frequently attacked by SPB.

Piedmont

The only factor similar for Piedmont and Coastal Plain infestations was reduced radial growth of infested trees. Otherwise, infestations typically occurred in shortleaf pine growing on greatly eroded, heavy clay soils. Also, littleleaf disease is more prevalent in the Piedmont.

Mountains

Relatively few plots were established in the North Georgia Mountains. Again, overstocking and reduced radial growth were associated with SPB infestation. Also, shortleaf and pitch pines were preferred host species as evidenced by the proportion of beetle attacks in stands of those species relative to their presence in the forest. Virginia pine, the most abundant species in the North Georgia Mountains, was attacked less frequently than expected.

Southwide Conclusions

The underlying factors contributing most to host susceptibility to SPB throughout the South are low tree vigor and/or stress. This is evidenced by the consistent Southwide association of SPB with reduced radial growth and certain stand disturbances. Reduced radial growth (low vigor) occurs in overstocked stands in the Coastal Plain and Mountains and in the presence of certain soil conditions in the Piedmont. Lightning is associated with initial SPB attack throughout the South. Locally, many other factors may work independently or in combination with those mentioned above to predispose trees to beetle attack. For example, plantations on sandy sites are vulnerable to annosus root rot, which in turn reduces vigor and SPB resistance.

Very few "new" findings were elucidated by the Program. Researchers had previously identified the aforementioned factors in numerous independent studies. What the ESPBRAP did do was to quantify the effects of these variables, and through a coordinated effort provide geographic replication to identify regional similarities and differences. Our results, unlike those of preceding studies, are useful for developing stand hazard rating models and management recommendations. In fact, several such models are either complete or in preparation (*see* Chapter 8). These models will permit land managers to identify those stands that warrant special attention and remedial action to minimize SPB losses.

Another use of these data will be in developing recommendations for preventing or reducing further SPB damage. For example, problem sites can either be avoided or amended, overstocked stands can be thinned or harvested, and highly susceptible species can be phased out in high-hazard areas (Hicks, Coster, and Watterston 1979).

The work done to date is only the beginning, but it provides a solid foundation on which to build future research.

Population Dynamics

Robert N. Coulson[1]

5

Introduction

Understanding the causes for changes in the distribution and abundance of southern pine beetles is prerequisite to developing an integrated management system for the pest. This knowledge of population dynamics can help predict where and when infestations will occur, how big they will become, and how long they will last. We can also use it to evaluate the probable effects of treatment tactics on SPB populations.

The goal of this chapter is to organize and interpret existing information on SPB populations with emphasis placed on the dynamic features. Implications of population dynamics of SPB to pest management decisionmaking will also be considered. There are five specific objectives of this review. The first is to define the basic population system in individual trees and then to discuss how this system functions at the community (infestation) and ecosystem (forest) levels. The within-tree life processes will be used as elemental building blocks for understanding the community and ecosystem levels. Emphasis will be directed to the dynamic levels of the community and ecosystem. The second objective is to consider the role of the host in the population dynamics of SPB. The third objective is to consider the role of SPB in the population dynamics of the host. The fourth objective is to consider the role of weather in the beetle's population dynamics. The fifth objective is to discuss utilization of information on population dynamics in integrated pest management decisionmaking.

SPB Populations Within Trees, Infestations, and Forests

The approach of utilizing a hierarchy of organization levels has been used to describe population dynamics of bark beetles (Coulson 1979). This approach permits definition of unique attributes associated with individual trees, infestations, and infested forests. The first level, the individual tree, includes information generally classed as natural history. By far the greatest volume of literature on SPB has been written at this level. It is at the second and third levels (infestation and forest, respectively) that actual dynamic features of population come into play.

SPB Populations in Individual Trees

The first level of organization includes the inseparable interrelationships between the beetle, associated microorganisms, and the host tree. Since the SPB's life history is the starting point for a discussion of population dynamics, the following abstract scenario is provided here (*see also* Chapter 2). In the first stage of its life cycle, the adult SPB selects a suitable host tree, through either random or directed behavior (the exact mechanism is unknown). Colonization of the host is regulated by a blend of both insect-produced pheromones and host-produced attractants. Females initiate construction of egg galleries by boring into the inner bark region, where they are joined by males. Blue-staining fungi (*Ceratocystis* spp.) and other microorganisms are introduced at this time. Mating takes place within the galleries, and eggs are oviposited in niches at intervals along the lateral walls. Both males and females reemerge and are capable of attacking and colonizing new hosts. Eggs hatch shortly after oviposition, and the larvae excavate larval galleries at right angles to the egg galleries. There are four larval instars. The first three remain in the phloem region and the fourth migrates into the corky bark, where pupation and adult emergence take place. A large complex of natural enemies and competitors develops concurrently in the host. Figure 5-1 illustrates the general distribution of attacking adults (Coulson et al. 1976a), eggs (Foltz et al. 1976a), larvae, pupae, and emerging adults (Mayyasi et al. 1976a and b) in relation to the infested portion of the tree bole.

These spatial and temporal features of the beetle's life cycle can be included by structuring the life cycle into a series of component processes: colonization (including attack, gallery construction, and oviposition), reemergence, brood survival, and emergence.

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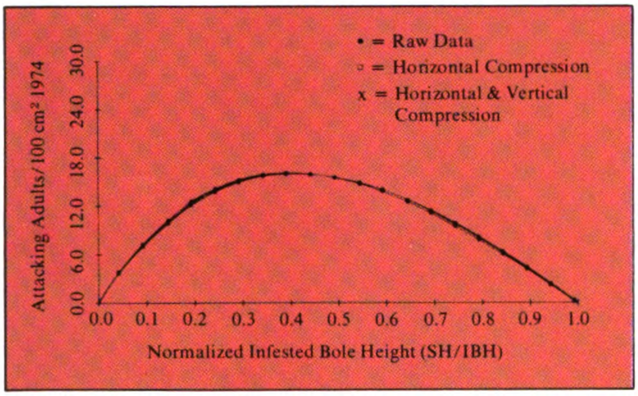
Colonization

The colonization process involves the location of a suitable host tree, identification of this tree for both SPB and its associates, aggregation (concentration) of sufficient numbers of individuals to overcome tree resistance mechanisms, inoculation of the tree with microorganisms, and establishment of an egg population. Successful colonization results in the death of the host (or a portion of it) and sets into motion a series of successional changes in the host tree that will subsequently have a pronounced influence on survival of the beetle population. For this reason, the colonization process will be discussed in considerable detail.

Attack. – The first phase of the attack process involves host selection by "pioneer beetles." These beetles must discriminate between host and nonhost species and between resistant and nonresistant hosts. The SPB's mechanisms for host selection are poorly understood but apparently involve primary attractants, visual cues, and random searching. Host selection is undoubtedly guided by sophisticated behavioral mechanisms, because the requirement for identifying relatively rare susceptible hosts has important consequences for perpetuation of the insect. The host selection phase ends when adults successfully enter the phloem. At this time insect-produced pheromones and host-produced attractants are released.



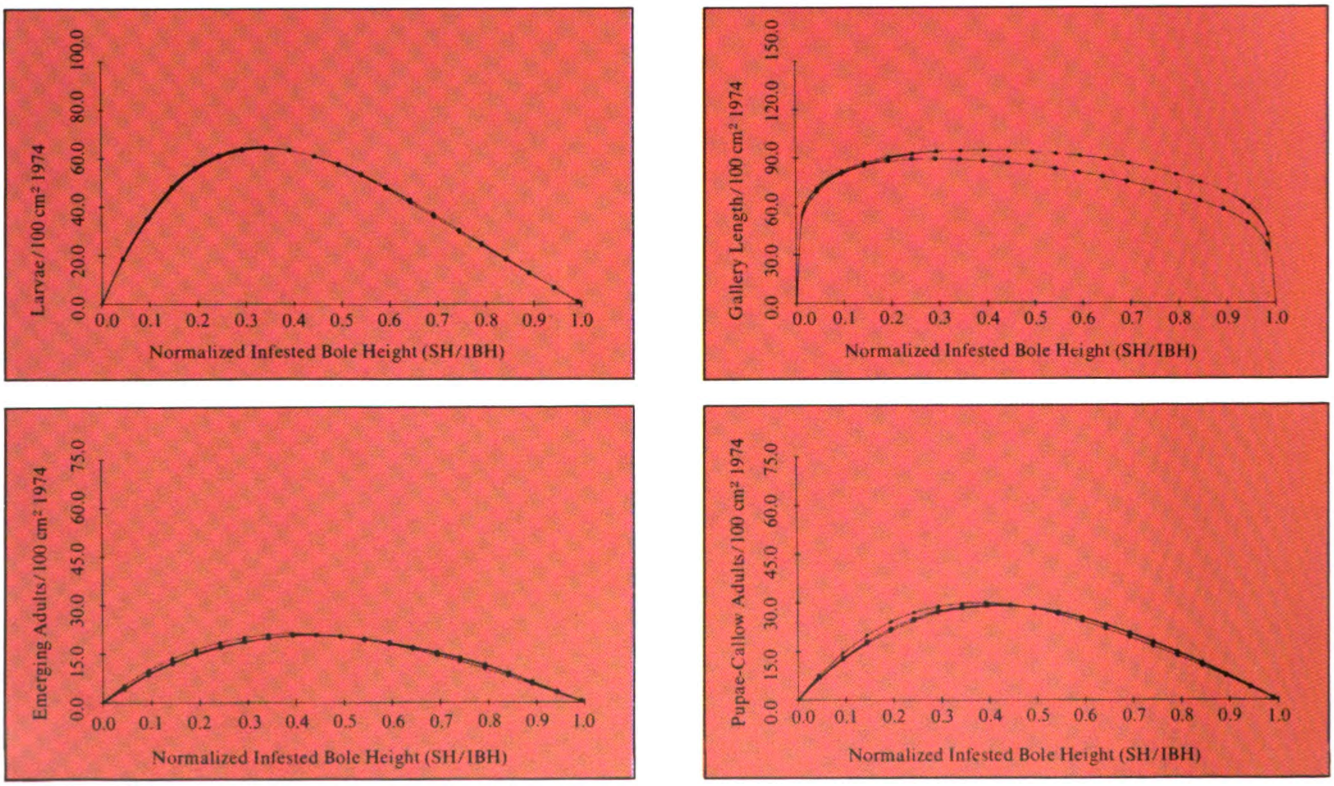


Figure 5-1. – Spatial distribution of SPB life stages (life stage density *v.* the normalized infested bole height).

The concentration phase follows host selection. Females respond to host trees marked by pheromones produced by the pioneering adults. These females initiate gallery construction, inoculate the tree with microorganisms, and produce additional pheromones. The pheromones, in combination with host attractants, stimulate the response of both sexes. After males arrive, mating, gallery elongation, and oviposition occur. These activities constitute the establishment phase, during which arrival of incoming beetles is apparently curtailed by production of inhibitor compounds. After oviposition is completed, the attacking adults reemerge.

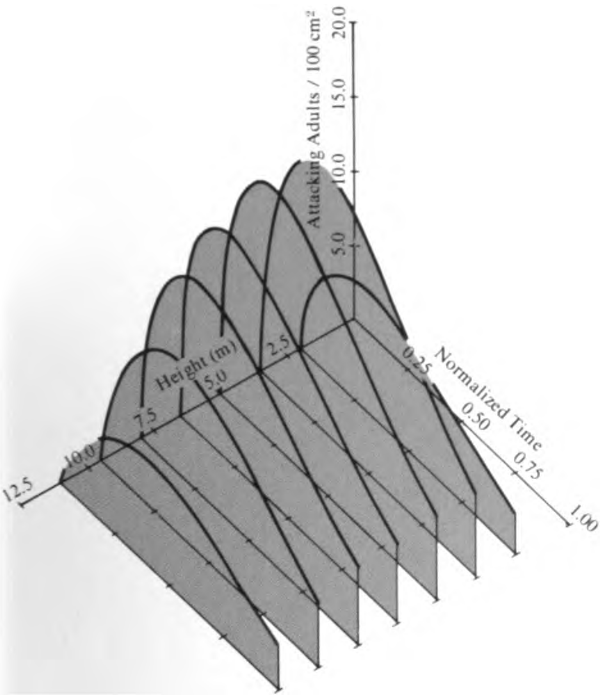


Figure 5-2. – Spatial and temporal distribution of attacking SPB adults (Y axis = adult density, X axis = height on infested bole, Z axis = normalized time). (From Fargo et al. 1978.)

Figure 5-2 shows the general spatial and temporal sequence of SPB attack (ATK), based on measurements of within-tree populations. The four principal characteristics of the ATK processes are (1) pattern (the configuration of the curve of adult density *v.* tree height), (2) extent (the amount of host tree utilized), (3) density (the amplitude of the curve of attack density *v.* tree height), and (4) duration (the length of time involved) (Fargo et al. 1978, Coster et al. 1977). Each of these characteristics is influenced by the interaction of many variables. Arrival of attacking adults precedes actual entry into the tree by 1 to 2 days.

One noteworthy consequence of the sequence of attack is that the age distribution of the population varies in a predictable manner over the infested portion of the tree bole. The central section of the tree is attacked first and at higher density than observed above and below this area. Attack extends from the center section out to the end sections over a period of several days. Generally, attack density is lower in the end sections than in the center. Originally, investigators believed this lower population density at the extremes of the infestations was related to difference in host tree quality or quantity. However, Fargo et al. (1979) found no consistent relationship between tree physical characteristics (e.g., bark or phloem thickness) and beetle density. The observed spatial and temporal pattern, therefore, is likely a result of the sequence of production of behavioral chemicals.

During the concentration phase of colonization, attacks occur first at midbole and later spread toward the top and bottom of the tree. These attacks are guided by both the beetle- and host-produced compounds. After 2 to 3 days, following an increase in population density and establishment of galleries, inhibitor compounds are produced. The center portion of the tree, where colonization is advanced, becomes unattractive. Production of inhibitor compounds gradually spreads to the extremes of the tree over a period of time that follows the age distribution of the within-tree attacking adult population. If the adult population available to attack a tree remained constant over the duration of the colonization process, the resulting pattern would be the same as observed in figure 5-2 (*see* Chapter 2). Production of pheromones by *Ips* spp. and the black turpentine beetle may also be important in the sequence of colonization and in resource partitioning.

Attack density on individual trees is highly variable. Fargo et al. (1979) reported a range of 1 to 19 beetles/100 cm², based on a study of 134 infested trees in east Texas. About three-fourths of the measurements taken were between 5 and 13 beetles/100 cm² (fig. 5-3). The sex ratio of adults in successful attacks is essentially 1:1.

The fate of the attacking adult population is influenced by many variables. The more prominent ones include meteorological conditions, predation, density, and quality of adults available for colonization, tree resistance, and physical attributes of the tree surface. The way these variables operate and interact through time and space is extremely important because for colonization to be successful, a population large enough to kill the host (or part of it) must be assembled.

The time frame for the attack process ranges from 8 days to 6 weeks depending largely on seasonal conditions. Figure 5-2 is representative of a "mass attacked" tree. In this circumstance attacking adult populations are generally high and the process is completed in a short time.

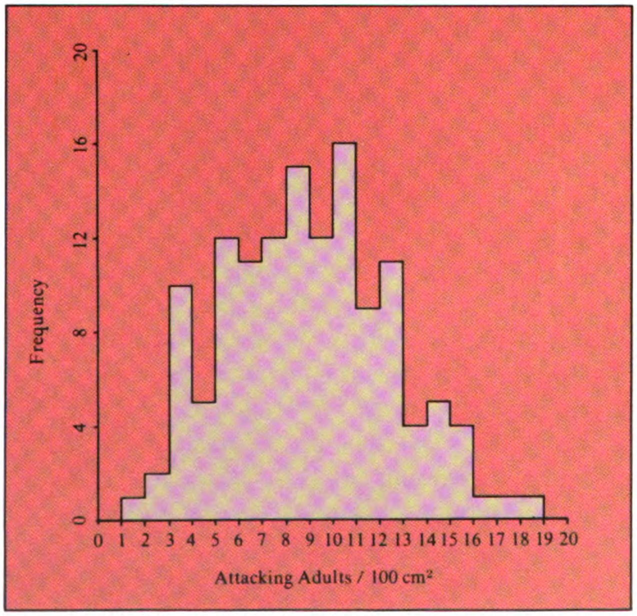


Figure 5-3. – Frequency histogram of density of attacking adult SPB, based on estimates taken from 134 trees in east Texas.

Gallery construction and oviposition.– Gallery construction (GL) is an important component of the within-tree population system of SPB because there is a relationship between gallery length and oviposition. Considerable research attention has been given to this relationship. Knowledge of the fecundity of SPB is of obvious importance in understanding population dynamics. Furthermore, it is substantially less difficult to observe and measure gallery length than the number of eggs.

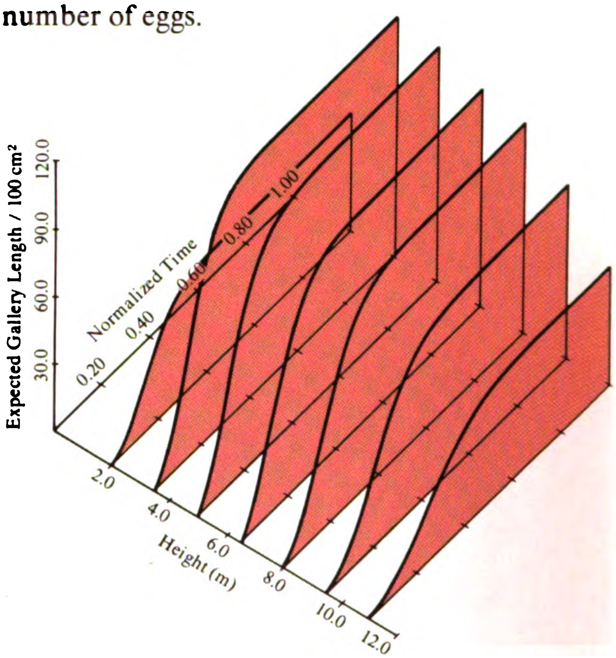


Figure 5-4. – Spatial and temporal distribution of cumulative gallery length for the SPB. Y axis = cumulative gallery length density. X axis = height of infested bole. Z axis = normalized time.

The general spatial and temporal pattern of GL is illustrated in figure 5-4 (Fargo et al. 1978). The GL process has the same attributes as described for ATK–pattern, extent, density, and duration. Gallery initiation generally occurs slightly below the center portion of the open bole. Gallery density is highest in this region and tapers gradually toward the top and abruptly toward the bottom of the infested bole (Fargo et al. 1978). Peak values for GL, based on a 3-year study in east Texas (Coulson et al. 1975a), ranged from 30 to 100 cm/100 cm² of bark (fig. 5-5).

Recent studies have revealed that the relationship between egg populations and gallery construction is rather complex. Foltz et al. (1976a) demonstrated a linear relationship between eggs and gallery length: E (no. of eggs) = 1.59 × GL. This field study, conducted in east Texas, utilized data collected throughout a summer season from several trees sampled at various heights and aspects. F. P. Hain (personal communication) obtained similar results for populations in North Carolina. Other studies have demonstrated statistically significant departures from the results of Foltz et al. (1976a) and Hain. Working in Mississippi, Lashomb and Nebeker (1979) reported that in their field-collected samples many egg niches did not contain eggs. In their Georgia laboratory studies, Clarke, Webb, and Franklin (1979) observed that oviposition did not begin immediately as galleries were constructed. Regression analyses of Mississippi and Georgia findings produced different results from those obtained in Texas and North Carolina.

The effects of temperature, adult density, and seasonality on gallery construction and oviposition were investigated in lab studies by Wagner et al. (1980b). Interactions of these variables affected total gallery construction and number of eggs per female, duration of gallery construction and oviposition, and the shapes or configurations of the curves of cumulative gallery construction or eggs per female over time. A mathematical model incorporating these variables was developed. This model provides a realistic view of SPB reproduction.

The effects of temperature and adult density on GL and oviposition are less difficult to understand and explain than is seasonality. Variation in

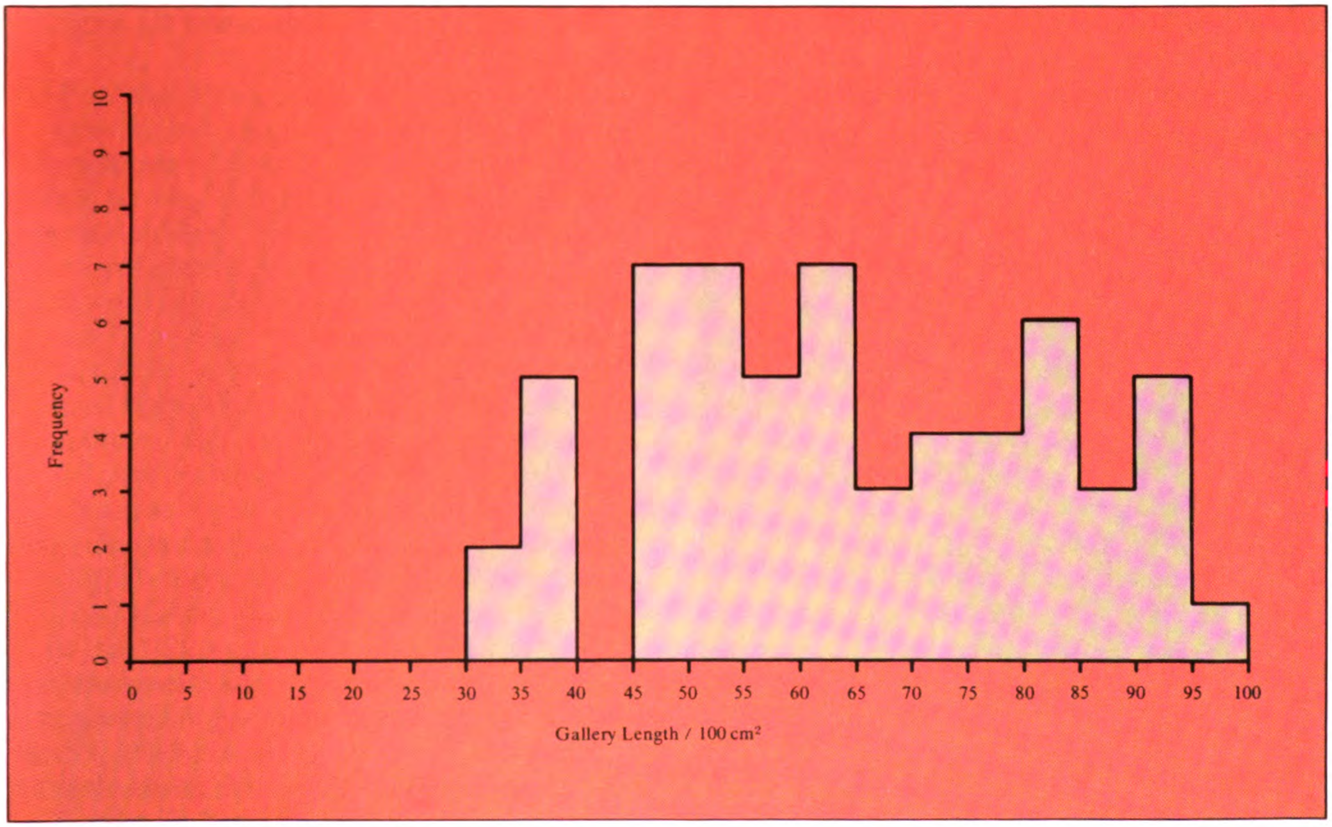


Figure 5-5. – Frequency histogram of density of gallery length of the SPB, based on estimates taken from 59 trees in east Texas.

population behavior associated with season has been observed by a number of workers, e.g., Thatcher and Pickard (1964 and 1967), and Thatcher (1971). Hedden and Billings (1977) reported seasonally related differences in fat content and size of adult beetles. Clarke et al. (1979) demonstrated that beetle size was associated with differences in fecundity. The relationships between beetle physical characteristics (size), energy reserves (fat), and fecundity are well documented. However, the importance of variations in beetle quality on population behavior in infestations and forests has not been examined in detail.

Resource utilization by SPB. – Obviously there are a number of important relationships between attacking adult and egg populations. One extremely critical relationship deals with the efficiency of host tree (resource) utilization. Each host has a finite quantity (or volume) of bark area suitable for brood development. The SPB has been shown to regulate egg populations through a density-dependent negative feedback mechanism that operates during colonization. The number of eggs per female varies as a function of the density of attacking adults (fig. 5-6). At low densities each female oviposits a larger complement of eggs. Conversely, at higher densities each female oviposits fewer eggs. Although information on within-tree SPB density has not been studied in detail, it is probably transmitted via acoustical signals.

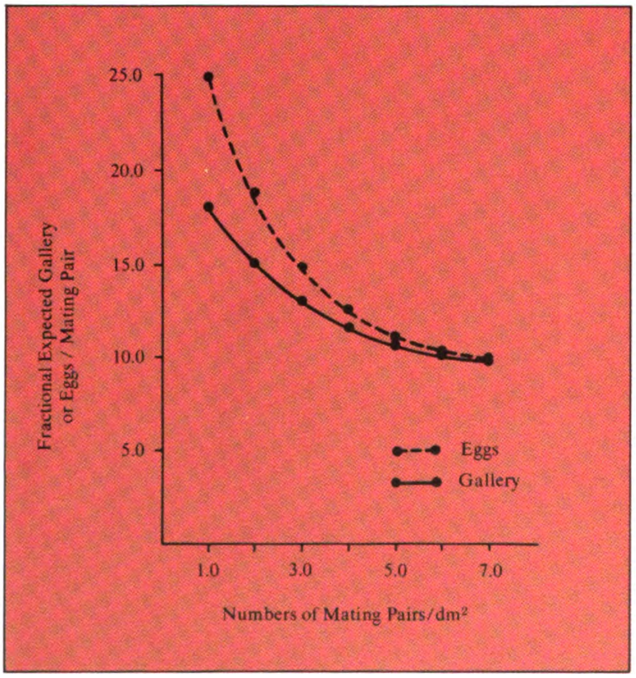


Figure 5-6. – Relationship between gallery length (solid line) and eggs (dashed line) *v.* number of mating pairs of adult SPB, illustrating a decrease in eggs and gallery length with increasing adult density.

In the original description of resource utilization by Coulson et al. (1976a), egg populations were estimated using the constant E = 1.59 × GL from Foltz et al. (1976a). Figure 5-6 illustrates resource utilization based on both gallery length measurements and actual egg numbers obtained in laboratory studies (Wagner et al. 1980b). Although many variables have been shown to influence the relationship between egg populations and gallery length, estimates of egg populations based on a constant multiplier provide a reasonable approximation of the actual number.

This mechanism of resource utilization permits efficient use of the host tree and prevents overpopulation that would result in mortality due to competition for available food material among brood life stages. Depletion of available host and food material is avoided by regulating the initial size of the egg population. Furthermore, rapid increases in populations are possible even though initial attacking adult numbers may be small. The insect, therefore, has the capacity to respond quickly to favorable host or weather conditions.

The resource utilization phenomenon has important implications in characterizing and forecasting population trends. A commonly used index of within-tree population trend is ratio of increase (Thatcher and Pickard 1964), which is defined as RI = (no. emerging adults)/(no. attacking adults/2). Because of the resource utilization mechanism, the expected egg complement per female is higher at low attack density. Therefore, even with identical survival, the RI would be higher at low than at high attack density (Gagne et al. 1980b). RI has been proposed for use as an index of population "vigor" (Moore

1978), e.g., high ratios being indicative of vigorous populations and low ratios indicative of low vigor. But the index cannot be used for this purpose, because of the resource utilization phenomenon.

Reemergence

Reemergence is the process where adult beetles attack one host, lay eggs, and then exit to attack another host. This aspect of the natural history of SPB was recognized and reported by MacAndrews (1926 unpublished) in the first description of the life cycle of the insect. The significance of reemergence to population dynamics was identified by Franklin (1969 and 1970a), based on a study of infestation development in Georgia.

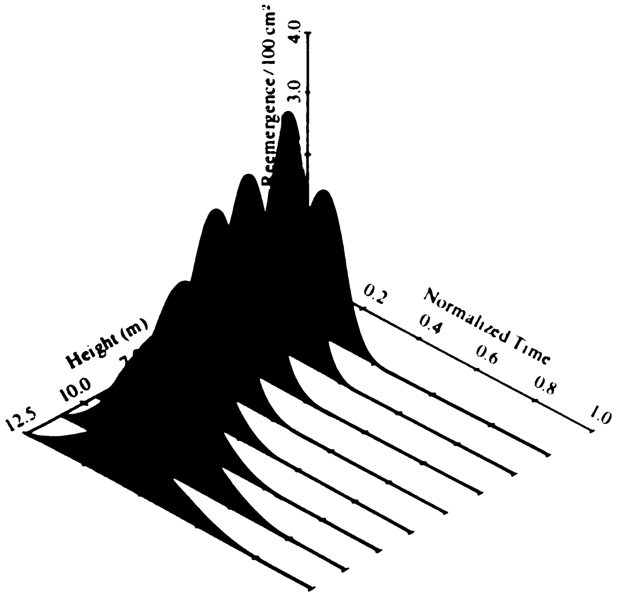


Figure 5-7. – Spatial and temporal distribution of reemerged SPB adults. Y axis = reemerged adult density. X axis = height on infested bole. Z axis = normalized time. (From Coulson et al. 1978.)

The spatial and temporal sequence of reemergence is illustrated in figure 5-7. The process has the same numerical features as reported for the components of the colonization process (pattern, extent, density, and duration). Reemergence begins at about the same time as peak arrival of attacking adults and continues for 10 to 14 days. The pattern and timing of reemergence follows the template established during oviposition. The number of beetles that reemerge ranges from 24 to 97 percent (Clark and Osgood 1964, Yu and Tsao 1967, Coulson et al. 1978 and 1980b, Cooper and Stephen 1978). The duration of the process over time is of survival value to the insect in that mortality agents affect only a portion of the population.

Several important features of the behavior of reemerged adults have been identified from both field and laboratory studies. Females are capable of establishing two or three brood populations (Clark and Osgood 1964, Thatcher and Pickard 1964). Additional matings may be unnecessary for production of viable eggs in later attacks (Yu and Tsao 1967), although males are present in galleries constructed by reemerged females in the field. Reemerged adults produce pheromones that attract field populations (Coster 1970). Reemerged adults perceive and respond to pheromone and host attractants (Coulson et al. 1978).

Reemergence is an important aspect of the beetle's population dynamics and influences the pattern of infestation growth. Assuming that host trees are available in an area, there are five basic requirements for infestation growth (Coulson et al. 1978): (1) There must be enough SPB adults nearby and capable of attacking trees. (2) Host trees must be identified by the attacking population. (3) Initial host resistance to attack must be overcome. (4) Colonization and brood establishment must take place. (5) Local attractiveness must be maintained in the infestation.

Brood as well as reemerged adults contribute to infestation growth. The only biological attribute in which reemerged adults are known to differ from emerged brood adults is age. T. L. Wagner (personal communication) conducted extensive laboratory studies on reproduction of reemerged *v.* brood adults and found fecundity to be equivalent in both.

The process of reemergence adds another dimension to the resource utilization mechanism described earlier. Reemerged adults can oviposit all their eggs in one host or a portion of the complement in each of several hosts. When adult population density is low in an area, the former circumstance probably occurs. Conversely, when populations are high, the latter circumstance likely results. Distributing the eggs through multiple reemergences in response to variable density of adult populations is clearly a survival-enhancing mechanism for the beetle. Reemergence and resource utilization, therefore, are complementary processes. The fact that reemergence takes place where infestations develop enhances survival further in that the distance between hosts is small.

Survival of Within-Tree Brood Life Stages

In discussing the survival of within-tree populations of the beetle, we must consider the fates of eggs, larvae, pupae, and emerging adults. Survival of adult populations en route between trees will be discussed later. Generally, the factors that modify the distribution and abundance of populations include weather, food supply, intra- and interspecific competition, parasitization, predation, and genetic responses. These mortality processes may operate simultaneously and are exceedingly difficult to measure. The biotic

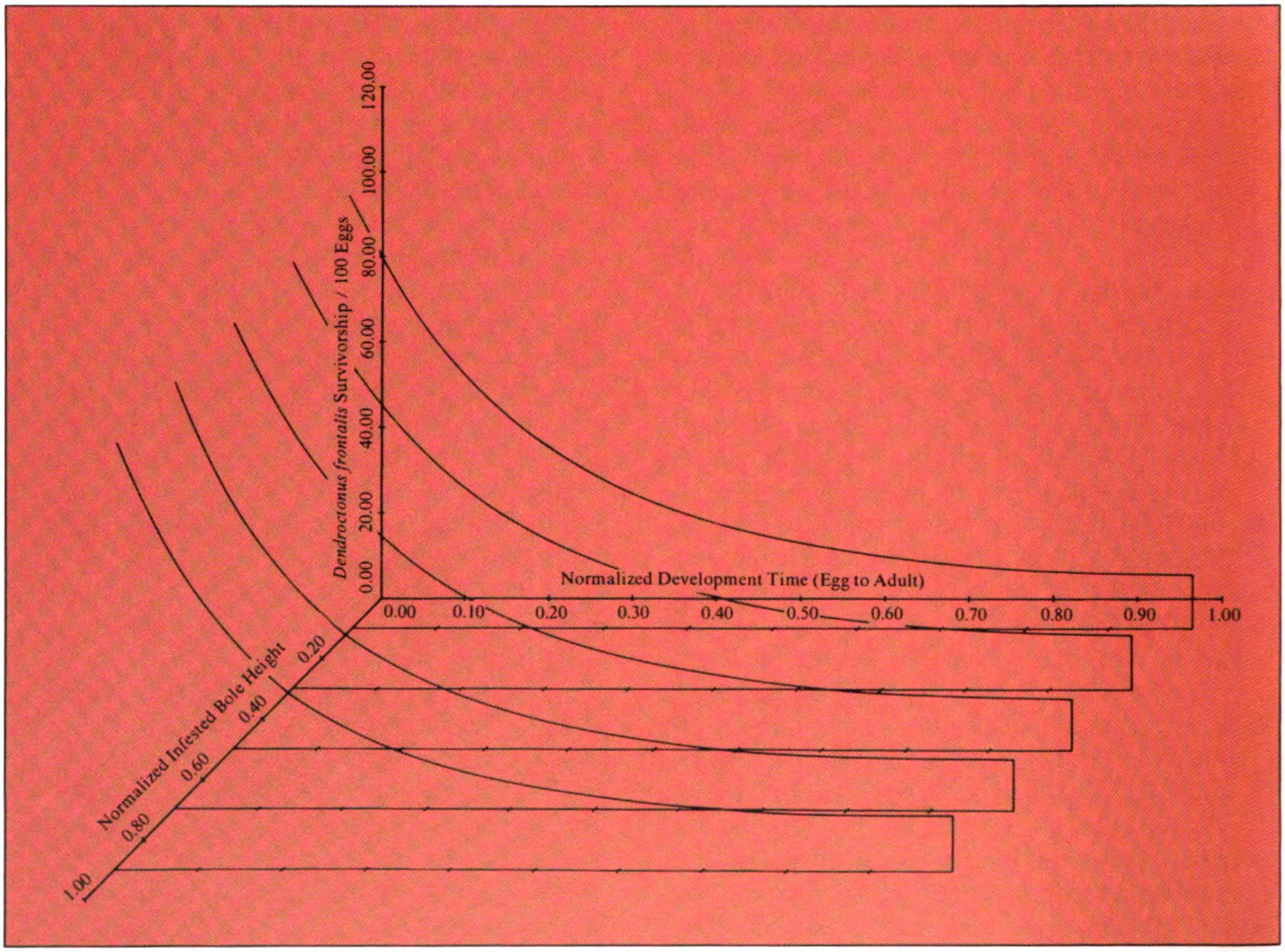


Figure 5-8. – Spatial and temporal pattern of survivorship for within-tree SPB populations. Y axis = survivorship/100 eggs. X axis = normalized infested bole height. Z axis = normalized time.

mortality agents have been studied in considerable detail and are reviewed in Chapter 3.

Determining exactly what has killed a southern pine beetle is complicated by the fact that the insect is a native pest with a large complex of natural enemies. These mortality agents tend to concentrate in different portions of the infested tree and therefore have distinct and clumped distributions (Dixon and Payne 1979b). Population estimation necessitates the use of large sample sizes (Stephen and Taha 1976) that are generally impractical for field studies. Furthermore, quantitative definition of the population systems of the natural enemies is complicated by the rapid developmental time, probable interactions between species, and continuous growth pattern of the natural enemies and SPB.

In view of these complications, survivorship has been described as a general process for the within-tree population (Coulson et al. 1977). The spatial and temporal pattern of survivorship/100 eggs is illustrated in figure 5-8, which is based on an analysis of 149 trees sampled during 1972–74 in east Texas. The survivorship process has the same numerical attributes as colonization and reemergence – pattern, extent, density, and duration. One noteworthy feature illustrated in figure 5-8 is that average within-tree survival at various

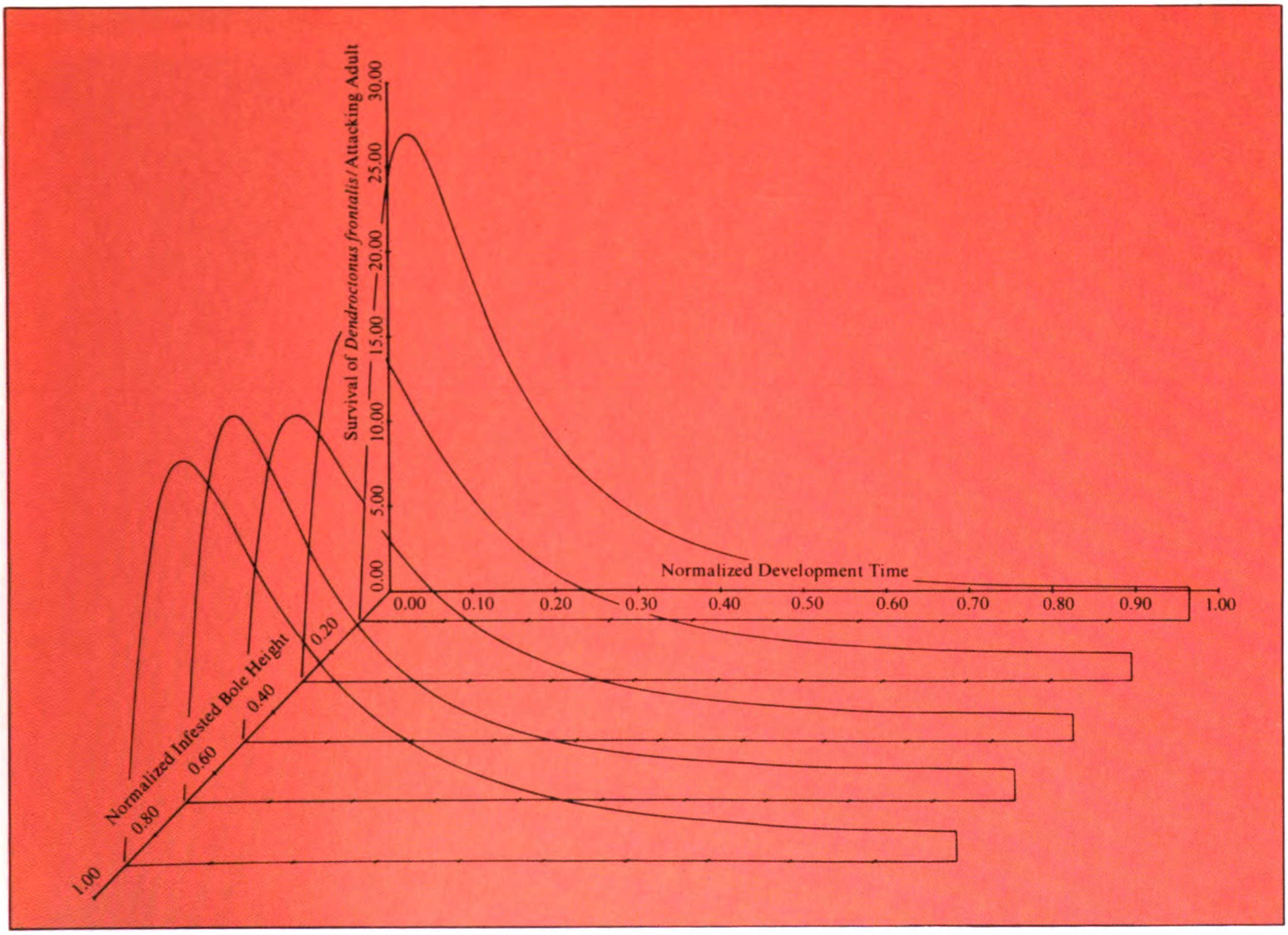


Figure 5-9. – Spatial and temporal pattern of generation survival for within-tree SPB populations. Y axis = survival of SPB/attacking adult. X axis = normalized infested bole height. Z axis = normalized time.

heights along the infested bole is virtually identical. However, survivorship varies among trees, host species, infestations, areas, and seasons. Also the mortality agents vary from one part of the tree to another. The net effect of the numerous biotic and abiotic mortality agents acting within the tree throughout development results in a uniform pattern of survivorship. The mortality agents therefore seem to have a similar net effect on the SPB, although different species operate in different regions of the same host trees.

The effect of the resource utilization mechanism on within-tree survival is demonstrated in figure 5-9, which illustrates survival of SPB/attacking adults over time and height on the infested bole. Although the beetle's attack density is greater toward the center of the infested bole (fig. 5-2), the number of eggs/adult is less at mid-bole. The significant point is that the pattern of survival is the same for each section of the tree, while the actual number of beetles present varies. This observation further emphasizes the problem of using the ratio of increase to characterize population trends.

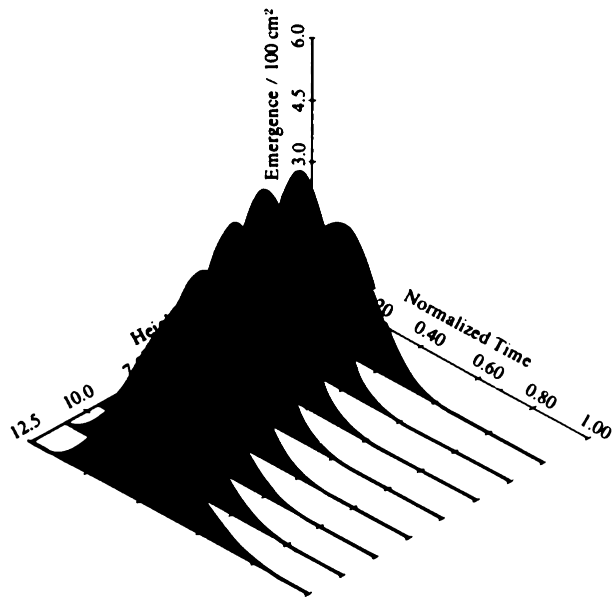


Figure 5-10. – Spatial and temporal distribution of emerged SPB adults. Y axis = emerged adult density. X axis = height on infested bole. Z axis = normalized time. (From Coulson et al. 1979b.)

Emergence

Emergence is the final process in the beetle's population system. Figure 5-10 illustrates the spatial and temporal pattern for the process. The same four numerical attributes occur – pattern, extent, density, and duration. Of the within-tree population processes, emergence has the highest degree of numerical variation. The observed spatial and temporal pattern of emergence reflects the net effects of all mortality agents acting on the population system.

The pattern for emergence is, again, a reflection of the original age distribution of the egg population. As with reemergence, emergence occurs in small daily increments over a period of ca. 14 to 28 days during the warmer months. This pattern likely has survival value for the species, as weather-related disasters would involve only a small part of the population. We also know that adults ready to emerge remain in the host during periods of inclement weather. Kinn (1978) described the diel emergence pattern for the SPB.

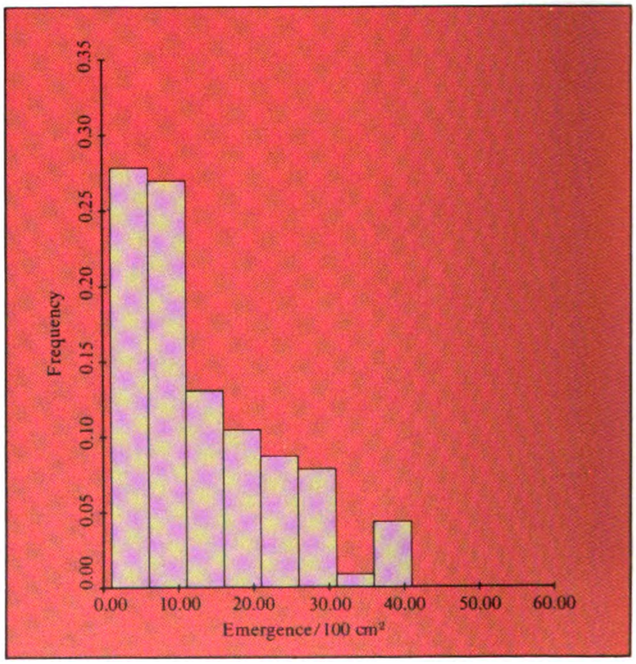


Figure 5-11. – Frequency histogram of density of emerged SPB adults, based on estimates taken from 134 trees in east Texas.

Densities of emergent beetles vary widely. Estimates based on 134 trees ranged from 2 to 42 beetles/100 cm^2 in east Texas (fig. 5-11). About three-fourths of the observations contained emergence densities in the range of 2 to 20 beetles/100 cm^2.

The influence of season on patterns of adult emergence in Texas has been investigated (Thatcher and Pickard 1967, Thatcher 1971, and Gagne et al. 1980a). Salient features of these studies are discussed below in conjunction with the influence of weather on populations of the beetle.

SPB Populations in Infestations

Populations of the beetle occur in clumps or infestations distributed throughout a forest. Infestations (= spots) are generally comprised of a number of trees, each containing beetles in one or more stages of development. Over the course of a summer, one spot can enlarge to include many infested trees. Spot growth is concentrated at one or more active fronts (or heads). This pattern of continuous spot growth is a unique feature of SPB populations.

Figure 5-12 illustrates a typical infestation. Although crown coloration is not always a good indicator of the stage of spot development, it does provide an acceptable means of illustrating the continuous growth pattern and variable age structure typical of infestations. In figure 5-12 the lightly faded green trees in the foreground have

Figure 5-12. – Aerial view of SPB infestation (spot) illustrating trees in several age classes. Gray trees in background no longer contain beetles in any stage, red trees contain late developmental stages and beetles ready to emerge, lightly faded trees contain early developmental stages, and green trees in the foreground (at the edge of the spot) are being attacked.

been colonized and reemergence of parent adults is occurring. The lightly faded red trees in the center contain developing brood life stages. Brood adults are emerging from the dark red trees in the background. The gray trees in the far background no longer contain beetles.

Figure 5-13 diagrammatically represents the sequence of development of a spot through the course of a summer season. The pattern of spot development is a function of the combined within-tree population processes in all trees in the infestation.

Patterns of Continuous Growth

To track the continuous growth of a spot, researchers need both quantitative estimation procedures and knowledge of the spatial and temporal patterns of within-tree beetle population processes. For SPB there are now available several different sampling plans that have defined accuracy and precision (*see* Chapter 6).

In the original description of the processes of colonization (Fargo et al. 1978), reemergence (Coulson et al. 1978), survivorship (Coulson et al. 1977), and emergence (Coulson et al. 1979b), it was found that the distributions for each process could be averaged to produce a single curve (density over time) and still provide a realistic representation of a particular process in a tree.

Figure 5-14 illustrates an example of the within-tree population processes, expressed in two dimensions, for several trees sampled at different times during the development of a single spot. Density and duration are highly variable for each tree, but the general patterns for the processes are quite similar. Continuous estimates of attack, gallery construction, reemergence, survivorship, and emergence, together with the spatial and temporal location of both infested and uninfested trees, provide the basic information needed for analyzing and interpreting population dynamics of the beetle within spots (Coulson et al. 1980b).

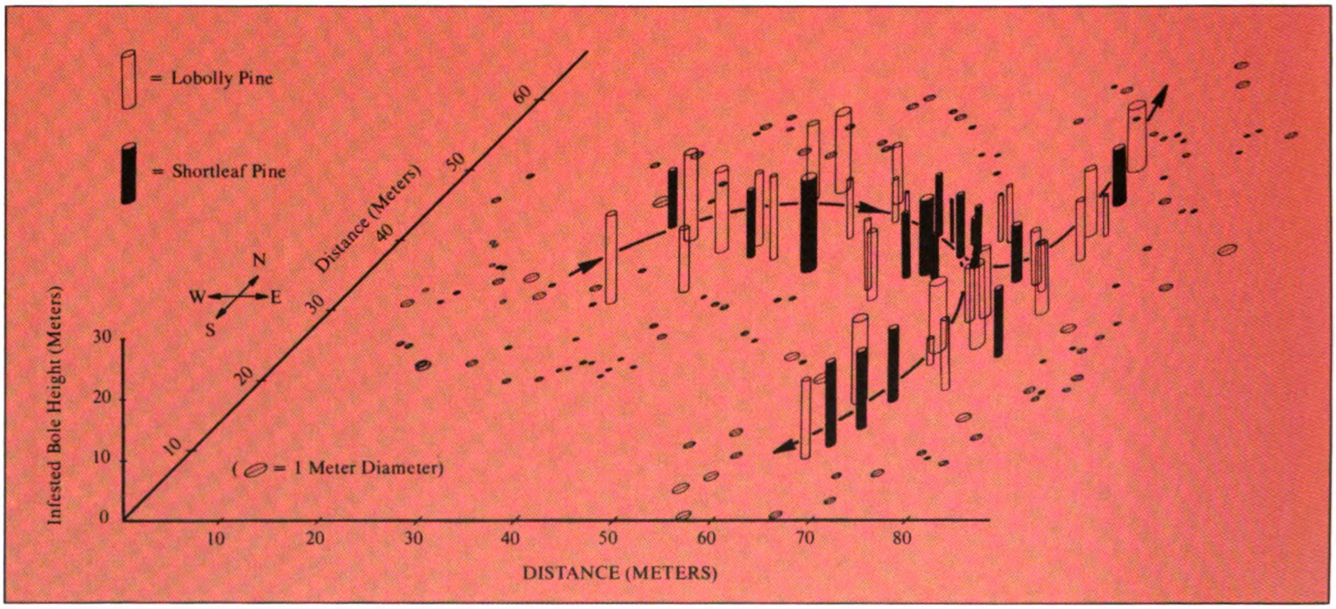


Figure 5-13. – Spatial arrangement of attacked and unattacked trees in an SPB spot. The cylinders represent attacked trees and are proportional to the actual size of the trees in the spot. The ellipses represent peripheral unattacked trees. The two axes indicate the actual scale in meters.

Using the quantitative estimation procedures and knowledge of the beetle's within-tree population processes, Coulson et al. (1980a) obtained daily estimates of populations from infestations. Figure 5-15 displays an example of the interrelationships between several of the beetle processes throughout the course of initiation, development, and termination of an SPB spot. Attack (A) is represented as a series of spikes occurring throughout spot development, as new trees are attacked. The attacking population is comprised of both reemerged (B) and emerged (C) adults. The two processes – reemergence and emergence (D) – were combined and termed "allocation" (Coulson et al. 1979b and 1980b). The two component processes of allocation vary throughout the summer. Furthermore, the total living brood within trees in a spot (E) influences the pattern of emergence. Numbers of infested trees and infested bark area are also illustrated in figure 5-15. The number of infested trees (F), total infested surface area (G), and average infested surface area per individual tree (H) have an important effect on the course and duration of spot development.

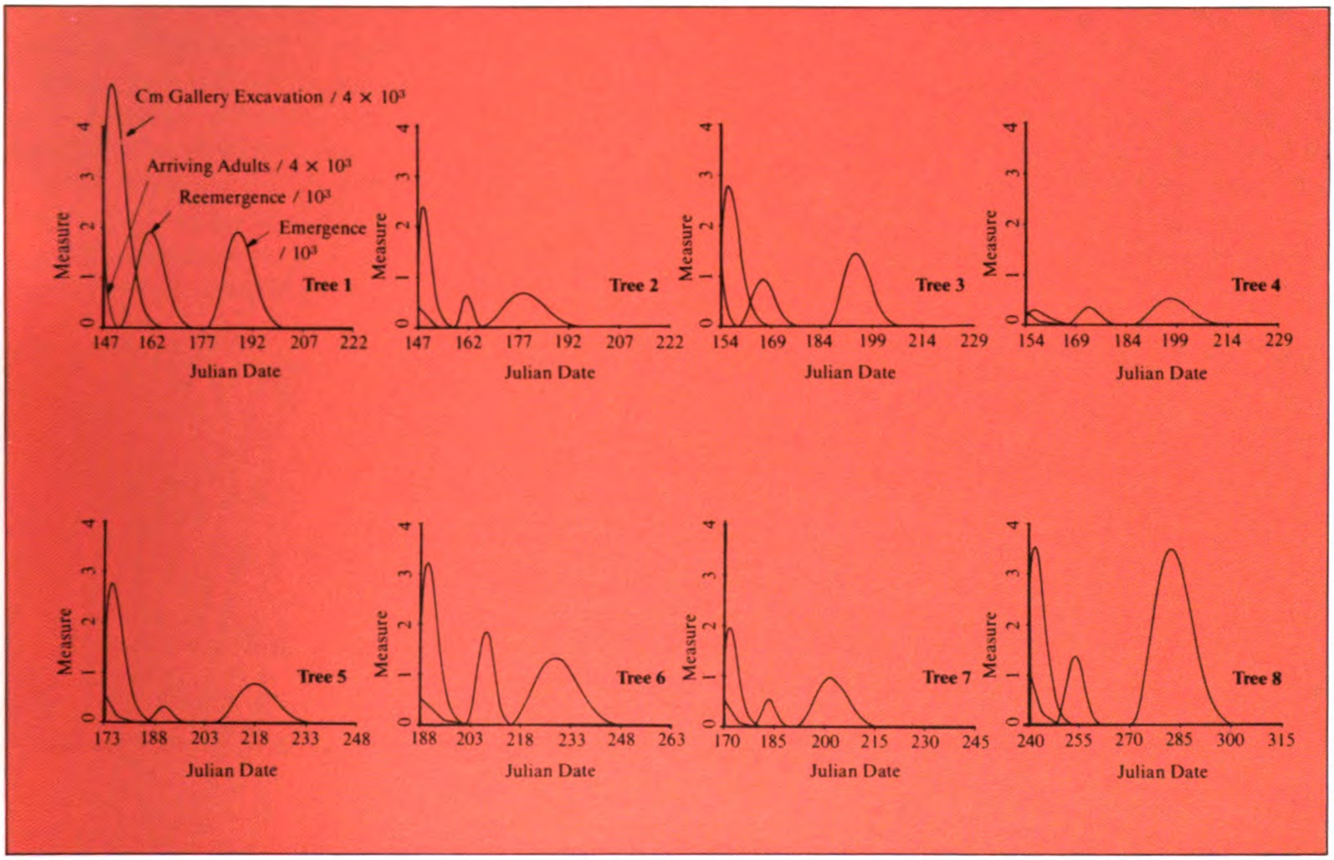


Figure 5-14. – Arriving adults, centimeters of gallery construction, reemergence, and emergence, based on daily estimates taken from trees throughout the course of development of a spot.

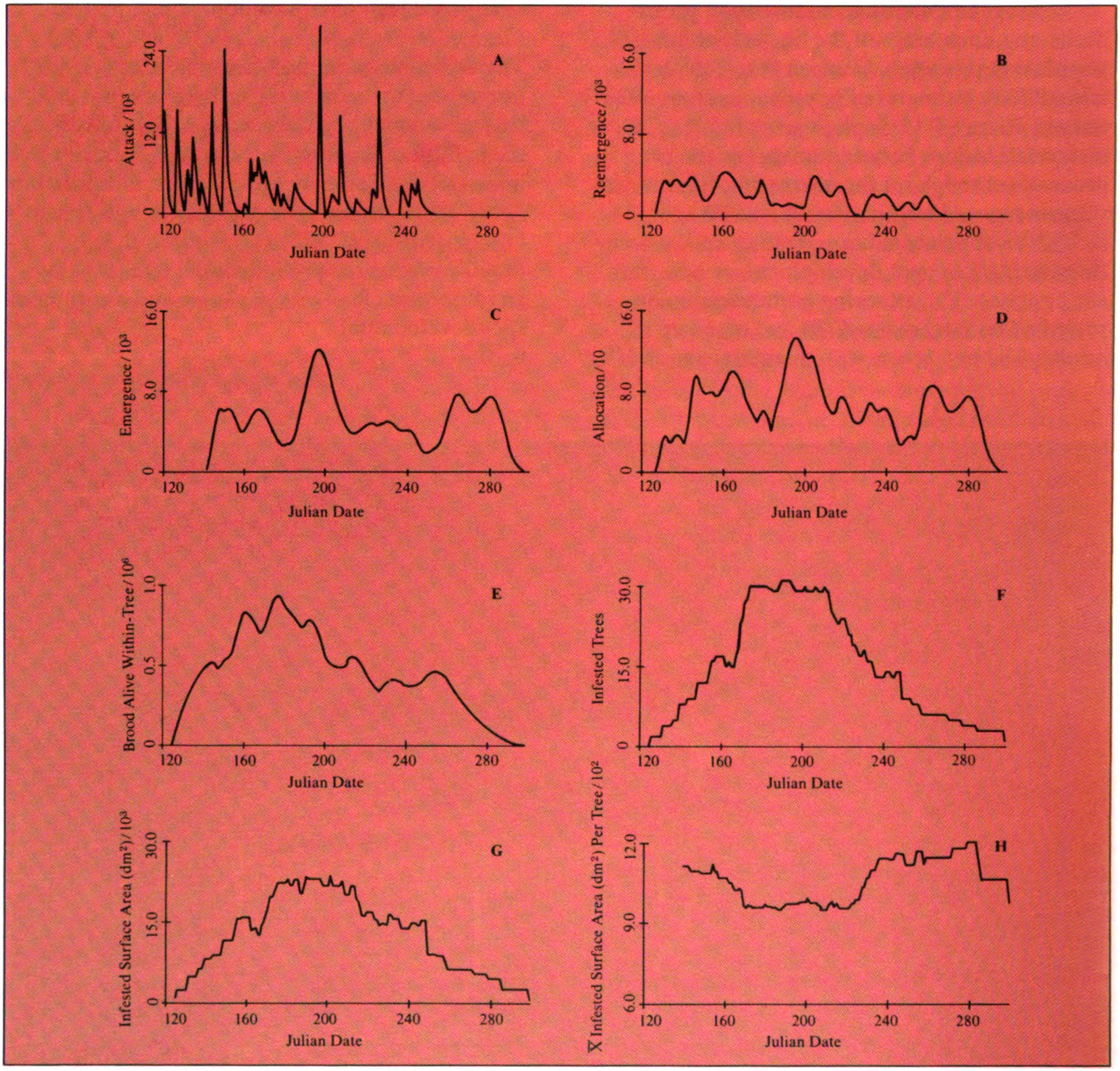


Figure 5-15. – Representative components of the population dynamics of the SPB, measured at the infestation level of organizational complexity. Measurements were made during the period of Julian dates 123 and 298 in a spot that occurred in east Texas during the summer of 1977. The beetle processes of attack, reemergence, and allocation are absolute numbers of beetles + 10^3; brood alive within the trees + 10^6. The host characteristics measured included the number of infested trees, the infested surface area ($100\ cm^2$) + 10^3, and the mean infested surface area ($100\ cm^2$) per tree + 10^2.

Analysis of continuous population data provides a means of interpreting processes unique to the infestations. Processes such as between-tree survival and allocation operate only at the spot level. These processes are important to understanding and predicting the distribution and abundance of the beetle. In addition, we can interpret the interrelationships between host and stand characteristics, weather, and population numbers using the continuous estimates.

Allocation of Adults

The distribution of beetle populations, whether in a tree, in a spot, or throughout the forest, is a function of the adult life stage. In any spot there are three categories of adults present: attacking parent adults, reemerging parent adults, and emerging brood adults. These classes can be catalogued further as within- or between-tree and of local or immigrant origin (Coulson et al. 1979b). Within-tree life processes that deal specifically with the adult life stage include colonization, reemergence, and emergence. A general depiction of these three processes in an individual tree is illustrated in figure 5-16. From this figure, it can be seen that a tree functions as a sink for beetle populations (attack), a sink and a source for beetles (attack and reemergence), or a source for beetles (reemergence and emergence). Within a spot there will be a mosaic of trees involved in each mode.

Insight into the manner in which SPB infestations develop can be gained by considering the combined processes of reemergence and emergence from a single tree, i.e., allocation. On an individual tree, allocation (1) is continuous for each tree in the spot and bounded by the length of the within-tree life cycle, (2) is distinct for each tree, (3) is bimodal in intensity, and (4) its two components may operate together in concert or independently (Coulson et al. 1979b).

An individual spot contains a number of trees having different characteristics. The combined reemergence and emergence from all trees in the spot determines the number of adults available for attack and the resulting infestation pattern illustrated in figure 5-15. During periods

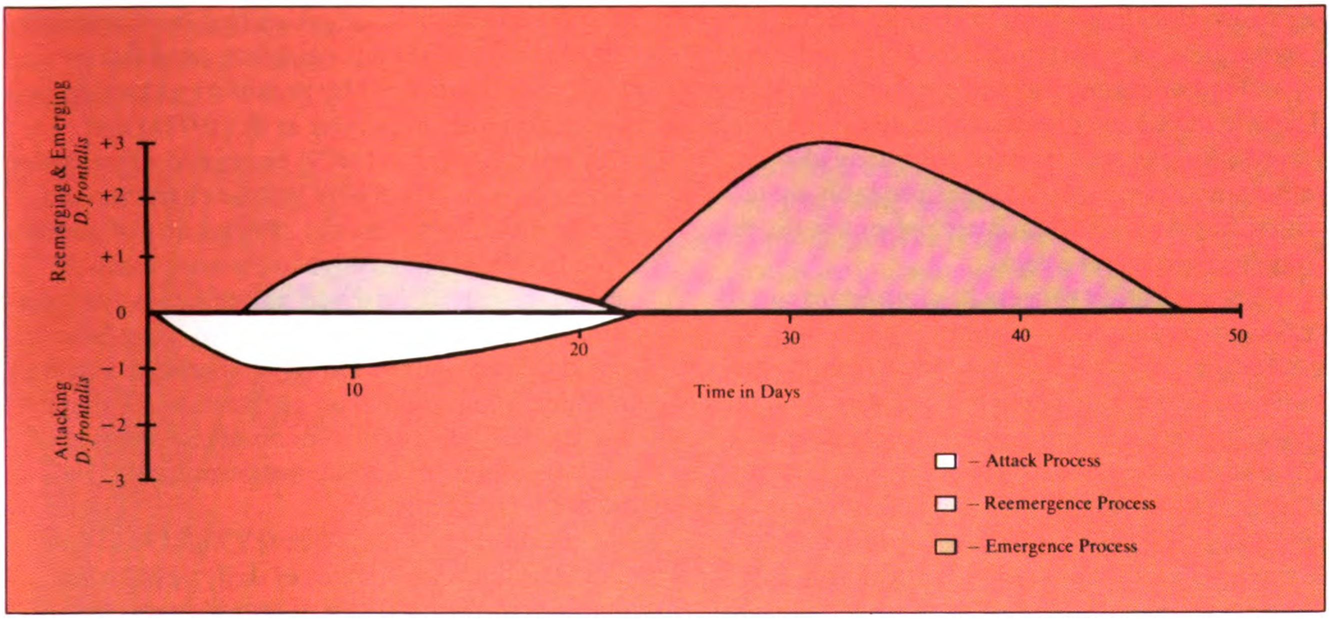


Figure 5-16. – Generalized plot illustrating the temporal relationship of the processes of attack, reemergence, and emergence for an infested tree. (From Fargo 1977.)

of close synchrony between the components of allocation, a continuous supply of beetles is available for colonization. The rapid enlargement of SPB infestations in short periods of time is likely a result of close synchrony between reemergence and emergence, coupled with favorable weather and stand conditions.

Since the allocation process is distinct for each tree, mortality is independent for each tree in the spot. This fact can be of considerable importance in spots comprised of hosts of variable size and age distribution.

The bimodal form and independence of the components of the allocation process enhance SPB survival in that variables which influence one component will not necessarily affect the other. For example, inclement weather during reemergence may not persist or recur at time of emergence. Furthermore, the incremental pattern of reemergence and emergence, which results from the prolonged colonization period, ensures that only a small part of the allocating population will be exposed to short-term weather-related mortality.

The implications of genetic diversity resulting from allocation have not been examined. Colonization of a particular tree is accomplished by a blend of reemerged and emerged beetles. These beetles have different ages and origins from within the spot. Immigration may also be important. Reemerged females probably mate with different males than were present in the first trees to come under attack.

The allocation process has important implications to population dynamics. First, allocation is clearly an infestation-level process, with attributes that cannot be defined by examination of individual trees. Second, the concept of distinct generations, used to describe many insect populations, is not applicable to the SPB since (1) the colonizing population consists of beetles of different ages and origins, and (2) attacks on different trees usually occur over an extended period of time. Third, the age distribution of the within-tree population resulting from allocation is highly variable.

Between-Tree Survival Probabilities

Quantitative information on the fate of adults en route between trees in a spot or between spots in a forest has been extremely difficult to obtain. This information is of paramount importance to understanding population dynamics.

Historically, most of the research on populations of adults, under field conditions, has been conducted in association with studies of SPB behavior in response to pheromones and attractants. Conclusions from the studies were based on relative estimates of populations obtained from interception traps (as opposed to absolute estimates).

The early studies by Gara (1967) and Gara and Coster (1968) were among the first to examine patterns of spot development as related to the beetle's response to behavioral chemicals. Spreading and collapse of infestations were found to be related to synchronization of beetle emergence (reemergence was not considered) with production of attractant compounds from nearby, newly attacked trees. The investigators also found that mass attack shifted from recently infested trees to vacant neighbors, and this behavior was influenced by proximity of host trees.

Subsequently, Coster et al. (1977a) and Coster and Johnson (1979) examined aggregation in response to attactive hosts and characterized the beetle's flight behavior. Probability of attack on a tree in a spot relative to distance from an attractive host was defined mathematically (Johnson and Coster 1978). These studies were based on advanced understanding of chemical communication and provided an explanation for dispersal that was consistent with observed patterns of spot development and known responses to behavioral chemicals.

Information on the beetle's flight behavior and quantitative estimates of daily populations involved in the processes of attack, reemergence, and emergence, taken together, provide the data needed to develop a model of allocation and a definition of between-tree survival for adults. Between-tree populations are composed of both reemerged and emerged adults during the time interval between leaving one host and successfully attacking another (entering its inner bark). Between-tree survival probability is the probability of an adult leaving one host and successfully attacking another. Allocation, in the present context, refers to the process wherein reemerged and emerged beetles are transferred from source to sink trees, i.e., from trees containing either reemerged or emerged beetles to trees being attacked.

Pope et al. (1980) and Coulson et al. (1980c) described two mathematical functions for transferring or allocating populations of SPB adults in a spot: a fixed probability function and a time- and temperature-dependent function. Both procedures produced similar results (fig. 5-17).

The transfer function hypotheses were developed and tested against quantitative estimates of populations of adults in infestations (e.g., fig. 5-15). The basic problem that the transfer functions deal with is accounting for the distribution of source beetles (reemerged and emerged beetles) and sink beetles (attacking beetles) over a prescribed and realistic period of time. The accounting procedures can be checked for accuracy by comparing test results with actual measurements.

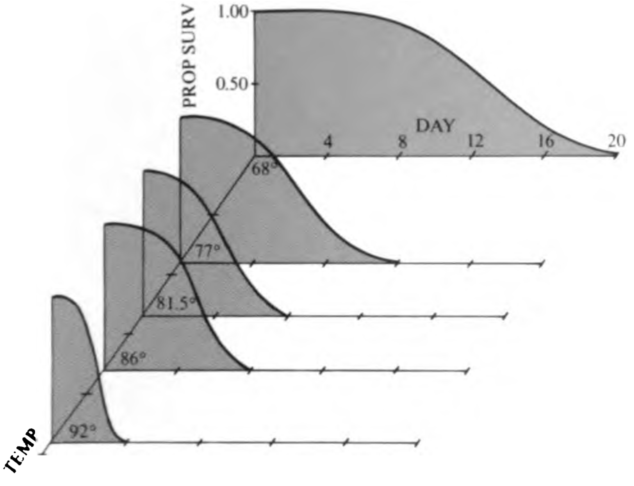


Figure 5-17. – Survival probability curves for emerged SPB adults held at five different constant temperatures (in °C) in the laboratory, illustrating the relationship between decreasing adult longevity and increasing temperature.

The assumptions of the fixed probability transfer function were that beetles could survive no longer than 6 days after leaving the host and that the proportion of surviving beetles on each day was a constant. The first assumption is probably reasonable; the second clearly is not. Nevertheless, the fixed probability transfer function provided a suitable description of actual field measurements.

The time/temperature-dependent transfer function utilized the same calculation procedure as the fixed probability procedure. However, adult longevity was based on temperature profiles defined from laboratory studies (fig. 5-17). Ambient conditions in the field were extrapolated from weather station data on temperature. Temperature had a significant effect on adult longevity. The time/temperature-dependent function provided a means of incorporating this important variable but, in doing so, added another degree of complexity to the model.

The probability of survival varies considerably over the course of development of a spot (fig. 5-18). The range covered an interval of ca. 0.75 to 0.05 survival.

By performing system perturbations on the time/temperature-dependent function, Pope et al. (1980) and Coulson et al. (1980c) demonstrated survival probabilities for segregated populations of reemerged and emerged beetles (fig. 5-19). The cyclic relationship between the survival probabilities for the two classes of beetles indicates that maintenance and perpetuation of a spot can be attributed to either reemerged or emerged beetles. In interpreting figure 5-19, it is important to recognize that the significance of increased or decreased survival probability is closely related to the absolute numbers of beetles available at any one time. For example, survival probability may be extremely high (day 249) but the number of beetles available small (day 249, fig. 5-15). The net result can be that the spot would not continue to enlarge.

Patterns of Spot Development in Relation to SPB Distribution and Abundance

In the previous sections I have discussed key elements of population dynamics of the southern pine beetle in spots. These elements included behavior of populations in response to pheromones and attractants; absolute population of attacking, reemerging, and emerging adults; the allocation process; and between-tree survival probability. Stand composition and geometry (the spatial arrangement of trees) together form the arena in which the life history processes take place. Therefore, it is not surprising that duration and intensity of spot growth are also linked, in part, to variables such as tree species, age, size, and density.

Characteristic pattern of SPB spot growth. – Development of beetle spots, by addition of newly attacked trees along one or more fronts throughout the course of a summer season, is a feature unique to SPB among the other *Dendroctonus* spp. There are at least three major reasons for this pattern of development. First, the reemergence process appears to be more pronounced with SPB than with other species. Reemergence takes place in the most recently attacked trees, i.e., adjacent to the next trees that

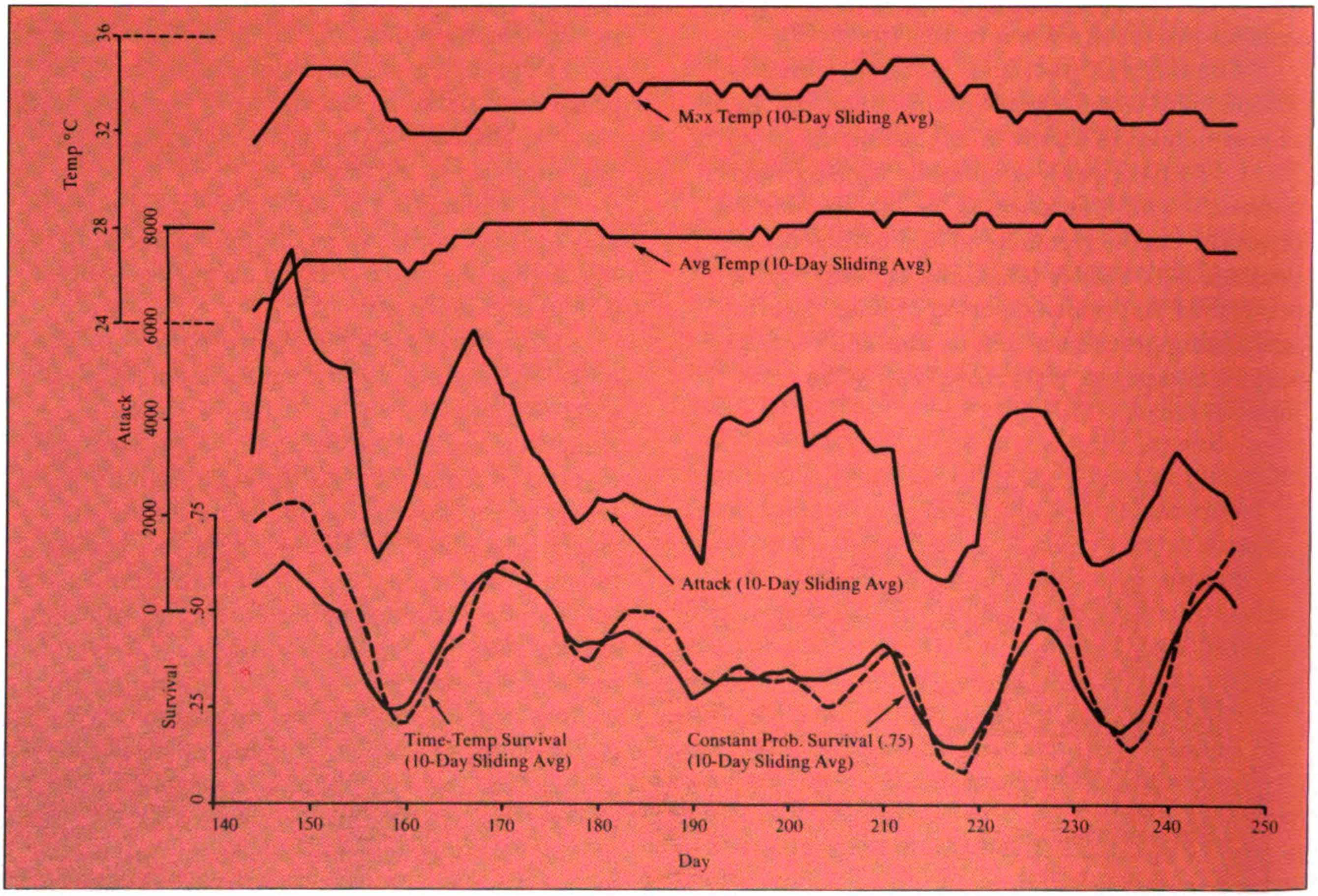


Figure 5-18. – Survival probabilities for between-tree populations of SPB adults and the pattern of attack observed throughout the course of development of a spot in east Texas during 1977. The average maximum and minimum temperatures (°C) are also included.

will come under attack. These trees form the active front(s) (Coster, Hicks, and Watterston 1978). Second, developmental rate of SPB populations in the field is extremely rapid (30 to 50 days during summer months), compared to that of other *Dendroctonus* spp. Brood life stages, therefore, develop to the emerging adult stage and enter the colonization process in a short period of time. Synchrony between emerging and reemerging adults can be quickly achieved and maintained under favorable weather conditions. And the allocation process provides a continuous supply of adults for the purpose of colonization. Third, the fact that new trees are being colonized means that pheromones and attractants provide a continuous focal point for communication. Without the focal point, emerging adults, which are removed in space from the active front by ca. 10 to 20 m, would likely disperse and suffer substantially higher between-tree mortality than actually occurs (Gara 1967). Obviously beetle density; tree species composition; host susceptibility, suitability, and spatial distribution; weather; and myriad biotic mortality agents also influence the final success of populations in a spot. Nevertheless, the characteristic pattern of spot growth often results in rapid increase in beetle numbers and a corresponding high rate of tree mortality.

Dispersal patterns of reemerged and emerged beetle populations in spot growth are depicted in figure 5-20. This figure was developed from quantitative estimates of beetle populations taken from the spot portrayed in figure 5-13. These estimates were also the basis for calculating the survival probalilities illustrated in figures 5-18 and 5-19. In figure 5-20 the arrows point in the direction of spot growth. The size of the arrows is proportional to the number of beetles present throughout the course of spot development. The numbers on the figure are Julian dates at various stages in spot development. The allocation process continues throughout the entire

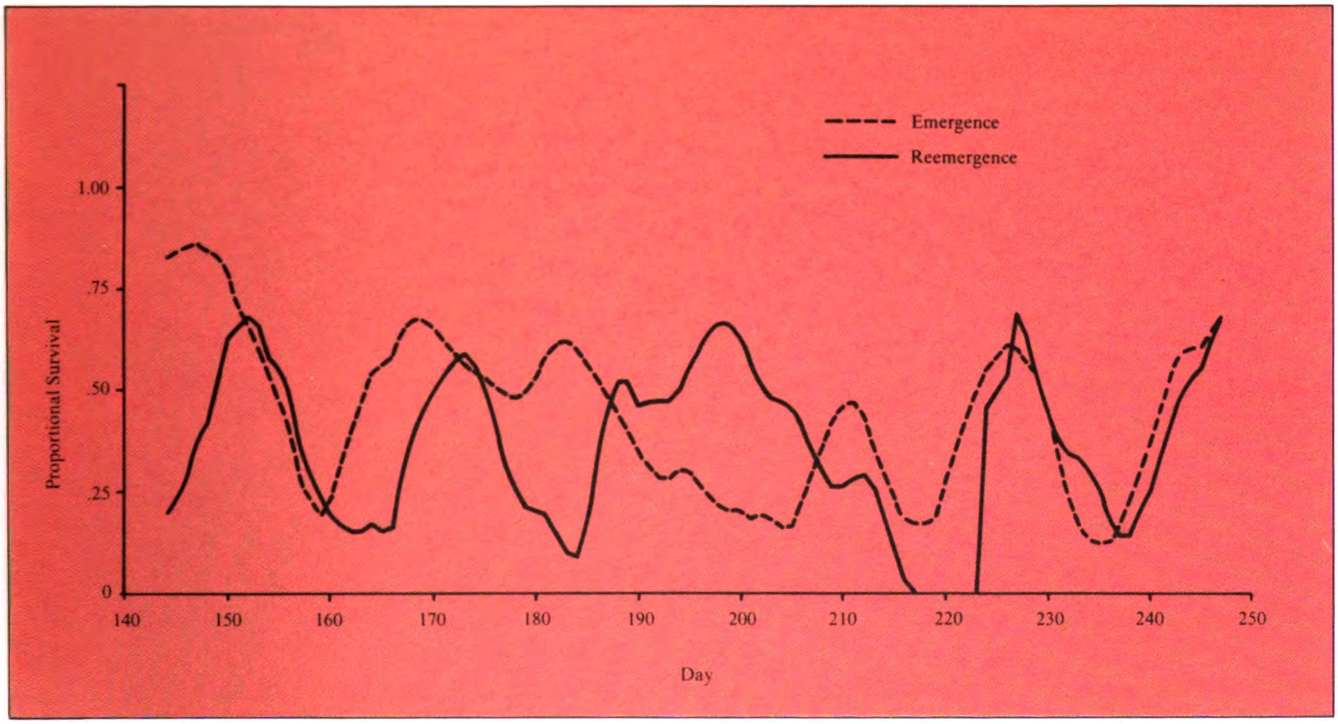


Figure 5-19. – Survival probabilities for between-tree SPB populations of emerged and reemerged adults throughout the course of development of a spot in east Texas during 1977.

period. At certain times either reemergence or emergence dominates in supplying beetles for colonization. Likewise survival probabilities for within-tree and between-tree populations and stand structure change throughout the course of spot development (figs. 5-18, 5-19, and 5-13). In the spot illustrated, about 50 trees were attacked during a period of around 100 days. This rate of attack is substantially less than often observed during epidemics, where 15 to 20 trees/day is not uncommon.

SPB generations.– The life histories of many insect species can be summarized conveniently by generations and cohorts; and, therefore, considerable attention has been devoted to development of analytical procedures for the concepts, i.e., the life table approach to population analysis.

The *within-tree* population system for SPB can be considered as a cohort. But, as evidenced in figures 5-2, 5-4, 5-7, 5-8, and 5-10, the age distribution of the life stages has a very important

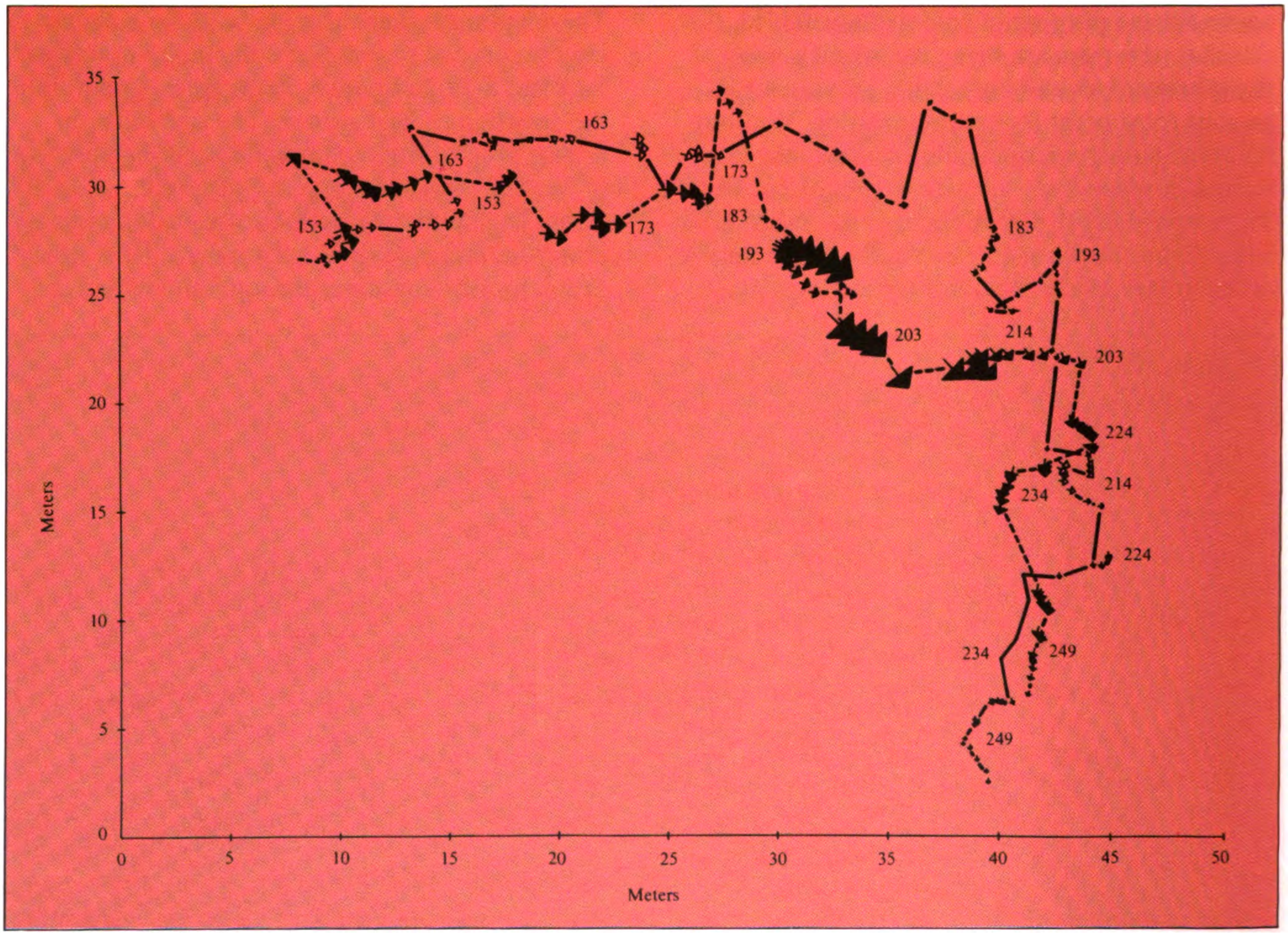


Figure 5-20. – Dispersal pattern followed by re-emerged (solid line) and emerged (dashed line) SPB throughout the course of development of a spot in east Texas during 1977. The arrows are proportional in size to the number of beetles in either the re-emerging or emerging mode. The numbers represent Julian dates in the development of the spot and range from 153 (June 2) to 249 (Sept. 6) in 1977.

temporal component. Therefore, analytical procedures based on the assumption of a stable age distribution for a population within a cohort in a generation do not strictly apply to SPB.

The production flow system approach, described by Coulson et al. (1976c), was based on point estimates of within-tree populations of SPB life stages. The life table approach was also used to evaluate the effects of a suppression tactic applied to within-tree life stages (Coulson et al. 1976d).

The pattern of continuous population growth in spots obliterates cohorts and generations of the beetle. This pattern results from the variable age distribution of beetle life stages in the attacked trees and the blending of populations in the allocation process. Therefore, the unique characteristics of SPB populations, which emerge at the spot level of organization, severely limit the applicability of analytical techniques developed for distinct cohorts and generations with stable age distributions.

At periodic intervals throughout the development of a spot there are surges or pulses in population abundance (fig. 5-21). In this figure population abundance for combined reemerged

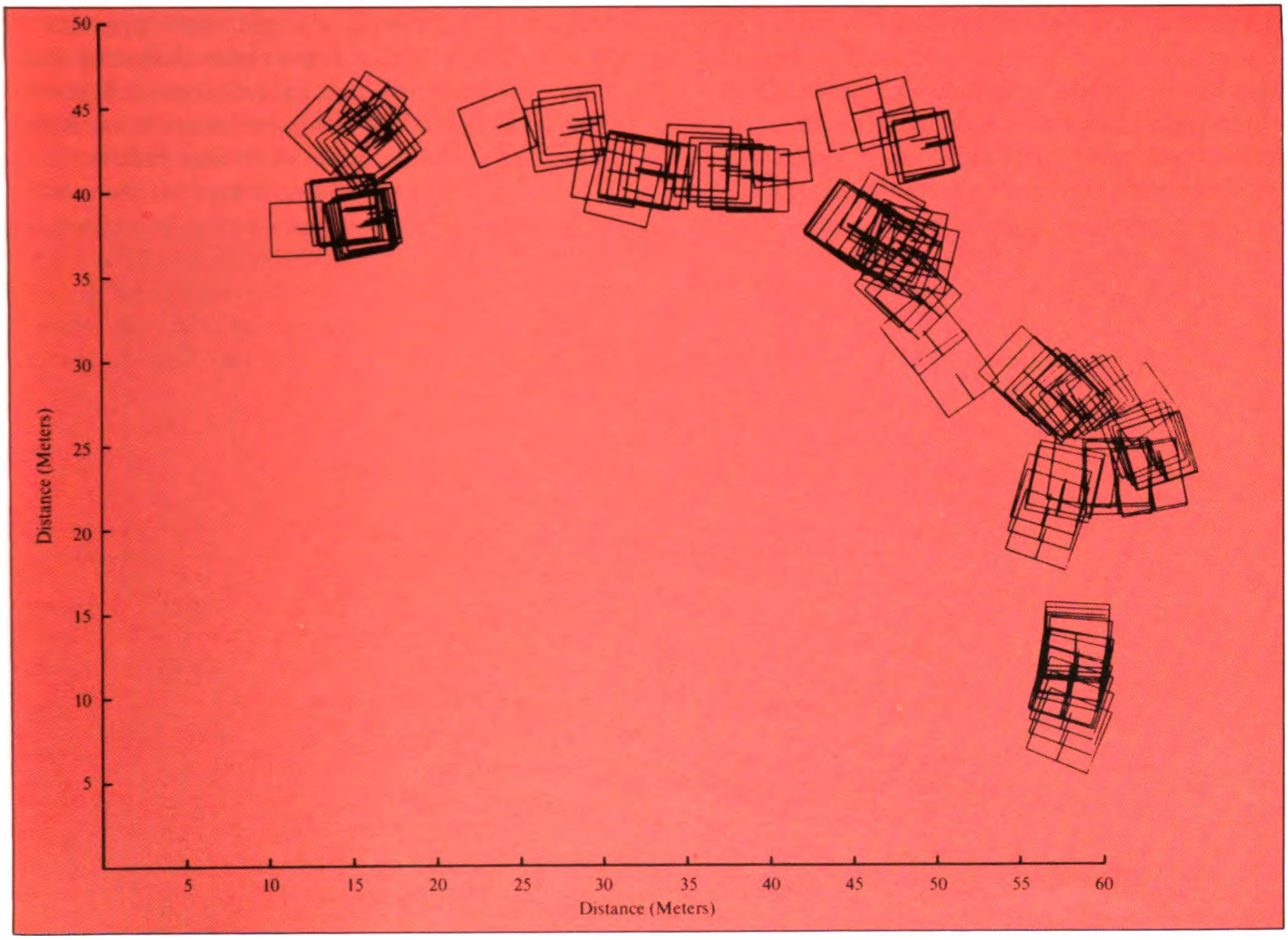


Figure 5-21. – Direction of dispersal followed by SPB adults throughout the course of development of a spot in east Texas during 1977. The boxes represent the direction (indicated by the line inside the box) of allocating SPB.

and emerged beetles is represented by the intensity of occurrence of the squares. The figure represents activity of populations of reemerged and emerged beetles throughout a spot's development. Population surges occurred near Julian days 153, 173, 193, 214, and 249 (*see* fig. 5-20). Probably the result of interaction among many variables, the pulses reflect the influx of increased numbers of emerged beetles from previously attacked trees in the spot.

Indices of spot growth and decline. – Many biotic and abiotic variables interact to produce the wide range of growth patterns observed for SPB spots. It is not reasonable to expect that simple indices of population growth, measured at one point in time, will provide a consistent or reliable means for predicting spot growth. For this reason complex mathematical models are generally employed for making predictions (*see* Chapter 6). When food resources are not limiting, the fate of a particular spot becomes a function of within-tree beetle production (input to output ratios), between-tree survival probability, and developmental rate.

Several indices are suitable for portraying certain aspects of within-tree beetle production (a quantity) and beetle productivity (a rate). Examples include emergence/attack, emergence/egg, reemergence/attack, emergence and reemergence/attack, and emergence and reemergence/attack/process timespan.

The main value of these indices is that they provide a simple representation of the net effect of the complex interactions of many variables. Gagné et al. (1980b) emphasized several limitations to the use of ratio estimators for characterizing population trends. Continuous population estimates for the processes of attack, gallery construction (oviposition), reemergence, survivorship, and emergence from each infested tree throughout the course of a spot's development were used to calculate these ratios. A description of the field methods and analytical procedures needed to obtain the estimates for spots has been published (Coulson et al. 1979a and 1980b).

Examples of calculated values for the various indices of population trend are illustrated in table 5-1. Mean values were obtained from measurements taken throughout the course of development of three spots during 1977 in east Texas. Each index provides different information about

Table 5-1. – Summary statistics for time and survival components for within infestations of *Dendroctonus frontalis.*

	Spot 20	**Spot 21**	**Spot 22**	**Pooled**
Number of trees	11	50	25	86
Mean $\frac{\text{emergence}}{\text{attack}}$	1.983	1.864	1.406	1.746
Std. dev.	.678	.886	.397	.775
Mean brood survival (emergence/eggs)	.187	.199	.192	.196
Std. dev.	.073	.101	.063	.087
Mean reemergence/attack	.583	.619	.626	.616
Std. dev.	.119	.167	.148	.155
Mean $\frac{\text{reemergence + emergence}}{\text{attack}}$	2.56	2.501	2.03	2.372
Std. dev.	.726	.895	.4709	.797
Mean brood development time (egg→adult) (days)	39.02	34.36	36.95	35.71
Std. dev.	8.15	4.97	3.85	5.4

the spots. None of the indices is suitable for predicting spot growth. The mean values of each index (table 5-1) for the infestations would probably not be statistically different.

The most commonly used index of population trend has been the ratio of emergence/attack (Thatcher and Pickard 1964, Coulson et al. 1976c and d and 1977, Moore 1978, and Gagne et al. 1980b). This index has also been termed "ratio of increase." The daily pattern for this index throughout the course of development of a spot is illustrated in figure 5-22. A value > 1.0 indicates that population output is increasing relative to the input. However, even when population numbers in a spot are large, a high value for the index may have little relationship to spot growth because of the variable nature of reemergence and between-tree survival of adults. This point is well illustrated by reference to the final days of development of the spot illustrated in figure 5-22. In this case the ratio was about 2.5, yet infestation growth ceased by Julian day 280.

The ratio of emergence/egg is a better index of within-tree brood survival than is ratio of increase. This index is substantially harder to obtain than ratio of increase because of the need to measure egg populations. However, the ratio is still preferable to ratio of increase since the number of eggs oviposited per female has been demonstrated to be a function of attack density (the resource utilization mechanism). This mechanism complicates interpretation of the significance of ratio of increase. Mean values for brood survival from three spots are contained in table 5-1. In these infestations the ratio for each spot was about 0.19.

The ratio of reemergence/attack provides an index of the amount of redistribution of beetles that is taking place within a spot. For the spots in table 5-1, the ratio was about 0.60. This index has

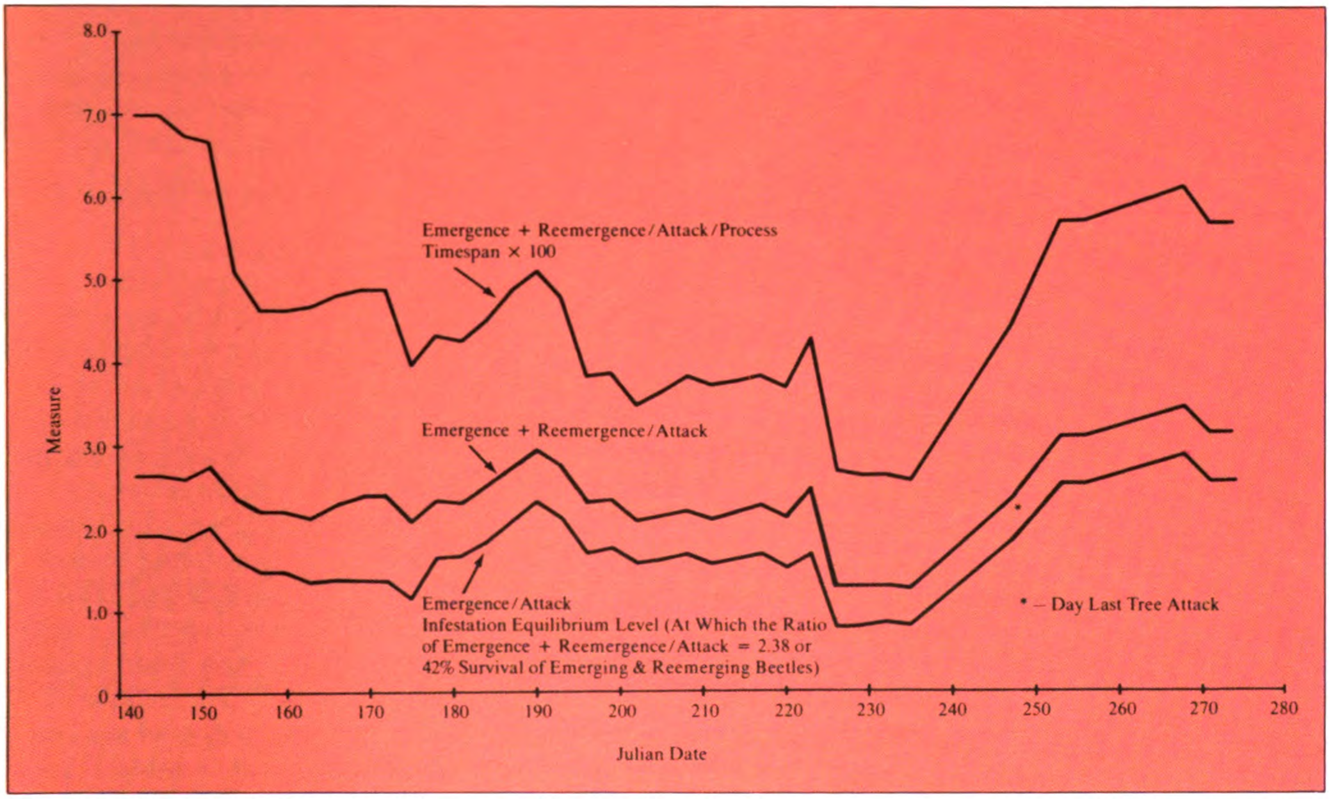


Figure 5-22. – Daily ratios of beetle output per input in an SPB spot in east Texas during 1977.

been shown to range from about 0.25 to 0.97 for *D. frontalis* (Coulson et al. 1978 and 1980b and Cooper and Stephen 1978).

The ratio (reemergence + emergence)/attack provides a measure of the actual beetle production per tree. This simple index incorporates both components of the allocation process (reemergence and emergence) and therefore is a better index of beetle production per tree than is ratio of increase. Mean values for the index from three infestations are contained in table 5-1. The index for each spot was ca. 2.4. The daily pattern for the index throughout one spot's course of development is illustrated in figure 5-22. Values for the the index would be extremely difficult to predict for an infestation because of the resource utilization mechanism. However, attacks, reemergence, and emergence can be measured in the field (Coulson et al. 1980b).

The index [(reemergence + emergence)/attack]/process timespan is probably the best single measure of beetle input-output per tree. This index represents the rate at which beetle production per tree is taking place. The main problem with the index centers on measuring the process time components in the field. Mizell and Nebeker (1978) described a procedure for estimating developmental time using field temperature measurements. The pattern observed for the index throughout the course of development of an infestation is also illustrated in figure 5-22.

Another seemingly useful measure of spot growth and decline is the number of living brood within the tree comprising the spot through time (fig. 5-23). Again, this index incorporates the interaction of many variables and ultimately reflects the number of beetles emerging into the spot. It is interesting to note that in this figure the

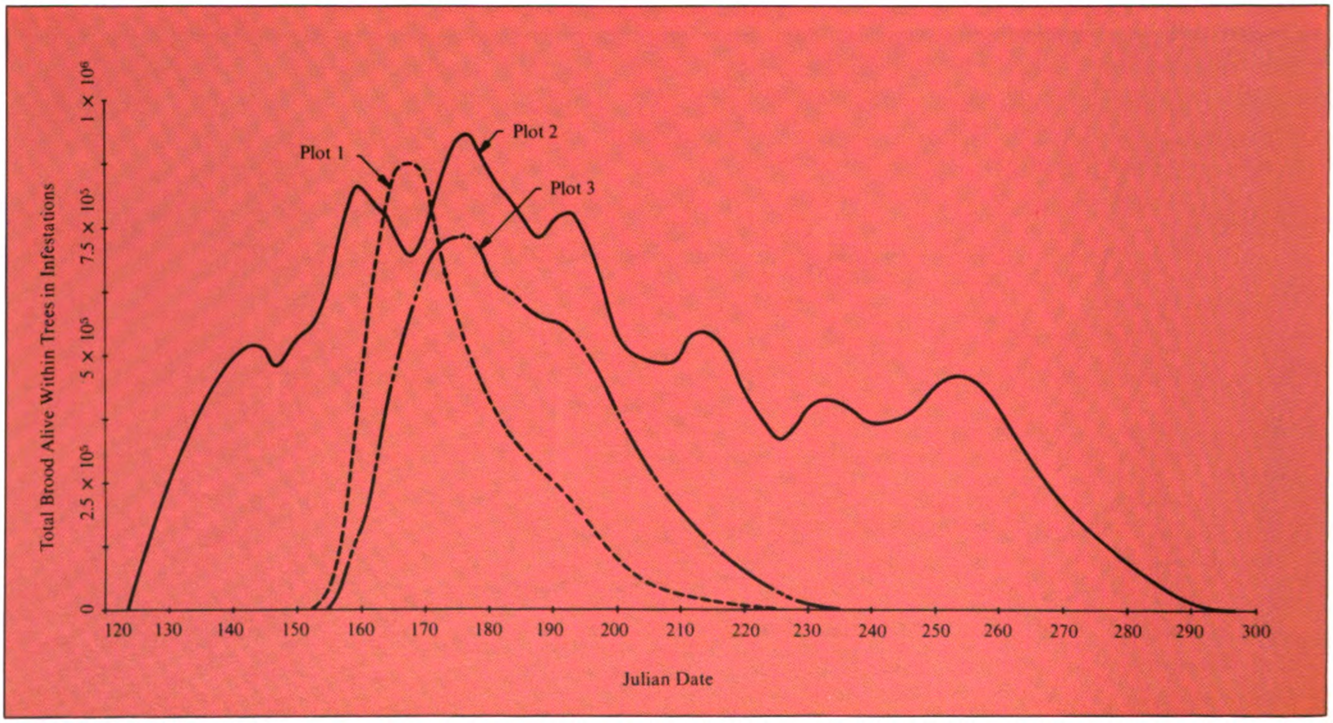


Figure 5-23. – Daily estimates of the total within-tree brood alive in three SPB spots in east Texas during 1977. These estimates span the duration the spots were active. Note that about day 275 all spots contained nominally the same number of living brood stages, yet the spots each became inactive at different times.

number of brood alive within the three spots illustrated was nominally the same at ca. Julian day 160, yet each spot declined at different times and at different rates. This observation simply illustrates the futility of attempting to utilize simple indices as a means of predicting population trends in spots.

Each of the five spot-growth indices described above provides information about the status of SPB populations in a spot. But none of the indices is suitable for predicting the future pattern of spot growth. Also, there are many other possible indices besides those presented above. Coulson et al. (1979c) described 12 different measurements that characterize spot growth patterns. All the indices require a substantial direct measurement effort in the field. For instances where these indices are used to characterize populations, calculated values will likely be generated as output from a model rather than measured directly in field studies. This output can then be used to define further basic principles of population dynamics, evaluate the efficacy of treatment tactics, predict timber mortality resulting from SPB infestations, etc.

SPB Populations in Forests

At the ecosystem level, emphasis on the beetle's population dynamics centers on the distribution, number, and size of spots. The same principles that govern SPB distribution and abundance on trees and in spots operate at the ecosystem level. Generally the main variables that limit the distribution and abundance of SPB at this level are climate and the availablity of susceptible and suitable host material. The effects of weather and climate on populations of SPB will be discussed below. The distribution and abundance of susceptible host type are influenced by a number of variables associated with tree species, soil and site conditions, and cultural practices. These variables have been discussed by Hicks in Chapter 4. Salient features of the interrelationship between population dynamics of SPB and tree species and soil, site, and stand conditions will be discussed below.

Host's Role in SPB Population Dynamics

Host susceptibility (= degree of resistance) to insect colonization and host suitability for brood development are subjects of considerable importance in understanding SPB population dynamics. The approach of employing trees, spots, and forests used previously is also useful for organizing concepts of host susceptibility and suitability. Again, the beetles interact with individual trees, stands, and forests.

Susceptibility and Suitability of Individual Trees

The concepts of host susceptibility to colonization and suitability for development are tied to inseparable interrelationships between the beetle, associated microorganisms, and physical and chemical characteristics of the host. Colonization initiates a series of events that eventually lead to the death and subsequent degradation of the host. The first step in the sequence involves overcoming tree resistance mechanisms. If this phase is successful, the tree, or a portion of it, will die. Without tree death, brood stages will not develop.

The blue-stain fungus, *Ceratocystis* sp., is considered to be the principal tree-killing agent, although many other microorganisms (bacteria, yeast, and other fungi) have been identified from the beetle's mycangium and body surface. Many details relating to beetle-fungi-host interactions have been described (*see* Chapters 2 and 4), but there has been no attempt to develop a comprehensive interpretation of the SPB's role in the scenario. Safranyik, Shrimpton, and Whitney (1975) have provided a conceptual statement for the mountain pine beetle (*D. ponderosae* Hopk.) in lodgepole pine (*Pinus contorta* Doug.) that is generally applicable to the SPB. The following description is based largely on their interpretation.

Attacking adults arriving on the host chew into the phloem and thereby begin to inoculate the host with blue-staining fungi. The spores germinate rapidly and penetrate the phloem and xylem as the beetles enlarge their galleries. Primary resin seeping from damaged resin ducts slows the attacking beetles but the production of secondary resin by ray cells is apparently the process that can prevent establishment. If the phloem and sapwood next to the wound become saturated with resin, the beetle will be killed (resinosis) or repelled (pitched out) and the fungus will die. This circumstance occurs when the tree response, in the form of resin production, is rapid and massive.

Longleaf and slash pines characteristically produce greater quantities of resin than loblolly or shortleaf pines. The latter two species have also been indentified to be more susceptible to SPB attack than the former two (Hodges et al. 1979). If the tree resin response is not sufficient to repel the beetles and isolate the inoculum, the fungi will quickly kill the living host cells and thereby prevent further response. The fungi penetrate the ray cells and grow radially and vertically into the bole. Circumferential spread is influenced by the construction and elongation of gallery by adults and perhaps mining by larvae. Eventually a girdle of nonfunctional sapwood is effected, and the tree dies (Safranyik et al. 1975 and Coulson et al. 1980b).

Successfully attacked hosts continue photosynthesis for a period of several days to weeks after successful colonization, even though death of the host has been assured (K. W. Brown, unpublished observation). This continued photosynthesis results in a characteristic pattern of tree drying that subsequently will have an important influence on brood survival. It is not uncommon to observe an infested host, containing late-stage larvae, that still retains a green or lightly faded crown. Brood adults will later feed on fruiting bodies of the blue-stain fungus that line the walls of the pupal chamber. This maturation feeding may be a requirement for completion of development. Transfer of inoculum to the next generation is also assured.

Host Susceptibility

Although the exact mechanism controlling susceptibility to SPB attack is unknown, there seems to be little doubt that the primary host defense is the resin system. Therefore, factors that disrupt or impair functioning of the resin system will influence host susceptibility. Increased susceptibility is usually associated with reduced tree vigor, and the condition is often reflected in reduced radial growth (Coulson, Hain, and Payne 1974); phloem thickness; and resin flow rate, quality, and pressure (Helseth and Brown 1970, Hodges and Lorio 1968 and 1971, Hodges et al. 1979, and Lorio and Hodges 1968a and b).

Among the variables thought to contribute most to susceptibility are tree age, stand density, root pathogens, lightning, water imbalance, and cultural damage (Alexander 1977; Alexander, Skelly, and Webb 1978; Coulson et al. 1974; Lorio 1968 and 1973; Hodges and Pickard 1971; Lorio and Hodges 1977; and Hodges and Lorio 1973 and 1975).

Variations in degree of host susceptibility influence beetle populations in several ways. First, resin flow can pitch attacking adults out. Beetles pitched out often die in the resin accumulation at the point of attack. Second, adults and eggs often die within the gallery due to resin crystallization. This phenomenon, termed resinosis, often occurs when the number of attacking adults is insufficient to successfully inoculate and kill the host. Third, when resin flow is sufficient to repel attacks, the insect is exposed to prolonged predation. *Thanasimus dubius* F. (Coleoptera: Cleridae), a common predator, exploits this circumstance during the spring and fall of the year. Fourth, any event that prolongs the period of time an adult is outside the host will greatly affect survival. Adult longevity between trees is short, particularly at high temperature (*see* fig. 5-17). Therefore, beetle confrontation with host resistance mechanisms that interfere with rapid entry into the tree usually results in insect mortality.

Habitat Suitability

The suitability of the habitat as a substrate for growth is a critical issue to beetle survival during brood development. Habitat suitability has components related to the physical characteristics of the host, such as surface area and volume of inner bark (Foltz et al. 1976b), and qualitative characteristics such as nutritive value to the developing insect (Hodges, Barras, and Mauldin 1968a and b; Hodges and Lorio 1969). These characteristics and qualities vary with tree species, age, and state of deterioration following attack. The physical properties of the host affect the rate at which the tree dries (Gaumer and Gara 1967), the temperature of the inner bark of the tree (Powell 1967), accessibility to natural enemies (Dixon and Payne 1979b), and the amount of living space available to the insect (Coulson et al. 1976b and 1980a). The chemical qualities of the habitat substrate affect the nutrients available for development of the SPB and associated arthropods, as well as the culture medium for microorganisms.

Successful colonization by SPB sets into motion a continuous process of deterioration of the habitat. An arthropod community composed of several hundred species of arthropods and microorganisms develops. This community is represented by numerous parasitoids, predators, and competitors that directly affect SPB populations. Many of these organisms have been identified (*see* Appendix, table 2), but most have undefined or questionable functions. Chapter 3 provides a discussion of the effects of natural enemies on populations of *D. frontalis.* Considerable resource partitioning occurs as a result of the development of the community. The presence of the various organisms directly influences the condition and suitability of the habitat for SPB colonization and development.

The within-tree habitat can be divided into two basic regions: the phloem (or inner bark), and the outer or corky bark. The nutrient-rich inner bark, which is utilized by virtually all members of the community, is an ephemeral habitat that changes dramatically following colonization. Conditions in the nutrient-poor outer bark are stable, relative to the inner bark, and this region is utilized sparingly.

The developmental life history of the beetle is tied closely to changes in the physical condition of the habitat. Oviposition and development of 1st- through 3rd-stage larvae take place in the inner bark. Development of 4th-stage larvae, pupation, and emergence of adults usually take place in the outer bark (Goldman and Franklin 1977). This migratory behavior of 4th-stage larvae is probably an adaptation to escape the changing conditions of the inner bark. It is not known if the migration is a response to unsuitable living conditions or unavailability of accessible food supplies. Furthermore, migration could serve as a means of avoiding natural enemies and competitors (Coulson et al. 1976b and 1979c).

Investigations of microhabitat conditions, under field conditions, have been directed primarily to studying changes in the moisture status of the tree through time (Webb and Franklin 1978 and Wagner et al. 1979). The basic pattern of SPB development in relation to measures of xylem water potential, xylem moisture, and phloem moisture is illustrated in figure 5-24. In general, development through the egg and early larval stages occurs before appreciable drying of the habitat. Migration into the outer bark occurs as drying becomes pronounced. Development of SPB life stages and the rate of deterioration of the habitat are therefore synchronized, under ideal conditions. Disruption likely results in mortality to the insect.

It seems clear that habitat-related mortality is important to within-tree SPB populations, although the evidence is somewhat circumstantial. First, life table studies that include natural enemies cannot explain the amount of within-tree mortality observed. Second, attempts to rear the beetle under laboratory conditions have produced variable results. Most researchers have related the failures to problems associated with moisture condition (either too much or too little). Third, atypical elongated larval mines and failure of larvae to establish "phloem cells" have been associated with high moisture content (Webb and Franklin 1978 and Wagner et al. 1979). This condition, which may reflect unsuitable substrate conditions for growth of microorganisms (Franklin 1970b, Barras 1970 and 1973) or unfavorable conditions for insect development, results in mortality to SPB.

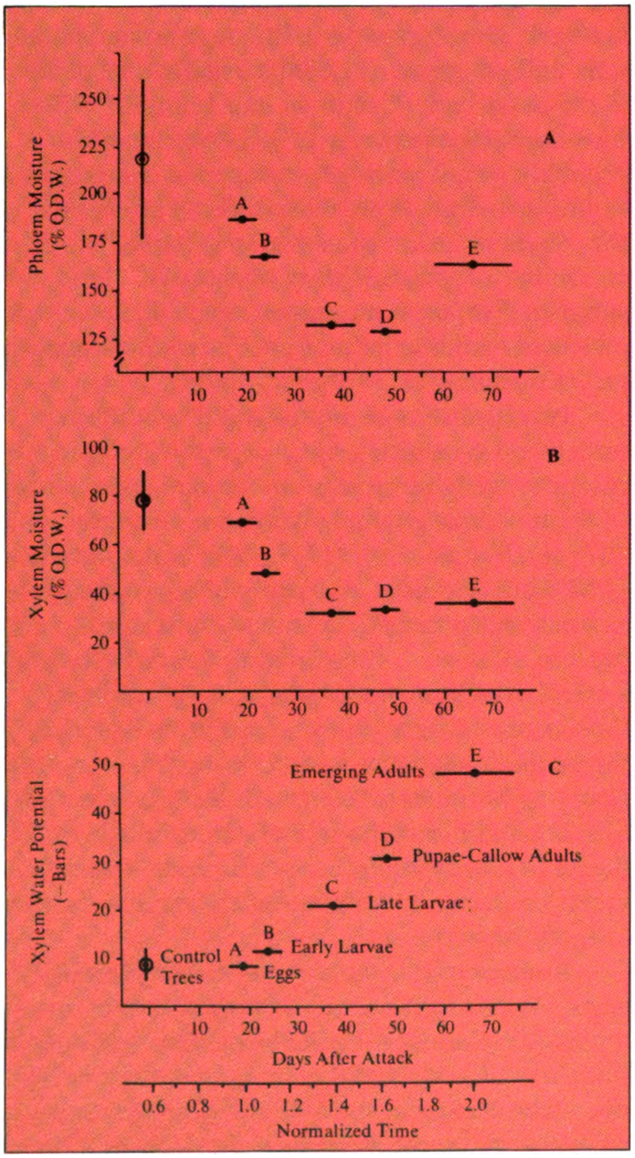


Figure 5-24. – Predicted phloem moisture (A), xylem moisture (B), and xylem water potential (C) at various SPB life stages, illustrating the systematic pattern of habitat degradation that follows colonization.

Many variables can influence the rate of drying of the host and the SPB's development (Fares et al. 1980). Prominent among these variables are ambient weather conditions (Kalkstein 1976, Gagne et al. 1980a), physical characteristics of the host (Fargo et al. 1979), initial tree vigor (Lorio and Hodges 1977), and perhaps attack density. SPB adults cannot perceive relative degrees of habitat suitability at the time of colonization. Therefore, the variable age structure of the egg population likely enhances survival of the insect, as all members of the within-tree cohort are not in the same stage of development. Even though portions of the habitat might be unsuitable for development, not all life stages would be equally affected.

Host Susceptibility and Suitability in Stands

Stand dynamics and beetle population dynamics are highly interrelated. In stands, interest focuses on the distribution and abundance of the variables that were credited with influencing susceptibility and suitability in individual trees. Individual stands vary in susceptibility and suitability throughout their life. Furthermore, within a particular stand, varying degrees of susceptibility and suitability exist. Considerable research has been devoted to identifying soil, site, and stand conditions that contribute to SPB incidence (e.g., Belanger, Osgood, and Hatchell 1979b; Coulson et al. 1974; Ku, Sweeney, and Shelburne 1977; Leuschner et al. 1976; and Lorio 1968). One goal of this research has been to develop a system for risk rating stands (*see* Chapter 8).

The basic conclusion reached in most studies has been that SPB incidence is associated with poor tree vigor (*see* Hicks et al. 1978). Stand factors that contribute to poor vigor are age, density, species composition, soil texture and type, drainage patterns which lead to water imbalances, disease, and recent cultural disturbances. Within a particular stand these variables are unevenly distributed and in fact occur as a mosaic of conditions that result in varying degrees of host susceptibility and habitat suitability. Coulson (1979) provided a description of how changing conditions within a stand influence development of an SPB infestation. Microsite conditions vary substantially within a stand (Lorio 1968 and Lorio and Hodges 1971). Observed patterns of spot growth for the beetle are tied not only to number of beetles per se but also to the quantity and quality of food and habitat available to the insect. Therefore, infestation geometry, which includes both the spatial arrangement of the trees (Hedden 1978a) and susceptibility factors, is of considerable importance in spot development.

Host Susceptibility and Suitability in Forests

In the forest, we are interested in the distribution and abundance of susceptible *stands*. Land-use patterns and physiographic characteristics influence the general frequency of occurrence of susceptible stands. Nevertheless, the same variables that contributed to host susceptibility and suitability on individual trees and within stands operate at the forest or ecosystem level. As with individual stands, susceptible hosts within forests are characterized by clumped distributions at any one time. Forest susceptibility is a dynamic process related to the mosaic of conditions that contribute to susceptibility and suitability as well as the pattern of utilization of the forest.

Clearly, all susceptible stands within a forest do not become infested during a given SPB epidemic. Many of the variables that influence the distribution and abundance of the SPB have been described above. Availability of susceptible host type and suitable climatic conditions appear to be the basic requirements for development of beetle infestations. The SPB's rapid appearance in response to these conditions is remarkable. Given that climatic conditions are favorable for insect development and that susceptible hosts are available in a forest, two major obstacles influence potential development of spots. First, the insect must be able to recognize susceptible host material, and second, it must be able to migrate to this material.

Primary host selection (recognition) by the beetle was discussed briefly above and in greater detail in Chapter 2. Although authorities do not agree as to the mechanism of primary host selection, two options have been proposed – directed behavior, based on visual cues or olfactory stimuli, or random searching. Obviously, olfactory stimuli would be of limited value to SPB searching large areas. Since the insect lands on host as well as nonhost species (Coster et al. 1977), it is unlikely that the beetle can discriminate between susceptible and nonsusceptible hosts by sight. This latter observation suggests that random searching is involved in initial or "coarse level" host selection.

Movement (migration) of the beetle within forests is also poorly understood. Two major hypotheses are used to explain the phenomenon: (1) migration over long distances, and (2) movement over short distances to highly susceptible hosts that serve as reservoirs. The evidence for long-distance migration is based on estimated capacity for flight, as measured by the use of flight mills, and the presence of fat reserves needed to sustain the beetles for long periods of flight (Borden 1974, Hedden and Billings 1977). But there is some evidence to suggest that long-distance migration is not the usual means of distributing populations over a forest. First, adult survival outside of the host is short *(see* fig. 5-17), particularly at high temperatures. Second, for a host to be successfully colonized, a large number of beetles must be aggregated in a short period of time. Third, a susceptible host apparently cannot be identified readily by the beetle. Obviously these three factors are related.

An alternative hypothesis for explaining movement of the beetle is that the insect is generally present in low numbers at many locations throughout the forest. The distribution and number of highly susceptible hosts (e.g., trees struck by lightning, infected with disease, damaged by cultural activities, injured by fire, etc.) has not been examined in detail. These trees act as reservoirs for many subcortical insects. With all the possible conditions that create highly susceptible trees, it is not difficult to envision perhaps 5 to 10 such trees occurring per 100 acres. These reservoirs would likely be able to supply limited populations from which outbreaks arise. Long-distance migration would not be a necessary requirement under such conditions.

The distribution and abundance of these reservoir trees is generally unknown, as organizations involved in survey and detection of forest pests normally do not record cause of death for single or small groups of trees. Furthermore, during periods of low population density, the distribution of SPB with the other southern pine bark beetles *(I. avulsus, I. grandicollis, I. calligraphus,* and *D. terebrans)* appears to be more equitable than during periods of high population density. Since the reservoir trees are already weakened or previously attacked by one or more of the other bark beetles, large numbers of SPB would not be required to overcome tree resistance mechanisms.

Role of SPB in Dynamics of the Pine Ecosystem

Pine forests in the South today represent second- and third-generation forests. Although the degree of management varies considerably, virtually all pine is now the result of cultivation by people. Given this circumstance, SPB has assumed (and earned) the role of a major mortality agent of pine forests. Intervention of SPB as a mortality agent in pine culture is disruptive to long-term forest management goals. Leuschner (Chapter 7) has discussed impacts of the insect in forests.

Research has documented the forest conditions associated with beetle outbreaks *(see* Chapter 4). Generally, the SPB is a serious pest in senescent stands occurring on poor sites. Often these stands have high basal areas and are composed of large-diameter, slow-growing trees. Of the four commercially significant pine species, loblolly and shortleaf pines are considered more vulnerable to colonization than longleaf or slash pines. In the population dynamics of commercial forests, the beetle's major role is in killing mature pines prior to a scheduled harvest date. This mortality not only results in direct loss of revenue but also disrupts the sustained use of the forest. In addition, the beetle affects other values besides timber production, such as watershed, recreation, wildlife, and grazing *(see* Chapter 7).

Evaluating the beetle's ecological role(s) in forests is somewhat more difficult than defining its social and economic impacts. Several basic problems complicate an interpretation. First, the evaluation should be directed to conditions that existed prior to the intervention of forest cultivation and management practices. Second, forests in the South are represented by more than 20 species of pine, although loblolly, shortleaf, longleaf, and slash pines are the most widely distributed species. Third, each of these tree species has characteristic ecological requirements and adaptations. Fourth, the distribution and abundance of the tree species today bears little resemblance to the pattern that existed in primitive forests. Fifth, forest management goals emphasize timber production with varying efforts to suppress mortality agents such as SPB, other insects, disease, and fire. Therefore, an evaluation of the probable roles of the beetle in forest ecosystems must be based on an interpretation of historical evidence and cast into a framework of ecological theory. Fortunately, there has been considerable research conducted in recent years on basic pattern and process of forest ecosystems (e.g., Bormann and Likens 1979).

Schowalter et al. (1979) developed an interpretative view of the role of fire and SPB in the Southeastern forest biome. This biome, which is a subdivision of the Eastern deciduous forest biome, historically was prevented by fire from reaching the climax hardwood stage (Oosting 1956 and Walker 1962). Physiographically, the biome extends from coastal plains into mountain regions.

Periodic perturbation is a primary factor influencing evolution of ecosystem structure and function (Bormann and Likens 1977, Christensen and Muller 1975, Grubb 1977, Loucks 1970, and Sprugel 1976). Many ecosystems have become dependent on periodic perturbation for regeneration and cycling of limiting nutrients (Amman 1977, Christensen and Muller 1975, and Daubenmire 1974). Functionally both the SPB and fire serve as natural harvesters and as such were responsible for periodic perturbations. In combination, fire and the beetle likely maintained uneven-aged pine forests and successional openings on upland sites, as well as diversity of herbaceous, pine-hardwood, and hardwood lowland communities. These "consumers" tailor the nutrient turnover rates of the subsystems to fit resource availability and slow loss of nutrients to the marine ecosystem.

The shifting mosaic of communities within the ecosystem is important for its persistence. Ecosystem research reported by Bormann and Likens (1977) supports Loucks' (1970) view of perturbation as a means of truncating community development at a point in time prior to senescence. Senescent communities show reduced ability to regulate ecosystem function and reduced availability of r-selected or exploitive species that increase ecosystem resilience following perturbation. Fire periodically rejuvenates patches of the ecosystem by restarting development at an early stage. The SPB potentially regulates this process by (1) thinning old or stressed stands as a means of maintaining community diversity and vigor, and (2) providing concentrations of fuel to enhance the effect of subsequent fire. The resulting dynamic mosaic of communities, representing various stages of succession, increases the relative stability of the ecosystem by reducing the impact of perturbation (Bormann and Likens 1977).

The preceding scenario is based on an interpretation provided by Schowalter et al. (1980). A general view of the interaction of fire and the beetle across a gradient from lowlands to highlands is illustrated in figure 5-25. The potential roles of the SPB and fire in forest succession and nutrient cycling have not been investigated experimentally. It is likely that new insights into forest management practices could be gained by scrutiny of the historical roles of these "consumers."

Role of Weather in SPB Population Dynamics

Along with the availability of susceptible and suitable host material, climate and local weather conditions in the South significantly influence the distribution and abundance of SPB. Several studies examined various aspects of the interaction of the environment and the beetle. Most have dealt with the association of weather conditions and outbreaks of the insect. The following discussion includes consideration of the effects of weather on populations occurring within trees and in spots, as well as general patterns of climatic conditions associated with outbreaks in forested areas.

Effects of Weather on Populations Within Trees and in Spots

Local weather conditions exert a significant influence on beetle survival within and between trees in a spot. Few studies actually measured weather-related mortality under field conditions. Most of the information on the subject was obtained from work oriented to describing within-tree population structure, or inferred from laboratory studies.

The most obvious effect of weather is on developmental rate of populations, which, in turn, influences the rate of spot growth. SPB population growth is continuous during much of the year, particularly in the mild, temperate regions of the Gulf Coastal Plain. This circumstance creates the basic requirement for the rapid growth of beetle spots often observed.

Both temperature and rainfall exert direct effects on survival of within-tree populations. Lethal low temperatures were reported by McClelland and Hain (1979) following severe winters in North Carolina. Likewise, Gagne et al.

(1980a) reported an association of high temperature (and rainfall) with increased larval and generation mortality.

Weather exerts an indirect effect on brood survival by influencing the rate of drying of the habitat. Mortality results if the habitat dries either too rapidly or too slowly (Wagner et al. 1979). The relationship between habitat deterioration and host suitability was discussed earlier.

Adult longevity has been related to temperature conditions (Coulson et al. 1980c). Adults survive only a short time at high temperatures (fig. 5-17). Therefore, the processes of reemergence, emergence, and dispersal are greatly limited during periods of hotter weather. The effect of temperature on these processes is manifested through increased between-tree mortality and hence a reduction in the rate of spot growth.

Local weather conditions have an extremely important influence on the beetle's ability to communicate by pheromones and attractants *(see* Chapter 2 for a discussion of behavioral chemicals). Fares, Sharpe, and Magnuson (1980) developed a model that demonstrates the effects of weather on dispersal of pheromones and attractants. This model explains many of the phenomena that scientists have observed concerning the aggregation patterns of the SPB in response to behavioral chemicals. For example, the pattern of diurnal activity for adults is likely a response to inversion conditions prevalent in the forest during morning and afternoon hours. Likewise the lapse conditions during midday result in funneling of the chemicals through the canopy. The first condition is extremely well suited for chemical communication; the latter is not. Furthermore, the decline in spot growth, often observed in August throughout much of the South, is likely because of the prevalence of lapse conditions during this time, coupled with high temperatures.

General Patterns of Climate and SPB Outbreaks

Indices of temperature and rainfall and wind direction have been compared to relative estimates of beetle populations in order to identify conditions that influence growth and collapse of outbreaks (Wyman 1924, Craighead 1925, Beal 1927 and 1933, St. George 1930, Merkel 1956, King 1972, and Kalkstein 1976). These studies have not provided a single set of conditions that are consistently associated with outbreaks in different sections of the South or at different times in the same section. The type of data used in the studies has contributed to the inconsistent results obtained.

Surveys of SPB-caused damage have provided most of the data used to characterize beetle populations. Survey data may be inaccurate for this specific application because crowns of infested pines fade at different rates (Doggett 1971, Billings and Kibbe 1978), there are large and generally undefined observation errors in collecting the data (Mayyasi et al. 1975), small infestations (< 10 trees) are often not reported by surveying agencies, and there is no simple and direct relationship between the number of dead or faded trees and beetle populations (Thatcher and Pickard 1964 and 1967).

The weather data used in the studies, which generally consisted of temperature and rainfall information, were more uniform in quality than insect population data, because the former were taken at weather stations and standard procedures were used to calculate indices. However, these indices were often expressed as deviations from regional averages. King (1972) pointed out that beetle-host interactions may not be governed by simple deviations from average conditions.

The temperature data from the weather stations probably provided a reasonable approximation of conditions in nearby forests, given that topography was similar. But a forest is generally 1 to 3° C cooler than an open field during the day and 1 to 3° C warmer at night (Geiger 1957). Rainfall is more variable locally than temperature. The correspondence between rainfall beneath the forest canopy and in an open field is further complicated by stemflow and interception of rain by tree crowns. Therefore, measurements of rainfall in a local area probably do not correspond well with measurements taken at weather stations several kilometers away.

The final point regarding the type of data used is that the weather variables were likely too simple to capture the complex relationships of the SPB and its environment. As indicated earlier, the numerical expression of beetle populations at the ecosystem level is the result of complex interactions among variables. So it is not surprising that studies of climatic patterns have not revealed consistent results suitable for explaining the SPB's distribution and abundance. It should be emphasized also that most of the studies on weather and SPB outbreaks have not been directed to explaining the effects of weather conditions on the insect per se. Rather, weather variables were interpreted to influence host susceptibility and suitability, which, in turn, were related to the occurrence of outbreaks.

Two studies have utilized absolute estimates of within-tree beetle population in conjunction with weather station data on temperature (McClelland and Hain 1979) and temperature and rainfall (Gagne et al. 1980a). In the first study, conducted over a 2-year period in North Carolina, severe winter temperatures resulted in nearly 100 percent brood mortality and the subsequent collapse of spot growth. During 1 year of the study, however, winter temperatures were not low enough to kill brood life stages, and yet the infestations still collapsed.

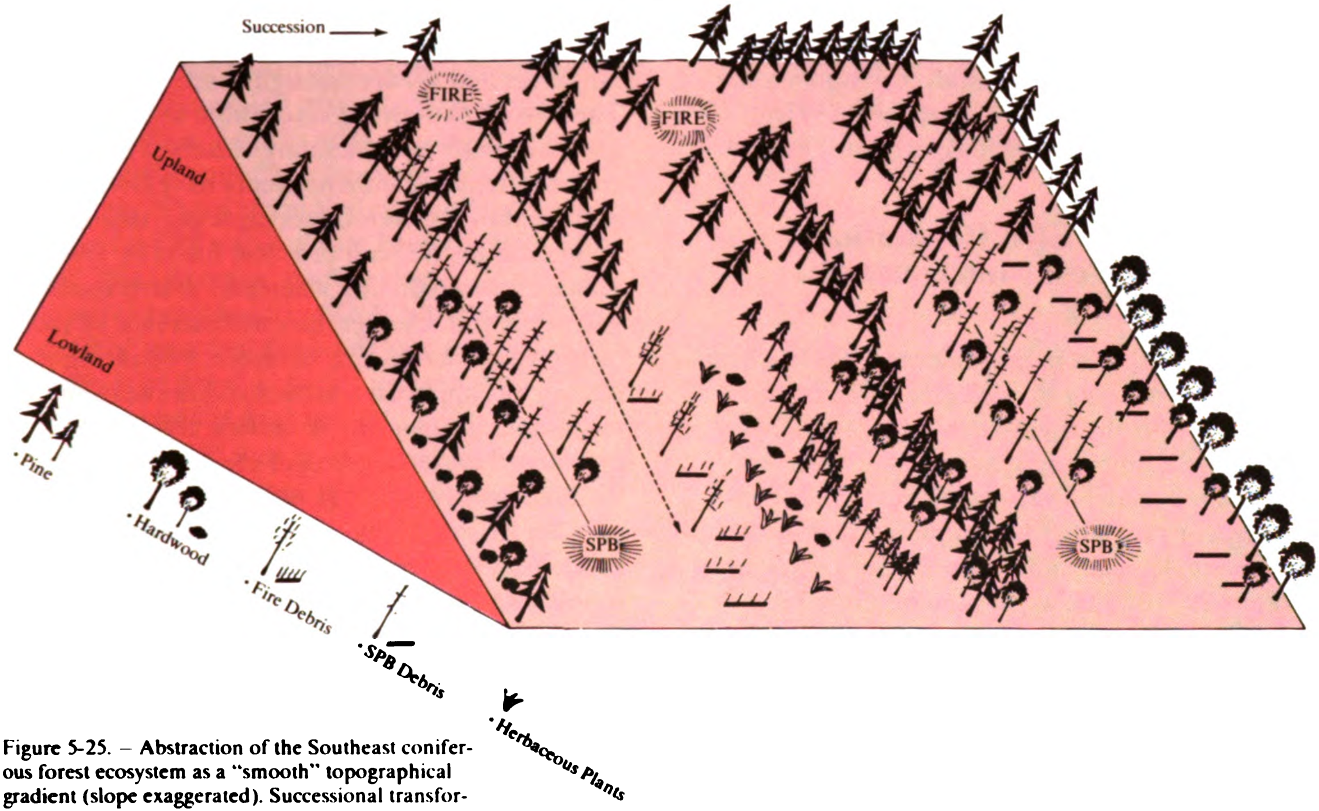


Figure 5-25. – Abstraction of the Southeast coniferous forest ecosystem as a "smooth" topographical gradient (slope exaggerated). Successional transformations resulting from fire and SPB extend at right angles to the plane of the page. Dotted arrows indicate direction of movement. Fire, a regular feature of the drier uplands, invades lowlands where drought and SPB both create favorable fuel conditions. The beetle, in turn, depends on fire to regenerate pine stands. The hardwood climax reached in the far right lowland results from suitable intervals without fire and can be reduced by fire.

In the Gagne study, survival of larvae and generation survival were both associated with temperature and rainfall indices over a 3-year period in east Texas. The most useful indices in regression equations describing larval survival and generation survival were day-degree accumulation and the proportion of the infestation period when at least 0.6 cm or more of rain fell per day. Increases in both of these indices were associated with decreases in larval and generation survival. The authors believe these indices the most useful for describing associations between weather and beetle populations because they measure both the size and duration of temperature or rainfall. The interaction of the two indices was complementary (Gagne et al. 1980a). This study did not substantiate King's findings (1972), which suggested that outbreaks were preceded by above-normal rainfall in January and February, or the findings of Kalkstein (1976), which suggested that outbreaks were triggered by dry soil conditions.

Implications of SPB Population Dynamics in Pest Management Decisionmaking

Integrated pest management (IPM) has been defined in a number of ways (*see* Chapter 11). Simply, IPM is the maintenance of destructive agents, including insects, at tolerable levels by the planned use of a variety of preventive, suppressive, or regulatory techniques and strategies that are ecologically and economically efficient (Waters 1974). IPM, a component of total resource planning, has evolved during the last decade (Coster 1977). Generally an IPM system for insects in a forest has four basic components that must be defined and understood: (1) pest population dynamics, (2) forest stand dynamics, (3) treatment tactics and strategies, and (4) impacts. Each of these subjects is discussed in various chapters in this volume.

Information on Population Dynamics in Relation to Decisionmaking in Pest Management

In this chapter, the SPB's population system was presented in a hierarchy of increasing complexity beginning with events taking place at or in individual trees, progressing to spots (or infestations), and ending at the ecosystem level. The spot level of complexity was highlighted because it is at this point where actual dynamic features of both the insect and host systems come into play. Much of the accelerated research on SPB-host dynamics has been undertaken because we now recognize the vital roles of these components in pest management decisionmaking. The problem of beetle-induced tree mortality in forests is a function of the distribution and abundance of both *trees* and *beetles* through space and time. The mosaic patterns of susceptible and suitable hosts in forests and the many variables that influence beetle population numbers have been described above. Given this complexity, one can appreciate the difficult problem faced by forest managers in predicting when and where spots will occur and whether they will increase in size or become inactive. Furthermore, evaluating the efficacy of suppression tactics and prevention techniques is not a simple matter: it requires sophisticated understanding of the interaction of the host-insect systems (Coulson et al. 1979c).

Because of the extreme complexity of the beetle-host systems, researchers have developed sophisticated mathematical models to predict populations of the SPB and the timber mortality resulting from its activity (*see* Chapter 6). The models can also be used in evaluating efficacy of treatment tactics aimed at suppression of populations. Regarding population dynamics, there is a distinct relationship between understanding, prediction, and decisionmaking (Campbell 1973, Coulson 1974). Mathematical models, based on detailed understanding of the population system of the SPB and interaction of this system on the host, enhance decisionmaking capability.

Population Dynamics Information and the Evaluation of Treatment Tactics

If we know how the population system of the SPB operates, we can develop and test new treatment tactics proposed for the insect. Scrutiny of information on the beetle's population dynamics has revealed a highly evolved and complex array of survival mechanisms, including (1) density-dependent regulation of egg populations, (2) reemergence of parent adults, (3) blending of emerged brood adults and reemerged parent adults to form the attacking adult population, (4) incremental allocation of both emerged and reemerged adults, (5) migratory behavior of within-tree larval populations possibly to escape competitors and changing habitat conditions, (6) variable age distribution of within-tree life stages, (7) coutilization of hosts by several species of bark beetles during periods of low population numbers, (8) utilization of highly susceptible hosts, and (9) communication via behavioral chemicals. There are probably many more mechanisms for SPB survival that have not been identified. The important point is that since the SPB is a native pest that coevolved with its host, it should be expected that elaborate survival mechanisms exist which enhance perpetuation of both the insect and the host species.

If a goal of forest management is to maintain pest populations at tolerable levels through application of remedial tactics, then it is imperative that the survival mechanisms of the insect be considered. A treatment tactic can be viewed simply as another mortality agent imposed on the SPB life system. Knowledge of how the beetle responds naturally to other mortality agents provides insight into the probable success or failure of a proposed treatment tactic. Mathematical models of SPB population dynamics are the tools for such evaluations. Failure of past suppression projects against SPB can be directly attributed, in many cases, to lack of understanding of the survival mechanisms of the insect and to our inability to predict the outcome of a treatment on the population system.

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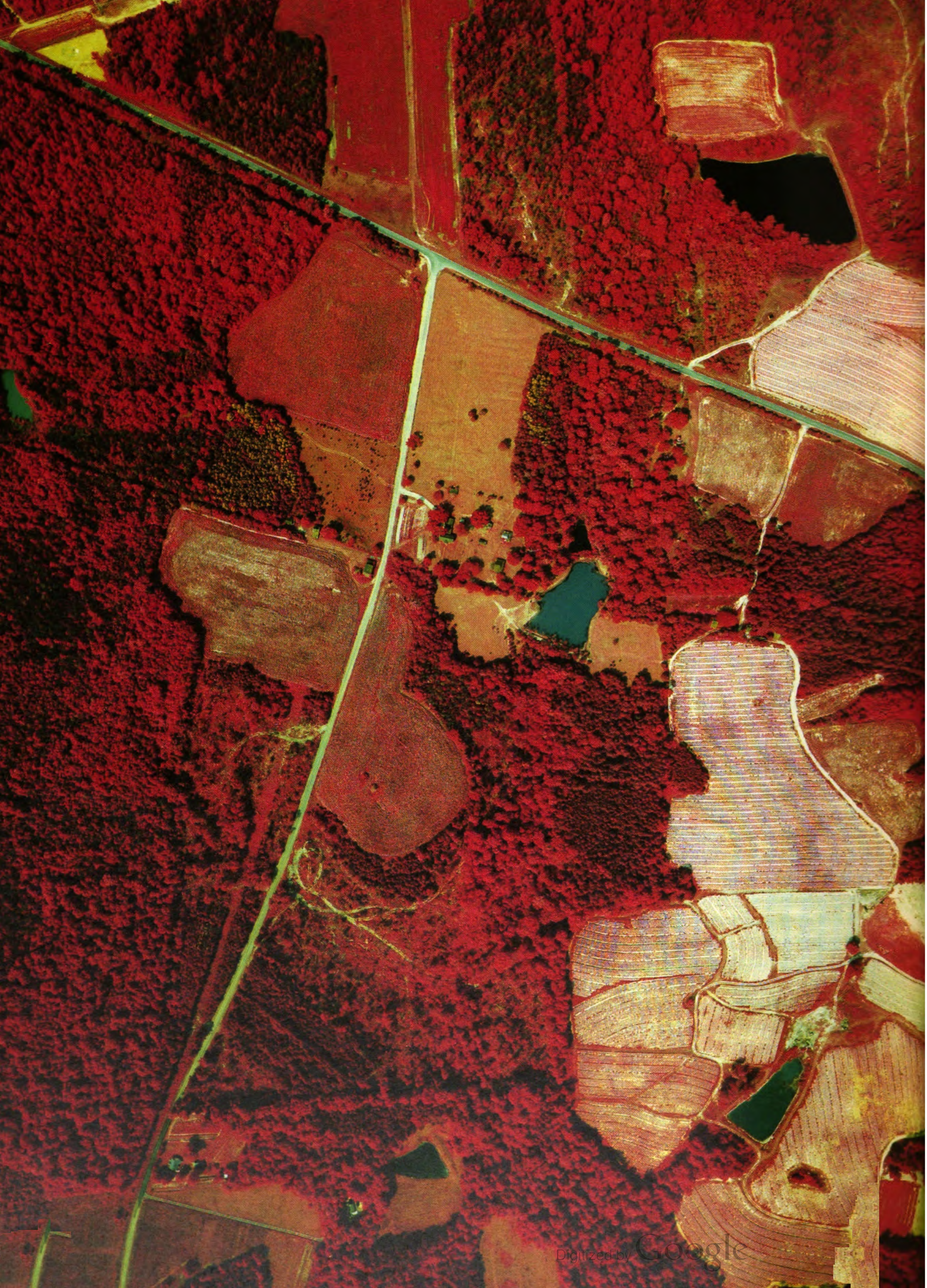

Sampling and Predicting Population Trends

Fred P. Hain[1]

6

Introduction

One of the primary goals of the Expanded Southern Pine Beetle Research and Applications Program has been to develop means for predicting trends in beetle activity. This requires precise and accurate sampling procedures, which are based on an understanding of SPB spatial distributions, as covered in Chapter 5. Accurate prediction of population trends is prerequisite to the development of management strategies to prevent or suppress beetle damage. With adequate forecasts, management can deploy its resources to prevent or mitigate expected outbreaks. Or during severe epidemics, management can direct its suppression efforts against those infestations likely to kill the most trees.

Adequate sampling procedures have other functions as well. They are necessary for evaluating the success of SPB control tactics. One of the basic problems in evaluating control strategies has been the lack of sampling techniques. Without proper sampling, results will be inconclusive because management is unable to measure treatment populations and tree mortality before and after treatment. Standard sampling techniques are also essential in estimating biological and socioeconomic impacts of infestations over large areas of mixed ownership. Survey information is required for making appropriate management decisions and budgeting resources to implement these decisions.

Of course, sampling techniques can also be used in research. Studies on the population dynamics or community ecology of the SPB would probably require more intensive procedures but basically the same techniques. The four uses, then, of SPB sampling plans are prediction of population trends, control treatment evaluations, damage surveys, and population dynamics studies.

The intensity of a sampling effort depends upon how accurate and precise the estimates must be to meet the objectives of management. For example, within-tree sampling to evaluate treatment effects need not be as intensive as sampling to evaluate the impact of a particular parasite on the host population. Important variables to consider in determining the accuracy and precision of a sampling plan are sample unit size, number of samples to be taken, spatial and temporal sampling interval, and distribution of the organism being sampled.

Because the southern pine beetle is a wide-ranging pest that affects several host species (*see* Chapter 2), there is considerable value in developing standardized sampling techniques and adhering to them when sampling objectives and target organisms are the same. Similarity in sampling techniques greatly facilitates comparing regional, temporal, and host species differences. Furthermore, analytical techniques developed at one institution can be readily employed at another. Of course, standardized techniques can be employed only after it has been clearly demonstrated that there is no significant change in the beetle's distribution through space and time or with host species, and after the procedures have been shown to produce accurate, precise estimates for the stated sampling objectives.

Certain practical considerations must also be taken into account when developing a sampling plan. Expense is of paramount importance. Financial resources will determine the degree of accuracy of the sampling plan. Compromises on sampling intensity are often required. Sampling procedures should be kept as simple as possible so that field technicians can readily understand and use the system with a minimum of special training. Unnecessarily elaborate and complicated procedures inevitably result in errors. Also, sampling to predict population trends must provide predictions far enough into the future that management can use the data in making action decisions. Finally, the area of applicability for sampling and prediction procedures must be considered. What works in Louisiana may not work in Georgia or Virginia. Thus, extensive testing must be done in several regions of the SPB range to validate the procedures.

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This chapter describes the survey, sampling, and prediction procedures developed by several investigators in the Expanded Southern Pine Beetle Research and Applications Program. Relevant knowledge from other studies will also be considered. Specifically, this chapter covers (1) survey methodologies developed for monitoring beetle activities over large areas; (2) quantitative sampling schemes for estimating within-tree and within-spot (= infestation) populations; (3) a practical means of estimating areawide populations; (4) although not yet quantitative, procedures for tagging dispersing beetles to study the insect outside the tree; and (5) various models that have been developed for predicting spot growth and areawide populations. In many cases, several procedures or models have been developed. I will attempt to describe the merits and limitations of each.

Surveys for Monitoring Beetle Activity

Computer-aided systems for acquiring, comparing, locating, and filing tree mortality information obtained from sequential aerial photographs are available as a survey and research tool. Means for more accurately positioning aircraft during aerial photo or sketch-mapping missions have been evaluated using the Loran-C radio navigation system. When cost effective, this system greatly improves the accuracy and reliability of aerial photo and sketch-map surveys. Multistage sampling systems also provide a systematic means for obtaining aerial survey and ground-check information.

Aerial Photography: Computer-Aided Systems

Aerial photography is an effective tool for detecting dead trees with discolored foliage. Although costly and difficult to conduct, photographic surveys are far more precise than sketch-map procedures in locating SPB infestations. Sequential aerial photographs also measure the dynamics of tree mortality. They reveal which infestations are expanding and where new ones are starting, once crown discoloration has begun. Photos may also prove useful in predicting beetle population and tree mortality trends and in evaluating treatment effects.

Although sequential aerial photographs have been used in the past (DeMars et al. 1973, 1980; Heller 1968, 1974; Heller and Wear 1969) for bark beetle surveys and research, the task of evaluating two or more sets of photos has been strictly manual and quite tedious. Without sophisticated navigational guidance systems like Loran-C, no two sets of photos would cover exactly the same territory. Furthermore, there would be differences in altitude, camera angle, and visibility. These and other variables would make the job of locating and comparing infestation trends in large areas very difficult.

PISYS

Orthophotography and aerotriangulation procedures can solve these problems. However, these methods are expensive, time consuming, and more accurate than necessary for SPB surveys. The linear regression method employed by PISYS – photographic interpretation system – (DeMars, Slaughter, and Green 1977 unpublished; DeMars and Aldrich 1978 unpublished) is less expensive and time consuming but still provides adequate accuracy. The materials needed to operate the system include a digitizer, a light table, a scanning stereoscope, a data logging calculator, a small plotter, small-scale aerial photographs, and topographic maps.

PISYS acquires, compares, locates, and files sets of point locations that represent infested spots detected from aerial photographs (figs. 6-1 and 6-2). The system computes the reference map location and, after establishing control points, computes the average accuracy of the spot location points identified on the photograph. In one study (DeMars et al. 1977 unpublished), the position of the infested spots was mapped with an average accuracy of ± 89 ft. Graphics (fig. 6-3) that permit the production of map overlays can be made. Maps of photo-detected infestations can be prepared at scales other than the photo scale. The system is most accurate for infestations on flat terrain.

With sequential photographs, PISYS can measure tree mortality that has occurred in previously identified plots or larger areas since the last photos were taken. The system can also be used (both for sequential photography and for single-occasion photography) to prepare maps at different scales and to array the findings.

PISYS has utility both as a survey and research tool. It will accurately define the extent of an areawide outbreak and accurately locate infested plots for ground checking. When sequential photos are used, tree mortality trends can be measured as well. PISYS can also provide a data base useful in formulating and testing predictive models and conducting computer simulation studies of pest management strategies. PISYS's utility in evaluating treatment effects was discussed by Hain et al. (1979) and DeMars, Hain, and Slaughter (1979). And data collected from an epidemic area in North Carolina were used to evaluate the effect of wind and barometric pressure on the proliferation of infested plots over a wide area (DeMars and Hain 1980).

One of the system's limitations is that it works less accurately on terrain that is not flat. But even in mountainous terrain, the error can be minimized if the sequential photo centers are at nearly the same point. Direct photo-to-photo fitting would then eliminate the need for a reference map. Such photos could be obtained only with an accurate navigational system such as Loran-C.

Figure 6-1. – In the PISYS system, an operator views aerial photographs using a scanning stereoscope. Points on the photographs are digitized with a Numonics graphics calculator interfaced to a desk-top minicomputer.

DTIS

Clerke and Mahan (1978) have evaluated the utility of the Digital Terrain Information System (DTIS), developed by the U.S. Forest Service for use in mountainous terrain with large-scale aerial photographs. DTIS relies on a digital terrain model as a basis for computation and analysis. Terrain data sources are available. The least expensive source, the Defense Mapping Agency, covers the entire country; but the accuracy of the data is considered sufficient for general planning purposes only. More accurate data sources are more expensive and are generally not available for the entire country. DTIS is considerably more expensive and time-consuming than PISYS, but in mountainous areas DTIS's improved accuracy may be needed.

DTIS performs several functions. It (1) extracts the position of features from aerial photographs, (2) displays the boundaries of the extracted feature on maps or aerial photographs, (3) displays the results of the terrain model analysis, and (4) stores the digitized information and associated data in computer-accessible files. More functions can also be implemented.

DTIS was tested in mountainous terrain on the Chattahoochee National Forest in northeastern Georgia. Preliminary results indicate that the Defense Mapping Agency terrain data may be effectively used for SPB surveys, with acceptable precision.

Thus, two systems (DTIS and PISYS) are now readily available for use in storing and analyzing aerial photographic data. The choice of systems depends upon the objectives of the user, financial resources, availability of terrain data, and the type of terrain to be covered.

Loran-C Navigation System

Aerial navigation equipment can significantly improve the accuracy and reliability of aerial photographic and sketch-map surveys. It will improve the ability of ground crews to locate infested plots, and it will increase the accuracy of aerial photography in photographing the same plots sequentially. The Loran-C[2] radio navigation system can also be used for navigation and position location by ground personnel.

Most surveys of southern pine beetle damage by pest management personnel have been made by aerial sketch mapping. The accuracy of this procedure is highly variable and depends upon many factors including the experience of the crew and their familiarity with the area, the topography and availability of suitable land-

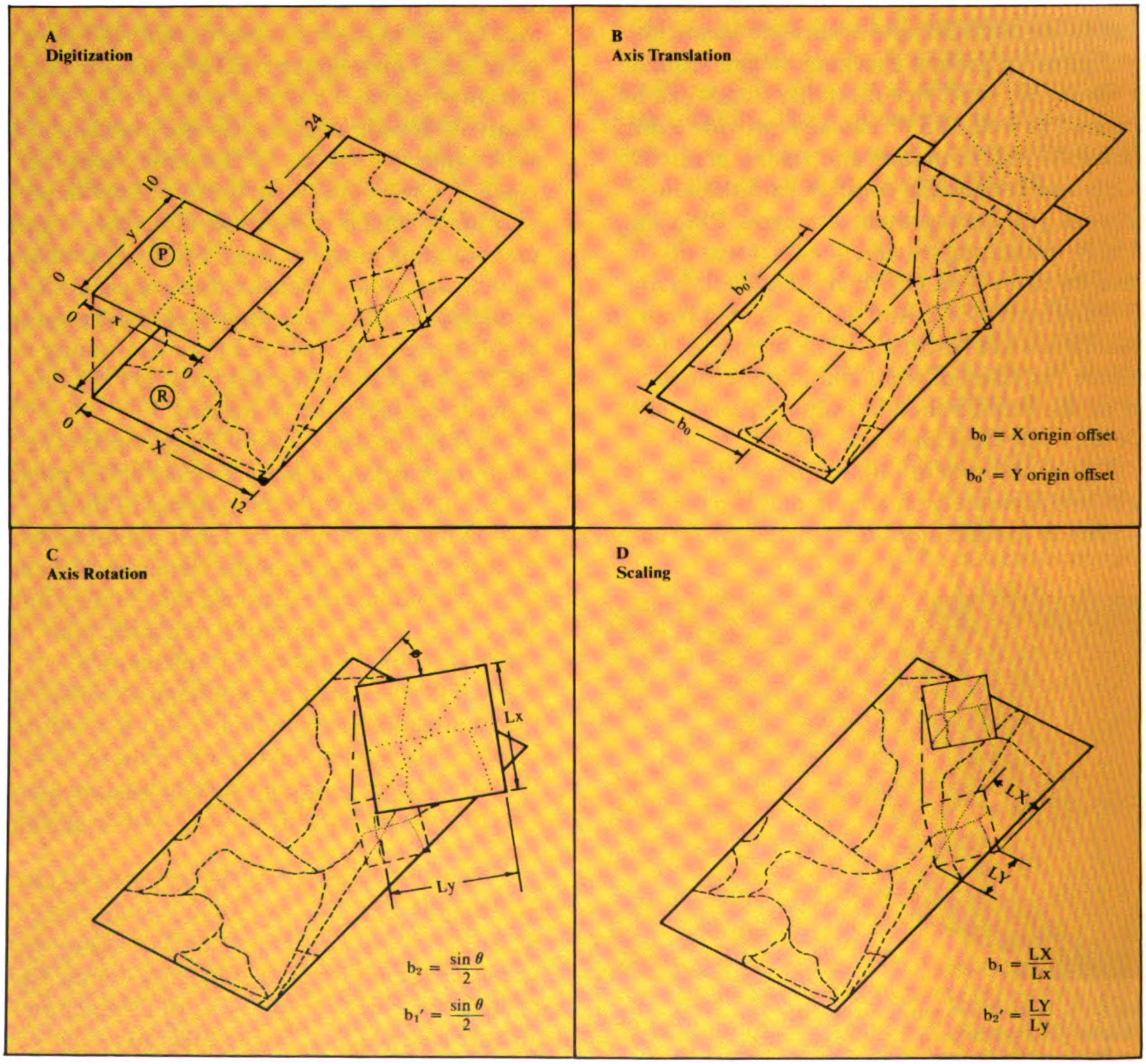

Figure 6-2. – Transforming the digitized locations of points on a large-scale photograph to the corresponding position on a smaller-scale map.

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[2] Loran-C is an acronym for long-range aid to navigation.

marks, visibility, and the accuracy of maps and photos used in the sketch mapping. It is not surprising that unacceptable errors in flightline navigation and SPB spot detection are frequently encountered (Dull 1980).

Loran-C is an operational, highly accurate radio navigation system (Clerke and Dull 1978 unpublished). The station configuration for the coverage of the Coastal Confluence Zone is shown in figure 6-4. Two-thirds of the United States is now covered, with complete coverage scheduled for 1985. Transmitters for Loran-C are arranged in chains consisting of a master station and a series of secondary stations. The aircraft's position is determined by the differences in arrival time between signals from the master and two secondary stations. The apparatus – Loran-C receiver, navigation computer, output interfaces, and display – weighs only 9 lb (fig. 6-5). Portable receivers are also available to transmit the positions of ground vehicles and aircraft over standard radio channels.

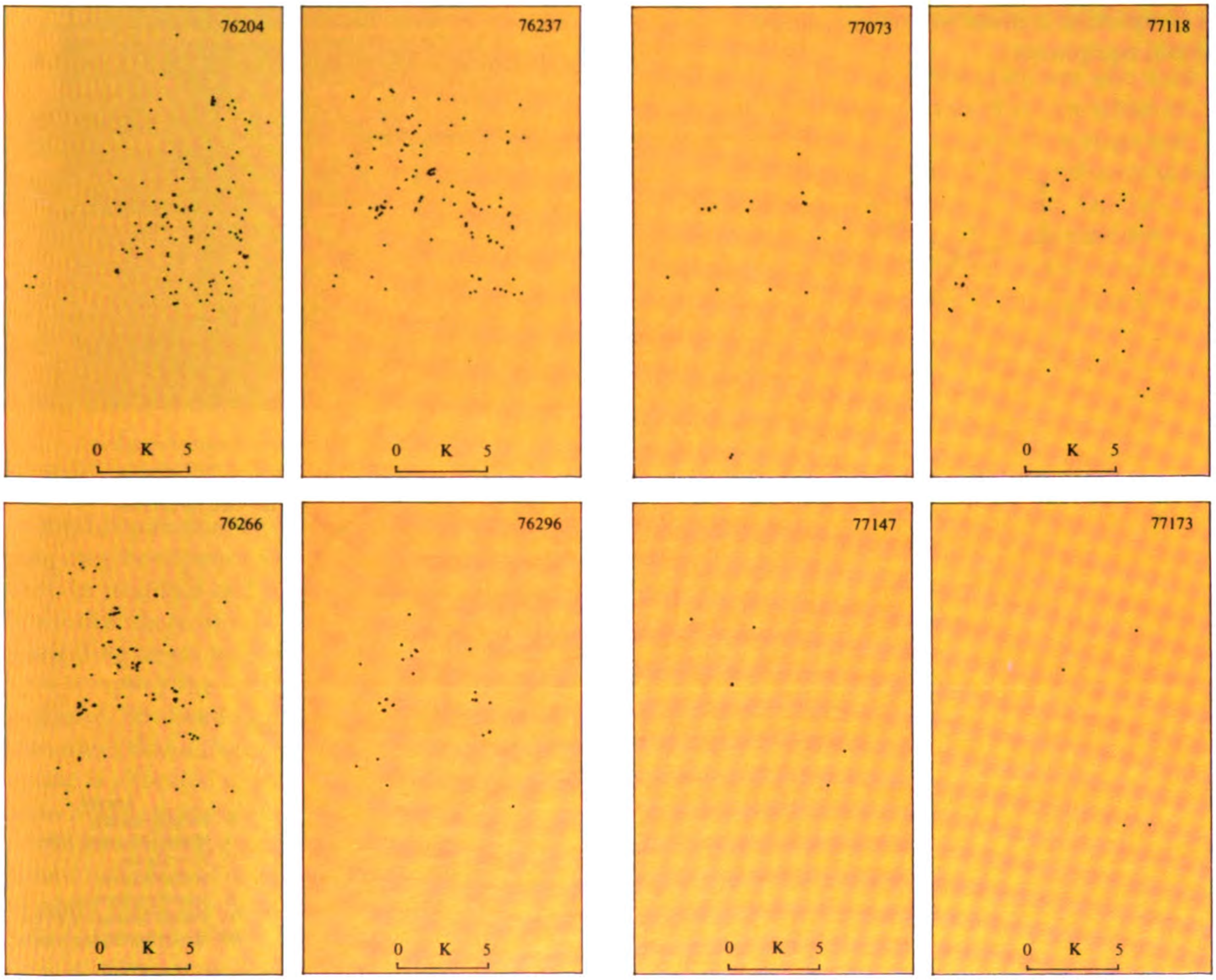


Figure 6-3. – PISYS graphic displays. Each point represents an SPB-infested spot. The identification numbers refer to the year and the Julian date.

Dull and Clerke (1979 unpublished) found that the accuracy and reliability of Loran-C for southern pine beetle surveys is more than adequate. Figure 6-6 illustrates the actual track of the aircraft compared to the desired track for a sample survey mission.

When Loran-C aerial photography is used, 93.7 percent of the beetle spots are correctly located. This compares with a desired probability of 95 percent (Dull and Clerke 1979 unpublished). However, the suitability and accuracy of Loran-C should be appreciated even more when a comparison is made to surveys using conventional equipment.

Multistage Sampling Procedures

Two-Stage Design for Tree Mortality Estimation

Researchers have developed two sampling procedures that can utilize the aerial techniques discussed above to estimate southern pine beetle mortality. Schreuder, Clerke, and Barry (1977 unpublished) reviewed some of the multistage sampling procedures that have been used in forestry. Emphasis has been placed on the development of designs that provide efficient and unbiased estimators through the use of sampling with the probability proportional to size (p.p.s. sampling). A ratio estimator is used to estimate

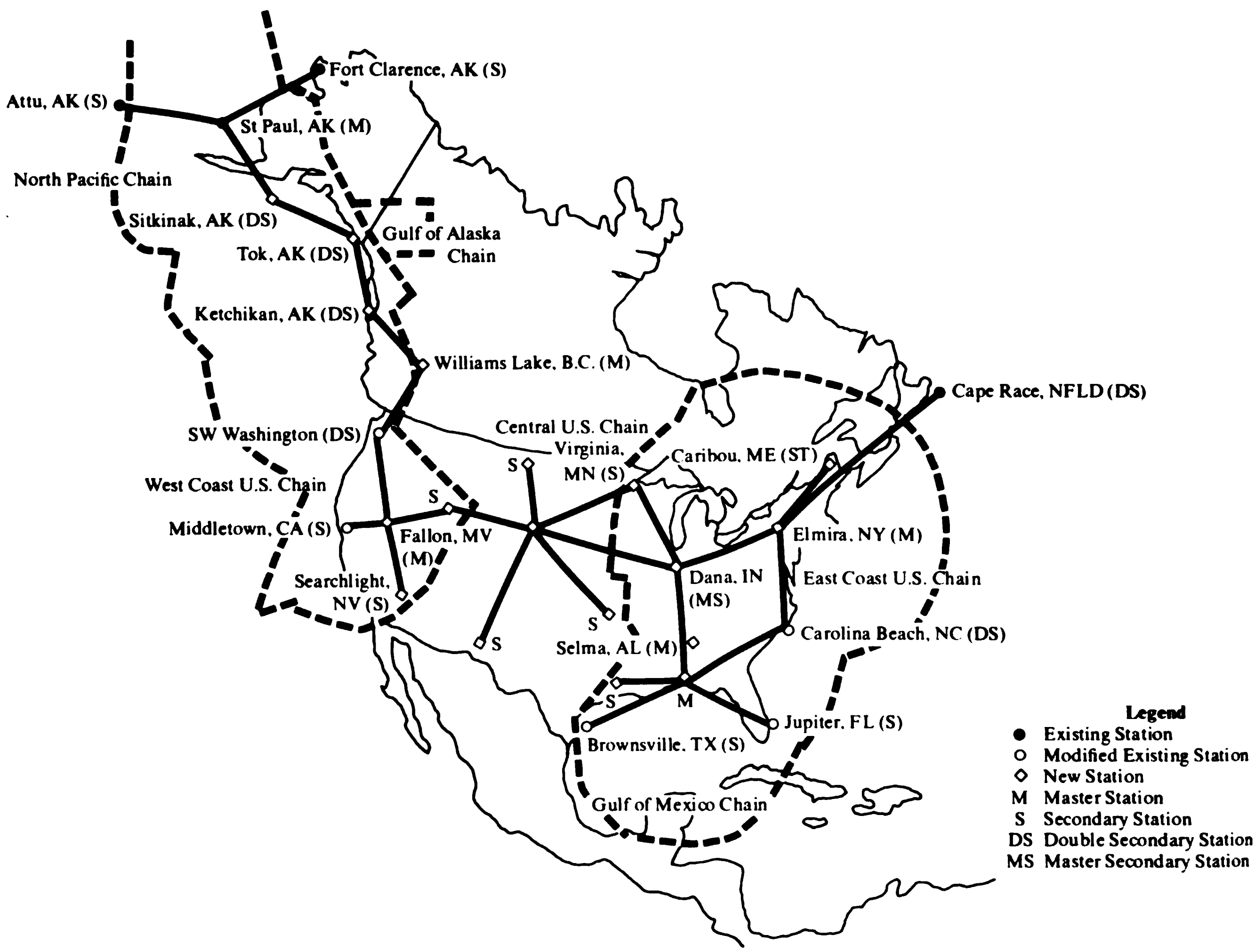


Figure 6-4. – Proposed Loran-C coverage.

Figure 6-5. – Loran navigation system, by Teledyne Systems, Inc. Less expensive Loran-C systems are available.

the total population. However, stratified sampling may be superior to p.p.s. samping in some cases. In stratified and p.p.s. sampling the basic idea is that there should be a higher probability of selecting larger units than smaller ones. But in p.p.s. sampling the selection of larger units is left to chance. Stratified sampling, on the other hand, guarantees that a fixed, desired percentage of the sample is allocated to each stratum of the population being surveyed.

In one stratified sample design, the on-the-ground variables of interest are correlated with variables obtained through aerial surveillance (Schreuder et al. 1980). The sampling design consists of two-stage sempling with double sampling estimation at the second stage. The design was tested on three ranger districts of the Chattahoochee National Forest in Georgia. The first sampling stage divided the population (beetle infestations) into subpopulations (timber types) which were more alike in regard to the variables of interest. In the Georgia test, the three ranger districts were divided into six strata based on timber types and on the level of SPB activity (number and size of infestations) observed during a sketch-map survey.

Information from the second stage was used in two ways. First, the strata were divided into substrata that were even more homogeneous. Based upon a second, more intensive aerial survey, the frequency and distribution of spot sizes were estimated.

The second-stage information was also used in a linear regression analysis of the variables of interest. The aerial information at this stage was much easier and cheaper to obtain and correlated well with hard-to-obtain ground data. On-the-ground measurements were done on a random sample of spots in each substratum. Schreuder's team planned their ground checking of the Chattahoochee to ensure that no less than 5 spots and no more than 90 were sampled in each substratum. Ground checking gave greater emphasis to larger spots. The double sampling estimation refers to the fact that a large sample of second-stage aerial information was used in regression estimation with a smaller sample of ground information (Schreuder et al. 1977 unpublished).

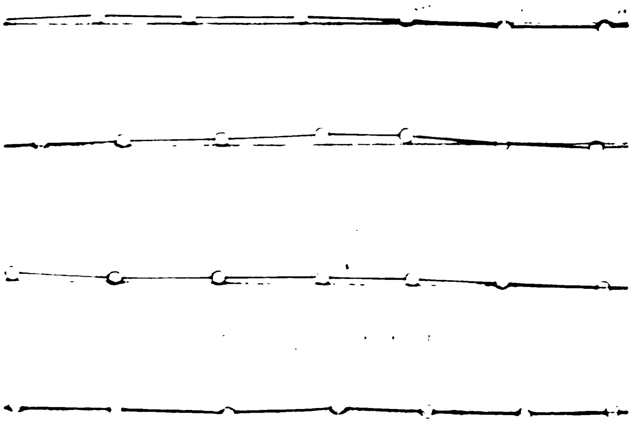


Figure 6-6. – Comparison of actual flight track to desired and Loran-C-indicated track.

Sampling Design for Periodic Mortality Estimation

A second technique for estimating beetle mortality was developed by Ghent and Ward (1977 unpublished). Their sampling procedures are designed for practical use by State or Federal agencies concerned with extensive areas. The technique provides an annual estimate of timber loss, requires little or no ground checking, and has a satisfactory level of precision (± 20 percent). The system uses sequential aerial photography and local aerial volume tables to meet these requirements.

A modified random sampling plan was employed in a 3-million-acre area in seven central Mississippi counties. Forty-five 500-acre plots of pine type were used. Photo plots were stratified by the proportion of pine in each county to the overall study area. However, stratification by outbreak would have been desirable (Ghent and Ward 1979a unpublished).

Sequential photographs were taken in the spring, summer, and early winter of 1978 and 1979. Loran-C navigational equipment aided in the task of rephotographing the same plots.

The data were analyzed according to a simple procedure developed for plots of different sizes. The ratio of volume loss to acreage is computed and multiplied by the total acreage in the study area (3 million acreas) to obtain an estimate of the total volume loss. Volume estimates are computed from aerial volume tables (Ghent and Ward 1980 unpublished). During 1978 approximately 645,000 fbm of timber were lost to the SPB in the central Mississippi study area (Ghent and Ward 1979b unpublished).

Choosing either of these two sampling procedures, or any other, depends upon the requirements of the user and the availability of resources. Regarding the two estimating procedures just discussed, Schreuder's procedures (1977 unpublished and 1979) do provide greater precision and accuracy but at a considerably higher cost. The authors gave a very detailed accounting of their operational expenses. Per-acre costs, using their techniques, ran to almost 4 cents. Estimated costs for the procedures described by Ghent and Ward (1977 unpublished) were half a cent per acre.

Sampling to Estimate Beetle Populations and Tree Mortality

To evaluate the effects of treatment on beetle populations at the spot level or to study the within-tree community ecology, investigators need precise population data. Several attributes of SPB populations can be either beneficial or detrimental to the development of quantitative estimating procedures (Pulley, Coulson, and Foltz 1979). The complicating attributes are (1) asynchronous beetle development with multiple overlapping generations, (2) variations in the length of the life cycle depending upon season of the year and climate, (3) a pattern of colonization that results in clumping of dead trees, (4) variations in life stage distributions within trees, and (5) the number of life stages that may be of sampling interest (attacking adults, reemerging adults, eggs, larvae, pupae, callow adults, and emerging adults). There are at least three ***simplifying*** attributes. A major portion of the insect's life cycle is spent within the tree. The length of the infested bole and the number of trees infested represent a discrete sampling universe. Finally, precise measurements of the beetle population and its habitat can be obtained.

Sampling Within-Tree Populations

Several authors have discussed bark beetle sampling (Berryman 1968; Carlson and Cole 1965; Coulson et al. 1975, 1976a and e; Foltz et al. 1976a; DeMars 1970; Dudley 1971; Pulley et al. 1977b; and Safranyik and Graham 1971). For sampling SPB populations specifically, Stephen and Taha (1976) and Nebeker et al. (1978a) addressed the problems of optimum sample unit size, number, and placement.

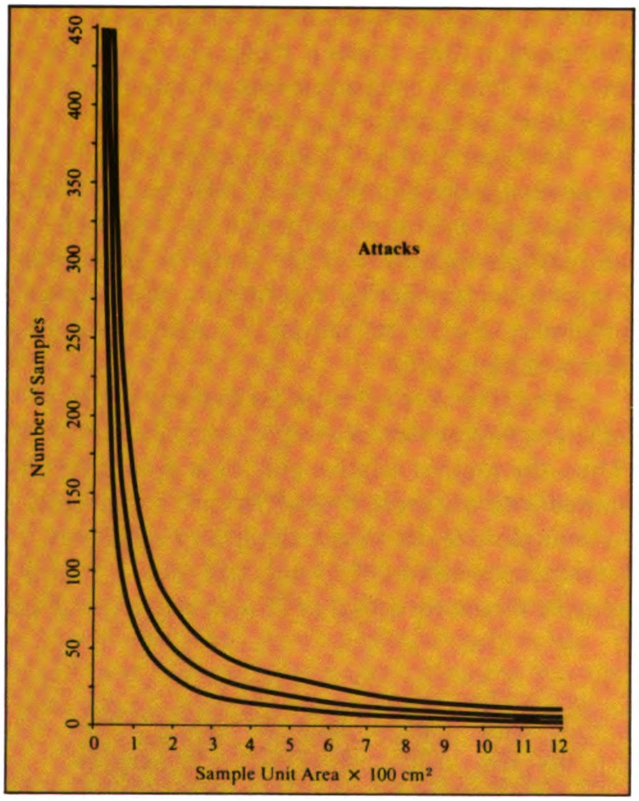
Stephen and Taha (1976) also considered the sampling requirements for the natural enemy complex. Infested bark from southern Arkansas was X-rayed and the resulting radiographs (fig. 6-7) were used as negatives to produce prints. The prints were reassembled to form a complete mosaic of infested bark. SPB attacks, egg gallery length, total brood, parasites, and predators were measured and recorded within each grid cell of the mosaic. This permitted the selection of computer-generated random samples, which could vary in size. Figure 6-8 shows the relationships between sample unit size and the number of samples necessary to estimate the density of a variable.

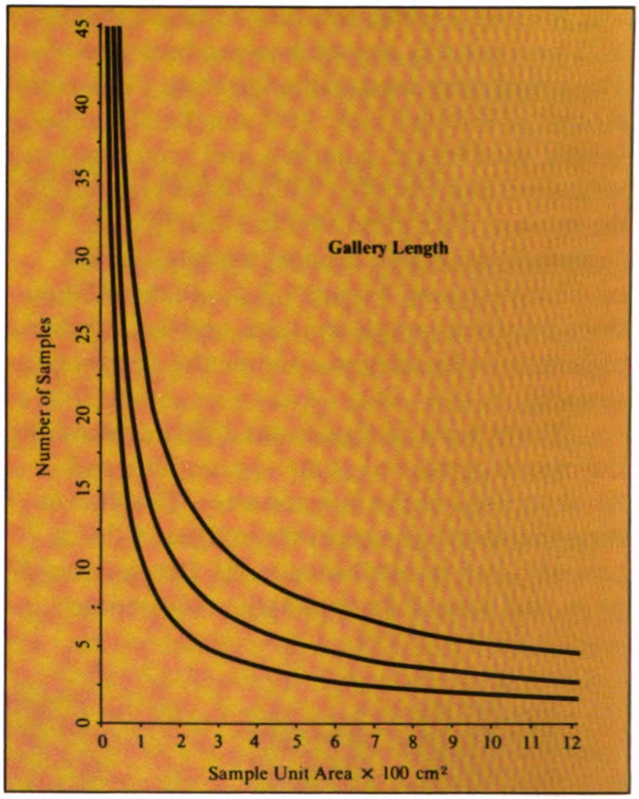
There were no significant differences among the means computed at the top, middle, and basal sections of the infested trees. This contradicts the distributions shown in figure 5-1 but probably can be attributed to the fact that Stephen and Taha did not sample at the extreme upper or lower portions of the infested bole. Sampling at three levels is recommended, however, for density measurements of individual predator and parasite species.

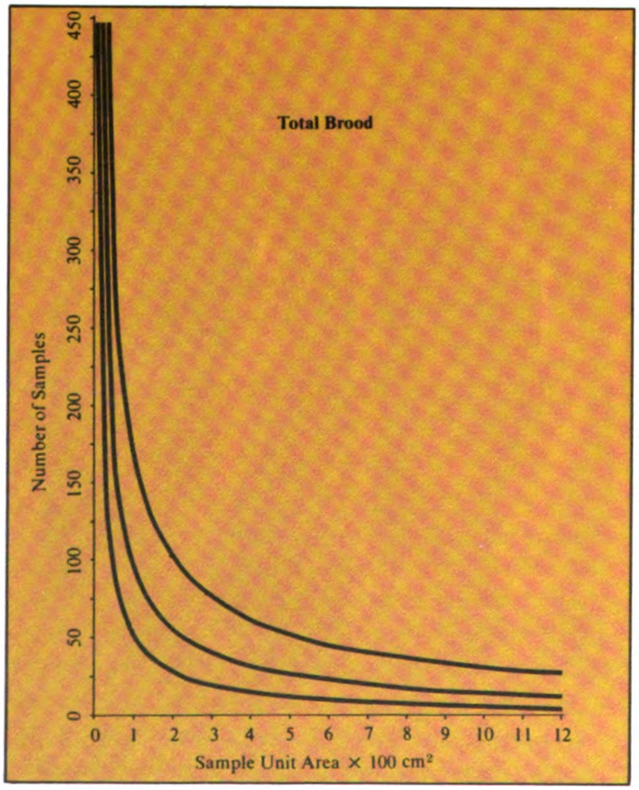
Nebeker et al. (1978a) did a similar but somewhat more detailed study. His team considered sample unit size, strata size and number, and sample allocation. They also took their analysis one step further by determining the relative efficiency of different sampling schemes and different sample sizes.

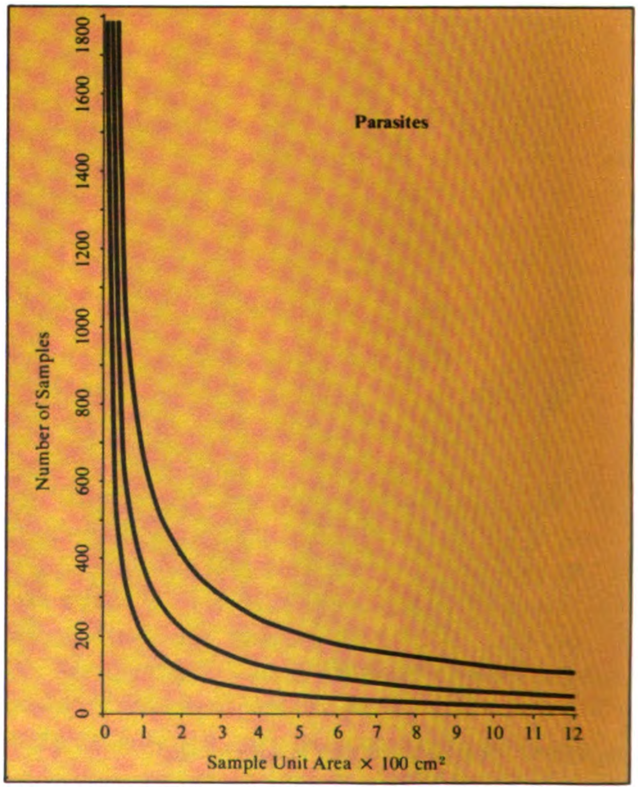
The Nebeker team found that the relative efficiency decreases as sample size increases. Thus, the highest relative efficiency would be obtained with a sample unit of 16 cm^2 – the smallest sample size. However, the loss in efficiency becomes less dramatic as unit size increases and may be inconsequential at unit sizes greater than

Figure 6-7. – Radiograph of bark samples infested with southern pine beetle.


Attacks
Number of Samples
0
50
100
150
200
250
300
350
400
450
0 1 2 3 4 5 6 7 8 9 10 11 12
Sample Unit Area × 100 cm²


Gallery Length
Number of Samples
0
5
10
15
20
25
30
35
40
45
0 1 2 3 4 5 6 7 8 9 10 11 12
Sample Unit Area × 100 cm²


Total Brood
Number of Samples
0
50
100
150
200
250
300
350
400
450
0 1 2 3 4 5 6 7 8 9 10 11 12
Sample Unit Area × 100 cm²


Parasites
Number of Samples
0
200
400
600
800
1000
1200
1400
1600
1800
0 1 2 3 4 5 6 7 8 9 10 11 12
Sample Unit Area × 100 cm²

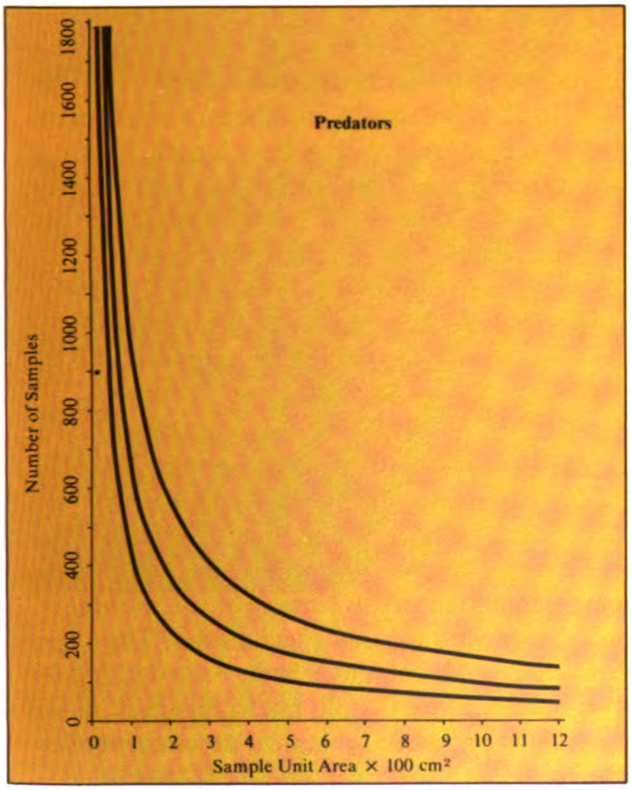
64 cm². Thus, if larger units are selected as a matter of convenience, their selection can be based upon other criteria, such as cost (larger units being easier to collect, handle, and analyze). Relative efficiency increases with the number of strata and with unequal stratification. Unequal stratification allocates the strata toward the center of the infested bole, where more information is obtainable.

Both Stephen and Taha (1976) and Nebeker et al. (1978a) stressed the limited nature of their respective studies – a few trees were sampled very intensively – and cautioned against generalization. However, the procedures they have developed are an important step in the development of sampling methodologies.

A different approach was selected by another team (Coulson et al. 1975a). Rather than intensively sampling a few trees, they devised a convenient sampling scheme, based upon previous work with other bark beetles (DeMars 1970, Safranyik 1968). The scheme allowed for sampling a large number of trees and thus was more representative of the highly variable conditions found in nature.

Bark disks (100 cm²) were removed in four directions at each sample level. Beginning at 2 m and continuing to the top of the infested bole, crews established sample levels at every 1.5-m interval. The bark disks were removed from the infested trees at three time intervals corresponding with different life stages (egg-attacking adults, late larvae-pupae, emerging adults). The bark disks were collected with a circular hole-cutting saw by climbing rather than felling the tree (fig. 6-9). The disks were X-rayed and insect inclusions and gallery lengths were counted on the radiographs. Host tree parameters also measured included tree height, height of the infestation, diameter, and bark thickness at each sample level. A total of 134 trees were sampled during the study (Pulley et al. 1979).

Figure 6-8. – Curvilinear relationship between number of samples needed to estimate total mature brood and the corresponding sample unit area. The 90 percent confidence limits are also included. (Taken from Stephen and Taha 1976.)



Attacking Adults

Other investigators have used modified versions of Coulson's procedures to sample different southern pine beetle life stages. Linit and Stephen (1978) investigated several techniques that can be used for estimating attacking adult populations: (1) X-ray determination of attacking adults, (2) dissection for attacking adults, and (3) attack site determination.

Linit and Stephen concluded that each of the three methods can provide reliable estimates of numbers of attacking adult southern pine beetles. But the attack-site method eliminates the need for precise timing of the sampling and the need for taking sapwood with the disk sample. The sapwood can decrease the quality of the radiograph image or require tedious laboratory procedures for removal.

Attack sites were recognized by the following criteria. First, pitch tubes were present at the suspected attack site. Second, the attack hole was slanted in relation to the bark surface and filled with an oleoresin/frass mixture. Finally, the position of the suspected attack site to the egg gallery was logical, e.g., at the "beginning" of a gallery (fig. 6-10).

But the attack-site method is not without its limitations. Sample timing cannot be totally ignored. If samples are taken too late, the substantial foraging of cerambycids and buprestids will partially or totally obliterate SPB egg galleries.

Eggs

Various methods for sampling southern pine beetle eggs have been reported. In a Texas study, bark disk samples of 100 cm² were removed just after mass attack was complete (Foltz et al. 1976a). Eggs and egg niches were counted following bark dissection in the laboratory. It was assumed that empty egg niches contained an egg that was destroyed during the dissection. A statistical analysis showed an average of 1.59 eggs per centimeter of gallery.

Figure 6-9. – Sampling an SPB-infested tree.

Lashomb and Nebeker (1979), working in Mississippi, felt that counting egg niches might result in an overestimate of egg deposition. So they took precautions to include the remains of eggs that were destroyed during dissection. They concluded that counting egg niches caused a 36 percent overestimate in egg deposition.

However, in a North Carolina study, Hain (unpublished data) sampled for egg production when the brood were in late larval stages. Live egg counts were made if egg niches were associated with a larval gallery. Dead egg counts were made if the egg was still present or if an empty egg niche without a larval gallery was observed. By this method, less than 5 percent of the egg niches were empty or had unhatched eggs. Using the same method in Arkansas, F. M. Stephen (personal communication) also found less than 5 percent empty niches or dead eggs.

In all three studies numbers of eggs had a linear relationship with gallery length. Thus, measurements of gallery length can be used to estimate egg deposition. The differences in egg density reported by the three studies could result from regional differences in the insect's biology or population characteristics, or reflect errors associated with the sampling techniques used.

Emergence

Various modifications for sampling bark beetle emergence have also been devised. McClelland et al. (1978) reviewed several of these approaches and proposed the use of a new emergence trap to solve many of the problems associated with the other techniques. They stated that emergence estimates have been derived by two means: those that do not interrupt or modify ongoing physical or biological processes within the tree (nondisruptive), and those that do (disruptive).

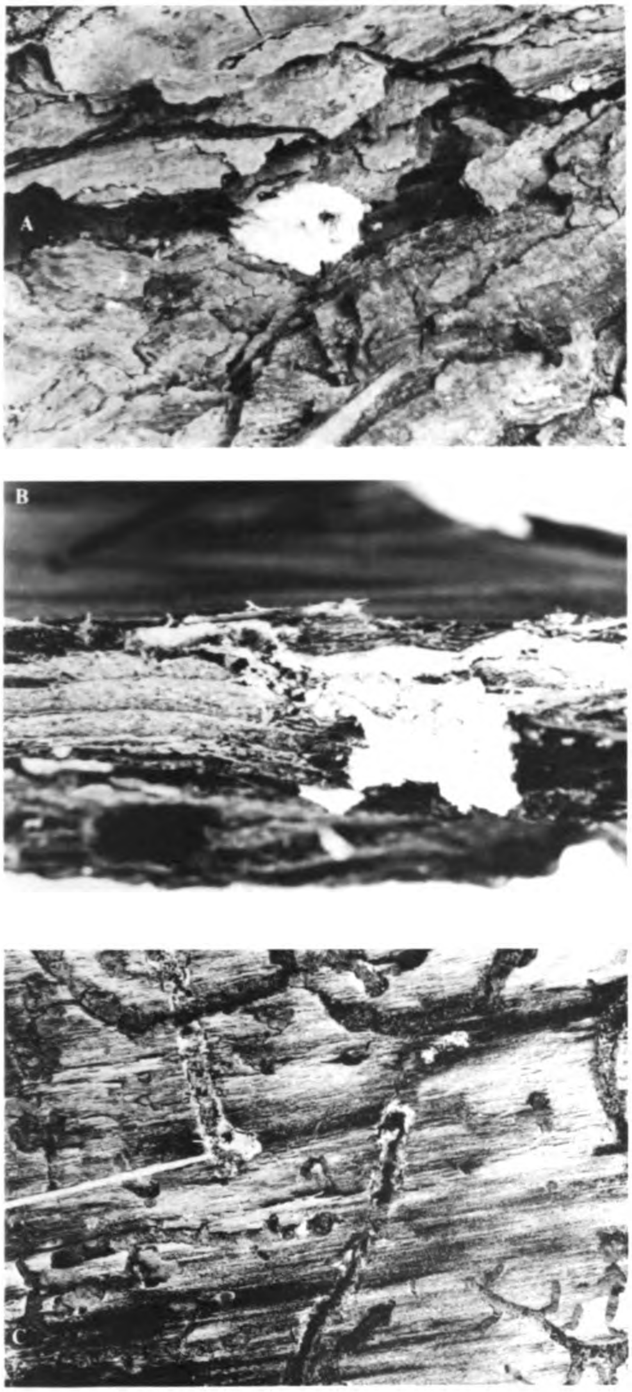


Figure 6-10. – Criteria used for the identification of SPB attack sites: (A) the outer bark surface showing a pitch tube that marks the point of attack; (B) a cross section of bark showing the pitch tube on the outer bark surface, and (C) the inner bark surface showing the entry point of an attack and the construction of egg galleries. (Taken from Linit and Stephen 1978.)

The nondisruptive techniques correlate emergence with counts of exit holes. Thus the tree remains unaltered until emergence is complete. Unfortunately a one-to-one relationship between exit holes and emergence does not always exist. Multiple use of a single hole and utilization of bark cracks and fissures commonly occurs.

The disruptive techniques include (1) removing samples before emergence to count callow adults within the bark (potential emergence), (2) placing bark slabs or bolts in field cages to monitor emergence under "natural" conditions, (3) placing bark slabs or bolts in environmental chambers to simulate natural conditions, and (4) attaching emergence traps to the tree. All methods involve some interference with biological processes operating during late brood development and emergence. The degree of disruption varies with the technique but is usually quite substantial.

The authors concluded that the most practical and unbiased estimates of emergence can be obtained by using on-tree traps constructed and installed to minimize the disruption of biological processes. They describe a basic trap design, with modifications, that utilizes a nylon screen and collecting bottle. The trap is designed to fit over a circular bark surface of 100 cm^2. McClelland's team acknowledged that the screening inhibited parasitism of late brood stages. But this inhibition could be minimized by placing the traps on the tree as late as possible, but before emergence begins. The traps are rugged, pliable, simple to construct, and easily attached and removed.

The emergence traps have also been used to sample reemergence of parent adults (*see* Chapter 5 and Coulson et al. 1978). Emergence traps were placed on infested trees when attacking adult density was judged to be at a maximum. Field crews placed traps at several heights on the infested bole and monitored them daily for the duration of reemergence (16 to 20 days) (fig. 6-11).

It is not always practical to monitor the traps daily or to revisit the trees more than once. Cooper and Stephen (1978) used laboratory rearing techniques to determine reemergence. With daily observations, lab workers determined a lag time between reemergence and brood adult emergence. All beetles collected up to this lag time were considered reemerging parent adults. Attack density, as determined by the attack-site method, and reemergence holes were linearly related to reemergence and had significant predictive value. Holes that penetrated the bark perpendicular to the inner surface and directly connected to an egg gallery were considered reemergence holes. Workers must take care not to confuse these with holes caused by other SPB associates. Both of the above studies found high reemergence rates.

Figure 6-11. – Infested loblolly pine tree equipped with pole steps to permit access to reemergence traps. (Courtesy of the Entomological Society of Canada.)

Estimating Total Within-Tree Populations

With an understanding of the various procedures and modifications for sampling southern pine beetle populations, let us proceed with a discussion of analytical methods for estimating total within-tree populations. Basically this involves the techniques that were developed from the data base of 134 infested trees sampled by Coulson et al. (1975a).

As mentioned earlier, an essential step in the development of precise estimating procedures is a clear understanding of the spatial and temporal distribution of the population being sampled. We must first consider the within-tree distribution of SPB. Beetle distribution within an "average" sample disk is uniform (Foltz et al. 1976a). In comparing the samples taken at four aspects (NE, SE, SW, NW) at each sample height, Foltz's team found no consistent directional bias. The population density along the infested bole varied with life stage but was generally greatest near the center of the infested bole and lower at the extremes (Mayyasi et al. 1976a and b, Coulson et al. 1976a and e, Foltz et al. 1976a). The generalized spatial and temporal within-tree distributions were depicted in figures 5-2, 5-4, 5-7, and 5-10. The functional distributions of the attacking adults, eggs, larvae, pupae-callow adults, and emerging adults in relation to the normalized infested bole (sample height/infested bole height) were described. Probability density functions for the various within-tree life stages have been determined (Mayyasi et al. 1976b). The probability density function (PDF) is the ratio between the insect density at a given height and the average insect density along the entire infested bole.

With regard to nonlinear models for describing the within-tree distributions, Nebeker et al. (1978b) analyzed these models with gallery length data collected from shortleaf pine in Mississippi. Figure 6-12 shows the curves of the various models they analyzed. Model I-A is the two-parameter model described by Coulson et al. (1976a) and Mayyasi et al. (1976a and b). They forced the density to be zero at the bottom and the top of the infested bole. The model explains about 25 percent of the total variability in the data. Model I-B forces the density to be zero only at the bottom of the infestation and explains about 32 percent of the variability. Model I-C places no restrictions on the density and raises the explanation percentage to 34. In contrast Model II, which was proposed by Foltz et al. (1976a) to describe the within-tree distribution of gallery length, explains only 25 percent of the variability when no conditions are placed on the parameters. Model III is model I-D with the following tree parameters added: (1) average inner-bark thickness at the middle of the infested bole, (2) infested bole length/tree height, and (3) diameter at breast height multiplied by the infested bole height. Model III explains 68 percent of the variability.

Pulley et al. (1976) developed the topological mapping routine for computing the total number of beetles on a tree using data provided by Coulson et al. (1975a). This procedure used all the data available to derive a best estimate for the total population.

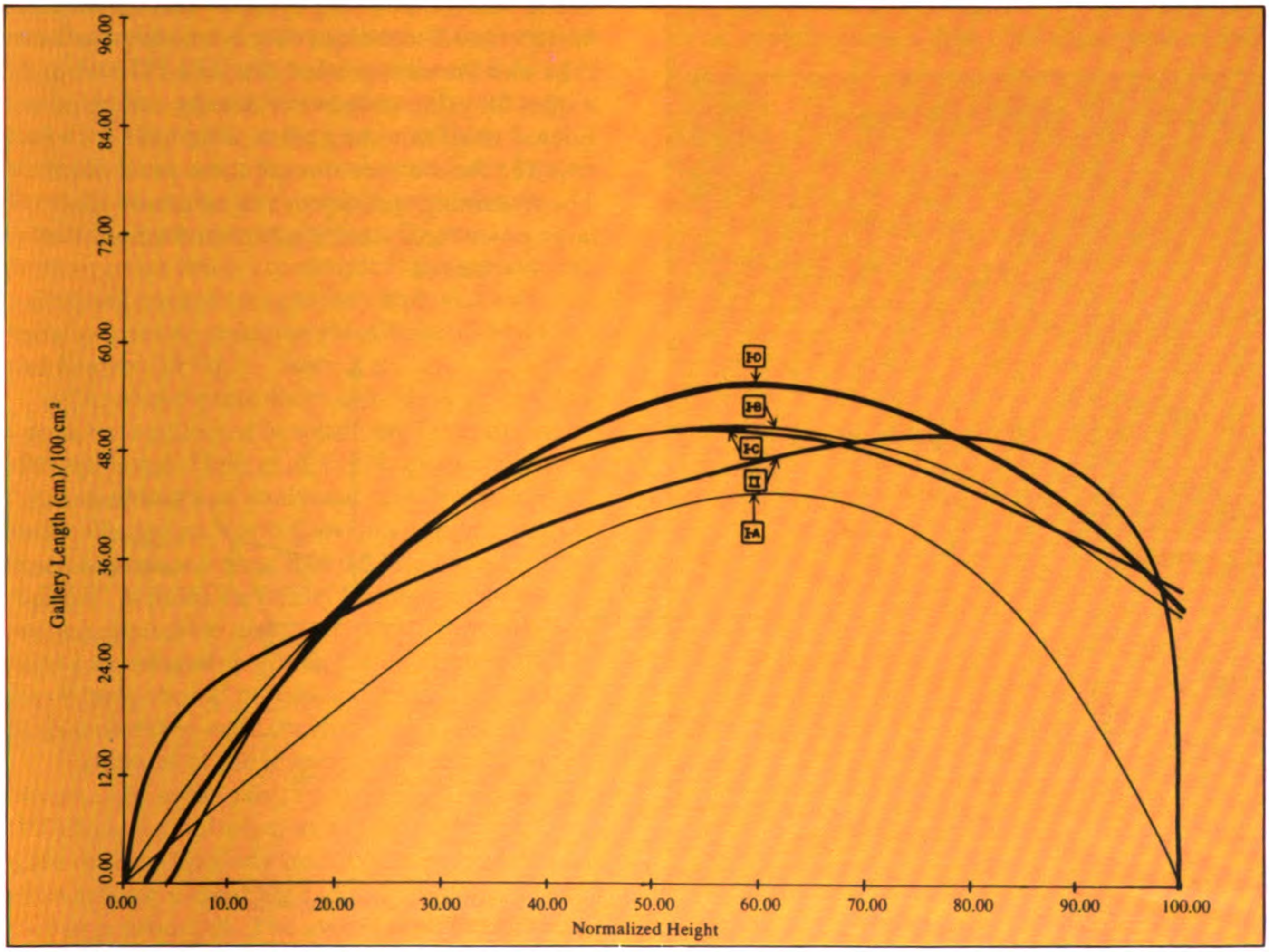


Figure 6-12. – Plot of raw data and resulting curves for various models discussed in Nebeker et al. (1978b). Models I-D and III are the same when all trees are combined. (Taken from Nebeker et al. 1978b.)

The topological estimates were used as a basis of comparison with all other estimating procedures. To understand this procedure, visualize a film of uneven thickness surrounding a tree. The thickness of the film is proportional to the insect density. If the volume of the film can be determined, the number of insects on the tree can also be determined. The topological technique assumes a gradual change in insect density between observation points.

The topological mapping procedure starts by considering the interval between sample heights as a truncated cone and transforms the surface of the cone to a plane. The individual segments between sampling points are transformed to trapezoids (fig. 6-13). A model to describe this surface was selected. To determine the volume and hence the insect count, it is necessary to derive the specific contour associated with a given section, as depicted in figure 6-14 (Pulley et al. 1976). Summing for all the sections then yields the estimate of beetle numbers for the infested tree.

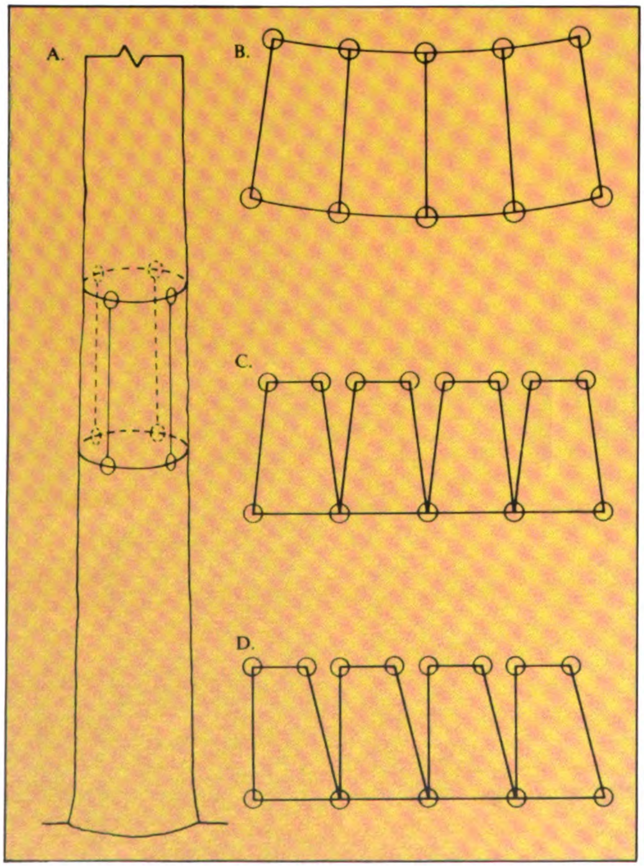


Figure 6-13. – Successive transformations of the tree surface. A. Truncated cone and sample locations on the standing tree. B. Flattened surface of truncated cone. C. and D. Sections of the conical surface transformed to trapezoids of equivalent area. (Taken from Pulley et al. 1976.)

Pulley et al. (1977a) selected a series of sampling plans and tested their suitability for estimating within-tree populations of attacking SPB adults. Later other life stages were estimated and the procedures evaluated (Coulson et al. 1976e). The accuracy and precision of the various estimating techniques was determined by comparing the estimates to the topological estimates.

Two types of estimates are necessary to obtain an estimate of total within-tree population: an estimate of the surface area or bark volume of the tree, and an estimate of the beetle density within the tree. Pulley et al. (1977a) selected five procedures each for calculating surface area and beetle density. The long cylinder and the tree geometry model techniques for estimating surface area, and the extrapolated disk and PDF techniques for estimating beetle density can be considered small sampling plans since little data is required for the execution of these procedures. The remaining techniques can be considered large procedures since a substantial amount of data is required.

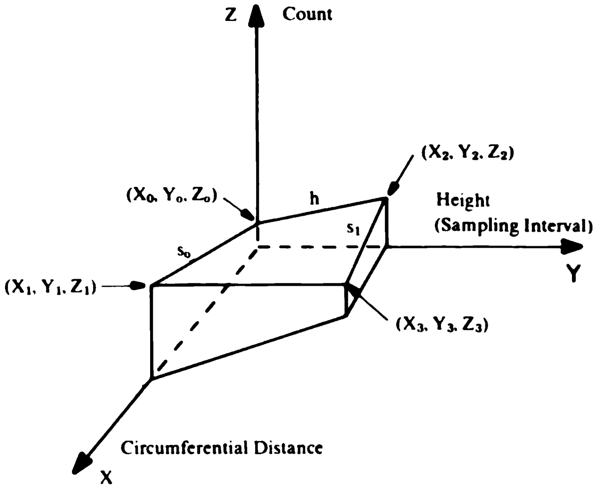


Figure 6-14. – Solid of volume-equivalent to the insect count on a particular section of the tree. (Taken from Pulley et al. 1976.)

The small sampling schemes are inherently more interesting because they are likely to have practical applications. The primary function of the large schemes would be as research tools. There are several possible combinations of the small surface-area estimation techniques and the small beetle-density techniques.

The tree geometry model PDF combination (TG-PDF) illustrates a small sampling plan (Coulson 1976e). The tree geometry model utilizes the nonlinear model developed by Foltz et al. (1976b) to estimate surface area. Tables of surface area based on the tree geometry model are provided for three bark thickness classes of loblolly pine in Coulson et al. (1976e). To estimate the number of beetles in a tree using the PDF technique, the observed density is divided by a PDF value tabulated in Coulson et al. (1976e) and multiplied by the surface area of the infested bole. The TG-PDF procedure is illustrated in figure 6-15. The procedure requires only one sample or set of samples at a given level, but multiple-level sampling can also be done. Procedures for multiple-level sampling are also discussed in Coulson et al. (1976e). Of course, if three or more levels are sampled, the topological estimating procedures can be employed with equal or greater precision (McClelland, Hain, and Mawby 1979).

The above procedures were developed from a data base collected in southeast Texas during an SPB epidemic. Hain et al. (1978) evaluated the same sampling and analytical procedures using data collected in North Carolina during a period when SPB populations had declined to a "sparse" population phase. If the procedures proved applicable under the population conditions experienced in North Carolina, then the procedures should be applicable on a regional basis (subject to validation).

Estimates of the infested surface area were obtained from the tables provided in Foltz et al. (1976b) and Coulson et al. (1976b). These tables were derived from the tree geometry model. The estimates were compared to the topological surface area estimates. The average relative error of the tree geometry estimate for the North Carolina trees was +4.19 percent and compared favorably with the +3.50 percent bias found in Texas.

The within-tree distribution of life stages in North Carolina was evaluated using the model of Mayyasi et al. (1976a and b). There were no significant differences between North Carolina and Texas, and the authors concluded that the PDF values given in Coulson et al. (1976b) are suitable for use in North Carolina.

Thus the TG-PDF procedures for estimating within-tree populations should be applicable in North Carolina as well as Texas and other regions of the South. As a final analysis, the North Carolina estimates were obtained using North Caro-

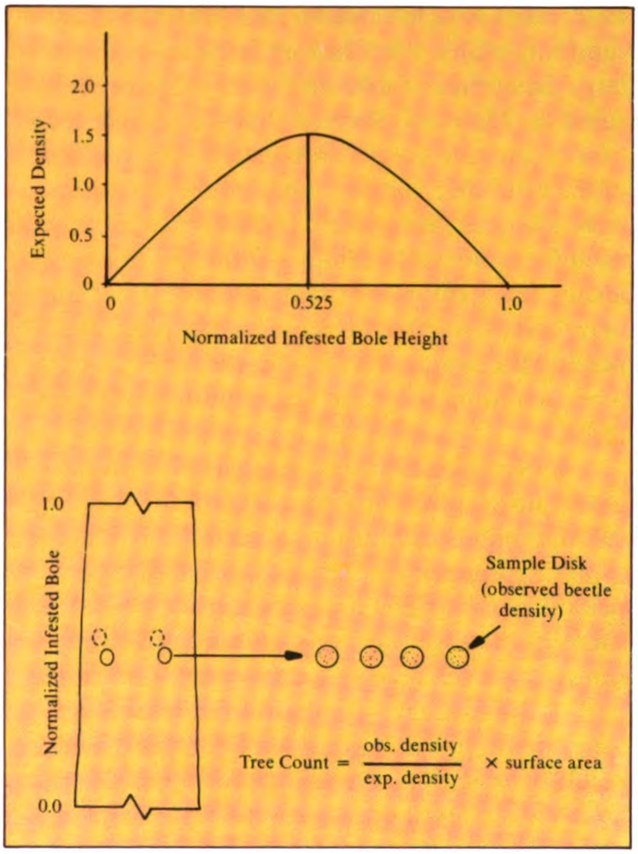


Figure 6-15. – Schematic illustrating the use of the probability density function (PDF) method of estimating within-tree attacking adult populations of southern pine beetle. (Taken from Pulley et al. 1977b.)

lina parameters (PDF values and correction weights) and compared to estimates for the same trees using Texas parameters. A comparison of mean relative errors showed only minor differences (Hain et al. 1978).

In comparing the within-tree distribution of infested shortleaf and loblolly pines, researchers found no significant differences between the two host species (McClelland et al. 1979). Hence a standardized approach to a regional research effort may be taken to determine regional differences in population parameters.

Pulley et al. (1977c) described the advantages of a sampling plan derived from a knowledge of the within-tree distribution of southern pine beetles. These authors contrasted the TG-PDF procedure to random and stratified random sampling plans. The random techniques required large quantities of data and were therefore less suitable. They also showed that the sample location on the tree greatly influenced the precision of the estimate. Various sample level locations were analyzed using the TG-PDF procedure with sampling intensities ranging from one to seven levels. The gain in information content became marginal after three levels were sampled. Dispersing the sample levels over the infested bole, while avoiding the extremes, produced the best results.

Pulley, Coulson, and Kelly (1979) investigated the accuracy and precision of the topological mapping procedure for a variety of different sampling intensities. Results showed that the penalties in bias and lack of precision due to sampling at wider spacings and taking fewer samples at each level were not large. For example, taking just one sample from the northeast aspect at a sampling interval of 250 cm would result in an underestimate of 10.29 percent, which is the largest proportional error. The sampling plan described by Coulson et al. (1975a) would result in an underestimate of 1.38 percent.

Nebeker (1979) presented a view of the hierarchy of within-tree estimating procedures based upon their level of precision. A complete census is, of course, the most precise, followed by estimates from large sampling plans, small sampling plans, and indirect procedures. The indirect procedures utilize host characteristics to determine the estimate rather than taking samples of infested bark. Model III, described earlier in this chapter and depicted in figure 6-12, can estimate the within-tree population by utilizing host characteristics as the only input parameters.

Estimating Within-Spot Populations

The next step in the development of quantitative sampling procedures is estimating beetle populations within an entire infested spot. Intensively sampling each tree is not practical. But since procedures do exist for nonintensive within-tree sampling, it should be possible to extend these methods to an entire infestation.

At least four factors need to be considered in sampling an infestation (Pulley et al. 1977a): (1) precision of the within-tree estimates, (2) total number of infested trees, (3) number of trees to sample, and (4) methods of selecting sample trees and scaling the observed counts.

Using the 134-tree data base, infestations of various sizes were simulated (Pulley et al. 1977a, Foltz et al. 1977). The infestations were considered a population of infested trees stratified by the SPB life stage. Sample trees were selected and estimates made of the within-tree populations. The information was then extrapolated to all the trees within each stratum.

Ten procedures were evaluated by Pulley et al. (1977a). The single-level (5.0 m) TG-PDF procedure and the two-level (3.5, 6.5 m) TG-PDF procedure were compared for precision. Researchers chose these sample heights because they were among the most precise of the single- and two-level estimating procedures. Methods of selecting the trees were evaluated by comparing random selection with the intentional selection of the largest trees. Methods of extrapolating sample tree estimates to calculate within-spot estimates included scaling according to the proportion of the tree numbers, tree diameters, or infested phloem areas included in the sample.

The best precision was obtained by selecting trees with the greatest infested phloem area or the largest diameter. The least costly procedure for obtaining a desired level of precision consisted of selecting the trees of the largest diameter and sampling at the 5-m level. A guide to using these estimation procedures has been published (Foltz et al. 1977).

Estimating Areawide Populations

Stephen and Taha (1976) outlined the following procedure for sampling SPB in an area of Arkansas consisting of several to many infestations: (1) Determine the number of samples for the sample unit area to be used. (2) Survey the area to estimate the number of spots. (3) Allocate a proportionate number of the samples to each infestation, depending on the number of infested trees with pupae or callow adults. (4) Subdivide the infested bole into at least three sections and sample each section.

Stephen and Taha expanded these techniques to permit estimations of the total numbers of SPB or their natural enemies within a defined area. The methods were specifically designed to provide the forest manager or pest control specialist with a tool to determine if treatment was necessary. Two methods have been described – one fairly simple but less precise, the other requiring intensive data collection and resulting in more precision. The simple method, which I will call the "prediction" method (Stephen and Taha 1979b), is practical, does not require intensive within-tree sampling, is relatively inexpensive, does not require highly trained specialists nor specialized sampling and X-raying equipment, and reduces the time between data collection and estimation. The other method is more complicated and does require within-tree sampling and the analysis of those samples. I will refer to this method as the "sampling and tree measurement" method (Stephen and Taha 1979a).

Both methods incorporate aerial survey information with ground survey information, and estimations of age structure, beetle density, and infested bark area. The aerial survey determines the location and relative number and size of infestations within a given area. The ground surveys for the prediction method locate each infestation to assess the predominant life stage at breast height, to measure the d.b.h. of each infested tree, and to obtain an estimate of the average height of infestation within each infested spot. In the prediction method, the authors have assumed a constant life stage along the length of the bole. Of course, this is rarely the case, but a large error should not be incurred if a relatively large, heterogeneous population is measured.

Estimates of beetle density were obtained for the prediction method from a 3-year data base of 181 trees in Arkansas. During all seasons, samples were collected from the full spectrum of infestation sizes available there. Stephen and Taha felt that such data should provide a reliable range in mean densities for each SPB life stage that would be encountered if intensive sampling were conducted over a large area.

An alternative to this simple, less precise approach is to determine the mean densities for infested trees in the study area using the "sampling and tree measurement" method. The procedures described above (Stephen and Taha 1976) represent a part of the sampling and tree measurement method.

To estimate the absolute population density in a given area, two variables are required: an estimate of the average beetle density, which can be obtained by either of the two methods described above, and an estimate of the total infested bark area. Using the 181-tree data base, the investigators calculated infested bark areas. A model was developed to predict infested bark area based upon d.b.h. measurements. But the authors felt a measure of the height at the top of the infestation (HTI) was also necessary because a control treatment could have an influence on the physical limits of the infestation. The trees were classed by HTI and d.b.h. A table of infested bark areas was prepared using the d.b.h. classes and height classes represented in the data bank. This table is used in predicting areawide population densities.

Stephen and Taha developed an alternative model for estimating infested bark area. They found the tables presented by Foltz et al. (1976b) to be inadequate since a substantial number of infested trees in Arkansas were in a size class not included in the tables. However, the techniques are quite similar and the differences are insignificant. This model is used in the "sampling and tree measurement" method. The amount of infested bark over the entire area is obtained by multiplying the average infested bark area per tree by the number of infested trees in the area.

Given the estimates of average beetle density for each life stage, plus an estimate of the total infested bark area, investigators can readily obtain an estimate of the total beetle population in an area. Stephen and Taha (1979a and b) compared the two methods for estimating total SPB populations. The sampling and tree measurement method produced an estimate of SPB attacks (on 16 trees) of 188,235 ± 18,929. Using the prediction method, the researchers obtained an estimate of 164,310 ± 14,922. Although the population totals differ by 13 percent, a substantial area of overlap occurs between the confidence limits of the two estimates.

Monitoring Emerging SPB Populations

Thus far this chapter has dealt with monitoring infested trees and sampling populations within infested trees. Since a high percentage of the SPB's life cycle is spent within an infested tree, this is not unreasonable. But a significant, though small portion of the life cycle is spent in flight to new host trees. Monitoring or sampling dispersing populations is extremely difficult. And the technology for doing this is not as well developed as the technology for sampling within-tree populations or for monitoring bark-beetle-caused tree mortality from the air.

The use of pheromone traps for monitoring beetle dispersal has been discussed in Chapter 5. Procedures for quantitatively estimating between-tree mortality based upon observations of spot growth and within-tree population were also covered. Here we will discuss a technique that has been developed to monitor beetles as they emerge from an infested tree. The implications of this technique are far-reaching since it would allow researchers to identify the source population of a newly infested tree. Therefore, it has applications for beetle dispersal studies.

The procedure involves the use of radioisotope tagging as reported by Moore and Taylor (1976), Taylor and Moore (1978), and Moore, Taylor, and Smith (1979). In selecting a potential tagging isotope, the authors were looking for the following properties: (1) The material should be able to soak into the bark of treated trees or stick to the outside and adhere to emerging beetles. (2) The isotope must have a half-life that will allow for the detection of SPB that have emerged and attacked another tree. (3) The material must not adversely affect the beetles' behavior.

Moore and Taylor found that emerging beetles carried the tag (^{32}P) from infested bolts to fresh bolts and were still tagged after entering the fresh bolt. The investigators concluded that part of the radioactivity rubbed off during excavation because frass and pitch collected from the entry holes were also radioactive. When the experiment was repeated on living trees, the pitch tubes were found to be radioactive and could be detected with a portable ratemeter. The beetles from treated bolts could be identified for at least 19 days, well beyond the 14-day half-life of the isotope.

The ^{32}P tagging technique was successfully applied in the field to evaluate the dispersal and attack potential of beetles emerging from felled brood trees. (This was done because cut-and-leave is a recommended control tactic in some States.) An infestation as far as 365 m from the felled trees was found, and 75 percent of the 12 infested trees contained radio-tagged pitch tubes. Radioactivity could still be detected 41 days after the study began. Other studies (Coster and Johnson 1977 unpublished) have had mixed results with the ^{32}P tagging technique.

Predicting Population Potential

Models for predicting the potential growth and expansion of a southern pine beetle population have been developed at the spot level and the area level. Models at the spot level have been referred to as "spot growth" models. For a more detailed discussion of population modeling, *see* Stephen, Searcy, and Hertel (1980).

Spot Growth Models

Regression Models

Hedden and Billings (1979) monitored the growth of 62 east Texas infestations during the summers of 1975 and 1977. Field crews visited the infested spots upon first detection and again at 2-week intervals during the summer or until the individual spots became inactive. Two thresholds of summer spot growth activity were identified. First, infested spots having 10 trees or fewer seldom experienced further tree killing. The proportion of infested spots that became inactive was inversely related to initial number of brood trees. Second, when rates of attack exceeded ca. 2.5 trees per day (>80 active trees), spot expansion became largely independent of stand density. Between these thresholds, spot expansion was correlated with the number of infested trees per spot, total BA, and average d.b.h.

Two increase ratios were calculated to compare infested spot growth trends among spots and among years. These were:

$$\text{Spot Growth Index (SGI)} = \frac{\text{BA of new trees killed/day}}{\text{BA of active trees at first visit}}$$

and

$$\text{Active Tree Index (ATI)} = \frac{\text{BA of active trees at day 30}}{\text{BA of active trees at first visit}}$$

Sample plots were then categorized into four groups based upon spot growth trends: (1) no infestation growth (ATI or SGI = 0); (2) declining growth ($\text{ATI} \leq 0.8$); (3) static growth ($0.8 < \text{ATI} < 1.2$); and (4) increasing infested spot growth ($\text{ATI} \geq 1.2$).

The mean rates of spot growth in summer-infested spots varied among years, directly reflecting the annual changes in areawide beetle population levels. As a result, the spot growth models of Hedden and Billings (1979) are appropriate only for increasing or peak populations in the Gulf Coast region during summer months.

Hedden and Billings's models were tested in 24 infestations located in Texas, Louisiana, and Mississippi, but principally in Louisiana (Twardus, Hertel, and Ryan 1978). The test was run during a general collapse in populations: 18 of the infestations were inactive by the second visit. The remaining six spots were inactive by the third visit. The results do not compare well with those of Hedden and Billings (1979). For example, of the six infestations in which additional tree mortality occurred, four had 30 or more active trees at the initial visit. Of the 18 spots that went inactive, seven had 30 or more infested trees at the initial visit. Hedden and Billings found that all infestations with 30 or more infested trees continued to grow. Basal area and average d.b.h. did not significantly differ between active and inactive infestations. They also observed that spots which later became inactive had no freshly attacked trees. In the Twardus team's study, however, the number of freshly attacked trees was not found to be correlated with additional tree mortality.

The results discussed in Twardus et al. (1978) do not invalidate the spot growth models of Hedden and Billings (1979) – they simply emphasize our lack of understanding about what causes a general collapse in SPB populations, as occurred during the three-State study. Hedden and Billings point out that their models are appropriate only for increasing or peak beetle populations. And, of course, it is during such times that the forest manager is most concerned about timber losses.

A nonlinear spot growth model (Reed et al. 1980) was developed using the data collected by Hedden and Billings. The model simulates the spread of SPB infestations using stand-level variables. The model consists of two principal functions: (1) a function to predict the rate of spread, in terms of trees killed per day, and (2) a function to predict the probability of a spot becoming inactive. The model was tested on 11 infestations from northern Georgia and underpredicted the total number of trees killed by 6 percent. It was not very precise in estimating damage from individual infestations, however.

Moore (1978) and Moore, Hertel, and Bhattacharyya (1979 unpublished) developed a trend predicting procedure that relies almost exclusively on evaluating beetle population parameters – specifically, attack:emergence ratios determined from bark samples taken during the first visit to an active spot. When the attack: emergence ratio (A:E) exceeded 1:10, the active spot was considered to be increasing. That is, the spot would have 1.5 times as many dead and infested trees at the second visit as it had at the first visit. If the A:E ratio fell between 1:5 and 1:9.9, the infested spot was considered static. That is, the number of dead and infested trees at the second visit would be between 0.5 and 1.5 times as great as at the first visit. The infested spot was considered to be decreasing if the A:E ratio fell below 1:4.9. In that case, the number of dead and infested trees at the second visit would be less than 0.5 as great as at the first visit.

The time between first and second visits of 4 months was considered adequate for summer predictions, when infestations were growing rapidly. Timing of sampling was critical. Bark samples had to be taken at 2 and 5 m from recently abandoned trees. If sampling was too late, large portions of the egg and brood galleries were obliterated by wood borers feeding in the inner bark. All beetle counts, from attacking adults to emerging adults, were determined from this one sample. In this respect, this procedure differs from all other sampling procedures discussed here.

Two subcategories (static-declining and static-increasing) were added, to account for infestations where the beetle activity was static (A:E 1:5 – 1:9.9). To make this prediction, the investigators examined secondary factors. These included percent brood emergence, relative amount of disease, length and condition of egg and larval galleries, number of clerid larvae, number of SPB emerged per unit area, number of infested trees, and pine BA.

In 11 infested plots located in the Georgia Piedmont, Moore's team concluded that if those infestations classified as increasing had been removed, 80 percent of the subsequent damage would have been prevented. If those infestations classified as increasing or static-increasing had been removed, 96 percent of the damage would have been prevented.

Moore et al. (1979 unpublished) developed a continuous model to predict the number of trees killed over a given period. The only variable in the equation was the attack:emergence ratio. Continued evaluation of the models and procedures described by Moore is in progress.

All models that have been discussed to this point are statistical regression models. In other words, these models are used to summarize data collected under changing environmental conditions. Such models highlight the important variables contributing to the system's dynamics. However, they can be used only under conditions similar to those that prevailed when the original data were collected.

Mechanistic Models

In contrast, biophysical mechanistic models require an understanding of the mechanisms responsible for the observed behavior. As explained by Coulson et al. (1979c), this modeling approach describes processes in mathematical terms and then integrates them into a model of the entire system. If the individual hypotheses are correct, such a model would allow for predictions outside the range of the original data.

Often a combination of the statistical approach and the biophysical approach can be used in developing the system model. But usually the model will be predominantly one or the other. The following is a description of a predominantly biophysical spot growth model.

TAMBEETLE

The TAMBEETLE model (Coulson et al. 1979c) is a biophysical mechanistic spot-growth model that accounts for the reproduction and mortality of beetles within an infested spot. The model is organized around trees which are active (currently infested), inactive (dead and vacated trees), or potentially active (trees that are in close proximity to active trees). The basis of the model is a series of submodels that are mathematically interconnected, to account for beetle reproduction and mortality. At present, the component submodels simulate the following processes: (1) brood emergence, (2) oviposition, (3) reemergence, (4) beetle allocation, (5) pheromone emission and distribution, and (6) tree drying.

The model follows the progress of the developing beetle cohorts as well as the infested tree cohorts. At present, the development, reproductive, and mortality components of the model are driven by temperature only. But there are plans to include a moisture variable.

The model is set up on a daily increment basis, and all the temperature-driven processes are calculated at the start of each day. Beetle cohorts initiate flight, attack trees, construct galleries, lay eggs, develop, pupate, and emerge. Emergence follows an extended probability distribution whose shape is determined by the previous temperatures experienced by the brood. The between-tree population, which consists of all emerged and reemerged beetles, forms the nucleus for beetle attack on active and potentially active trees. Figure 6-16 illustrates the organization of the model.

The TAMBEETLE model allocates the between-tree population to active and potentially active trees. Potentially active trees are defined by their proximity to active trees. The effective distance is a function of the size and shape of the pheromone plume emanating from the active tree. This plume, in turn, is affected by climatological conditions. Once the beetles have been allocated (equivalent to landing on a tree), the probability of a successful attack is a function of the amount of gallery construction already completed within the tree (equivalent to an inhibitor of further attack). If the beetles do not attack, they are available to attack other potentially active trees.

A potentially active tree becomes an active tree, in the model, if it has become "susceptible" to beetle attack. Susceptibility is a tree vigor parameter measured by the number of beetles initially required to overcome the natural resistance of the tree. Once this resistance is overcome, the tree is subject to mass attack (aggregation).

At the end of each day, the between-tree populations are combined for allocation the next day. If the between-tree population is not successful in colonizing a tree, the beetles will disperse, retarding spot growth. Factors that limit the growth of a spot are high tree resistance, wide tree spacing, and weather factors which interrupt pheromone communication and/or flight activity.

Little or no knowledge of computer technology is required to use the model. An interactive question-and-answer routine is available for the

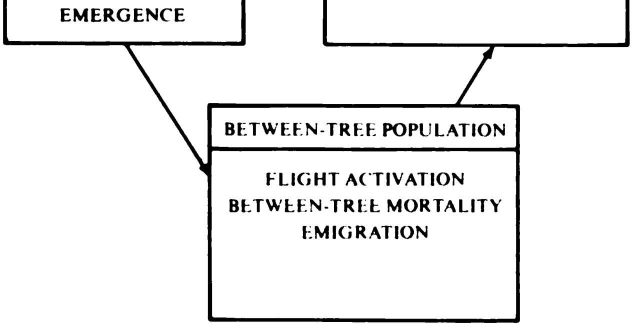


Figure 6-16. – Population growth sequence followed in the TAMBEETLE infestation dynamics model.

user to input information about an infested spot. The routine is set up to follow the sampling procedure described by Coulson et al. (1976e) and Foltz et al. (1977), and reviewed earlier in this chapter. The input values that the user must supply to activate the model are (1) the number of active trees, (2) an estimate of the beetle population (the number of beetles per bark sample), (3) the infested phloem area for each tree, (4) the mean and standard deviation of all d.b.h. and infested bole height measurements, (5) mean bark thickness, (6) tree susceptibility (assumed to be between 100 and 500 beetles per tree), (7) immigration (usually set at 0), (8) pine BA, and (9) daily minimum and maximum temperatures. Other input parameters that will be added to the model include wind, cloud cover, and precipitation. An effort is being made to reduce the number of input parameters so as to make the model more practical for pest control specialists.

The user can then output a vast array of predicted information for any given day. The output could include the numbers of trees killed, trees under attack, trees with brood, attacks per day, reemerging beetles per day, and emerging beetles per day. The model cannot provide the specific geometry for the location of infested trees. Nor is it a spot initiation model. A cohort of beetles and infested trees must be present to activate the model.

Figure 6-17 illustrates the flow logic of the model. The first three blocks initiate the model. The next six blocks are recycled on a daily basis. Field validation is complete for some components of the model and is in progress on the others.

Arkansas Spot Growth Model

Another spot growth model was developed by Hines (1979) and Hines, Stephen, and Taha (1980). This model predicts not only spot expansion but also the monetary loss on beetle-killed pulpwood and sawtimber, based on current stumpage prices.

Figure 6-18 illustrates the information flow within the model. It shows the basic SPB life cycle with assigned rates and variables. Rates (bottlenecks) regulate the rate of flow of materials through the system and thus control the magnitude of change. Variables alter the rates through time.

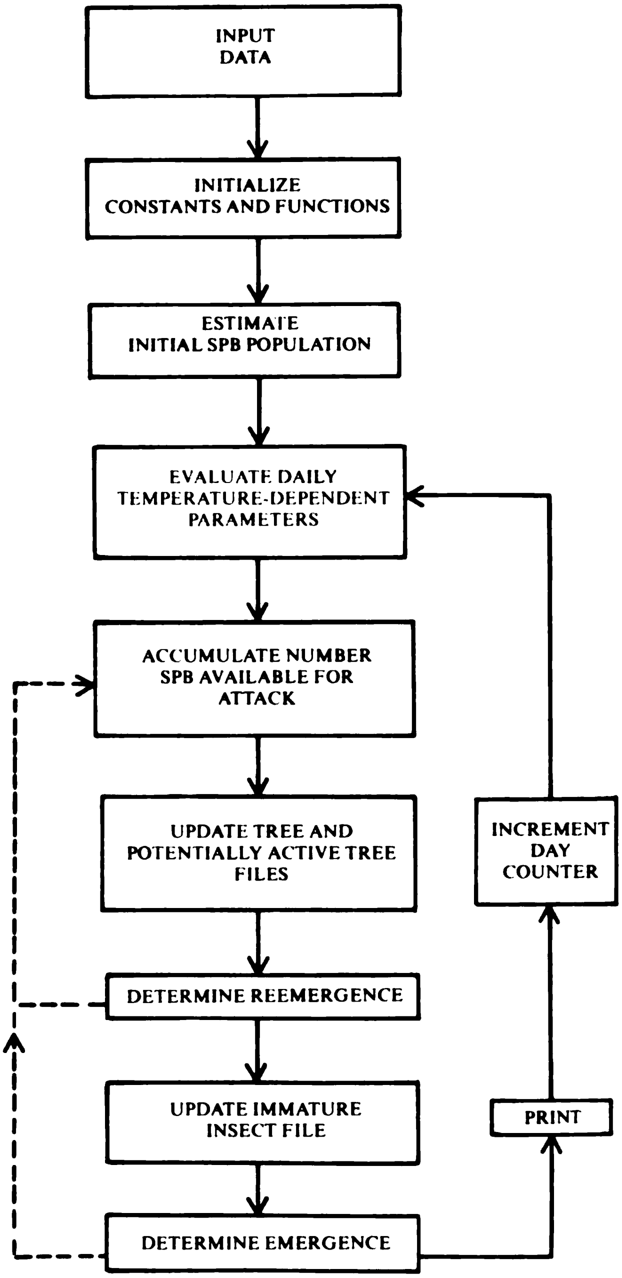


Figure 6-17. – Information flow chart for the TAMBEETLE infestation dynamics model.

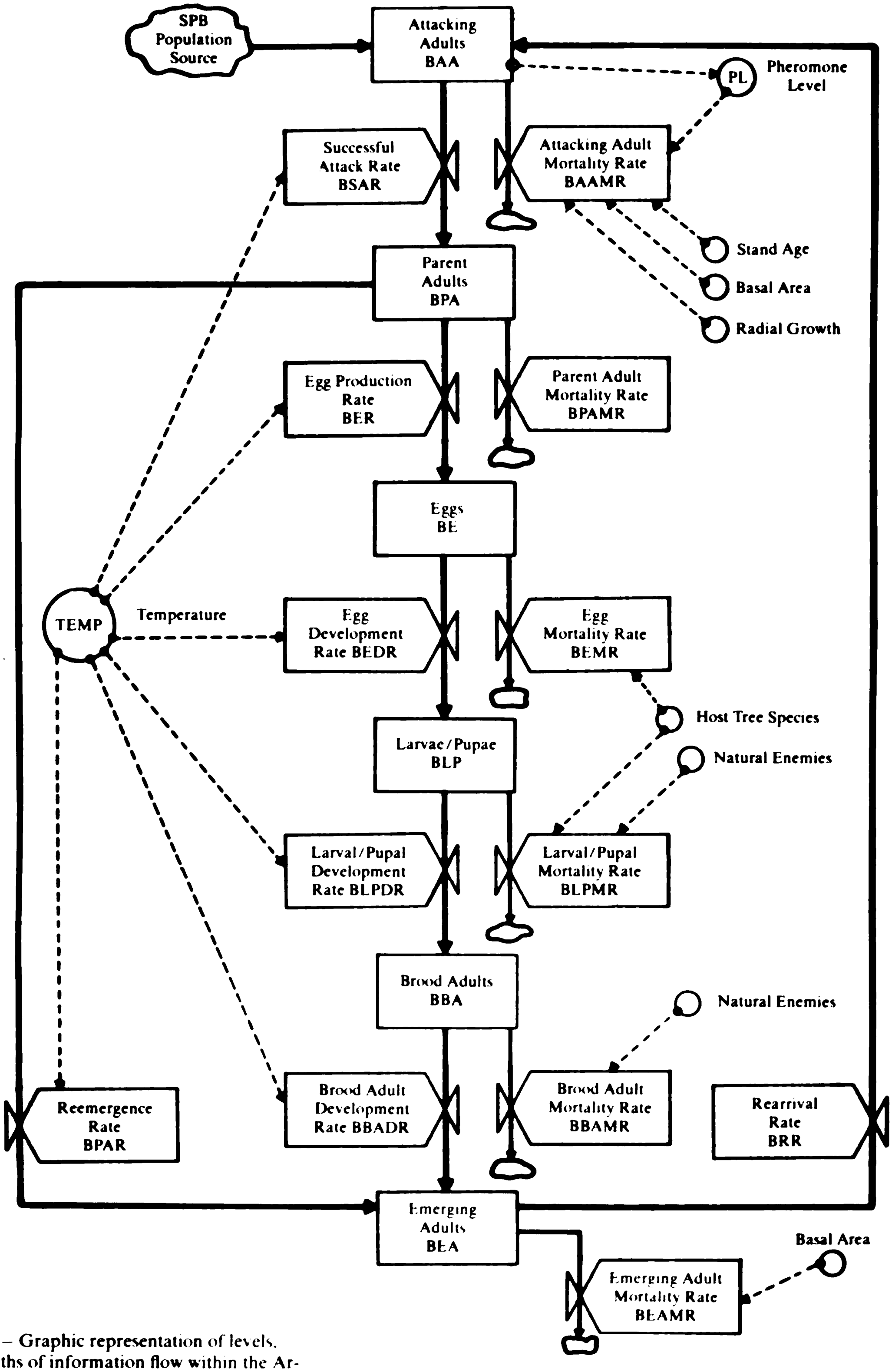


Figure 6-18. – Graphic representation of levels, rates, and paths of information flow within the Arkansas spot growth model.

The input parameters necessary to initiate the model can be obtained by a forest technician. A computer interactive question-and-answer program is available. The forester or pest management officer needs only a description of site and stand conditions. The input values are (1) date of observation, (2) length of time the user wishes to simulate, (3) geographic location, (4) BA, (5) tree growth rate, (6) tree age, (7) species composition of the stand, (8) d.b.h. class, (9) a tree count by SPB life stage (parent adult, larvae, pupae, or brood adult), (10) the average height at the top and the base of the infested portion of the trees, (11) average circumference at the top of the infestation and at breast height (optional), and (12) current stumpage prices.

Detailed information on beetle density is not needed because the model assumes an average density for each life stage based on previous intensive within-tree sampling. An estimate of the infested bark area is converted to numbers of beetles in each life stage.

The mortality rates of the various life stages are affected by the stand's basal area, growth rate, age, and species composition. The model employs geographic area and date to access the appropriate temperature files. And, of course, the current stumpage price is needed to assign a dollar value to the predicted timber loss.

The model outputs a weekly prediction of the number of dead and infested trees classified by life stage, a volume estimate of the timber loss, and a monetary value of that loss. The infested tree prediction is obtained by converting the number of beetles to an equivalent amount of infested bark and dividing that by the average amount of infested bark per tree.

The Arkansas model has certain assumptions and limitations. Many of these can be refined as more data becomes available. For example, the system is closed, allowing neither emigration nor immigration of flying adult beetles. The food supply is unlimited, and there are no physical barriers within and no disturbances of the habitat. Average beetle density and average infested bark area are constants. Finally, the model is appropriate only for the months of April through September and for a period of not more than 90 days.

Areawide Modeling Efforts

Several efforts have been made to model southern pine beetle activity on an areawide basis. Since forest management plans are developed for large areas and the cost for management's decisions and actions is frequently budgeted well in advance of actual implementation, some means of predicting SPB incidence and severity is desirable. The following is a discussion of those modeling efforts that are attempting to address this question.

FRONSIM

Leuschner, Mattney, and Burkhart (1977) developed a simulation model to estimate timber mortality in future years over large geographic areas. The Frontalis Simulator (FRONSIM) estimates damages by simulating the number of infested spots for a given year. This model, although rudimentary, is available for use now with only basic data required. After estimating the number of infested spots in a year, the model applies a frequency distribution of the number of trees per spot to estimate the total number of trees. It then applies a frequency distribution of infested tree d.b.h. measurements to estimate the number of trees in each d.b.h. class. Timber mortality and monetary value are estimated using a local volume table and current stumpage prices. The procedure can be done for any number of years in the future and summed over all years. The number of spots can be simulated by a completely random model or a regression model.

This model has some built-in assumptions and limitations. First, because the model averages the results for any one year, severe outbreaks or collapses cannot be predicted. In fact, extreme beetle activity cannot be predicted. Second, FRONSIM estimates the value of timber lost in future years but does not include other, less tangible losses such as the impact on the subsequent stand, recreation, wildlife, or water.

Third, the areawide data required for the model are relatively unavailable at this time, although some data are being collected. Lack of data naturally hinders validation and implementation. Finally, the model provides predictions on a regional basis by averaging the experience on all infested lands in the region and projecting it into the future. Thus it is not useful to the small landowner.

Estimating Incidence of Outbreaks in a Stand

Daniels et al. (1979) discussed a methodology for estimating the probability of an outbreak (= incidence) in a stand. The method does not predict the severity of the infestation. It is based upon a logistic probability function with total basal area and the proportion of the BA in pine as the independent variables. Other variables (e.g., average height, age, average current radial growth, and soil variables) were also evaluated but gave similar results.

Table 6-1 documents the results of fitting the model to data collected from disturbed and undisturbed, natural stands. Disturbances included lightning strikes and harvesting activity during the past year. Table 6-1 shows that the probability of an infestation increased as total BA and proportion of pine BA increased. And the probabilities in disturbed stands were considerably higher than in undisturbed stands.

Daniels et al. concluded that the model has two major advantages. It provides a continuous measure of probability, even in low-susceptibility stands – a probability that can be partitioned into categories within the context of the users' objectives. Also, the probabilities can be used in more sophisticated decision guideline models or outbreak severity models.

Hicks, Howard, and Watterston (1980) also developed a methodology for estimating the probability of an outbreak in a stand. The model was developed by a stepwise discriminant analysis and requires pine BA, average tree height, and a categorical evaluation of landform (e.g., flood plain, lower slope, ridge) as input parameters. The predicted probabilities of attack were valid for data collected in east Texas when assumptions were made about the beetle population level. Thus the actual frequency of attack depends on both stand characteristics and SPB population levels.

DAMBUGS

By combining a spot growth model with a spot incidence model, it should be possible to derive an estimate of southern pine beetle damage for a region. DAMBUGS (Reed 1979 unpublished) represents such a combined model. It utilizes the spot incidence model of Daniels et al. (1979) with a spot growth model that relies solely

Table 6-1. – Test probabilities for *Dendroctonus frontalis* incidence in nonplantation stands. (From Daniels et al. 1979.)

Total basal area		Proportion pine basal area					
(ft^2/ac)	(m^2/ha)	0.5	0.6	0.7	0.8	0.9	1.0
Undisturbed Stands							
50	11.48	0.0016	0.0022	0.0031	0.0043	0.0060	0.0083
100	22.96	0.0027	0.0037	0.0051	0.0071	0.0099	0.0137
150	34.44	0.0044	0.0061	0.0085	0.0118	0.0164	0.0226
200	45.93	0.0073	0.0101	0.0141	0.0195	0.0269	0.0371
Disturbed Stands							
50	11.48	0.0014	0.0022	0.0036	0.0056	0.0093	0.0150
100	22.96	0.0045	0.0073	0.0117	0.0188	0.0301	0.0478
150	34.44	0.0135	0.0217	0.0345	0.0547	0.0855	0.1312
200	45.93	0.0396	0.0625	0.0972	0.1482	0.2195	0.3126

on stand conditions as input parameters (e.g., forest type, stand age, site class, total BA, mean d.b.h.). In this system, the incidence model estimates the size of each infestation. The damage from all simulated infestations is summed to arrive at an estimate for the region. SPB population parameters are not included in the model.

Modeling the Endemic-Epidemic Cycle

Modeling the severity of southern pine beetle activity over large areas is still at the conceptual level. Models that can predict with a reasonable degree of accuracy when and where outbreaks are likely to occur would undoubtedly be a useful management tool. Gold, Mawby, and Hain (1980) have set up a framework for modeling the transition of SPB activity from the endemic (low level) to the epidemic state. By necessity, the model includes the insect-host interaction in a hierarchy of four levels: the individual tree, local neighborhood (group of trees that influence the dynamics of a given tree, or all trees that are influenced by a given tree), quasi-uniform patch (the partitioning of a larger region), and large region. Individual trees can be described in terms of attack threshold, potential brood productivity, stress state, relative attractiveness to beetle attack, pheromone emission, and beetle production.

Certain stress factors substantially reduce the susceptibility and the brood productivity of the tree. This effect is made the basis of a distinction between endemic and epidemic modes of infestation within an individual tree. An endemic mode tree may have been predisposed to SPB attack by lightning strikes, *Ips* bark beetles, water stress, or disease (Hain 1980 unpublished). Thus its susceptibility and capacity for beetle production have been substantially lowered. In this mode SPB is a secondary invader. The span of time over which beetles attack and subsequently emerge is commonly longer than in epidemics. Since brood emerge over a longer period, their ability to attack en masse is lessened. An epidemic mode tree is mass-attacked by SPB as the primary invader, resulting in the tree's death. In the modeling framework, the degree to which epidemic mode trees dominate the dynamics of the neighborhood, patch, and region is made the basis of the endemic-epidemic transition at these levels.

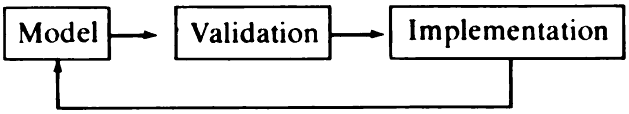
The dynamics of a local neighborhood are determined by the states and interactions between the individual trees of which it is composed. The dynamics of a patch are determined by the states and interactions of the local neighborhoods, thus allowing for the introduction of environmental fluctuations as disturbances within the patch. The dynamics of the region is determined by the states and interactions between the patches of which it is composed, allowing for consideration of regional differences.

The regionwide description can be in terms of a mosaic of probability distributions of endemic mode and epidemic mode trees. Hopefully these descriptions can be drawn from a common distributional family and quantified for each patch. The probability distributions of each patch must be adjusted for the microheterogeneities, such as edge effects and proximity to infested trees. Therefore, it is clear from this framework that an understanding of the overall system requires a consideration of all four levels in the hierarchy (tree, neighborhood, patch, and region).

Model Validation

Little has been stated about model validation. Hines (1979) points out that a model is valid when it can predict changes with reasonable accuracy. The first stage of model validation is to determine if the model duplicates previously obtained field data. This is done implicitly in estimating unknown parameters. The second stage of validation is carried out concurrently with implementation of the model. The results of the model's prediction are compared with what is observed in the field.

As observed and predicted changes occur during implementation, model improvements can be initiated. This procedure is repeated indefinitely until the model predicts changes with a reasonable degree of accuracy. Thus the model is in a constant state of evolution from a primitive to a sophisticated structure.



Of course, changes in the model structure must be based upon a sound understanding of the beetle's biology and its interaction with the host.

Summary

A great deal of subject matter and information has been covered in this chapter. At first glance, the topics may appear unrelated. However, the underlying theme has been the development of procedures for monitoring and/or predicting population trends. Depending upon the objectives of the user, a procedure can be used singularly or in conjunction with other procedures. As an example of a user objective that would require several of the procedures discussed in this chapter, let us consider a case study of a control treatment evaluation. This case study was discussed during a recent symposium (Smith and Twardus 1979). The objective is to evaluate cut-and-leave as a tactic for controlling SPB over a large area. The change in timber volume loss and the effect on beetle populations needed to be determined.

Coulson et al. (1979c) outlined a stepwise protocol for evaluating treatment tactics. The first step is to consider the probable effects of the proposed treatment in light of current knowledge on beetle dynamics and host tree interactions. For the purpose of illustration, we will assume that cut-and-leave can affect within-tree survival and dispersal mortality. The second step is to simulate the infested spot conditions in both the presence and absence of the treatment using the TAMBEETLE population dynamics model. Variables can be manipulated to test the treatment under a variety of conditions and thus indicate the conditions under which the treatment would be effective. This step eliminates expensive field testing of tactics with low utility potential. The third step is to compare the cost of applying the treatment with the value of the expected timber protected.

If the procedure still appears promising, the next and most expensive step is field testing. For discussion purposes, two areas with about equal distribution of susceptible host type and active spots could be used as treated and check blocks, respectively. Sequential aerial photography with navigation guidance by Loran-C can monitor tree mortality and infested spot proliferation before and after treatment. PISYS can store and analyze the aerial data. With ground checking, volume loss can be estimated. To determine within-tree survival in selected treated and untreated areas, the within-tree sampling and estimating procedures (Coulson et al. 1975a, 1976e) should be employed. The areawide populations can be estimated in both areas using the approach of Stephen and Taha (1979a and b). Also the probability of beetle's emerging from treated areas and contributing to infested spot proliferation can be examined using radioisotope tagging techniques (Moore and Taylor 1976, Moore et al. 1979, and Taylor and Moore 1978).

The final step would be to reevaluate costs and benefits in light of the experimental results. If the procedure becomes operational, continued monitoring and evaluation can be done using multistage sampling techniques (Ghent and Ward 1977 unpublished, and Schreuder et al. 1977 unpublished and 1979).

Impacts of the Southern Pine Beetle

William A. Leuschner[1]

7

Introduction

In the most general terms, the impact of the southern pine beetle is that it kills trees. But this phenomenon may be just the first in a series of events. SPB-related tree deaths cause openings in the forest canopy, and these openings affect the amount of sunlight reaching the understory below. Changes in sunlight alter both the overstory and understory species that grow back after a beetle infestation. Canopy reduction also changes water yields. This chain of cause-and-effect relationships can go on and on, until an economic impact is reached. The purpose of this chapter is to examine economic impacts of the SPB, as they relate to forest products (timber, recreation, wildlife, etc.). Statistical procedures exist for estimating some economic impacts in quantifiable units. By using these procedures, foresters can make pest management decisions on a carefully thought out, rather than intuitive, basis.

"Impact" is a word with a variety of meanings (*see also* Stark 1979 and Johnson 1973). For our purposes, an *impact* is simply any change brought about in the forest by an insect population. It may be positive or negative, affecting either flora or fauna.

A *physical impact* is any impact measurable in physical units, such as a change in numbers of woodpeckers or cords of pulpwood. A physical impact may or may not be of value. An *economic impact* is any change in (1) a socially useful forest product, (2) socially useful items needed to produce a fixed level of forest products, or (3) the distribution of forest products, the income derived from them, or their cost of production. Thus economic impact has three elements: production level, inputs for production, and the distribution of production and costs. This chapter will focus mainly on the first element – the beetle's impact on forest products.

If a result of beetle activity can be measured in physical units and affects at least one of the three economic impact elements, then the activity is said to result in a *physical economic impact.* In addition to measuring the result of beetle activity in physical units, its value to society must be determined. *Social value* is often estimated by the market price of the product that is affected. The product of a physical economic impact and social value is the *impact* value. To illustrate, consider this hypothetical example of the impact value of SPB in a campground area:

Physical economic impact	×	Social value per unit	=	Impact value
2,000 fewer visitor days at campground	×	$5.00 per visitor day	=	$10,000

But determining the impact value is not as straightforward as the campground example suggests. Difficulties may arise. It may be hard to quantify the physical impact in readily understood units. For instance, with the campground example, one impact of SPB may be the loss of enjoyment experienced by campers using an SPB-attacked campsite. Scientists in human behavior may be able to quantify changes in enjoyment by using various indices, but foresters and pest managers would have a hard time using these. And it may be difficult, or impossible, to place a monetary value on some impacts. For example, even though we could measure the increased number of birds found in outbreak areas, we could not estimate their dollar value.

Sometimes, then, economic impact can be measured in dollars or physical units. In other cases, we may be able to state only the direction of a change, not its amount. Economic impact is finally determined not by our ability to measure but by the usefulness of the changed element to society.

We can also distinguish between *primary* and *secondary* impacts. A primary impact is caused by the direct action of the insect (killing a tree). A secondary impact flows from the primary impact (e.g., changes in water yields caused by the canopy reduction from the dead tree). The chain of secondary impacts can continue almost indefinitely ("for want of a nail . . . the war was lost"), until finally an economic impact occurs.

Forest managers are interested in southern pine beetle impacts precisely because they are

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economic — they affect products, inputs, or distributions desired by society. The economic impact must be assessed so society (governmental agencies or the private sector) can decide whether control efforts are worthwhile.

To assess beetle impact for a forest or an outbreak, we must aggregate the impacts of individual spots. The impact on one or several spots may be economic but not large enough to make control actions cost-effective. Aggregate impact must be assessed to make that decision. The aggregate attack configuration also affects impact and must be determined. The impact of a single 50-acre spot will be different from that of 100 half-acre spots. These differences are reflected in the secondary impacts on several diverse forest products.

Timber Impacts

When southern pine beetles kill trees, harvested volume may be sharply reduced. This reduced volume is due to either unsalvaged merchantable trees, harvesting trees ahead of schedule, or both. The value of salvaged timber may also be reduced by decay, stain or insect holes, or increased logging and handling costs. There may also be an impact on the stand replacing the one killed by SPB. The tree species in the subsequent stand may be more or less commercially desirable, so the stumpage price may change. Stocking can be either increased or decreased, resulting in a yield change. And regeneration may be delayed, resulting in increased management costs when the time value of money is considered. In the subsequent stand, other impacts unique to the individual attack and stand conditions may occur.

Physical Timber Impact

Timber impact determination is simple to outline but complex to apply. The physical impact on the original stand is the difference between the volume of timber that would have been harvested had the stand not been attacked and the volume of timber that was salvaged after the attack. Differences in product quantities (e.g., decreased sawtimber volume) should be taken into account. The volume and species in the post-SPB stand, plus those stands that would continue into perpetuity, should also be estimated. These are subtracted from the stands that would have replaced the original stand in perpetuity if it were unattacked and grown to full rotation. Thus, the difference in timber volumes harvested, by species and in perpetuity, is estimated for the stand with and without SPB attack. This difference is the physical timber impact.

Estimates of future timber volumes can be obtained with growth simulators. PTAEDA is one such model. It stimulates stand growth for loblolly pine plantations using individual trees as the basic growth units (Daniels and Burkhart 1975). It includes a stochastic element to provide for probability in the prediction function. Randomly chosen probabilistic factors are used to generate mortality and to represent microsite and/or genetic variability when projecting growth. Work is currently underway to include SPB-specific mortality. The response of stands to site preparation, thinning, and fertilization may be simulated and outputs are basal area per acre, number of trees per acre by diameter class, total stem cubic foot volume, total above-ground biomass, and frequency of tree mortality by diameter class. PTAEDA was developed for simulating tree growth and stand development in managed loblolly pine plantations, but a second version — seed PTAEDA — is under development for naturally regenerated loblolly pine stands (Daniels et al. 1979).

Present Net Worth Model

Next, the management costs and stumpage prices for the timber volumes are estimated and the present net worths (PNW) are calculated for the stand in perpetuity with and without the SPB attack. PNW calculations are not discussed here but may be found in forest or financial management texts. The difference in PNW with and without attack is the value of the economic timber impact.

This present net worth model, without the perpetual rotation or subsequent stand impacts, is

$$\begin{aligned}\text{Impact} &= PNW_{wa} - PNW_{woa}\\ &= \Delta D_1PQ + P\Delta Q + \Delta PQ + \Delta P\Delta Q\\ &\quad - D_2\Delta C - \Delta D_2(C+\Delta C) \qquad (1)\end{aligned}$$

where:

PNW_{wa} = present net worth per acre with attack
PNW_{woa} = present net worth per acre without attack
P = stumpage price per unit of volume harvested
Q = volume harvested per acre at rotation
Δ = algebraic change in the variable caused by attack
D_1 = discount factor for the present value of a single payment
D_2 = discount factor for the present value of a terminating series of payments
C = management cost per acre per year.

This model was demonstrated by Leuschner et al. (1978) using data from the Trinity District of the Davy Crockett National Forest in east Texas (Leuschner et al. 1976). The demonstration used the Timber Benefits Analysis Program (TBAP), which included the subsequent stand and perpetual rotations. The estimated value of the economic timber impact determined after the damages were done was $5,764 for 44.31 acres infested from July 1, 1974 to June 30, 1975.

These results were compared to the traditional timber impact model, which is the sum of (1) the volume salvaged multiplied by the difference between the salvaged and unattacked stumpage price, plus (2) the unsalvaged volume multiplied by the unattacked stumpage price. The traditional model estimate was $17,877 – over $12,000 more than the PNW model. The traditional model usually (1) underestimates damages by the value of timber lost due to premature harvest, (2) overestimates damages by the change in the present value of total revenue due to earlier harvest, and (3) overestimates damages by the change in the present value of the management costs no longer incurred. The volume lost due to premature harvest – the element traditionally underestimated – is generally small because SPB prefers to attack more mature stands. Hence the traditional model tends to overestimate SPB damages.

Both the PNW and traditional models assume that the observed stumpage prices for unattacked and salvaged timber reflect their social value. The salvaged stumpage price is usually less than the unattacked price because, it is assumed, the salvaged timber cannot be converted into the same products as the unattacked timber due to rot and decay. Also, the logging and milling conversion costs may be higher. Studies were performed to verify these assumptions. The economic timber impact could be decreased if conventional beliefs about rate and amount of deterioration are wrong and if the potential purchasers are informed of the facts. Impact could be decreased by increased salvage stumpage prices, increased amounts of attacked timber being salvaged, or both.

Timber Deterioration

Deterioration of beetle-killed sawtimber and pulpwood trees was studied in Virginia, North Carolina, and east Texas. Trees were harvested from SPB spots at different times after being killed by beetles and then sawn to determine the grade and yield of lumber. Lumber strength and pulping characteristics were determined with laboratory tests and were compared to results from green, unattacked trees from the same areas.

Both lumber grade and yield were lower from the beetle-killed logs. For example, in Virginia (Sinclair and Ifju 1979) the green logs yielded 71 percent high-grade lumber (No. 1 Structural, 8/4) from butt logs. Logs that had been dead for 20 months produced only 17 percent high-grade lumber (fig. 7-1). Yield, as measured by the lumber recovery factor, was only slightly reduced (fig. 7-2). Decreased yield from beetle-killed logs was mainly from increased slabbing and more cull boards.

Logically, the rate of sawtimber deterioration differed across the South. Recovery in the warm, humid east Texas region had dropped to about 75 percent of the control value at 90 days after the trees were killed (Walters, Weldon, and Rutherford 1979 unpublished). Similar recovery loss took 360 days in the cooler, drier climate of Virginia.

The strength of beetle-killed timber from Virginia was measured using standard toughness tests (Sinclair, McLain, and Ifju 1979) for trees dead 2, 12, and 20 months (fig. 7-3). About half to two-thirds of the strength was lost after the dead tree had gone through the first warm season, and there was no statistical difference between strength losses and time since death beyond that period. Similar results were obtained for radially loaded toughness tests.

Thus, the yield and grade recovery and strength of SPB-killed timber, although lowered, are still acceptable in many circumstances. An economic guide for purchasers of beetle-killed sawlogs (Sinclair 1979) takes these factors into account and illustrates how to calculate a break-even sawlog purchase price.

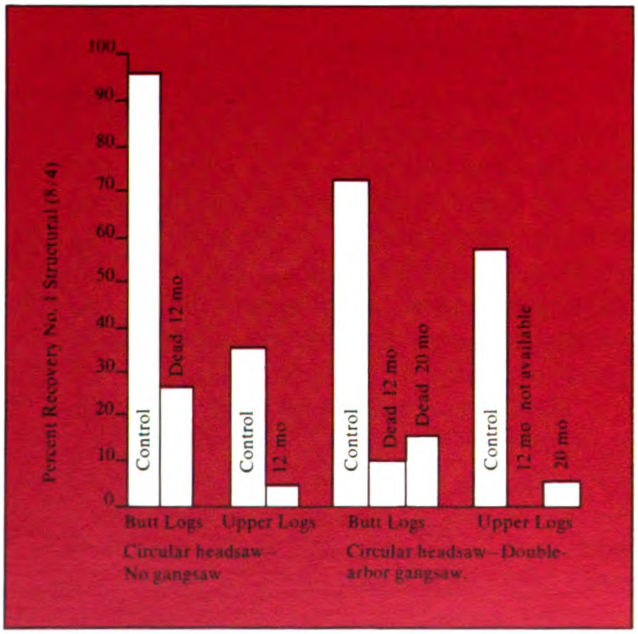
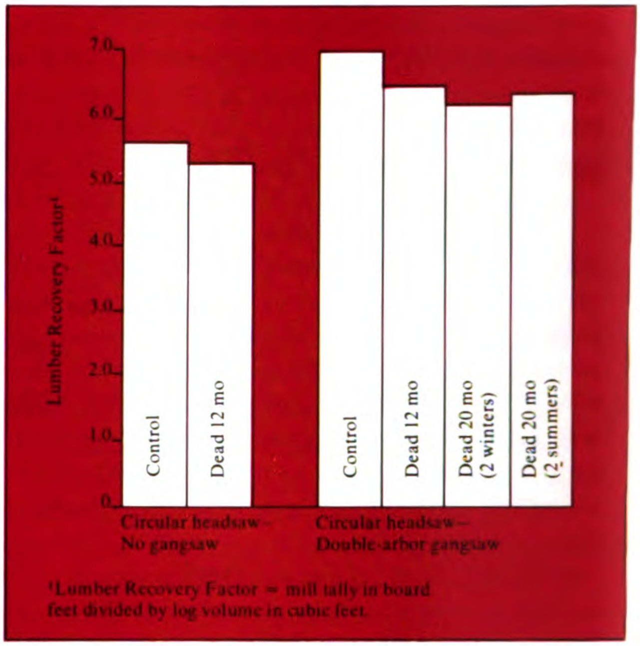


Figure 7-1. – No. 1 Structural Grade recovery from control and SPB-killed trees in Virginia.



¹Lumber Recovery Factor = mill tally in board feet divided by log volume in cubic feet.

Figure 7-2. – Lumber yield from control and SPB-killed trees in Virginia.

Gross Kraft pulp yield from SPB-killed timber was not significantly altered for up to 2 years after death in Virginia (Ifju et al. 1979) and 1 year after death in east Texas (Walters et al. 1979 unpublished). Again, differences in deterioration time are probably due to climatic differences. Paper properties (Canadian Standard Freeness, tear strength, and tensile strength) were somewhat less from beetle-killed trees. But wood scientists concluded that these trees could be pulped up to 24 months after death, depending on the climate, with only a slight effect on paper properties.

Beetle-killed timber may also be used for plywood, but the trees must be harvested quickly. Veneer grade and wide sheet recovery were evaluated in an operational plant in east Texas. They were unchanged up to 45 days after death but then decreased until the logs were unusable for plywood after 360 days (Walters et al. 1979 unpublished). Changes in moisture content of the beetle-killed trees cause some problems when normal production processes and schedules are used. Oven drying of plywood panels must be avoided, and gluing procedures may require alteration in order to produce plywood that consistently meets commercial standards.

Recreation Impacts

When southern pine beetles attack a high-density recreation site, recreation impacts occur. Tree death results in reduced shade and screening, leaves unsightly dead snags, and creates a safety hazard to recreationists. Three kinds of impacts can accrue: the cost of removing the attacked trees, the decreased satisfaction of those recreationists who no longer use the site because of the attack, and the decreased satisfaction of those recreationists who continue to use the site. The value of the economic impact can be estimated for the first two impacts but not for the last.

The cost of removing the dead trees may be estimated by a straightforward accounting procedure that accumulates the labor, equipment, and materials costs for the removal. Total cost will vary depending on the removal technique, the distance traveled to the recreation area, and other variables unique to the specific infestation. In one study, Leuschner and Young (1978) estimated the impact at $3.96 per tree.

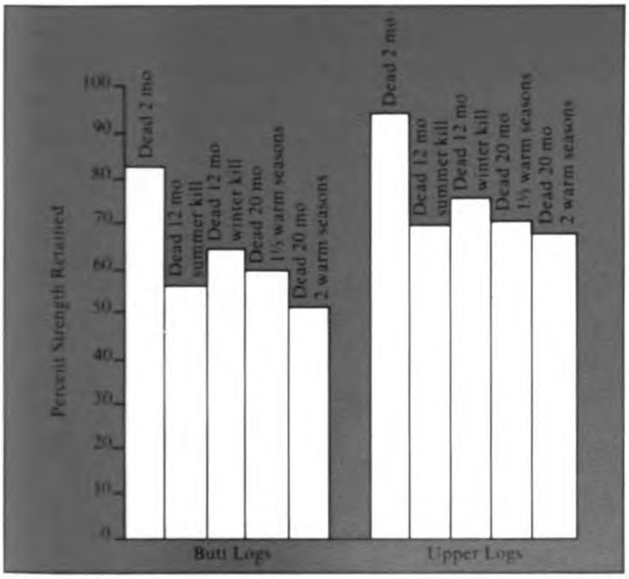


Figure 7-3. – Strength retained by SPB-killed trees in Virginia, measured by tangentially loaded toughness tests.

Estimating the value of the economic impact for recreationists who stop using the site is more complex. Outdoor recreation market values are seldom observable; therefore, a substitute measure is used. The Hotelling-Clawson-Knetsch (HCK) method (Clawson and Knetsch 1966), which uses travel costs as a price substitute in constructing a demand curve, has gained wide acceptance. The value of the recreation is the area under the demand curve, which is a measure of the recreationists' willingness to pay for the recreation and hence a measure of social value. SPB impact is estimated by including the proportion of the recreation site covered by pine crowns as an independent variable in the demand function. An SPB attack reduces the pine crown cover, causing a shift in the demand curve. The area under the shifted demand curve is the value of recreation on the site after the attack. The difference between the area under the curve before and after the attack is the onsite value of the economic impact on recreationists no longer using the site (fig. 7-4).

However, recreationists no longer using an attacked site may either stop recreating or may substitute another recreation site for the attacked

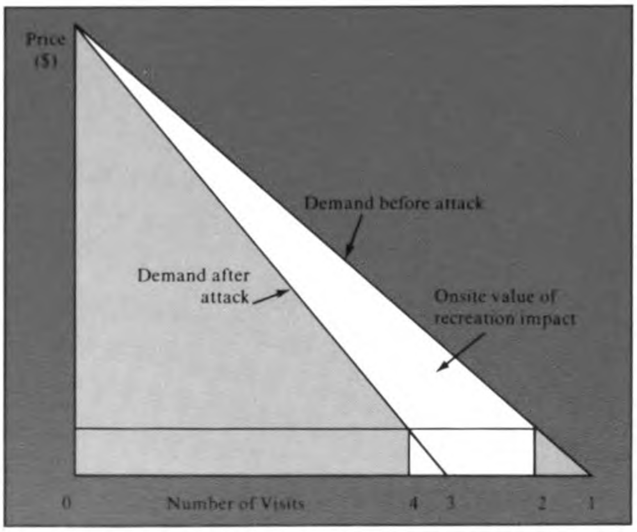


Figure 7-4. Technique for estimating recreation impact.

one. The social value of the substituted recreation site should be added back to reduce the onsite impact and provide an aggregate estimate of impact for the recreation system.

Leuschner and Young (1978) examined campground recreation during 1973 at the Rayburn and Steinhagen Reservoirs in east Texas. Demand functions were fitted for both U.S. Forest Service (USFS) and U.S. Corps of Engineers (COE) campgrounds because of their different characteristics. The general forms of the fitted equations were:

$$LFSV_{ij} = Lb_0 + b_1LC_j + b_2LTP_j + b_3LTC_{ij} + b_4LAOI_{ij} + b_5LP_i \quad (2)$$

and

$$LCOEV_{ij} = Lb_0 + b_1LC_j + b_2LTP_j + b_3LTC_{ij} + b_4LAOI_{ij} + b_5LP_i + b_6LTH_j + b_7LEH_j \quad (3)$$

where:

L = the natural logarithm of the variable or coefficient
FSV_{ij} = the annual number of visits from origin *i* to USFS recreation site *j*
$COEV_{ij}$ = the annual number of visits from origin *i* to COE recreation site *j*
C_j = the number of designated camping units without electrical hookups at site *j*
TP_j = the percentage of site *j*'s area covered by pine crowns
TC_{ij} = the total cost per visit from origin *i* to site *j*
AOI_{ij} = an alternative opportunity index, the sum of the number of reservoirs closer to origin *i* than the reservoir at which site *j* is located
P_i = thousands of households at origin *i*
TH_j = the percentage of site *j*'s area covered by hardwood crowns
EH_j = the number of electrical hookups for trailers at site *j*

The functions were fitted with estimates of travel costs and with travel costs plus an allowance for the time spent traveling. The estimated recreation value in 1973 was $7.7 million excluding travel time costs (but including travel costs) and $12.4 million with travel time costs. Onsite impact depends on the particular site, the amount of crown reduction caused by an attack, and whether travel time costs are included. For example, the impacts on the Cassells Boykin and Ebenezer sites were $22,000 and $35,000, respectively, at 10 percent crown reduction (table 7-1). The impact at the Ebenezer site increased from $35,000 to $110,000 to $415,000 as crown reduction increased from 10 to 30 to 90 percent. And the Ebenezer impact at 10 percent crown reduction without travel time cost was $35,000 and with travel time cost, $59,000. Adjustments for substituting unattacked sites within the recreation system were made for two campsites (Twin Dikes and East End) that are near the high and low end of the impact value distribution. These adjustments indicated that the recreation system impact is only 10 to 15 percent of the onsite impact (table 7-2).

The HCK methodology is useful for assessing SPB recreation impact, but system-wide substitution must be included and aggregate rather than onsite impacts must be used to guide management decisions. The methodology is limited to high-density use sites, however, and may be so complex as to be used only where obviously large recreation values exist.

Recreation impact can be relatively important, as indicated by aggregate impacts as high as $76,000 on the Twin Dikes site (compared to the $6,000 timber impact on the 85,000-acre Trinity Ranger District). This high potential impact may well justify intensive beetle prevention and/or suppression programs on these sites. However, recreation impacts should not be averaged with other forestwide impacts to justify larger control programs because the recreation impact is separable and site-specific. Certainly, the proportion of pines in the overstory stand will influence potential impacts on individual sites.

Esthetic Impacts

The deterioriation of attacked stands also causes an esthetic impact. Esthetic impact on heavily used sites is at least partially measured in recreation impacts. But esthetic impacts can also occur with dispersed recreation. This impact can be divided into that occurring when people view SPB damage from within the forest and when they view it from outside the forest. For example, hunters and hikers view damage from within a forest and pleasure drivers or casual passersby view it from the outside. One might speculate that damage viewed from within has less total impact because those viewing it are concentrating on another activity (such as hunting) or may see less of it per person because they cover less ground by foot, and because they are usually fewer in number.

The impact of SPB damage on those viewing

Table 7-1. – Estimated onsite campsite impacts without and with time cost, in dollars, east Texas, 1973.

	Percentage of pine crown coverage reduction							
	Without time cost				With time cost			
Site	10	30	60	90	10	30	60	90
Sam Rayburn COE Sites								
Cassells Boykin	22,221	69.553	151,228	262.929	36,985	115,452	249,642	429,326
Ebenezer	35,160	110.056	239,292	415.882	59,183	184,743	399,471	687,874
Hanks Creek	50,426	157.840	343,186	596,449	83,176	259,646	561,452	965,577
Jackson Hill	46,259	144,794	314,820	544,147	76,374	238,408	515,518	886,576
Mill Creek	33,822	105,865	230,179	400,045	55,986	174,764	377,892	649,917
Powell	35,444	110,943	241,220	419,233	56,617	180,977	393,652	678,428
Rayburn	19,948	62,439	135,758	235,943	33,564	104,770	226,544	389,602
Sam Augustine	21,337	66,786	145,212	252,373	35,615	111,176	240,396	413,425
Twin Dikes	62,652	195,706	425,514	739,531	103,739	323,828	700,206	1,204,207
B. A. Steinhagen COE Sites								
Campers Cove	28,005	87,659	190,595	331,247	46,259	144,402	312,241	536,982
East End	10,674	33,409	72,639	126,243	17,657	55,116	119,177	204,956
Magnolia Ridge	31,283	97,919	212,901	370,015	52,003	162,334	351,016	603,666
Sam Rayburn USFS Sites								
Bouton Lake	3,485	10,868	23,446	40,145	5,859	18,244	39,254	66,876
Boykin Spring	13,434	41,889	90,369	154,735	22,281	69,379	149,274	254,309
Caney Creek	36,825	114,821	247,706	424,136	60,991	189,920	408,626	696,156
Harvey Creek	11,078	34,541	74,516	127,590	18,402	57,299	123,282	210,027
Letney	12,365	38,556	83,177	142,420	20,755	64,627	139,049	236,889
Sandy Creek	10,860	33,861	73,049	125,079	18,128	56,450	121,454	206,914
Townsend	21,467	66,935	144,400	247,249	35,409	110,258	237,226	404,149

Source: Leuschner and Young 1978.

Table 7-2 – Estimated onsite and systemwide campsite damages for East End and Twin Dikes sites, without time cost, east Texas, 1973.

% TP_j Reduction	East End				Twin Dikes			
	Number of Visits		Dollar Value		Number of Visits		Dollar Value	
	Onsite	Aggregate	Onsite	Aggregate	Onsite	Aggregate	Onsite	Aggregate
10	2,283	337	10,674	1,411	13,154	1,492	62,652	6,430
30	7,146	1,028	33,409	4,287	41,173	4,609	195,706	20,223
60	15,538	2,297	72,639	9,298	89,522	10,138	425,514	43,677
90	26,959	3,865	126,243	16,316	155,586	17,625	739,531	75,938

Source: Leuschner and Young 1978.

it from outside the forest has been estimated by showing people photographic slides of forests with varying amounts and stages of beetle damage. The slides are controlled for season, physiography, sky composition, vegetation patterns, and several other variables. Two slides are shown simultaneously, each on a separate screen, in all possible combinations. Respondents thus see 45 different pairs of slides put together from 10 original slides. The respondent has 5 seconds to indicate whether the right- or left-hand slide is preferred before the next pair of slides is shown. Thurstone's (1927) Law of Comparative Judgment is then used to compute an interval preference scale for each slide.

Buhyoff and Leuschner (1978) reported the results when this technique was applied to 277 persons with backgrounds representing different levels of knowledge about forestry. Each study group was randomly divided into two subgroups, one informed that they were viewing SPB damage and one not informed. Industrial and Federal foresters were not divided because it was assumed that they would know that they were viewing damage. The proportion of vegetation damaged in each slide was calculated with a ¼-inch grid overlay on an 8 × 10-inch print of each slide. The logarithmic function $Y = b \ln X$, where Y = landscape preference value and X = proportion of landscape damage, was fitted for each subgroup. The functions were not statistically different between the two observer groups, so data were pooled by informed-uninformed categories and the regressions reestimated to obtain

$$Y_I = 1.03 - 0.28 \ln X \qquad R^2 = 0.84 \qquad (4)$$

$$Y_U = 1.46 - 0.14 \ln X \qquad R^2 = 0.33 \qquad (5)$$

where:

Y_I = the landscape preference value for the informed group
Y_U = the landscape preference value for the uninformed group
$\ln X$ = the natural logarithm for the proportion of the vegetation damaged

Buhyoff and Leuschner drew several conclusions. (1) Preference apparently was unaffected by forestry background. (2) People apparently evaluate damage differently based on whether or not they know it is damage. And, as shown more clearly by a plot of the functions, (3a) the informed group had a stronger preference for undamaged stands but lost it more rapidly once damage occurred; (3b) the informed group lost more preference than the uninformed group as damage increased; and (3c) preference loss was very small in both groups when damage exceeded 10 percent.

These results have several management implications. First, the increased impact on those knowing they are viewing SPB damage should be weighed against the benefits of publicity campaigns. Second, professional foresters may have faith that their reactions to SPB esthetic impact are similar to other people's. Finally, to reduce esthetic impact, it is probably more important to prevent or control initial SPB damage than deal with extensive loss.

Hydrologic Impacts

Hydrologic impacts are usually measured by quantity of water obtained from a watershed (yield), the timing and duration of the high and low flows (regimen), and water quality. Generally, water yield increases as vegetation decreases. SPB may temporarily increase yield by killing vegetation and reducing transpiration and the amount of precipitation intercepted by healthy pines. The regimen is determined by precipitation timing and intensity, soil permeability, soil water deficits, and soil depth. SPB impact on regimen depends on the distance of the spot from the stream: the more distant the spot, the less likely it will affect stream flow. Quality has several dimensions, of which only sediment, nutrient content, and water temperature are considered. SPB can have a quality impact if infestations cause increased erosion (and hence sedimentation) or increased nutrient leaching. Water temperature impacts occur only if SPB removes sufficient shade from streams.

Hydrologic impacts can be examined by using existing hydrological models that contain a measure of crown cover or stand density as an independent variable. We can then examine the beetle's impact on yield by changing these variables to reflect different levels of attack, much the same as in the recreation impact technique. Regimen and quality impacts can then be examined by synthesizing water yield changes as shown by the hydrologic model, the established hydrologic relationships, and the characteristics of the SPB outbreak. This technique may not be as accurate as direct observation, but it requires less time and money.

Such a study was performed by Leuschner, Shore, and Smith (1979) using the Rogerson model (1976). They selected sites within the SPB's range, representing high, average, and low water yields (Corinth, Miss.; Dalton, Ga.; and Blackstone, Va., respectively) and examined changes in these yields as stand basal area changed. Yield changes were examined for original stand BA of 150 and 90 ft^2/acre, although any original BA can be used.

Results showed that yield increased between 9.0 and 0.3 acre-inches/year for an acre of SPB spot depending on the site, original BA, and the amount of BA reduction (table 7-3). A rough indication of forestwide physical impact can be obtained by using the Trinity District data (Leuschner et al. 1976), where about 44 acres of SPB spots occurred on about 85,000 acres of host type in 1 year. The largest spot was 2.17 acres; assuming maximum yield, the annual increase would have been 19.53 (9.0 × 2.17) acre-inches from that spot. Similarly, the increase from all spots would be 396 acre-inches (9.0 × 44). But the average is only 0.0047 acre-inches (396/85,000) per acre of host type. These increases are small, considering the total area affected. The estimates are conservative because (1) increases will decrease to zero as vegetative cover returns, (2) they are based on maximum yield changes, and (3) the yield change for a spot will be less the further the spot is from a stream.

Water quality is also unlikely to be affected by SPB attacks. Studies show that erosion, and hence sedimentation, is not adversely affected by overstory removal (e.g., Aubertin and Patric 1974, Dickerson 1975, and Hornbeck 1967). Nor is nutrient loss significantly accelerated by usual management practices (e.g., Swank and Douglass 1977 and Pierce et al. 1970). Further, the relatively small and dispersed spots make a large impact on water temperature via shade removal improbable.

The economic impact is most likely to occur in water yield, and that should be valued as close as possible to the watershed, not at higher levels of production, after the water has become "more valuable." But throughout the beetle's range, water at the watershed is generally zero valued because it is usually replaceable from alternative sources. Economically, it is a "free good" (Young and Gray 1972 and Gregory 1972).

In summary, the southern pine beetle's physical economic impact on water yield is small and its impact on water quality is zero. The economic

Table 7-3. – Change in water yield at the spot in acre-inches per year by percent reduction in basal area and site-precipitation combination.

Percent total BA reduction	Stand basal area before attack					
	150 ft^2/acre			90 ft^2/acre		
	High site High precip.	Avg. site Avg. precip.	Low site Low precip.	High site High precip.	Avg. site Avg. precip.	Low site Low precip.
100	9.0	7.3	2.7	4.9	4.2	1.9
80	8.0	6.5	2.3	4.5	3.9	1.7
60	6.4	5.2	1.7	3.8	3.1	1.4
40	4.0	3.1	0.8	2.8	2.2	0.9
20	1.9	1.3	0.3	1.2	1.1	0.4

Source: Leuschner, Shore, and Smith 1979.

value of these impacts is also zero. The reader is cautioned, however, that these conclusions are based on the Trinity District infestation configuration, which had small and dispersed spots. The conclusions could change if large contiguous areas are attacked, particularly in rougher terrain, or if water is in short supply and not a free good. Therefore, a separate analysis might be desirable if these conditions are likely to hold.

Wildlife Impacts

The southern pine beetle's direct, or primary, wildlife impact occurs when it is a food for some species, most notably woodpeckers. The indirect, or secondary, impacts occur either by increasing associated insect populations that can act as food or by killing trees and decreasing crown cover. Reduction in crown cover can result in increasing stream temperature and sedimentation, increasing edge, changing the availability of nesting sites, and changing the understory vegetation. The latter causes changes in shelter and cover as well as the amount and kind of food (fig. 7-5). The impacts on individual wildlife species will differ because each species can have unique requirements. For example, the SPB is a food for woodpeckers but not for squirrels.

Direct observation and measurement of SPB wildlife impacts is difficult, if not impossible, due to the state of population censusing technology and the costs of such work. Further, exact production relationships between amounts of food, shelter, etc., and wildlife population numbers are still being developed. Therefore, the analyst is dependent on synthesizing published data with known biological relationships and qualitatively analyzing results to examine suspected impacts.

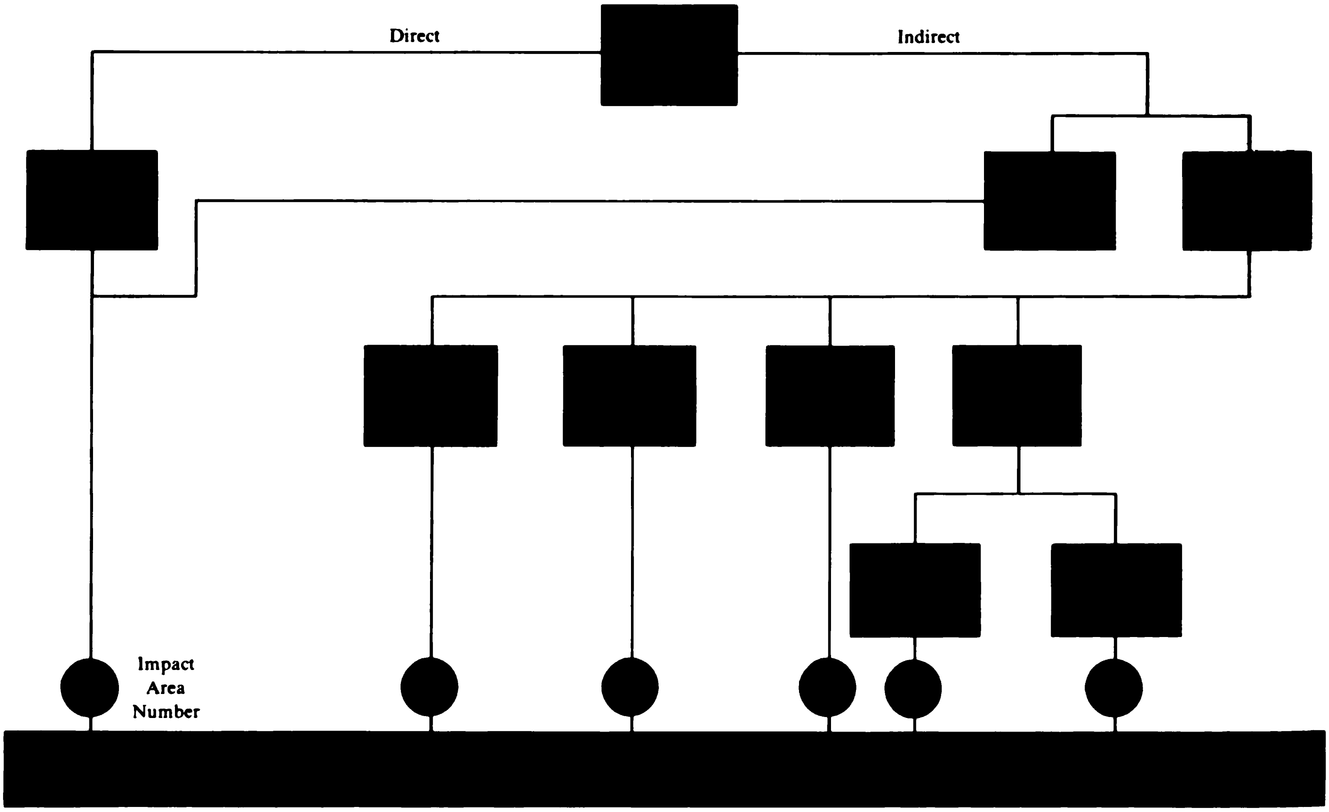


Figure 7-5. – Qualitative model of SPB impacts on wildlife populations. (Source: Maine, Leuschner, and Tipton 1980.)

Figure 7-6. – Snags containing a pileated woodpecker's nest cavity. (From Kroll, Conner, and Fleet 1980.)

Maine, Leuschner, and Tipton (1980) performed this kind of study. Impact on amount and kind of food due to changing understory vegetation was assessed by inferring changes in crown cover from Leuschner et al. (1976) and Ovington (1957), translating these into changes in the amount and kind of browse and herbage using Schuster's (1967) model and results, and obtaining an average change by weighting by the spot size distribution found on the Trinity District (Leuschner et al. 1976). SPB attacks also provide edge by causing forest openings. Linear feet of edge were calculated by assuming circular, triangular, and rectangular spot shapes and weighting by the Trinity District (Leuschner et al. 1976) spot size distribution. About 2,000 ft of edge per acre of SPB spot was found. This amounts to about 660 ft of edge per square mile of forest [(2,000 × 44 × 640)/85,000].

These techniques apply to several species and hence were discussed in one place. Other techniques are species-specific, and the interested reader should refer to Maine, Leuschner, and Tipton (1980) for a discussion of impacts on ten species or species groups.

Woodpeckers

Downy, hairy, and pileated woodpeckers are major SPB predators (Coulson et al. 1972b and Kroll, Conner, and Fleet 1980), and SPB can provide winter food for them. In fact, the availability of SPB often limits woodpecker populations (Kroll and Fleet 1979). SPB could also increase woodpecker populations by providing dead, standing trees for nesting sites (fig. 7-6). The size of these impacts is unknown but is probably limited because of the small proportion of the forested area with spots.

Turkey

The southern pine beetle's impact on turkey habitat in pure pine stands is likely to be negligible because turkeys usually frequent hardwood or pine-hardwood stands. There may be a slight positive effect in mixed stands when SPB serves as a direct food, increases edge, or favors increases in grasses and legumes that are part of the turkey diet. However, this increase may be offset by the large decrease in dogwood species, a preferred turkey food. Thus, the net effect of SPB on turkey is probably negligible.

Quail

Quail is an "edge species" requiring five types of cover plus food, all within a limited cruising radius. SPB spots increase edge and understory vegetation, thereby providing additional cover, particularly in the purer pine stands. Legumes, an important quail food, also increase slightly with SPB spots. Hence the food impact may be slightly positive. There is, therefore, a positive net impact from increased edge and slightly increased food.

Other Birds

This is a catchall category including predators, such as owls and hawks, and nongame species. Edwards (1978) found high populations of small mammals and members of the finch family in newly cut stands. These animals are food for predatory birds. Hence SPB can have a positive impact on their food, which might be partially offset by increased cover. Meyers and Johnson (1978) state that nongame bird population diversity and density are high in early stages of loblolly-shortleaf succession but decrease with stand age. Thus SPB can have a positive impact on nongame birds by returning pine stands to early succession stages. We conclude that the net effect of SPB on other birds is positive because food and other habitat requirements are increased.

Rabbits

Rabbits are prey for nearly every carnivorous bird and animal (Madson 1959). Escape cover is, therefore, critical and can be limiting in the winter. The small home range of rabbits also requires interspersion of cover and food like that found in edge. SPB creates openings that promote increased cover, understory growth, and edge. Rabbits' favored food plants also develop in these openings. Thus, SPB has a positive impact on rabbits.

Squirrels

Grey and fox squirrels, the two major species within the beetle's range, inhabit hardwood forests where mast, other food, and den trees are found. They rarely inhabit pine monocultures, brush, or cutover land. And their small cruising radius keeps them close to the hardwood types. Thus impacts in the purer pine types are unlikely. A slight positive impact in pine-hardwood types might occur if SPB removed pine competition, thereby increasing mast production. But this positive impact might be offset by destruction of old pines that could serve as leaf nest trees. Therefore, the net SPB impact on squirrels is likely to be negligible.

White-Tailed Deer

White-tailed deer inhabit almost any wooded or brushy area that provides thick cover from predators during the day, while the deer sleep. Pine and pine-hardwood forests can provide this cover, but winter food is often the limiting factor. SPB attacks can increase honeysuckle and grasses in pine stands and mast production via decreased competition in pine-hardwood stands. Harlow and Hooper (1971) found honeysuckle, acorns, and grasses made up over 70 percent of winter food in the Coastal Plain. Hence SPB can have a positive impact on deer. Maine, Leuschner, and Tipton (1980) estimated that 1 acre of SPB spot provided 14.5 deer days' increase in food. Thus 25 acres of spots are needed to increase carrying capacity by one deer. This is the equivalent of one deer per 50,000 acres of host type if the infestation has the characteristics of the Trinity District (Leuschner et al. 1976). Deer browse open areas at night and retreat to thick cover during the day. The interspersion caused by edge is, therefore, another positive impact. The net impact of SPB on deer is positive through increased food and edge.

Small Mammals, Fish, and Other Animals

The small mammal category includes mice, shrews, moles, voles, rats, and other small Insectivoria and Rodentia. Lack of published information makes this analysis even shallower than others. The major impact might be through bringing vegetation closer to the ground, thereby increasing food and shelter. But the importance of this effect is undocumented. Murray (1957) reported that edge effect is unimportant for these animals. The net SPB impact is assumed negligible based on the lack of published associations rather than firm evidence indicating no impact.

Southern pine beetle impact on fish would occur through increased sedimentation and water temperature. In the Hydrologic Impacts section we concluded that these would be negligible; thus the beetle's impact on fish is negligible.

"Other Animals" includes opossums, skunks, and other fur bearers. Again, lack of published information results in a particularly shallow analysis. However, we do know that many fur bearers are carnivorous, so SPB could have a positive effect by increasing rabbit and other prey populations. Other fur bearers, found mostly in and around water, would be unaffected by SPB-induced changes in food, edge, or cover. A negligible net impact is assumed, based, again, on lack of evidence rather than evidence of no effect.

Summary

The preceding analyses indicated a positive SPB impact on woodpecker, quail, rabbit, deer, small mammal, and other bird populations – mostly through increases in edge and food. Therefore, SPB control is a *cost* to wildlife because it reduces positive impacts of the beetle. The impacts' magnitude is difficult to determine but is likely to be quite small if outbreak characteristics are similar to those used in the analyses. Special analyses may be desirable if different outbreak characteristics are suspected or if unique local conditions prevail.

Grazing Impacts

Southern pine beetle attacks could increase grazing capacity by opening the overstory and thereby causing increased production of grazing herbage. But the usual SPB outbreaks appear to be so small and dispersed that the increase in herbage would not be enough to justify investing in grazing unless it were already present. Therefore, it is hypothesized that grazing impacts are likely to occur only on those 30.3 million acres reported by the Forest Range Task Force (U.S. Department of Agriculture Forest Service 1972b) as grazed loblolly-shortleaf type.

A rudimentary grazing impact estimate can be made following techniques described previously. More specifically, (1) the impact on crown cover or density is estimated, (2) this change is related to herbage using published models, (3) herbage changes are then translated to grazing capacity changes, and (4) capacity changes can be expanded to a region- or Southwide basis assuming the distributions and intensity found on the Trinity District (Leuschner et al. 1976). The value of the economic impact can be estimated by using either the market value of grazing leases for similar range or the cost of developing range to replace that which would have been generated by SPB attacks.

This technique was applied by Maine (1979), who wrote a computer program to make the calculations. The program used both the Halls and Schuster (1965) and the Wolters (1973) models to translate changes in basal area to changes in herbage. Herbage changes were translated to animal unit months, assuming that 100 lb of herbage are needed each day for year-long grazing (based on Pearson 1975, Duvall and Whitaker 1964, and other studies) and 75 lb/day are needed for seasonal grazing (based on Duvall and Linnartz 1967). An animal unit month was valued at $4.03, the average cost of production in 1970 (U.S. Department of Agriculture Forest Service 1972b).

Grazing impact of SPB varies depending on the distribution of spot sizes, the width of the shaded area within the spot, the hardwood BA present, the herbage model, and whether year-long or seasonal grazing is assumed. Maine (1979) estimated that maximum impact on the Trinity District would have been between 4.4 and 29.3 animal unit months (or a loss of between $18 and $118) if the entire District were grazed and if SPB were completely controlled. This dollar estimate compares to the $6,000 timber impact that would have been saved if there was complete control. Maine (1979) also estimated that the Southwide impact in 1 year would lie between zero and $42,000, again depending on the preceding assumptions. He concluded that although the impact is positive and hence a cost of SPB control, grazing impact is negligible Southwide or over large areas and hence not generally important for management considerations. He cautioned, however, that these results were based on crude estimates and broad averages that might increase if severe or concentrated outbreaks occurred.

Wildfire Impacts

Many foresters believe that insect outbreaks can cause increased fire losses either by providing snags or by increasing fuels and thereby increasing incidence or fire intensity and subsequent losses. Direct observation and field measurement are expensive and time consuming and hence impractical for most analyses. So we are once again dependent on synthesizing published information on insect outbreaks, fire studies in general, and those few studies relating insects and fire. Two general impact areas may be examined: losses due to increased fire control expenditures (an increased cost of production), and increased timber losses due to insect-induced fires (decreased production). Timber losses can increase if more fires start, the rate of spread increases, or more damage is caused.

Maine (1979) performed this type of study for southern pine beetles. He concluded that fire control expenditures were unlikely to increase because (1) Gobeil (1941) found they did not on the Gaspé peninsula for the spruce bark beetle *(D. piceaperda* Hopk.), and (2) the dispersed nature of SPB infestations supports extending this conclusion to SPB. The conclusion is also supported by his rough estimate that only 64 acres of SPB spots burn annually Southwide.[2]

Fire starts were considered negligible because only 3 percent of southern fires are naturally caused (U.S. Department of Agriculture Forest Service 1976). Increased spotting due to burning standing, dead trees could increase incidence. But small, dispersed spots and the low estimated SPB acreage burned imply this impact is also likely to be small. Rate of spread could be increased if ground-level fuel with a lower moisture content were increased. However, ground-level fuel increase is likely to be small at any one time due to the slow decay of standing trees and, again, the small, dispersed spots and low SPB acreage burned.

Maine (1979) found that the ability of fire to do damage was influenced by stand value, stand susceptibility, and fire intensity. Attacked stands have diminished or no value when burned because the pine trees are already dead, although there may be some value in hardwoods. Stand susceptibility and intensity might be slightly increased. But the usual low value of the dead pines and residual hardwoods makes it unlikely that SPB-related wildfires will do much damage.

Fire impacts may generally be ignored in management decisions. Rate of spread and intensity are probably increased by some small, unknown amount. But the Southwide impact is believed negligible because of the small, dispersed spots, because only an estimated 64 acres a year are burned, and because pines are already dead and the residual hardwoods tend to have a lower commercial value. The reader is again cautioned that these conclusions are based on crude estimates, broad averages, and the assumption that Trinity District (Leuschner et al. 1976) outbreak characteristics generally apply Southwide. The conclusions should be reassessed if large, contiguous areas of SPB damage occur.

Summary

Economic impacts of the southern pine beetle are those causing changes in the production, inputs needed for production, or the production distribution useful to society. Impacts can be measured in either qualitative, physical, or value terms. Timber, recreation, hydrologic, and grazing impacts can be estimated in dollars; esthetic impacts with an interval preference scale; and wildlife and wildfire impacts, only qualitatively (table 7-4). SPB usually decreases timber, recreation, and esthetic products; has slight positive effects on wildlife, wildfire, and grazing; and also

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[2] About 0.25892 percent of commercial forest acreage in the South is burned annually (USDA -- Forest Service 1976), about 0.05 percent of the commercial forest has SPB spots (Leuschner et al. 1976), and there are about 49.4 million acres of loblolly-shortleaf pine type (USDA – Forest Service 1973). Then, 0.0025892 × 0.0005 × 49.4 million = 63.95 acres. This assumes that the Trinity District outbreak characteristics hold Southwide and that fire incidence is independent of SPB attack.

slightly increases water yield, although the economic value of this increase Southwide is usually zero. Timber and recreation impacts have the highest dollar impacts and hence should be considered in making management decisions. Hydrologic, grazing, and wildfire impacts are generally too small to consider in making management decisions.

The reader is cautioned again about the weaknesses in specific analyses and the general nature of the results. Perhaps no one is more cognizant than a forester of the diversity of natural conditions over wide geographic areas and the ever-present possibility that unique local conditions will result in a different answer than the general case. The practitioner is therefore urged to make local analyses where the size of possible expenditures or losses justifies the expense.

The reader is also cautioned that many general conclusions are based on the Trinity District infestation characteristics and that they may not represent the entire South. Unfortunately, these were the only summarized data available at the time research was executed. They remain, to our knowledge, the only published data characterizing an infestation with frequency distributions. Parallel analyses can be made using the techniques reported herein when other data become available if an analyst believes the general conclusions would be substantially different. Similarly, the techniques and assumptions can be refined as more of SPB's interrelationships become known and quantified. These results are offered as guidelines for decisions that must be made between now and the time when new and better information is available.

Table 7-4.—Summary of SPB impacts.

Impact	Measurement Unit	Measurement Model	Usual Impact	Comments
Timber	Dollars	Present net worth	Negative	Traditional model usually over estimates impact.
Recreation	Dollars	HCK method	Negative	Relatively high impact for high-density use areas.
Esthetic	Interval preference	Psychological disutility	Negative	Attack prevention more important than spread.
Hydrologic	Dollars	Rogerson	Zero	Small yield increase but water is free good; hence zero dollars.
Wildlife	Qualitative	Synthesize pub. studies	Positive or zero	Positive impact on woodpecker, quail, rabbit, deer, small mammal, and other bird populations.
Grazing	Dollars	Synthesize pub. studies	Positive	Total usually too small for consideration.
Wildfire	Qualitative	Synthesize pub. studies	Positive	Total usually too small for consideration.

Rating Stands for Susceptibility to SPB

Peter L. Lorio, Jr.[1]

8

Introduction

Over the past 10 years, more and more emphasis has been focused on the possible prevention of bark beetle outbreaks through forestry practices. In order to prevent attacks, one must know a great deal about insect/host/climatic interactions. This chapter summarizes the state of the art in the application of available knowledge to the prevention problem. Identification of site-stand variables that are associated with SPB attacks has led to a first approximation on many stand rating systems. Development of descriptive and predictive models that would rank forest stands as to SPB susceptibility was a major objective of the Expanded Southern Pine Beetle Research and Applications Program's coordinated site-stand project. Results of this project can best be understood in light of the historical work done on risk or hazard classification. For the purposes of this chapter, terminology follows that used by researchers in discussing their work.

Early work in the western United States developed tree classification systems applicable to stands under a selection cutting system. Among others, Dunning (1928), Keen (1936, 1943), Keen and Salman (1942), and Salman and Bongberg (1942) developed tree classification systems silvicultural in character and use, but with the primary objective of reducing insect problems. Basically, high-risk trees were logged to reduce potential losses from bark beetles. Johnson (1949) used the percentage of pine volume recently killed by bark beetles, in addition to the percent of present volume of pine in high-risk trees, to develop indices of beetle hazard.

More recent developments in knowledge of bark beetle/site/host relationships have been applied to western forest management problems. Safranyik, Shrimpton, and Whitney (1974) summarized years of work on mountain pine beetle/lodgepole pine biology and ecology and developed management guidelines to reduce losses in Canadian forests. Infestations in stands with an average diameter over 8 inches, that are over 80 years old, and are in the hotter and drier areas of the species range (mild winters) are considered potentially epidemic.

In the Rocky Mountains of the United States, Amman et al. (1977) used tree diameter, tree age, and stand location (elevation and latitude) to predict risk of mountain pine beetle outbreaks in unmanaged lodgepole pine stands. Mahoney (1978) reviewed and tested several such approaches to stand risk classification. Schmid and Frye (1976) developed a system for spruce beetle (*Dendroctonus rufipennis* [Kirby]) based on psysiographic location, tree diameter, basal area, and percentage of spruce in the canopy. Schenk et al. (1977) and Moore, Schenk, and Hatch (1978) developed and tested a fir engraver stand hazard index for grand fir (*Abies grandis*) stands based on Crown Competition Factor (Krajicek, Brinkman, and Gingrich 1961) and tree species diversity. Application and evaluation of the utility of these varied forest management tools for the West are progressing, and similar approaches have been developed concurrently in the South.

Bennett (1965) reported the common association of dense pine stands (fig. 8-1) and slow tree growth (fig. 8-2) with southern pine beetle outbreaks. He further indicated the importance of stand age and composition in relation to susceptibility to bark beetle attack. By recognizing factors that enhance the probability of bark beetle outbreaks, and developing procedures to avoid those conditions, forest managers can substantially lessen the potential for SPB problems (Bennett 1968, 1971). Lorio and Hodges (1974) suggested that results of research on soil, tree, and stand characteristics associated with SPB could be applied to the development of stand risk classification. Their work indicated that dense loblolly pine sawtimber stands on moist to wet, productive sites were closely associated with outbreaks in southeast Texas and southwest Louisiana. It appeared that recognizable host and site factors which affect the quantity and quality of food and habitat for bark beetles could be used to determine SPB risk.

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Classification and Rating of Stands for Risk

The primary task of the coordinated regional project to study site-stand characteristics (*see* Chapter 4) was to determine what variables (e.g., species composition, stand density, stand age and/or size, site quality, and tree growth rates) were consistently related to outbreaks across a large segment of the beetle's range (figs. 8-3 and 8-4). Results of this work are summarized in Chapter 4 and in Coster and Searcy (1980). Using these data, researchers have approached stand rating in several ways: (1) Discriminant analysis with primary site, tree, and stand variables, as well as derived variables, from the coordinated regional project; (2) probabilistic models; and (3) qualitative stand risk rating.

Figure 8-1A. – A dense pure pine stand of the type favored by SPB.

Figure 8-1B. – Similar stand following SPB attack.

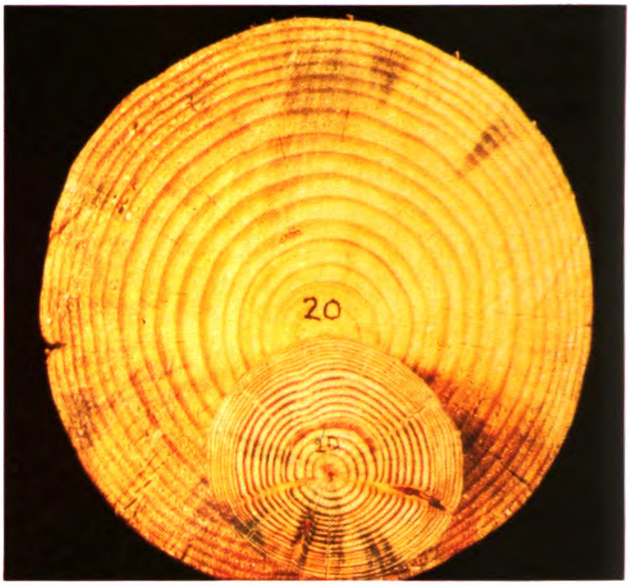

Figure 8-2. – Closely spaced rings near the outer margin indicate slow radial growth, a common characteristic of pines in SPB-attacked stands.

Discriminant Analysis

Discriminant analysis is analogous to multiple regression and the same implied statistical assumptions govern (Morrison 1967). In the application of discriminant analysis to the stand rating problem, the range in values of characteristics such as live-crown ratio, radial growth, basal area, and soil depth were examined for both SPB-infested and noninfested plots. Combinations of variates that would discriminate most effectively between infested and noninfested plots were selected for stand hazard models.

By inference, discriminant scores associated with noninfested plots indicate resistance to SPB attack. Those associated with infested plots indicate susceptibility. Noninfested plots consisted of baseline plots established in a line-grid fashion across study areas to characterize general forest conditions. Such plots may or may not have been associated with factors indicative of resistance to bark beetle attack.

Working in the Georgia Piedmont, Belanger, Porterfield, and Rowell (1980) used data from 197 plots (58 SPB-infested, 139 noninfested) to develop a discriminant model with six variables based on data from undisturbed, natural stands. This model correctly classified 86 percent of 64 SPB-attacked plots from an independent sample.

$$\text{Discriminant score} = 2.38664 - 0.02645\,(\text{LIVECRWN}) + 0.05551\,(\text{AVERAD 1}) - 0.10111\,(\text{SURCLAY}) - 0.08016\,(\text{SURDEPTH}) + 0.00530\,(\text{PERLOB}) + 0.07842\,(\text{SOIL 1}),$$

where

LIVECRWN = Percent live crown
AVERAD 1 = Radial growth for last 5 years (mm)
SURCLAY = Percent clay in surface (0 – 15 cm) horizon
SURDEPTH = Depth of A horizon (cm)
PERLOB = Percent loblolly in total pine component
SOIL 1 = Percent clay per cm A horizon depth.

A land manager's model was developed using four easy-to-measure variables that might be included in existing inventories. This model was only slightly less effective – 82 percent accurate – in discriminating between infested and noninfested plots from the 64-plot sample.

$$\text{Discriminant score} = 1.24082 - 0.04829\,(\text{LIVECRWN}) + 0.10006\,(\text{AVERAD 1}) + 0.00941\,(\text{PERLOB}) - 0.12903\,(\text{SURDEPTH}).$$

The sign and total discriminant score indicate the direction and degree of susceptibility. Average value for infested plots was -0.6312; average score for baseline plots was 0.3343.

Figure 8-3. – Field crew workers determine tree characteristics such as bark thickness (left) and age and growth rate (right).

Kushmaul et al. (1979) developed three discriminant models based on data collected in the Louisiana, Mississippi, and Texas Gulf Coastal Plain. Stepwise discriminant analysis of data from natural, undisturbed loblolly and shortleaf stands produced the following model.

$$\text{Discriminant score} = 2.33550 - 0.01906\,(\text{pine BA}) + 0.01484\,(\text{average last 10 years' radial growth}) - 0.00829\,(\text{understory \%}) - 0.00613\,(\text{surface soil depth}) - 1.71662\,(\text{bark thickness} - \text{fissure}).$$

Discriminant scores less than -0.13514 indicate infested plots; scores above this value indicate uninfested plots. Use of this model is illustrated in table 8-1.

Tests on a subset of the data not used in developing the model (15 infested and 20 noninfested plots) suggested about 74 percent overall accuracy. A model based on commonly measured variables in continuous forest inventory (CFI) plots correctly classified 80 percent of the infested and 70 percent of the noninfested plot subsets.

$$\text{Discriminant score} = 3.06315 - 0.018342\,(\text{pine BA}) - 0.00705\,(\text{age}) - 0.00002\,(\text{stand density}) - 0.00880\,(\text{site index}) - 0.04085\,(\text{total BA/acre}).$$

Scores less than -0.12736 indicate infested plots. Neither of these models was considered practical for users with limited resources, but each gave some insight into variables associated with infested stands.

A simple model, including only pine BA and last 10 years' average radial growth, correctly classified 93 percent of the infested plot subset, but only 65 percent of the noninfested subset.

$$\text{Discriminant score} = 0.93080 - 0.02004\,(\text{pine BA}) + 0.01827\,(\text{average last 10 years' radial growth}).$$

Scores less than -0.12917 indicate infested plots. Lower accuracy for noninfested plots is understandable considering that the noninfested subset did not necessarily represent resistant stands. These stands happened to be uninfested at the time of the data collection, but they could very well possess characteristics commonly associated with infested stands.

Further testing of this and similar simple models, over time and in controlled pilot studies,

Figure 8-4. – A field worker determines stand characteristics, e.g., basal area, trees per acre, diameter of stems.

may be warranted. The need to bore trees for growth measurements might inhibit routine use of the model, but a correlated variable that is easy to estimate, such as live crown ratio, could possibly substitute for growth measurements. Best results probably could be obtained by applying the model to stands that include species and tree size classes that represent favorable SPB habitat.

In Arkansas, Ku, Sweeney, and Shelburne (1980a and b), working primarily with shortleaf and loblolly pine, sampled 984 SPB-infested and 509 noninfested stands in a study of site and stand conditions related to a bark beetle outbreak. Their efforts led to an equation that accurately discriminated between infested and noninfested stands 75 percent of the time, both with a small subset and with 240 plots used to develop the equation. (Infested plots used had at least 10 infested trees.) The final equation, based on 268 plots in natural stands on upland flat sites, was

$$\text{Discriminant score} = -1.50\,(\text{total BA}) + 3.3\,(\text{stand age}) + 64.3\,(\text{last 10 years' radial growth}) + 0.93\,(\text{hardwood BA}).$$

Scores greater than 100 indicate low susceptibility, greater than 1 and less than 100 indicate medium susceptibility, and less than 1 indicate high susceptibility.

Ku, Sweeney, and Shelburne believe that this equation applies best to undisturbed natural stands on upland flats – sites from which the data base originated. Its utility on other landforms, in plantations, or on disturbed sites is questionable.

Everyone would like to see a generally applicable stand rating model for the Coastal Plain. Variations in site, vegetation, and climate across the SPB range in the Coastal Plain complicate the task, but Porterfield and Rowell (1980 unpublished) developed a working model that they consider useful.

Using data collected by collaborators from Texas to Virginia, Porterfield and Rowell developed a discriminant analysis to select a set of

Table 8-1. – Discriminant scores and susceptibility rankings for five selected stands.[1]

First discriminant model		**Values for each variable for stands I through V**					**Product (coefficient multiplied by variable value)**				
Coefficient	**Variable**	**I**	**II**	**III**	**IV**	**V**	**I**	**II**	**III**	**IV**	**V**
A				B					A × B		
-0.01906	Pine basal area (ft²)	10	70	90	110	220	-.1906	-1.3342	-1.7154	-2.0966	-4.1932
+0.01484	Avg radial growth last 10 yr (mm)	62	58	25	21	30	+.9201	+.8607	+.3710	+.3116	+.4452
-0.00829	Understory (percent)	50	10	30	70	40	-.4145	-.0829	-.2487	-.5803	-.3316
-0.00613	Surface soil depth (cm)	35	60	15	60	60	-.2146	-.3678	-.0920	-.3678	-.3678
-1.71662	Bark thickness – fissure (in)	.2	.2	.5	.5	.3	-.3433	-.3433	-.8583	-.8583	-.5150
	Constant term						2.3355	2.3355	2.3355	2.3355	2.3355
	Discriminant score (constant included)						+2.0926	+1.0680	-.2079	-1.2559	-2.6269
	Stand ranking based on discriminant score (1 = most susceptible)						5	4	3	2	1

[1] From Kushmaul et al. (1979).

site-stand variables that, in combination with each other, was most reliable in classifying stands as to infestation status. Individual plots were either SPB-attacked or unattacked, and were in naturally established, undisturbed stands. Infestations had to include five or more SPB-killed trees, an indication that site-stand conditions may have enhanced sustained activity. The data set included 547 infested and 474 uninfested plots and yielded the following discriminant model:

$$\begin{aligned}\text{Discriminant score} = {} & 1.02559\\ & - 0.00043\ (\text{total volume})\\ & + 1.33776\ (\text{proportion sawtimber})\\ & - 2.14726\ (\text{average bark thickness})\\ & + 0.01878\ (10 \text{ years' radial growth})\\ & + 0.03205\ (\text{slope})\\ & - 0.00791\ (\text{proportion of total BA in pine})\end{aligned}$$

where

Total volume = ft^3 of pine $>$ 4.6 inches d.b.h.

Proportion of sawtimber-sized pine $= \dfrac{\text{ft}^3 > 9.6 \text{ inches}}{\text{ft}^3 > 4.6 \text{ inches}}$

Average bark thickness = average of fissure and ridge bark thickness (nearest 0.1 inch)

10 years' radial growth = millimeters (at breast height)

Slope = ground slope in percent

Proportion of total BA in pine $= \dfrac{\text{ft}^2 \text{ of pine BA}}{\text{total BA.}}$

Scores below 0.044185 are best classified as SPB-attacked; those above, unattacked. This model correctly classified 79 percent of the plots used in developing it. With an independent sample of 119 plots (69 SPB-infested, 50 noninfested), it correctly classified 74 percent of the plots. Porterfield and Rowell suggest that the model tended to classify too many infested stands as baseline but note that many misclassifications were borderline. They point out that degrees of susceptibility are continuous, and that a stand's relative discriminant score in relation to other stands is more important than its classification. Intuitively, we know that many stands exist in a range of degrees of susceptibility to SPB attack. The problem is to find a practical and useful means of identifying the especially susceptible ones.

Porterfield and Rowell's model uses some variables derived from basic measurements made by collaborators, and would involve considerable effort to apply. It appears to have utility but needs to be tested with sample data from various locations across the Coastal Plain. Species is not an explicit variable in the model; one might consider its application to all southern pine stands, or perhaps to stands stratified by species. Experience indicates that longleaf and slash pine are less suitable hosts for SPB than either loblolly or shortleaf.

Probabilistic Models

Hicks et al. (1980) developed a probability of attack model for east Texas forests from site and stand data on 484 SPB-infested and 416 noninfested plots. They first determined the variables most strongly associated with infestations by stepwise discriminant analysis. A discriminant function, including bark thickness in fissures, pine BA, average tree height, and landform category, correctly classified 79 percent of the plots used to develop the function.

Subsequently, Hicks et al. determined that a discriminant function using only pine BA, average height, and landform category correctly classified 72 percent of the sample plots. Then, following an estimate of overall probability of SPB attack in east Texas based on prior incidence of attack per unit area of SPB host types (loblolly-shortleaf pine and oak-pine), they calculated the probability of attack (Pa) according to the general equation:

$$Pa = \sum_{i=1}^{3} Pi$$

where $Pi = A \times D \times W$.

Pi = probability due to an individual variable

A = overall probability of attack

D = ratio of percent of infestation in a variable class to the percent of noninfested plots in that class

W = variable weight based on the standardized coefficients from discriminant analysis.

For example, Pa for a loblolly pine stand averaging 25 m in height, with 28 m^2/ha BA, located on a stream terrace is determined as follows:

$A = 0.00093$ from Hicks' three-county study area estimation of the area ratio of sampled infestations to SPB host types in the study area (3-year period) (Hicks et al. 1980)
$D = 1.25$ for height $= 25$ m, 2.715 for BA $= 28\ \mathrm{m}^2$, and 6.857 for landform category = stream terrace
$W = 0.268$ for height, 0.498 for BA, and 0.234 for landform category

$$\begin{array}{lllll} & A & D & W & \\ \text{Pi (height)} = & 0.00093 \times & 1.25 & \times\ 0.268 & = 0.000311 \\ \text{Pi (basal area)} = & 0.00093 \times & 2.715 & \times\ 0.498 & = 0.001257 \\ \text{Pi (landform)} = & 0.00093 \times & 6.857 & \times\ 0.234 & = 0.001492 \end{array}$$

Therefore,

$$\text{Pa} = 0.000311 + 0.001257 + 0.001492 = 0.003050,$$

or about a chance of 1 in 328, if the succeeding 3 years of SPB activity is similar to the preceding 3 years in the area of interest.

Hicks et al. suggest several uses for their probability model, depending on institutional or landowner objectives. The model should be tested with independent data in east Texas. Variables used in the model are meaningful and relatively easy to measure, but the estimate of *A* for an area of interest and its application to the future years of interest may present serious difficulties.

Another probabilistic model was offered by Daniels et al. (1979). Their model involved use of the logistic function for estimating a continuous measure of SPB incidence or probability of outbreak. This approach provides a more general incidence index than categorical classification methods, and its validity is not dependent upon certain distributional assumptions, as is discriminant analysis.

A continuous probability function is most meaningful, according to Daniels et al., when applied to a specific forest land area and a specific time period (perhaps 1 year). Such a model would be most useful for decisionmaking if probabilities can be estimated as a function of site, stand, and insect population variables that (1) are associated with differences in outbreak probabilities, and (2) can be easily measured in the field or from aerial photographs. Insect population variables may reflect changes in probabilities between endemic and epidemic periods, but useful data are difficult to obtain.

The logistic function,

$$\hat{p} = \frac{1}{1 + e^{-(b_0 + b_1x_1 + b_2x_2 + \ldots b_kx_k)}}$$

cannot be estimated directly (p is not observable), but uninfested (0) or infested (1) may be taken as observed values of *p* and related to the *x* variables in the logistic function characterizing stands with and without outbreaks. Direct estimation of the coefficients of the *x* variables in the logistic function by the maximum likelihood procedure is preferred over discriminant function estimators because the former yields asymptotically unbiased coefficient estimates independently of any distributional assumption about the data (Halperin, Blackwelder, and Verter 1971).

Daniels et al. (1979) developed a logistic regression model based on site and stand variables measured by collaborators in the site-stand regional study (Chapter 4). They used data from 187 natural stands to fit a two-variable model for disturbed and undisturbed categories. Total stand BA (x_1) and proportion of the BA in pine (x_2) were chosen for the models.

Undisturbed $p = -8.599 + 0.044x_1 + 3.309x_2$
Disturbed $p = -9.998 + 0.088x_1 + 4.801x_2$

Models with additional independent variables gave similar results.

Differences in sampling intensities of infested and noninfested (baseline) populations required differential weighting of the data. Infested data were estimated to represent 100 times the sampling intensity of noninfested data, so noninfested plots were weighted by 100 in the estimation procedure. Stand size was not part of the basic data, so $\hat{p}$'s were for "average" stand sizes and stand size distributions were assumed to be the same for infested and noninfested populations.

The developers of this method believe it has distinct advantages in that (1) it provides a continuous estimate of incidence that may still be partitioned according to user needs or wishes, (2) the probabilities are meaningful since they indicate the chance of an outbreak, and (3) the probabilities may be combined in use with other guideline models for a variety of management objectives.

The approach is attractive and should be explored more extensively. Species or forest type, and tree age or size variations from the 187-plot samples Daniels et al. used would probably limit the utility of these specific models in broad applications.

Qualitative Stand Risk Rating

Efforts to develop qualitative methods of stand risk rating for southern pine beetle include work by Belanger and the Georgia Forestry Commission (R. P. Belanger personal communication). Their system for field evaluation of stand susceptibility to SPB attack includes stand, representative tree, and site characteristics, as follows:

Ranking the Susceptibility of Stands to SPB Attack

Stand

1. Shortleaf pine ≥ 50% total pine Yes__ No__
2. Hardwood component ≤ 25% total stand Yes__ No__
3. Pine BA ≥ 130 ft²/acre Yes__ No__

Representative Tree

4. Radial growth (last 5 years) ≤ ½ inch Yes__ No__
5. Live crown ratio ≥ 40% Yes__ No__

Surface Soils 0–6 inches

6. Micaceous red clays Yes__ No__

The yes answers are totaled and a hazard ranking and need for cultural treatment given according to the following diagram.

<table>
<tr><td></td><td colspan="4">Hazard Ranking</td></tr>
<tr><td></td><td>Low</td><td colspan="2">Moderate</td><td>High</td></tr>
<tr><td>Total of "yes" answers</td><td>0 1 2</td><td>3</td><td>4</td><td>5 6</td></tr>
<tr><td>Cultural treatment</td><td colspan="2">Not Needed</td><td colspan="2">Needed</td></tr>
</table>

This system is currently being tested throughout the Georgia Piedmont by Belanger and Georgia Forestry Commission personnel.

Lorio (1978) proposed the use of available forest resource inventory data such as forest type, tree size and/or age, stand density, and site index for evaluating stand risk to bark beetle attack. Some basic assumptions are made with this approach: (1) All southern pines are susceptible to attack, but loblolly and shortleaf are the primary host species. (2) Lack of knowledge about SPB population dynamics prohibits effective prediction of infestations over time. (3) SPB needs for food and habitat for abundant reproduction are related to recognizable stand characteristics. (4) Stands favorable for SPB food and habitat also constitute potentially large resource losses. (5) Routine forest inventory data, used for a wide variety of forest management planning and decisionmaking purposes, can also be applied effectively to stand risk classification for the SPB.

Continuous Inventory of Stand Conditions (CISC), an automatic data processing system used for National Forests in the South that continuously reflects an up-to-date description of timber stands, was used to classify stands on the Kisatchie National Forest in Louisiana. Five criteria in CISC are being used currently in classification: forest type, stand condition class, method of cut, operability, and site index. *Forest type* is self explanatory. *Stand condition class* includes consideration for damage, quality, density, and age. There are 15 classes, of which immature poletimber, immature sawtimber, and mature sawtimber are particularly important for risk classification. *Method of cut* describes the silvicultural treatment needed for the stand, such as clear cutting, thinning, seed tree. *Operability* indicates the kind and mixture of products to be removed by the method of cut and must be compatible with the method of cut. On the Kisatchie National Forest operable pine poletimber stands must yield at least 3 cords/acre, and sawtimber stands at least 800 fbm/acre (Scribner rule) under a silviculturally acceptable method of cut. In-operable stands contain very low volume of resource, representing low risk for SPB outbreak even though individual trees might be very susceptible to attack. *Site index* gives an indication of the quality or capability of the site. The more productive sites can produce larger trees and more of them per acre in less time than poorer sites, and these good sites with moist or wet water regimes constitute potentially greater risk of SPB outbreaks.

Initial retrospective tests of the classification, based on 25 months of infestation data (June 1975–June 1977), showed that stands classed as high risk had 10.5, medium 6.3, and low 3.2 infestations per 1,000 acres. A second predicitve test was extended another 30 months on the Catahoula Ranger District with the following results: high 12.1, medium 5.8, and low 3.1 infestations per 1,000 acres (fig. 8-5).

These results on over 100,000 acres over 4½ years strongly indicate some practical utility of the system. Stands classed as high and medium risk comprised only about 23 percent of the study area (fig. 8-6). Identification of such stands significantly reduces the area of primary concern relative to potential SPB outbreak and provides criteria that can be used in deciding which stands to thin or regenerate, what sequence of treatment to follow during a cutting cycle, and what stands to monitor for potential problems.

Tests and revisions of the approach are continuing on the Kisatchie National Forest. CISC does not include BA, so method of cut and operability are used as broad indicators of density in risk classification of stands. Currently, provisions are being made on the KNF so that foresters may include BA in CISC as well as enter an SPB risk classification code if desired. Criteria have been prepared for prescriptionists to use on a trial basis. These include basal area criteria based on thinning guides currently in use on the Kisatchie, and on stand data from 318 SPB infestations collected over a 25-month period (Lorio and Sommers 1980).

Aerial Approaches

Sader and Miller (1976 unpublished) developed a risk-rating system based on a study conducted in Copiah County, Mississippi. The study revealed that a trained interpreter could estimate four forest stand and topographic variables from 1:24,000 color infrared imagery. These primary variables were species composition, stand size (sawtimber, poletimber, etc.), stand density, and topographic position. Sader and Miller assigned a numerical weight to each variable according to their estimate of the degree of influence each has in creating conditions favorable for SPB attack. Secondary variables within each primary variable were assigned a numerical rank based on relative susceptibility to initial attack and potential for infestation spread.

Sader and Miller's weight and risk values for stand and topographic variables are given in table 8-2. In their study, dense pure pine stands with sawtimber-size trees on ridges (broad interstream divides) had the greatest probability of

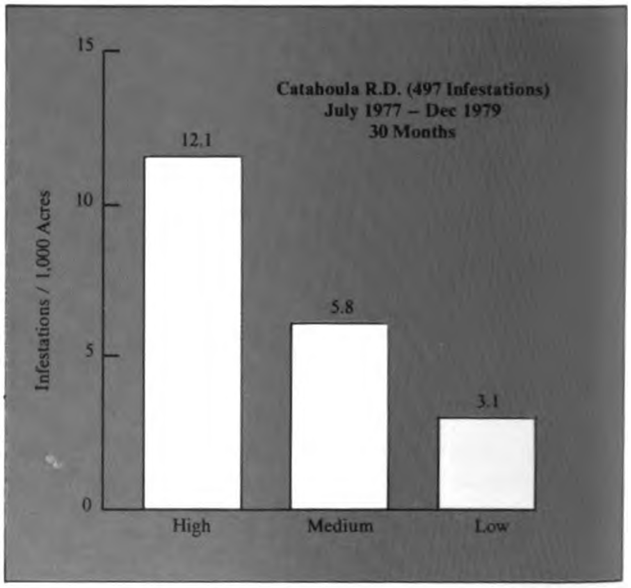

Figure 8-5. – SPB infestation frequency on the Catahoula Ranger District, Kisatchie National Forest, by stand risk classes over a 30-month period (July 1977–December 1979).

initial attack and infestation spread. Such stands also constituted the greatest potential resource loss.

Examples of use of their system are:

Stand 1: Pine, sawtimber, dense, ridge position
(PsDR) = 154 (high risk)

Stand 2. Pine-hardwood, pole, sparse, lower 1/3 slope position
(PHpSL1/3) = 53.5 (low risk)

No explicit differentiation of pine species was included in the system, but loblolly and shortleaf were the predominant species in Copiah County. Sawtimber was defined as trees over 11.5 inches d.b.h.; large poletimber to sawtimber as 9.6 to 11.5 inches d.b.h., and poletimber as 5.0 to 9.5 inches d.b.h. Stand density criteria were, dense $\geq$ 120 ft^2 BA/acre, normal 80-119 ft^2 BA/acre, and sparse < 80 ft^2/acre.

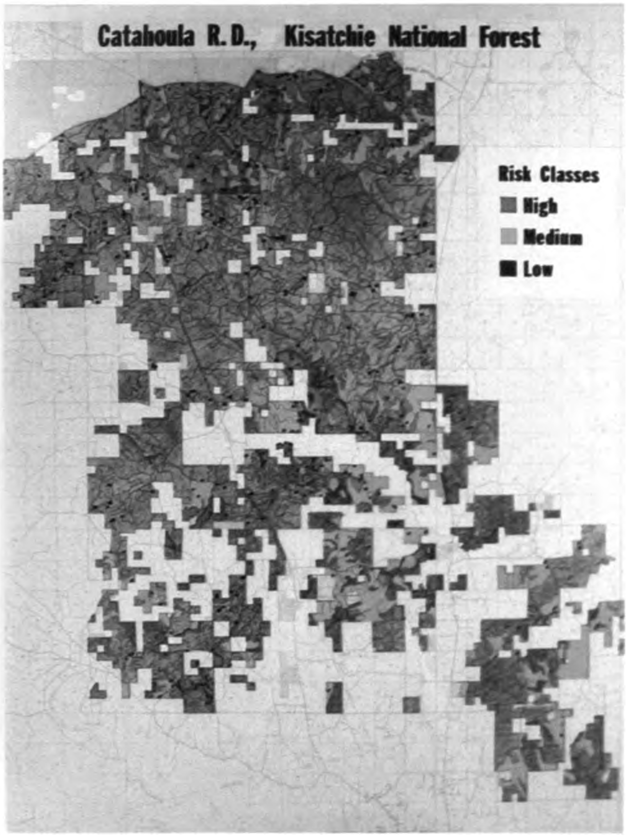

Figure 8-6. – Map of Catahoula Ranger District showing high-, medium-, and low-risk areas for SPB

Sader and Miller used 235 infestations from 1974 in developing their model and 42 infestations from the decreased activity in 1975 in attempting to evaluate it. Their evaluation did not include consideration of the relative area occupied by each of their five risk classes (high, moderately high to high, moderately high, moderate, and low). They concluded that the approach was encouraging but in need of further refinement through data input over a longer timespan.

Table 8-2. – Weight and rank values for stand and topographic variables (from Sader and Miller 1979 unpublished).

Weight	Primary variable	Secondary variable	Rank	Total
15	Species composition	Pine (P)	3	45
		Pine-hardwood (P-H)	1.5	22.5
7	Stand size	Sawtimber (s)	3	21
		Large pole to small sawtimber (pl)	2	14
		Pole (p)	1	7
12	Density	Dense (D)	4	48
		Normal (N)	3	36
		Sparse (S)	1	12
8	Topographic position	Ridge (R)	5	40
		Upper slope (U1/3)	4	32
		Middle slope (M1/3)	2	16
		Lower slope (L1/3)	1.5	12
		Minor bottom (Mb)	1.5	12

Mason (1979) has developed a similar approach to risk rating in east Texas, based on photo-interpretable variables. He first examined the work of Hicks et al. (1979) and determined which of the stand and site variables that they reported to be closely associated with SPB infestations could be assessed with reasonable accuracy by photo interpretation methods. These were total BA/acre, tree species, average tree diameter, average height, and landform.

After preliminary geographical and host type characterization with 1:250,000 LANDSAT false color composites, Mason selected 10 U.S. Geological Survey 15-minute quadrangles representative of the east Texas piney woods. Within each of these he chose an 18,000-acre test block for detailed habitat mapping with the use of large- and small-scale color infrared photography

(1:5,000, 1:10,000, and 1:60,000) (fig. 8-7 A–C). Using high-intensity dot grids (10,000 dots/in^2) and specially developed equations, he estimated percent pine stocking (composition), BA/acre, average d.b.h., and percent crown closure. Stand height was visually estimated within broad classes by stereo observation and field reconnaissance.

Data were extrapolated from large-scale strips to areas covered by small-scale photos, to produce habitat type maps and landform overlays at a scale of 1:24,000. Ground checks verified that photo estimates of mapping variables were 92 percent accurate, and stepwise discriminant analysis yielded two photo-applicable models:

$$\text{Infested stand characteristics} = 7.76(\text{HTC}) + 4.42(\text{BAC}) + 4.49(\text{LDC}) - 26.05$$

$$\text{Baseline characteristics} = 7.06(\text{HTC}) + 3.40(\text{BAC}) + 5.02(\text{LDC}) - 22.92$$

where

HTC = Height class
BAC = Basal area class
LDC = Landform class.

These equations were about as accurate (71 percent) as models based on more variables or on additional variables not suitable for photo interpretation (Hicks et al. 1979).

Hazard ratings were assigned to stands within the 18,000-acre test blocks. Results with one such block based on 1973–1979 SPB infestation data in the Texas Forest Service's Operational Control System were encouraging.

	Hazard Class			
	Very high	High	Moderate	Low
Infestation/1,000 acres	10	10	6	2
Trees killed/1,000 acres	92	399	107	2

Evaluation is continuing on the nine additional 18,000-acre test blocks, and plans are being developed to test the system outside the area where it was developed.

Mason (personal communication) recognizes the need to differentiate somehow between the terms "hazard" and "risk," which are often used interchangeably. In one sense hazard may be high for an individual tree or small group of pines within an essentially hardwood stand, but the risk in terms of potential loss of resource may be quite low for the stand as a whole. Aerial photo interpretation techniques provide a useful means of recognizing and sorting out such differences.

Aerial approaches like Sader and Miller's and Mason's should be especially useful in situations where resource inventory data are lacking or are not available in a useful form.

Current Status and Future Needs

Great effort has been marshalled by the ESPBRAP to focus on the development of useful tools for forest managers to avoid and deal with southern pine beetle problems. A variety of approaches has yielded valuable insight into some basic interrelationships between the SPB and its host and site environment. Some potentially useful tools have been developed. Conscious effort should be given to developing guidelines for specific potential users in the context of the entire forest management problem. The SPB is only one small aspect of the complexity involved in management of the southern pine forests. So the closer research can come to developing useful tools that are easily understood, and that can be easily integrated into forest management planning systems, the more likely managers are to use them. Getting consideration for potential SPB outbreak incorporated into overall planning systems would be a major accomplishment in forestry practice in the South.

The essential basic knowledge needed for developing practical guidelines to forest managers is at hand. A large vacuum exists, however, with regard to knowledge of the basic relationships between host stand characteristics and SPB population dynamics. Future work toward refinement of SPB population dynamics models should involve closely integrated studies of population dynamics and tree, stand, and site characteristics. Hope for methods to predict continued growth or collapse of individual infestations and for predicting the start, continuation, or collapse of outbreaks hinges on such integrated research.

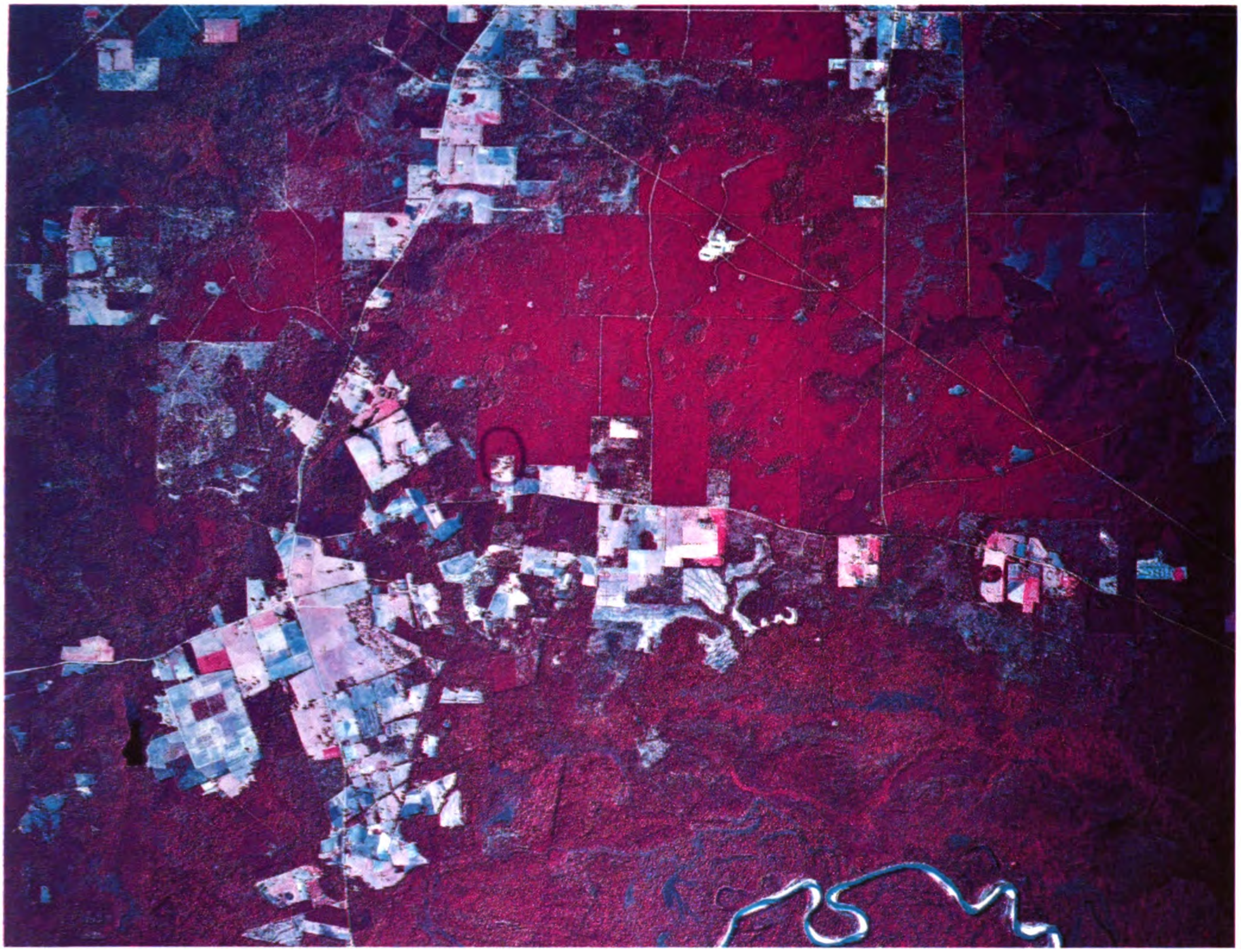

Figure 8-7A. – High-altitude, small-scale (1:60,000) color infrared photo used for stand type mapping and hazard classification.

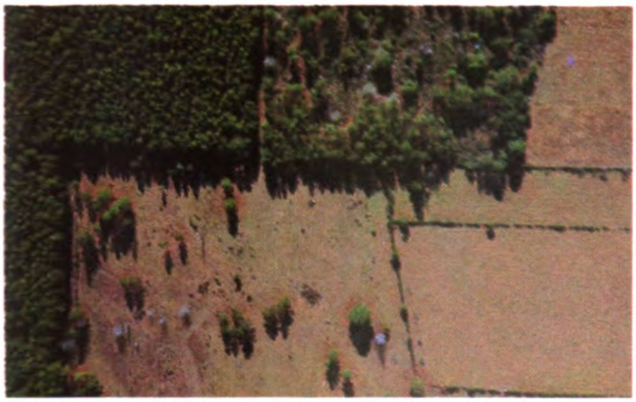

Figure 8-7B. – Medium-scale (1:10,000) 35-mm supplemental sampling photography for detailed stand evaluation.

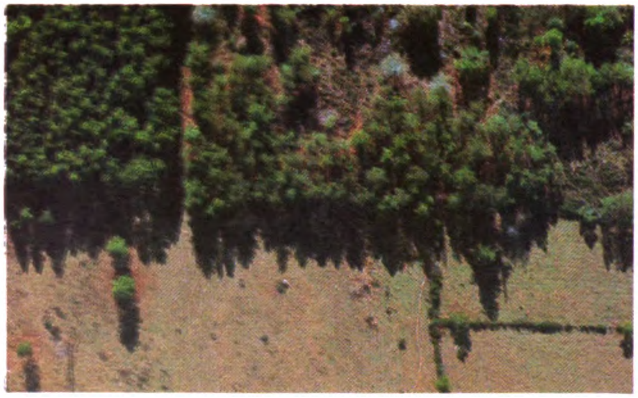

Figure 8-7C. – Large-scale (1:5,000) 35-mm supplement for stand and tree measurements.

Silvicultural Guidelines for Reducing Losses to the Southern Pine Beetle

9

Roger P. Belanger[1]

Introduction

The proper silvicultural treatment of forest stands is an essential element in developing strategies to achieve long-term success in suppressing the southern pine beetle. Intermediate cuttings and regeneration methods provide the means to produce environmental and biological conditions unfavorable to the attack, spread, and population growth of this forest pest. Yet silvicultural practices that promote stand resistance to insect damage are fundamentally lacking in management planning and practice. Severe timber losses and the recent decline of pine resources because of the SPB are evidence of this neglect.

Foresters in the South have long realized the opportunities for reducing insect damage through silviculture. General guidelines were developed to identify areas at high risk for SPB attack and reduce the potential for losses (Bennett 1968, 1971). Recommendations were sound and the message clear: good forest management provides protection against most insect pests. Detailed information was still lacking, however, to develop control tactics and prevention strategies that could be integrated with management operations and objectives. Forest pest managers did not know what stand, site, and host tree characteristics are associated with SPB infestations. Systems and methodology to rank the relative susceptibility of stands to beetle attack were needed. Studies had not been conducted to determine how host-insect relationships differed between and within the Southern Coastal Plain, Piedmont, and Southern Appalachian Mountains. Many of these questions have been answered by the accelerated efforts of the Expanded Southern Pine Beetle Program. Findings from this 6-year program provide the basic information used to develop the silvicultural principles and practices discussed in this chapter.

The purpose of silviculture is to produce and maintain such a forest as will best fulfill the objectives of the owner (Smith 1962). The practice of silviculture involves harvesting, regeneration, tending, and protecting the crop. Treatments are assigned according to economic considerations and management objectives. Cultural practices to promote long-term resistance to SPB attack can be in harmony with these goals. In many instances, "prevention silviculture" may be necessary to obtain the desired forest crops.

Protecting Stands from the SPB

To fulfill management objectives and maintain stable, healthy forest stands, the manager must understand tree physiology, the factors that influence the growth and development of stands, and the importance of site. Attention to these basic principles is required before proper practices can be defined to protect stands from the SPB. They are the keystones to the silvicultural techniques outlined in figure 9-1.

Promoting Individual Tree Resistance

Favor Most Resistant Species

Intermediate cuttings and regeneration systems should retrict the composition of the stand to species that are best suited to the site and most resistant to southern pine beetle attack. Slash pine, longleaf pine, Virginia pine, and eastern white pine tend to be more resistant to SPB attack than loblolly pine, shortleaf pine, or pitch pine (Hodges, Elam, and Watson 1977; Belanger, Osgood, and Hatchell 1979b). Differences in susceptibility are related to the physical properties and to the toxicity of the oleoresin system (Coyne and Lott 1976, Hodges et al. 1977). The oleoresins of highly resistant pines are extremely viscous, crystallize slowly, and continue flowing for long periods of time after wounding. Southern pines with a high limonene content may be more resistant to continued beetle attack than trees with a low limonene percentage.

Strains of southern pines highly resistant to SPB infestation are not available for planting. The potential does exist, however, for making genetic gains through selection. Hodges et al. (1977) found that in regard to oleoresin properties, 19

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percent of loblolly pine trees studied in central Louisiana resembled longleaf pine or slash pine more closely than the average for loblolly pine.

Physical properties of oleoresins are under strong genetic control. Squillace and Gansel (1968) have developed procedures for assessing the potential oleoresin yield of pines at 2.5 years from seed. Peters (1971) showed it is possible to select for oleoresin properties while at the same time selecting for form and vigor. An early evaluation of the relative susceptibility of selected individuals or established genetic strains to SPB attack appears possible without sacrificing other desirable traits.

Remove High-Risk Trees

Trees damaged by lightning, wind, ice, and other destructive agents increase the chances of attack and buildup of troublesome insects and should be removed from the stand. Pines struck by lightning (fig. 9-2) offer a favorable environment for the SPB and *Ips* beetles (Hodges and Pickard 1971). Stands damaged by wind, ice, or hail are more susceptible to bark beetle attack than undisturbed stands (*see* Chapter 4). Salvage cuttings should be completed as soon as possible after injury has occurred.

Sanitation cutting fells or removes damaged, infested, and high-risk trees to prevent the establishment, spread, or proliferation of the southern pine beetle. Cut-and-leave (Chapter 10) is recommended for infestations that are too small and scattered for practical salvage removal. Treatments appear most successful when applied to spots with 10 to 50 active trees (Texas Forest Service 1975). Often, spots with fewer than 10 active trees become inactive and require no treatment. Large, active infestations are difficult to control regardless of treatment. Cutting infested trees into an opening may increase mortality of developing broods, especially if the entire log is exposed to direct sunlight (Hodges and Thatcher 1976).

Promoting Stand Resistance

Maintain Proper Density

High-risk stands are characterized by slow radial growth (*see* fig. 8-2). Intermediate cuttings are a means of promoting and maintaining rapid growth of trees in young stands and reducing losses from the SPB (fig. 9-3). Thinnings in North Carolina (Maki, Hazel, and Hall 1978 unpublished) reduced the average spot size from almost 6 acres per infestation to less than 3 acres and

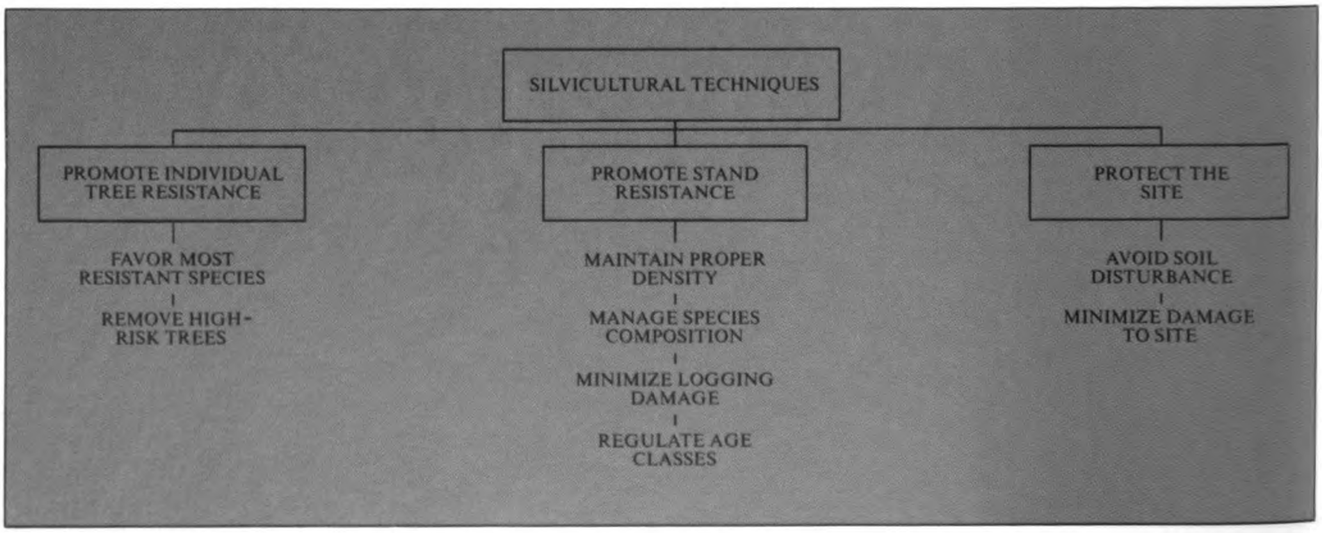

Figure 9-1. – Silvicultural guidelines to reduce losses from the SPB.

appeared to reduce the incidence of attack. Low thinning or "thinning from below" is recommended in natural stands and plantations to reduce competition and remove the types of trees most subject to SPB attack. The poorer crown classes – suppressed and intermediate trees – are cut first. These small, slow-growing trees are more susceptible to beetle attack than healthy trees (Haines, Haines, and Liles 1976; Ku, Sweeney, and Shelburne 1976). Dominant and codominant trees with large live crown/height ratios and desirable phenotypic traits should be favored as crop trees. They are best suited to respond with increased growth after release and have the most potential for high-value products.

Prescribed burning (fig. 9-4) can be used to eliminate suppressed, high-risk trees from overstocked stands (McNab 1977). Site-stand studies have shown no relationship between burning and SPB attack. The role of fire in pest management strategies deserves additional study.

Thinning schedules depend on the close relationships between site quality, age of the stand, stand density, live crown ratio of individual trees, and rate of growth. Root and crown competition among individual trees usually occurs at ages 10 to 15 years on good sites, later on poor sites. Thinning at this time is advised to maintain rapid tree growth. Delay will reduce live crown ratios and tree vigor to levels unfavorable for growth but attactive to the SPB.

Degree of thinning to reduce the risk of southern pine beetle attack is determined by the intensity of management, the kind of product desired, available markets, and natural conditions particular to each location. Reduction of basal areas to 80 to 100 ft²/acre is recommended for overstocked stands of immature trees. The risk of beetle attack in most instances will increase considerably at basal areas greater than 100 ft²/acre. Wide spacing distributes growth on a selected number of desired stems, resulting in the production of small saw logs by age 35 to 40 years on good sites. Heavy thinning should be avoided, however, in areas subject to severe wind and ice storms (Belanger and Brender 1968). Dense stocking is recommended if the management objective is high yields of wood fiber. Light thinnings may need to be repeated at short intervals to maintain vigorous growth.

Thinning on high-hazard annosus root rot sites (> 70 percent sand in topsoil) can lead to spread of the disease and severe infection followed by a reduction in radial growth and attack by the southern pine beetle (Skelly, Powers, and

Figure 9-2. – Pines struck by lightning are highly susceptible to beetle attack.

Morris 1974). Precautions can be taken to reduce the danger of annosus infection. Thinning should be scheduled during summer, when fewer annosus spores are produced and high temperatures kill those that are produced. Treating stumps with borax or *Peniophora* spores minimizes spread. Prescribed burning before and after thinning also reduces severity of annosus root rot in the South (Froelich, Hodges, and Sackett 1978).

Manage Species Composition

Favoring beetle-resistant species of pine and removing high-risk trees lower the hazard index of stands. Stand composition of pines and hardwoods also promotes resistance to attack and the spread of endemic beetle populations (Belanger et al. 1979b; Belanger, Porterfield, and Rowell 1980 unpublished). The SPB prefers host types that are uniform and continuous. Spread of infestations is greatest in dense pine stands (Gara and Coster 1968, Hedden and Billings 1979). Hardwoods limit these conditions by disrupting continuity between host trees. Intermediate cuttings should favor hardwoods that are suited to the site and are compatible with long-term management objectives. BA of the pine component should be maintained at < 100 ft^2/acre.

Minimize Logging Damage

Logging activity has a tendency to increase southern pine beetle attack (Porterfield and Rowell 1980). Careless cutting, skidding, and hauling often cause severe mechanical injury to above- and below-ground portions of residual trees. These disturbances are attractive courts for the black turpentine beetle, *Ips* species, and SPB.

Figure 9-3. – Intermediate cuttings promote the rapid growth and vigor of young stands.

The more recent the logging damage, the more susceptible the stand is to attack.

Increased beetle activity resulting from poor logging practices can quickly offset the benefits from silvicultural treatments. Harvesting systems should be developed that minimize damage to the stand and site. Use of small harvesting equipment and removal of short roundwood are recommended for intermediate cuttings. Heavy equipment and tree-length logging generally increase the amount of damage to residual trees. Equipment operators and ground crews can be trained to minimize damage to residual trees and promote stand conditions less vulnerable to insect attack.

Regulate Age Classes

Susceptibility of stands to SPB attack increases with age throughout most of the South (Lorio 1978, Belanger et al. 1979b, Coster and Searcy 1980). Overmature stands are characterized by slow radial growth, flat-topped crowns, and thin foliage. Trees in these advanced stages of decline are seldom able to respond to treatment. The best option is to regenerate these stands. Excellent guidelines exist that bring together information on methods of regenerating the southern pines (U.S. Department of Agriculture Forest Service 1973; Society of American Foresters 1981). The manager has the option of planting or natural regeneration. Quality trees of

Figure 9-4. – Prescribed burning can be used to eliminate small, high-risk trees from stands.

the most resistant host species should be retained as seed trees if the stand is to be renewed naturally. Planting provides choice of species and desired spacing. Close initial spacings will require intermediate cuttings at an earlier age than wide spacings in order to reduce risk of SPB attack.

Many overmature stands of pines are intentionally being preserved throughout the South for esthetic reasons, ecological study, and wildlife. Overmature pines add to the visual attractiveness of woodlands and are the required habitat of some wildlife species. Overmature stands are extremely susceptible to SPB attack and need to be monitored closely to prevent buildup of epidemic populations and loss of the entire pine component. Host trees attacked by bark beetles should be removed as soon as possible.

Figure 9-5. – Clay soils restrict root development.

Protecting the Site

Southern pine beetle infestations have been associated with soil and site conditions in the Piedmont (Belanger et al. 1980 unpublished) and the Southern Coastal Plain (Lorio and Hodges 1971; Belanger, Hatchell, and Moore 1977; Hicks et al. 1979). Piedmont soils are characterized by heavy micaceous clays that have a high erosion potential, limit the infiltration and percolation of water, and restrict expansive root development (fig. 9-5). Infestations on the Coastal Plain are more frequent on wet and waterlogged sites than well-drained sites. Harvesting methods and cultural operations should avoid disturbing soils and other site conditions whenever possible.

Fertilization plays an important role in the establishment and growth of many pine plantations in the South. Studies have not been conclusive, however, in assessing the relative susceptibility of fertilized stands to SPB attack (Haines et al. 1976, Maki et al. 1978 unpublished, Moore and Layman 1978). Fertilizer increases the growth of large trees while small trees are further suppressed. It is speculated (Haines et al. 1976) that SPB broods that develop in suppressed trees are not capable of successfully attacking neighboring, more vigorous trees of larger crown classes. This hypothesis still needs to be tested.

Regional Recommendations

Unhealthy stands are highly susceptible to attack by the southern pine beetle. This familiar and basic principle applies regardless of region or pine type. Although silvicultural practices can prevent or reduce losses from beetles by increasing the resistances of host trees, no "standard" recommendation will apply to all situations. Each forest condition and locality presents different management problems; each might require a different combination of methods to increase resistance to insect attack.

Southern Coastal Plain

The Southern Coastal Plain includes the seaboard extending from Maryland and Delaware along the Atlantic Coastal Plain and Gulf Coastal

Plain to Texas. The region can be further subdivided into the lower and upper Coastal Plain. The lower Coastal Plain consists of the low elevation "flatlands" and wetlands. Slash pine, longleaf pine, and planted loblolly pine are the principal SPB host species. The upper Coastal Plain lies inland from the flatlands. The topography is slightly rolling and the soils have good drainage. Between one-half and three-fourths of the area is forested. The principal pine species in the upper Coastal Plain are loblolly and shortleaf.

Natural stands most susceptible to southern pine beetle attack in the Coastal Plain are characterized by high stand densities (fig. 9-6), a large proportion of pine sawtimber, and declining radial growth (Coster and Searcy 1980; Chapter 4). Poorly drained soils and low-lying areas are also indicators of high-risk sites. Trees on dry or droughty soils are less commonly attacked. Timely cultural treatments can prevent or reduce stress conditions that favor attack and spread of the SPB.

Intermediate cuttings in heavily stocked plantations and natural stands will reduce competition between trees and reduce the probability for southern pine beetle attack. Initial cuttings should be early – not later than 20 years – to anticipate rather than relieve the adverse effects of severe crowding. Thinning may be required sooner on good sites than on poor ones, and possibly sooner in the Gulf Coastal Plain than on the Atlantic seaboard (Wahlenberg 1960). Overstocked stands should be thinned to a BA of 80 ft^2/acre to increase growth rate and vigor (Hicks et al. 1979, Toko and Landgraf 1979). Residual BA can be slightly higher as age and site

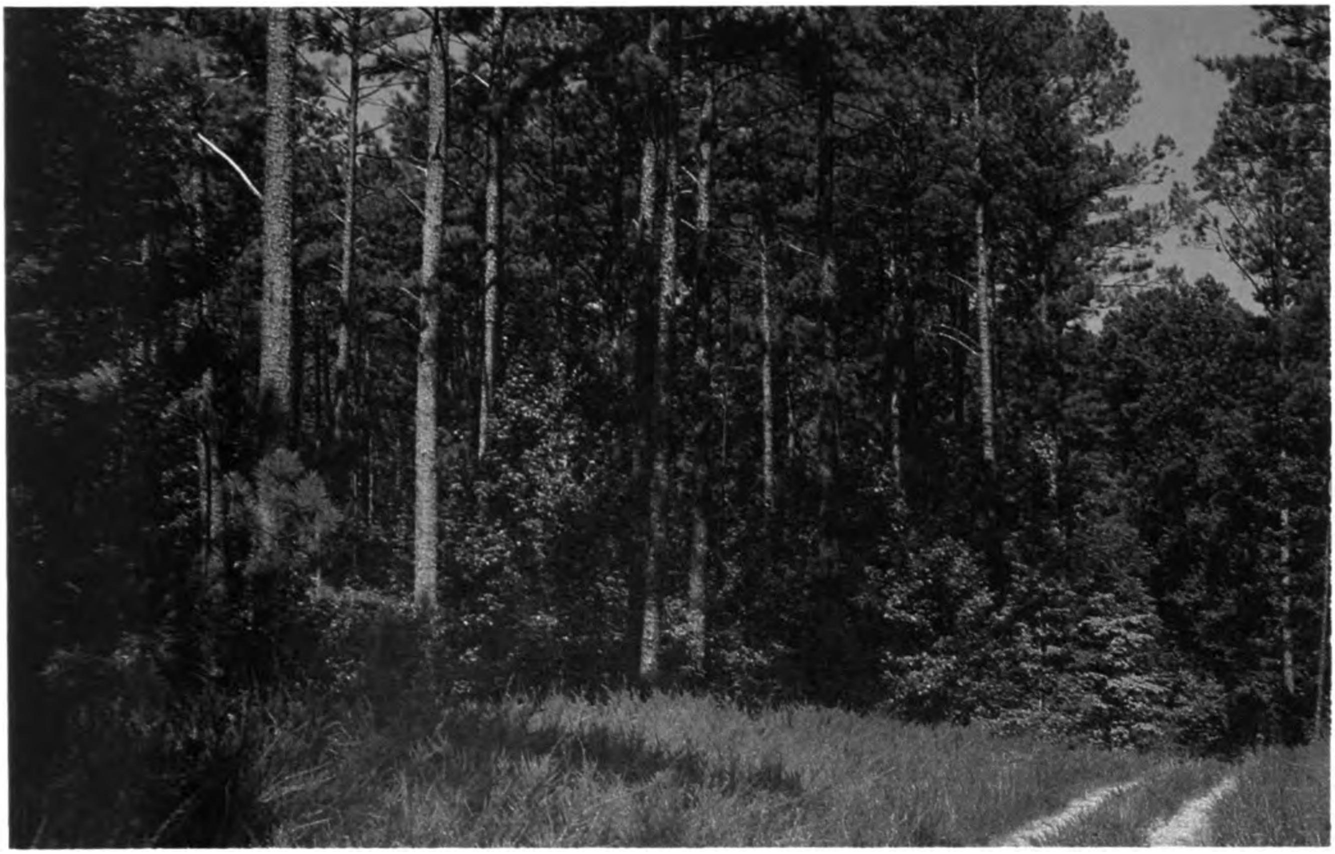

Figure 9-6. – Dense stands are subject to attack by the SPB.

index increase. Intermediate cuttings should be rescheduled as BA approaches 120 ft^2/acre.

Infestations in the Coastal Plains are more frequent on wet and waterlogged sites than on well-drained soils. There are 20 million acres of excessively wet, swampy sites in the Atlantic and Gulf Coastal regions (Zobel 1979). Trees on poorly drained sites are often deficient in mycorrhizal roots and are therefore subject to severe physiological stress during periods of drought (Lorio, Howe, and Martin 1972). Drainage systems designed to remove surplus water from low-lying areas will curtail the damage from rootlet pathogens and stem the decline of host pines (Bennett 1971). Drainage improvements have already bettered over 2 million acres of forest lands in the South. Logging damage on low-lying areas of fine-textured soils can be avoided by diverting operations to sandy soils during wet periods and using harvesting equipment of low bearing pressure (Hatchell, Ralston, and Foil 1970).

Wet sites should be regenerated with more beetle-resistant species, such as slash pine or hardwoods (Hicks et al. 1979). "Wet site" loblolly pine and pond pine grow well on wetlands (Zobel 1979), but their relative resistance to SPB attack is unknown. On high-risk sites – conditions too wet or too dry – resistance to pests may be more important than tree growth alone.

Potential for growth and yield in the southern Coastal Plain appears directly related to potential for beetle problems. Infestations occur more frequently on moist, high-quality sites than on poor sites (Lorio 1978, Kushmaul et al. 1979). Consequently, a disproportionate amount of silvicultural attention can justifiably be directed toward stands growing on good sites. Intermediate cuttings are required sooner and more frequently on quality sites than poor sites to reduce competition from hardwoods and understory vegetation, maintain rapid radial growth, and develop a species composition unfavorable to beetle attack. Quality sites have the potential for high yields of forest products. Extra care and protection may be necessary measures to meet these goals.

The southern Coastal Plain has a high frequency of thunderstorms, tropical storms, and glaze storms. These types of climatic damage to trees promote bark beetle attack and spot proliferation. Spot spread depends on size and vigor of the insect population and interrelationships of different bark beetles present within the stand. Damaged and dying trees should be salvaged promptly to reduce the numbers of focal points for infestations. If needed, other intermediate cuttings could be conducted at the same time to reduce stand density and the probability of spot expansion. The forester can do little to guard against increases in beetle activity associated with extended periods of drought or flooding (King 1972, Kalkstein 1976). Frequent surveillance during periods of extreme climatic stress makes prompt detection of insect attack possible and assists the manager in deciding what measures are needed to control the pest.

Piedmont

The Piedmont extends from Virginia through North Carolina, South Carolina, Georgia, and into Alabama. At one time or another most of this land was in clean-cultivated crop production. Soil depletion following continuous cropping and severe erosion resulted in widespread land abandonment. Forests quickly reclaimed the fields. Loblolly pine and shortleaf pine were the predominant pioneer tree species in the southern portion of the Piedmont; shortleaf pine and Virginia pine spread throughout the northern Piedmont.

About three-fifths of the Piedmont is now in forests, mostly farm woodlands. Approximately half of these forests are in natural and planted pines and the other half in mixed hardwoods. Destructive losses from the SPB are accelerating the natural succession from pine to climax hardwood species (*see* Chapter 5). Species composition in the Piedmont is widely varied, and forests are interspersed with agricultural lands. Ownerships and management objectives are numerous. Though these conditions complicate forest management, they need to be considered individually and collectively in developing silvicultural systems to prevent or reduce SPB-caused losses.

Natural stands susceptible to southern pine beetle attack in the Piedmont are characterized by dense pine stocking with a large percentage of the host component in shortleaf pine (fig. 9-7), slow radial growth during the last 10 years, and a high clay content in the surface and subsurface horizons (Belanger et al. 1980 unpublished, Maki et al. 1978 unpublished). Where loblolly and shortleaf pine are the predominant host species, regeneration systems and intermediate cuttings should favor loblolly whenever possible. A wide range of possible silvicultural methods is available for the management of loblolly pine (Wahlenberg 1960; Brender 1973; Brender, Belanger, and Malac 1981). Most loblolly pine stands require intermediate cuttings to realize maximum growth and yield, and to reduce their susceptibility to beetle attack. Basal area of approximately 80 ft²/acre is recommended for average Piedmont sites. Prescribed levels of density can vary slightly with age, site quality, and owner objectives. A live crown ratio of 40 percent for young trees and 33 percent for older trees is recommended to promote individual tree vigor (Brender 1979). Thinnings may have to be repeated at 5- to 10-year intervals to maintain these crown ratios.

Figure 9-7. – Shortleaf pine is highly susceptible to SPB attack in the Piedmont.

Selection criteria are more difficult when managing mixtures of Virginia pine and shortleaf pine. Virginia pine, although more resistant to beetle attack than shortleaf, is often characterized by poor form and persistent branches. These faults present difficulties in harvesting and processing for solid wood products. Virginia pine is recommended for hazard areas where high yields of wood fiber are the primary management objective. Shortleaf pine is recommended for solid wood products.

Most Virginia pine stands in the Piedmont resulted from natural seeding on abandoned agricultural lands during the 1930's and 1940's. Stocking is usually dense, stems are small, and radial growth is slow. Spread and proliferation of the SPB in these stands can be extreme once infestations occur. Intermediate cutting does little to increase stand resistance under these conditions. Height and diameter growth in mature Virginia pine stands do not respond to thinning as rapidly as loblolly pine or shortleaf pine (Belanger and Bramlett 1979). Mature, slow-growing stands should be harvested and regenerated naturally to Virginia pine or planted to loblolly pine.

The best management strategy to reduce losses from the southern pine beetle is to thin Virginia pine before age 15, with subsequent thinnings as needed to maintain rapid growth. Basal areas should be maintained at about 100 ft²/acre for high yields of wood fiber.

Figure 9-8. – Regeneration systems should favor species that are highly resistant to attacks by the SPB.

Shortleaf pine deserves special consideration and attention in the culture of Piedmont forests. The growth, yield, and quality of products from shortleaf pine stands can be excellent on good sites. There is little reason to discriminate against shortleaf pine under these circumstances. These stands can be managed much like loblolly pine to maintain rapid and vigorous growth (Belanger 1979). Susceptibility of shortleaf pine to SPB attack appears to increase as quality of the site decreases. Silvicultural options are limited on poor sites; heavy clay soils limit economic, biological, and environmental gains from treatment. Salvage cuttings are recommended to utilize dead trees; sanitation cuttings will remove the most susceptible trees and reduce chances of spread to healthy trees. Stands should be harvested at 25 to 30 years of age to prevent severe losses from both SPB and littleleaf disease. Loblolly pine should be favored over shortleaf pine when possible in the management of susceptible stands (fig. 9-8).

Managing pine and hardwoods in mixtures also reduces the probability of insect attack and spread in the Piedmont (Belanger et al. 1980 unpublished). Sweetgum *(Liquidambar styraciflua* L.) can be reproduced and managed with pine on upland sites. Yellow poplar *(Liriodendron tulipifera* L.), red oaks *(Quercus* spp.), sycamore *(Platanus occidentalis* L.), and sweetgum are suited for lower slopes and bottomland sites. Mixing stand components may be suited to owners of small, nonindustrial woodlands managing for products other than timber. Mixed stands often support diverse and dense wildlife populations, can be esthetically pleasing, and contribute toward a gradual improvement of poor sites.

Little can be done to make immediate or significant long-term improvements to soil and site conditions characteristically associated with high-risk stands in the Piedmont. These soils have a high erosion potential and require careful management to prevent further deterioration of the site. Intensive site preparation and cultivation with heavy equipment are recommended only where soils and slopes are suited for these practices. The application of intensive site preparation methods should be avoided on slopes greater than 10 percent. Burning appears to be a preferable alternative to intensive mechanical preparation from the standpoint of soil erosion (Nutter and Douglass 1978). Herbicides offer the greatest opportunity to control competing vegetation with minimum impact on soil physical properties. Logging practices and methods of site preparation need to be specific to site conditions. Further abuse of already fragile sites in the Piedmont will only intensify SPB problems in the future.

Southern Appalachians

During the last century, removal of large volumes of timber due to mortality from chestnut blight, domestic use of timber, damage from grazing, and woods burning has produced a general forest condition of low stocking and poor quality in the Southern Appalachians (Brender and Merrick 1950). Most of the forest types are mixed hardwood. In the mountains, SPB host types are primarily Virginia pine, shortleaf pine, eastern white pine, and pitch pine. Many pine stands resulted from natural seeding on remote and scattered farms that were sold or abandoned. Today most of this land is managed by Federal agencies for multiple uses. The accessibility of stands often determines the intensity of management and specific objectives. Private, nonindustrial holdings are mostly in the valleys, where topography is suited for farming and settlement.

The southern pine beetle has been a problem for decades in the Southern Appalachians. Several outbreaks have been reported since 1920 (King 1972, Price and Doggett 1978), the most recent activity having occurred from 1972 through 1977. Studies in the mountains of Georgia, North Carolina, South Carolina, and Tennessee showed that stands severely attacked by the SPB were characterized by dense stocking, slow radial growth, and a large proportion of overmature pine sawtimber (Belanger et al. 1979b). Short leaf and pitch pines are more susceptible to beetle attack than Virginia pine or eastern white pine. Findings indicate that management and silvicultural techniques offer means of reducing SPB-caused pine mortality in the Southern Appalachians.

Managing species composition deserves consideration as a method of reducing such losses. Managers should favor eastern white pine and Virginia pine over shortleaf pine or pitch pine whenever possible. The ability of vigorous-growing white pine and Virginia pine to "pitch out" SPB may account for the low rates of mortality of these species. White pine, economically one of the most important sawtimber species in the Southern Appalachians, can be regenerated by clearcutting and planting, clearcutting with seed in place (Moyers 1979), or planting under a residual hardwood overstory (Van Lear and Cox 1979). Seedlings should be released the third growing season if competition from hardwood sprouts and brush is severe. Intermediate cutting can be scheduled at ages 20 and 30 to obtain high-value products and maintain rapid growth. Harvest should be scheduled at 40 to 50 years. Older trees are susceptible to beetle attack (Belanger et al. 1979b).

Management recommendations for Virginia pine in the Southern Appalachians are similar to those for the Piedmont: some form of clearcutting for regeneration, early intermediate cuttings to maintain rapid growth, and harvesting at ages 40 to 50 years. Excellent stands of Virginia pine have been regenerated in the mountains by clearcutting, burning to reduce heavy slash and hardwood competition, and planting with superior stock.

Another preventive measure where nontimber values are an objective is managing pine and hardwoods in mixture. Hardwoods are a component of most pine stands and the climax species in the mountains. Favoring hardwoods during intermediate cutting will reduce the incidence of beetle attack as well as improve the quality of stands and sites.

A combination of thinning, improvement cuts, and salvage cuts may be used to reduce the BA of overstocked stands. Approximately 80 to 90 ft^2/acre of leave BA is recommended for these types of stands (U.S. Department of Agriculture Forest Service n.d.). Overmature, slow-growing trees should be cut to improve the age distribution and growth potential of the residual stand. It may be necessary to carry out two or three intermediate cuts to obtain the desired results. Overmature stands should be harvested and regenerated to species most resistant to SPB attack.

Intensive culture of forest stands is difficult in the Southern Appalachians. The most common deterrents to silvicultural treatments are the inaccessibility of stands, poor market conditions, and a lack of logging and planting contractors. Where pines contribute significantly to management objectives, these obstacles need to be overcome. Neglect of the pine component could increase the risk of attack and probability of severe losses should SPB outbreaks occur.

Discussion

In recent years SPB activity has increased in frequency and severity throughout the South. The problem appears closely related to changes in forest composition and stocking conditions (Hedden 1978b). Much of the present southern pine forest resulted from natural seeding and planting on abandoned agricultural lands from 1930 through 1950. Young stands grew rapidly with little or no management. Insect and disease problems developed as stands became crowded and vigor declined. Problems intensified as stand age, stocking, and sawtimber volume increased. Proper management can reverse this trend. Information and ranking systems are now available (*see* Chapters 4 and 8) to identify highly susceptible stands. Studies have shown that silvicultural treatments have been effective in reducing losses from the SPB (Morris and Copony 1974, Maki et al. 1978 unpublished).

Natural stands and plantations can be equally susceptible to SPB attack when mismanaged; they can be equally resistant to the beetle when treated properly. Planting offers the best opportunities to control seedling quality, species composition, stocking, and culture of the stand for high yields of wood products. Natural regeneration provides protection to the site, has low establishment costs, and can satisfy a number of forest management goals. Methods and intensity of silviculture depend on objectives of ownership.

Systems developed to determine the relative susceptibility of stands to southern pine beetle attack can be used to evaluate the effectiveness of silvicultural treatments. Intermediate cuttings to reduce stocking levels and stimulate radial growth will lower the probability of attack in most high-risk stands. Response to cutting will not be immediate after treatment. A period of 3 to 5 years may be necessary before roots and crowns of released trees can support rapid growth. Response time will increase with age of the stand and poor site quality. Overmature stands are usually past the point of physiological improvement and should be regenerated.

Cultural treatments are also needed in young stands and low-risk stands to maintain rapid growing conditions. Competition in the early life of the stand usually occurs at ages 10 to 15 years, depending on site quality and initial spacing. Initial thinning is recommended shortly after crown closure. The purpose of treating young stands is to prevent rather than remedy high-risk conditions. Periodic thinning and improvement cuts will maintain stand vigor.

Careful tending of host types is necessary to obtain effective and lasting management of the southern pine beetle. Most forest agencies and industries are experienced and respond quickly with the salvage of infested stands and control measures during epidemic beetle conditions. But silvicultural activities related to forest pest management generally lag during periods of low beetle activity. When SPB populations are down, planning and application of prevention strategies should be accelerated. High-risk stands can be identified and treated to reduce the susceptibility of beetle attack and probability of spot spread. Low-risk stands can be tended to maintain vigor and rapid growth. Stands and forests that are highly resistant to SPB attack should be a primary objective of management. Silvicultural practices offer the most practical and long-lasting means of achieving this goal.


BARKO
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Direct Control

Ronald F. Billings[1]

10

Introduction

The search for practical and effective methods to protect pine resources from the southern pine beetle has challenged scientists and forest managers for many years. Increasing emphasis is now being placed on proper forest management practices (silvicultural control) as the principal means for avoiding beetle problems (*see* Chapter 9). But outbreaks continue to occur in areas where host and climatic conditions favor SPB population increases. Direct control methods – salvage, cut-and-leave, insecticides, or pile-and-burn – provide the last line of defense for protecting pine resources from excessive losses once infestations are in progress.

Until about 1970, the primary approach for combating the southern pine beetle and other bark beetle pests was to destroy broods in infested trees. With limited knowledge of the insect and a lack of trained personnel, forest managers saw this strategy as the simplest and most efficient way to deal with bark beetles when they became a problem.

Before the 1960's, we knew little about the underlying causes of southern pine beetle outbreaks and relationships between beetle attacks and host condition. As a result, the SPB was considered a "beetle problem" rather than a "tree problem," to be dealt with in a manner similar to insect pests in agricultural crops. For many years, direct control was the first and only line of defense for protecting valuable timber resources. Conveniently enough, science helped us fight the beetle battle with chemical weapons.

Early methods for killing beetles were varied and imaginative: rapid utilization of infested trees (= salvage) and burning the slabs, tops, and unmerchantable trees; immersing infested logs in water (Hetrick 1949); exposing infested trees to solar heating (= cut-and-leave) (St. George and Beal 1929); and injecting poisons into the sap stream of recently infested trees (Craighead and St. George 1938). But some of these practices also proved inefficient and often impractical.

The search for more efficient means to maximize brood mortality led to the development of toxic chemical sprays. Orthodichlorobenzene in kerosene and later in fuel oil was successfully used on SPB during the 1940's (Thatcher 1960). Following World War II, a new chlorinated hydrocarbon insecticide – benzene hexachloride (BHC) – became available and was first used in 1950 to combat an SPB outbreak in east Texas (Morris 1951 unpublished).

With BHC and its gamma isomer lindane as weapons, pest control specialists firmly believed that outbreaks could be suppressed and beetle problems solved simply by treating enough beetle-infested trees to eliminate the beetle's pest status – if not the insect itself. State and Federal pest control agencies and industrial landowners pursued this "brute force" approach diligently. Chemical control had priority over salvage because of the belief that "salvage contributes little or nothing toward control of the beetle populations" (Texas Forest Service 1950).

But the insecticide treatments did have limitations. They were expensive and time-consuming; costs ranged from $1 to $10 per tree (Drake 1970). And chemicals required careful, thorough treatment in order to give high mortality (Anderson 1967). Further, their extensive use was charged with selectively eliminating beneficial insects (Williamson and Vité 1971).

These factors, along with the discouraging fact that beetle outbreaks continued year after year in spite of large-scale chemical control programs, ultimately put an end to their wide use for bark beetle control in the South. The BHC era had ended by 1970, and the search for new and environmentally acceptable alternatives began.

Pest managers are changing their philosophy toward direct control. Control programs that involve both preventive and remedial measures are being encouraged. Depending on the value of the resource threatened, the objectives of the landowner, and the season, the control strategy may be to minimize timber losses, to maximize beetle

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mortality, or to let nature take its course (Hedden 1979). Indeed, spots may go untreated if the likelihood for additional timber losses is small or if the landowner places little or no value on the threatened trees. New strategies will integrate insect control programs with total resource management and will neither exclude nor rely solely on direct controls (Coster 1977).

Current Control Methods

At present, forest managers or landowners faced with southern pine beetle infestations can choose from four direct control options: (1) removal and utilization or sale of infested trees (salvage), (2) cut-and-leave or cut-and-top, (3) fell and spray with insecticides, and (4) fell, pile, and burn infested trees. Options (1) and (4) are among the earliest controls recommended for use against SPB (Hopkins 1911).

Selection of a tactic usually depends on the value of the resource threatened, the scope of the pest problem, spot size and accessibility, the landowner's management objectives, and the season (Hedden 1979, Swain and Remion 1980). Also, each method has advantages and limitations that may either favor or preclude its use in a particular situation.

Salvage

Throughout the South, prompt salvage and utilization of infested trees has become the preferred method for minimizing the beetle's economic impacts and simultaneously reducing beetle concentrations.

Procedure

Salvage control consists of rapidly removing from an infestation all trees that contain SPB brood or attacking adults (Texas Forest Service 1976). In addition, a 10- to 100-ft buffer strip of uninfested trees around the active head of the spot is designated for removal (fig. 10-1). The buffer strip is especially important for large spots because it serves to disrupt spot growth.

Advantages and Disadvantages

Salvage is preferred over other direct controls because the owner can recover part of his losses by selling the merchantable trees. The prompt removal of logs with beetle-infested bark intact serves to reduce beetle concentrations in treated stands (Morris and Copony 1974, Billings and Pase 1979a). And removal of an adequate buffer strip prevents spots from spreading. Whether salvage operations reduce *areawide* beetle outbreaks remains in question.

Although the benefits of salvage seem obvious, it is not appropriate for all southern pine beetle spots (Kucera 1969). Clearly, to be controlled by salvage, a spot must be accessible to heavy logging equipment and contain sufficient merchantable volume to cover harvesting costs. Also, there must be a local market for beetle-killed trees. Because of these constraints, many spots are not suitable for salvage control. Despite

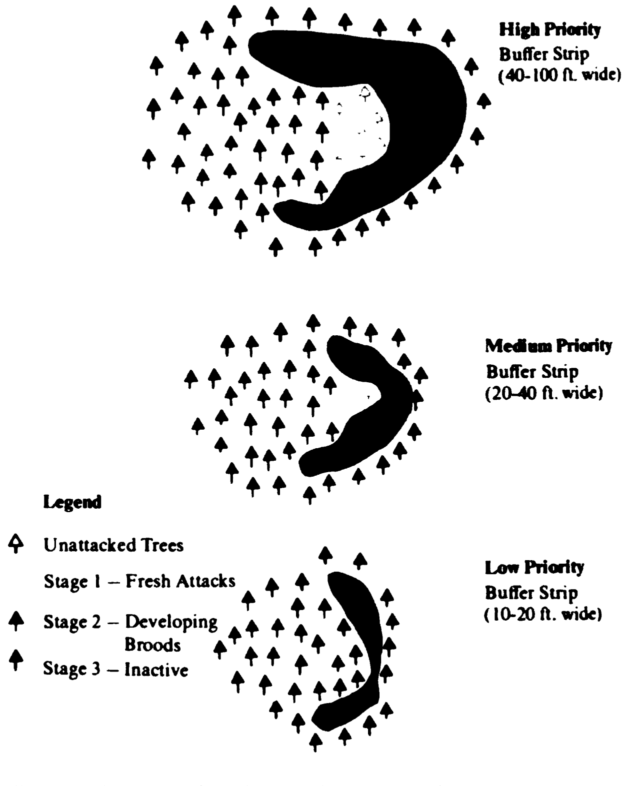


Figure 10-1. – Procedure for marking buffer strips for control by means of salvage.

these limitations, salvage, when properly and promptly applied, remains the most practical and economic control tactic for treating large, rapidly growing infestations (Swain and Remion 1980).

Cut-and-Leave (Cut-and-Top)

In east Texas a tactic known as cut-and-leave has been increasingly used on spots where salvage is not practical (fig. 10-2). In 1979, the tactic was added to the list of recommended SPB suppression procedures for which Federal cost-sharing funds may be obtained (Harvey Toko personal communication). To date cut-and-leave has been used only on a limited basis in other Southern States.

Figure 10-2. – Application of cut-and-leave requires felling those trees that contain SPB broods, plus a buffer strip of uninfested trees.

Procedure

The procedure for cut-and-leave, described in detail elsewhere (Texas Forest Service 1975, Swain and Remion 1980), is similar to salvage treatment, except that felled trees are not removed (fig. 10-3). Only currently infested trees and a buffer strip of uninfested trees are felled, with the crowns pointing toward the center of the spot. Cut-and-top is a variation of cut-and-leave in which the crowns of infested trees are severed from the lower boles. The use of cut-and-top in

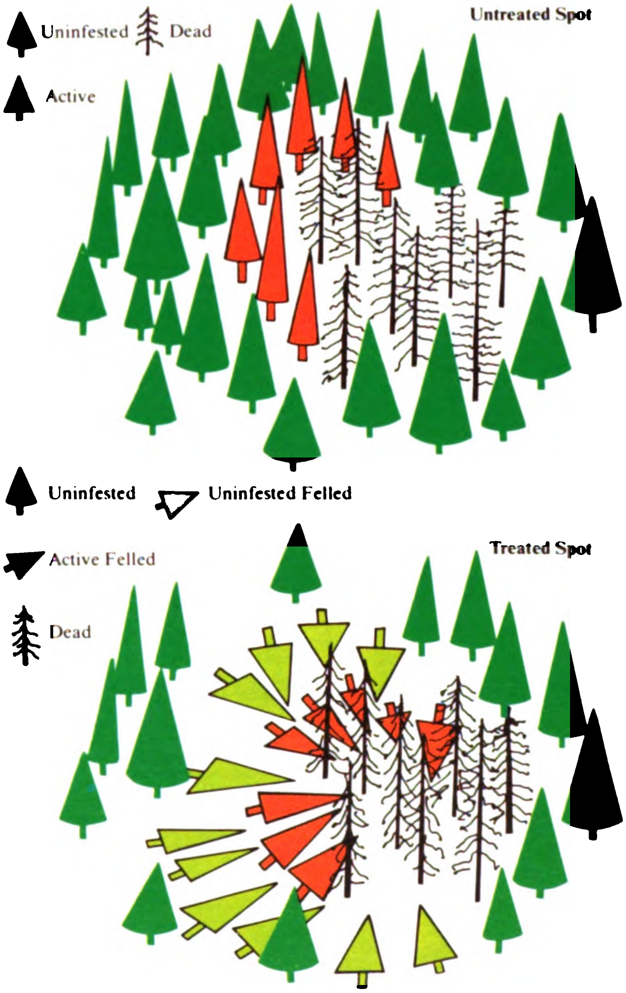


Figure 10-3. – Procedure for controlling southern pine beetle infestations by means of cut-and-leave.

east Texas largely has been discontinued in favor of the simpler and less time-consuming cut-and-leave method.

Rationale

Cut-and-leave and cut-and-top methods were initially designed to capitalize on biological limitations of developing broods (Ollieu 1969). Low moisture and high temperature in the inner bark area of the felled trees were expected to reduce beetle survival. But experimental tests of cut-and-leave did not demonstrate sufficient beetle mortality to justify its application solely on that basis (Hodges and Thatcher 1976, Palmer and Coster 1978, Hertel and Wallace 1980).

But cut-and-leave continues to see use in Texas, primarily because of another beneficial effect – when a buffer strip is included, it stops the expansion of a spot (Ollieu 1969).

The biological rationale for spot disruption by cut-and-leave is based on our understanding of how individual spots expand during the summer (*see* Chapter 2). Continuous spot growth requires at least three factors: emerging beetles, nearby pine trees, and a source of secondary attractants (fig. 10-4). Felling the most recently attacked trees eliminates the attractant source (Vité

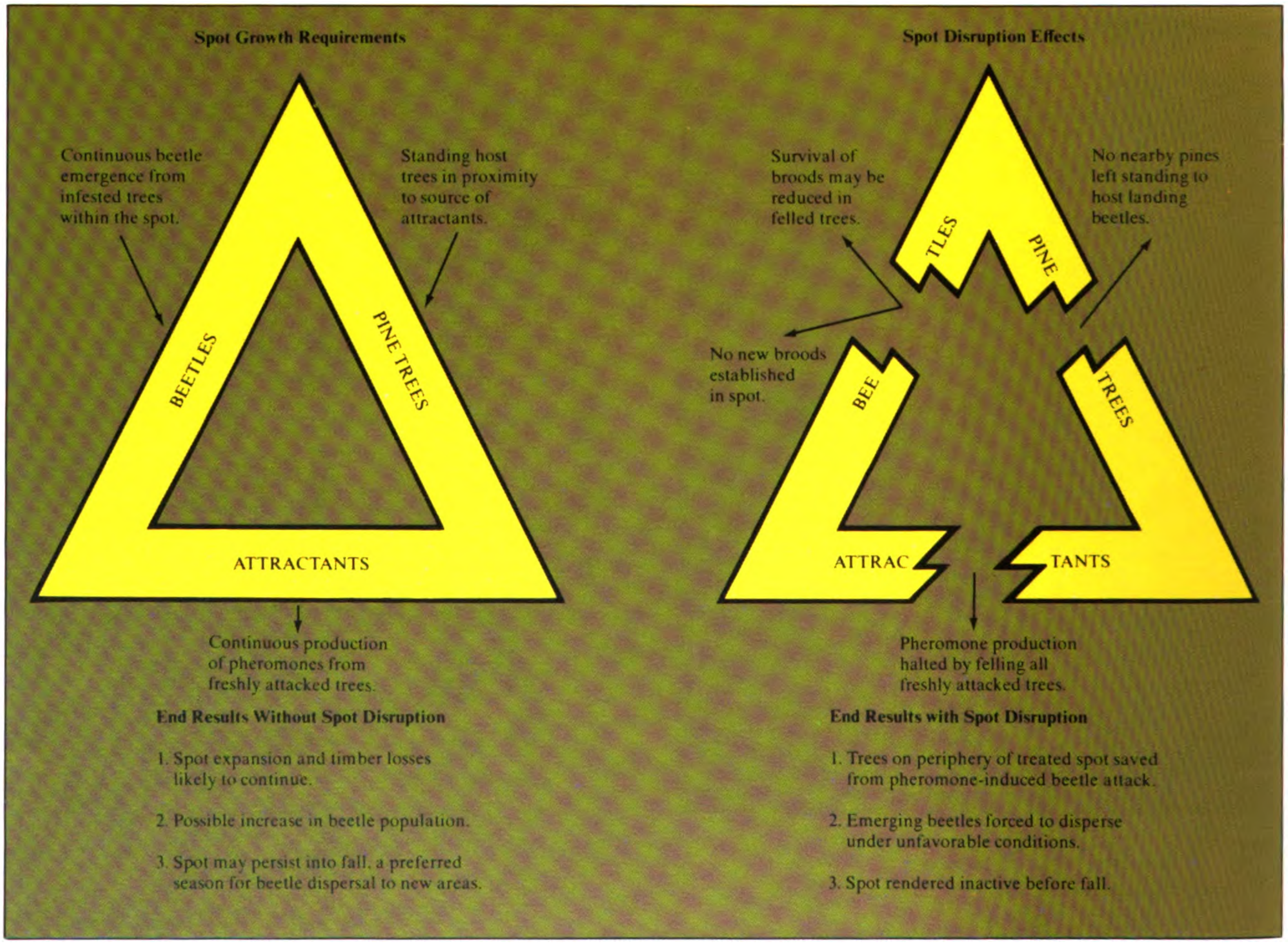


Figure 10-4. – Summary of biological and economic rationale for summer treatment to disrupt spot expansion.

and Crozier 1968), the felled buffer strip eliminates nearby unattacked pines, and beetles emerging from the infested trees tend to disperse in the absence of attractants (Gara 1967).

What becomes of the adult beetles that emerge in treated spots? Their fate is unknown, but during the hot summer months, mortality may be high since the beetles' energy reserves are low (Hedden and Billings 1977).

Could the dispersing beetles aggravate the pest problem by causing new spots? This possibility is difficult to test, but a computer analysis of recent detection and control records for east Texas, where spot disruption tactics are commonly used, suggests that summer control by cut-and-leave or salvage did not contribute to the number of new spots in the area. On the contrary, new spots appeared most frequently in the vicinity of uncontrolled active spots and those controlled after September (Billings and Pase 1979a).

Advantages and Disadvantages

Cut-and-leave provides a simple and practical treatment for preventing spot spread in small to medium-sized spots (< 100 active trees) where salvage is not feasible. It requires little equipment and can be applied by a two- or three-man crew, often at time of first ground check. As a result, the average lag time from detection to control by cut-and-leave is considerably less than that for salvage (Texas Forest Service 1980). This time lag becomes an important consideration when a landowner is faced with a large number of spots to treat.

There is evidence that greater numbers of predators and parasites emerge from SPB-infested trees treated by cut-and-leave or cut-and-top than from standing infested trees during the summer (Baker 1977). This potential benefit deserves further study.

The disadvantages relate primarily to the need for a buffer strip of uninfested green trees. Many landowners are reluctant to sacrifice this buffer if the trees cannot be salvaged. Particularly in small spots (< 20 active trees), more trees may be cut for the buffer than would be killed were no treatment applied (Hertel et al. 1980), since spot growth in small spots may not occur. Expanding spots with more than 100 active trees are more difficult to stop with cut-and-leave, and reinfestations (breakouts) are more likely to occur. Salvage is preferred for such large spots.

Insecticides for Remedial and Preventive Control

Lindane

Since 1950, BHC and lindane have been the standard chemicals recommended for control of the southern pine beetle and other bark beetles (Hetrick and Moses 1953, Coulson et al. 1972b). Both chemicals are effective when applied in fuel oil or in water emulsion to infested logs for destroying broods or in water emulsion to standing trees to prevent SPB attacks. Although BHC is no longer available, lindane is still registered for remedial control and prevention of bark beetles.

In recent years, however, the use of pesticides in forestry – particularly chlorinated hydrocarbon insecticides such as lindane or BHC – has become highly controversial (Koerber 1976). Drawbacks include safety hazards, toxicity to nontarget organisms, and persistence in the environment. In November 1969, the Mrak commission on pesticides and their relationship to environmental health (U.S. Department of Health, Education, and Welfare 1969) recommended that the use of persistent insecticides, including lindane, be restricted to essential purposes and be replaced by safer alternatives whenever possible.

Chlorpyrifos

With the goal of developing acceptable and effective chemical substitutes for lindane, researchers have screened numerous alternative insecticides in the laboratory for contact toxicity to SPB adults (Hastings and Jones 1976) and efficacy for reducing brood survival in infested log sections (Ragenovich and Coster 1974). Several proved to be more toxic to SPB adults or developing broods than lindane. One of the most promising was chlorpyrifos (Dursban ® 4E), an organophosphate insecticide.

Subsequent field tests have documented the efficacy of chlorpyrifos for remedial control (killing broods in trees). In three independent field tests (Louisiana, Georgia, Mississippi), formulations of 1- and 2-percent chlorpyrifos were found to be equivalent to 0.5-percent lindane in water for reducing numbers of emerging beetles from treated bolts (Ragenovich 1977 unpublished; Brady and Berisford 1977 unpublished; Fitzpatrick, Neel, and Lashomb 1979). The same concentrations can be used as a topical spray on standing trees to prevent SPB attack for up to 4 months (Ragenovich 1977 unpublished, Brady and Berisford 1977 unpublished). These efficacy data, when combined with the necessary support information on safety, toxicity to nontarget organisms, and the environment (Hastings, Jones, and Kislow 1977), have enabled the manufacturer to obtain EPA registration for a 1-percent chlorpyrifos spray. It can now be used for the remedial control or prevention of SPB.

Fenitrothion

Another organophosphate insecticide successfully field tested for remedial control or prevention of southern pine beetle is fenitrothion (Sumithion®). Both 1- and 2-percent formulations have proven superior to lindane in water for remedial control (Berisford and Brady 1978 unpublished, Mizell and Neel 1979 unpublished). As a protective spray, a 2-percent solution provided protection up to 3 months in the presence of moderate SPB population pressure. Efforts are currently underway to obtain EPA registration for fenitrothion.

Advantages and Limitations of Insecticides

Because of high cost and increasing Federal restrictions, we will probably never again see the large-scale use of toxic chemicals for control of bark beetles in the South that prevailed in the 1950's and 1960's. Nevertheless, there remains a need for fast-acting, effective tactics to reduce bark beetle concentrations or to prevent tree mortality in high-value or special use situations. To date, only insecticide sprays can assure this level of protection (Swain 1976, Roettgering et al. 1976). In commercial forests, insecticides are useful for treating small spots during the winter or those inaccessible to salvage equipment. Also, insecticides provide an effective means to protect high-value trees from bark beetle attack in pine seed orchards, naval stores, or urban, home, and recreational areas (Thatcher, Coster, and Payne 1978).

Cost, the need to fell and spray all surfaces of infested trees, safety precautions, and toxicity to nontarget organisms are expected to limit the use of the new insecticides in forests. Chlorpyrifos, a cholinesterase-inhibiting insecticide, is labeled for restricted use to be applied only by or under the supervision of pest control operators or other trained personnel. This chemical also is more costly to apply than lindane or fenitrothion.

Pile-and-Burn

The practice of felling, piling, and burning infested trees to destroy developing broods represents one of the earliest approaches to bark beetle control. This method is still recognized as an option for SPB, and broods can be destroyed if all infested bark is completely burned. This practice has been largely abandoned as an operational method, however, because of the labor and logistical problems involved. In most cases, heavy equipment is required to pile the trees. In wet areas, burning felled trees becomes difficult if not impossible. In dry areas, the procedure increases the chances of wildfire, and burning as a control is necessarily restricted to the seasons when fire danger is low. Nevertheless, fire is still available as a control tool for whoever prefers this mechanical method of destroying beetles.

Potential Control Methods Evaluated

Scientists have continued the search for new methods of direct control. Among possibilities explored by the ESPBRAP have been fertilization of infested stands, use of systemic insecticides, and manipulation of beetle populations with synthetic behavioral chemicals (pheromones).

Fertilization of Infested Stands

Fertilization of forest stands promotes rapid growth and presumably increases tree vigor. Moore and Layman (1978) conducted tests in North Carolina to determine the extent to which fertilizers increase resistance of pines to bark beetle attack. A 9- to 11-year-old loblolly pine plantation infested with SPB and black turpentine beetle was treated with a summer application of 10-10-10 fertilizer at a rate of 1,000 lb/acre. Over an 80-day study period, beetles continued to kill similar numbers of trees in both fertilized and unfertilized plots. The investigators speculated that fertilizers applied in the spring might prove more successful. The trees would have more time for nutrient uptake and response before beetle activity increased during the summer. Because of collapsing beetle populations, no additional fertilizer tests have been conducted to date.

Systemic Insecticides

A systemic insecticide applied aerially to the foliage of beetle-endangered trees would be a useful tool for direct control of the southern pine beetle. To be effective, such a chemical would need to be absorbed into the needles and rapidly transported through the inner bark (phloem) in concentrations sufficient to kill beetles where they feed. One insecticide that showed early promise as a phloem-mobile systemic was acephate (Orthene®). Extensive field evaluations of acephate for reducing within-tree populations of SPB have been conducted (Crisp, Richmond, and Shea 1979 unpublished). Foliage applications at two different rates prior to beetle attack reduced survival of larvae. But the treatment had no effect on eggs, pupae, or callow or parent adults. The investigators concluded that systemic insecticides will need to be more phloem-mobile, more toxic to all life stages, and more persistent than acephate if this approach is to succeed.

Behavioral Chemicals

Most bark beetle species select and colonize suitable hosts by using species-specific systems of chemical communication. For SPB, host selection involves both attractants and inhibitors (*see* Chapter 2). The concept of controlling SPB by exploiting its own behavioral chemicals has captured the interest and imagination of entomologists for many years.

Pioneering field experiments conducted in 1963 demonstrated that the southern pine beetle's aggregating pheromone could be used to concentrate and subsequently decimate a beetle population on resistant trees (Gara, Vité, and Cramer 1965). These early studies utilized log sections infested with virgin females as the source of attractant because the pheromone had yet to be identified.

The primary component of the aggregation pheromone produced by attacking southern pine beetle females has since been identified as frontalin (Kinzer et al. 1969, Payne et al. 1978). Frontalure, a synthetic attractant composed of frontalin in α-pinene, is available for experimental use. Behavioral chemicals that repel beetles, such as *endo*-brevicomin (Silverstein et al. 1968) and verbenone (Renwick 1967), also are being evaluated for control purposes.

Frontalure might be used in several ways for southern pine beetle control. One technique, based on a knowledge of SPB attack behavior and the effects of the herbicide cacodylic acid (Vité 1970), was tested on a limited basis on private lands in east Texas from 1970 to 1973. The procedure involved baiting uninfested trees with frontalure on the periphery of active spots and simultaneously treating the baited trees with cacodylic acid. Emerging beetles were thereby induced to attack and colonize the "trap trees" and most of the broods failed to develop due to the excessively high inner bark moisture resulting from the herbicide treatment (Ollieu 1969). A similar procedure was successfully tested in Virginia for controlling spring-emerging populations of SPB during outbreak years (Copony and

Morris 1972). The tactic, however, has not been adopted operationally. Apparently its success was dependent upon too many unanticipated and uncontrollable variables for the method to be applied by nonprofessional personnel (Coulson et al. 1973a and b, and 1975b).

The transfer of frontalure from experimental to operational use for southern pine beetle control has been slow, but potential applications are still under investigation. An experimental attempt to "confuse" emerging SPB in a summer infestation by permeating the active front with frontalure applied from the air proved unsuccessful (Vité, Hughes, and Renwick 1976). The frontalure intensified the infestation rather than disrupting it, presumably by preventing dispersal losses and attracting beetles from surrounding stands. These investigators concluded that inhibitory compounds may hold more promise than attractants for future aerial permeation experiments.

In a more recent test in east Texas, frontalure applied from the ground to nonhost trees and pines containing late brood stages behind the front of an expanding spot successfully interrupted the natural process of spot growth. No additional trees were killed in the spot until the frontalure was removed 6 days later (Richerson, McCarty, and Payne 1980).

The test was repeated in Georgia in 1979. After 50 days, no additional spot growth occurred in a previously expanding spot following similar application of frontalure to trees containing developing brood. The treated spot eventually went inactive, while untreated spots nearby continued to expand during the course of the experiment (T. L. Payne personal communication).

The treatment presumably disrupts spot growth by preventing emerging beetles from responding to natural, but more distant, pheromone sources at the spot's active head. Further tests are planned to evaluate the effectiveness and practicality of this application as an operational control tactic.

Recent tests on protecting individual trees within an active spot from attack with various inhibitory pheromones also have proved encouraging. Although the inhibitor-treated trees were killed by a combination of SPB and *Ips avulsus*, a mixture of *endo*-brevicomin and verbenone reduced SPB landing on traps by 84 percent and egg deposition by 88 percent during the 17-day treatment period (Richerson and Payne 1979). Reductions in both number and length of beetle galleries in treated trees suggest that this treatment could significantly reduce brood production and lead to the early disruption of spots.

It is possible that permeating an area with these compounds to inhibit beetles from perceiving and/or responding to attractants may be more successful and practical than baiting individual trees. The necessary tests and evaulations are currently underway to determine if these inhibitors can be developed into practical pest management tactics (T. L. Payne personal communication). Progress has also been made toward the development of sustained-release delivery systems for bark beetle pheromones (Payne, Coster, and Johnson 1977).

Since behavioral chemicals are not yet available for operational use, a discussion of their advantages and disadvantages for southern pine beetle control is largely speculative. Among advantages, behavioral chemicals are natural, nontoxic compounds that are considered nonhazardous to the environment. Unlike current control methods, the application of behavioral chemicals does not require felling trees. The chemicals could be formulated for easy application by nonprofessional field crews or small landowners. The use of frontalure for spot containment shows promise as a simple and viable substitute for cut-and-leave that eliminates the need to sacrifice unattacked trees for a buffer. Conceivably, the same approach could be combined with salvage to prevent further tree mortality until all brood trees were removed from the spot. Aerial applications of inhibitors may permit the treatment of a large number of spots within a short period. This capability would place operational controls for the first time in the hands of a few highly trained pest control specialists.

The operational use of behavioral chemicals for southern pine beetle control must await EPA registration and development of safe and practical delivery systems. Costs may prohibit use over extensive forest areas. Perhaps most importantly, we must keep in mind that success under experimental conditions does not assure that a new tactic will become operational. But treatment efficacy is essential and represents the first step along the path to eventual application.

Practical Considerations and Complexities of Areawide Control Programs

In nature, southern pine beetle populations occur at three different levels of "organizational complexity" (Coulson 1979c; *see also* Chapter 5): beetles in trees, beetles in spots (groups of infested trees plus attacking adults), and beetles in areas (groups of spots plus dispersing adults). Control efforts, in turn, may be directed at any one of these three levels. Experience has shown that efficacy at the first level (high beetle mortality in treated trees) or the second (spot disruption) doesn't necessarily imply equal success at the third level (suppressing outbreaks). In fact, the desired goal of control efforts, choice of tactics, and measures of treatment efficacy may vary, depending upon which level is addressed (Hedden 1979).

Suppression of beetle outbreaks over wide areas by means of direct control action has seldom been achieved, with one possible exception (Lorio and Bennett 1974). The apparent failure to curb outbreaks in progress is often blamed on deficiencies in available control tactics. In reality, to achieve effective control at the area level requires prompt treatment of all active spots over a broad area within a relatively short timespan. This goal is seldom attainable due to various practical constraints that enter the control picture at the area level. These obstacles include the multitude of land ownerships involved and seasonal influences on the insect, host trees, and man. Also, until the recent development of population estimation techniques, we have been unable to evaluate the efficacy of areawide control tactics. For a more complete discussion of this subject, *see* Chapter 6 and Coster and Searcy 1979.

Landownership Constraints

More than 70 percent of the forest acreage in the South is held by small private owners, many of whom do not live on their holdings. The remaining acreage belongs to forest industries, National and State forests, biological preserves, and wilderness areas. Forest management objectives on these diverse ownerships vary widely, as does recognition of SPB as a pest. Emphasis given to direct control and abilities of different landowners to respond to the problem range from complacency to rapid action. Beetle infestations can increase in situations where no control is practiced, spreading directly by spot growth (fig. 10-5) or indirectly through beetle dispersal to adjacent lands, where losses may be less acceptable. The very fact that SPB infestations do not generate the same level of concern among all landowners severely complicates efforts to suppress populations on an areawide basis.

In certain States, laws have been passed requiring landowners to control SPB infestations promptly. In some cases, State forest agencies have legal authority to control spots on private lands in situations where landowners are reluctant to do so. Originally intended to aid areawide control programs, such laws have proven difficult to enforce. State forest agencies simply do not have the manpower, equipment, or money to assume responsibility for all spots that develop during SPB outbreaks.

Seasonal and Regional Constraints

Seasonal limitations also complicate direct control efforts, particularly in the Gulf Coast region. What we know about the reproductive potential and seasonal habits of the SPB clearly suggests that, to reduce beetle populations, direct control should be applied primarily during the winter (Hopkins 1911, Thatcher and Pickard

1964, Franklin 1970a). In practice, however, control programs along the gulf coast are applied primarily during the summer (fig. 10-6), because detection of new infestations is seasonally dependent. From 45 to 75 percent of all multiple-tree spots are reported from May through July (Coulson et al. 1972b). Also, access to spots is often hampered during fall, winter, and spring months by wet ground conditions, particularly in lowland areas.

When outbreaks occur, new spots are reported faster than available resources can be marshalled for direct control action. The 1979 outbreak in Georgia is an excellent example. Over 11,000 spots averaging 50 trees in size were detected over a 69-county area by August (Price and Thomas 1979). But due to rapid beetle development, many summertime spots may already be inactive (abandoned by SPB) by the time they are ground checked, and ground crews must devote much time to checking spots that may no longer contain beetles.

By winter, much of the beetle population in the Gulf Coast region has become distributed in single trees and small new spots scattered throughout the forest. Because new infestations during the fall, winter, and early spring are difficult to detect (Billings 1979), as many as four consecutive beetle generations may effectively escape control pressure. And this is the very season when the attack: emergence ratio of the insect is at its highest (fig. 10-6). It is possible for beetle populations to recover to outbreak levels the following year, largely counteracting control efforts the summer before. The cycle repeats itself as long as such factors as favorable climatic and host conditions prevail.

Control during the winter is less problematic in the northern part of the beetle's range (Tennessee, the Carolinas, and Virginia). Cold winters

Figure 10-5. – Small plantation invaded by southern pine beetles as infestations spread from adjacent sawtimber stand.

tend to restrict beetles to the multiple-tree spots they occupied during the fall; this fact simplifies winter detection. Since the beetles complete only three to five generations per year in this area, overwintering broods seldom emerge before late April or May. This schedule allows more time for control prior to beetle dispersal. It is not unusual for landowners to control as many SPB infestations during the winter in these States as during the summer (Coleman A. Doggett personal communication).

Finally, the recurrence of southern pine beetle infestations in an area from one year to the next should not necessarily be attributed to "ineffective" control tactics. Recurrence may also be a symptom of high-hazard stand conditions (Hedden 1978b). Such stand management problems remain largely unaltered by direct control treatments.

Learning to Cope with SPB Outbreaks

In recent years, pest managers have accumulated much historical information from southern pine beetle outbreaks and direct control programs (Price and Doggett 1978, Pase and Fagala 1980). With this information and recent research on SPB population dynamics, patterns of infestation development, and susceptibility of forests, we are better prepared to suggest how forest managers can more efficiently confront SPB outbreaks.

We now recognize that once SPB populations reach outbreak levels (e.g., more than one multiple-tree spot/1,000 acres host type), it is probably too late to change drastically the course of events (i.e., total number of spots). But we can reduce considerably the ultimate size of spots and their economic impact by setting realistic

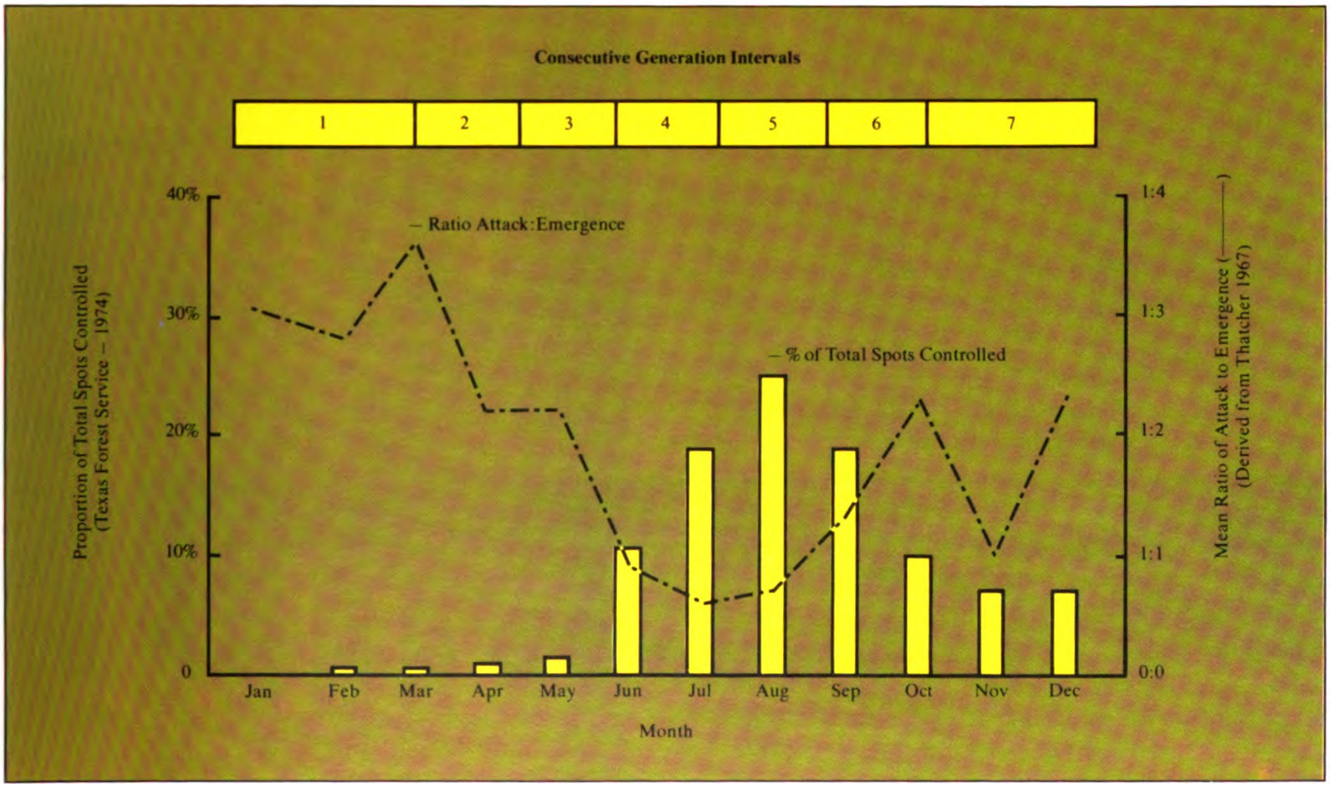


Figure 10-6. – Typical patterns of control application in relation to seasonal trends in the attack: emergence ratio for seven overlapping generations of SPB in the Gulf Coast region.

priorities and establishing "action thresholds" (Chant 1966) at each level of operation: detection, ground check, and control. By recognizing that all spots do not pose the same threat, we can focus control efforts on those spots likely to have the greatest impact on resources if left unattended.

Improving Detection and Ground Check Operations

We now have enough empirical evidence to approximate the action threshold level for detection and control of southern pine beetle spots. Experience has shown, for example, that it is impractical to detect single-tree spots during the summer for purposes of control. Most State agencies in the South restrict detection to those spots containing a minimum of 5 to 10 red- and yellow-crowned trees. This action threshold has been set because smaller spots are mostly inactive at the time of ground check (fig. 10-7) or are the result of causes other than SPB (Billings 1974 and 1979).

The efficiency of ground-check operations can be further increased if aerial observers estimate the size of each new spot they report and assign each a ground-check priority (Billings and Doggett 1980). When the size of individual spots is estimated from the air, unavoidable errors occur (Mayyasi et al. 1975). The extent of the error varies with spot size, season, and the experience of the observer. Nevertheless, an aerial estimate of beetle activity based on the number of trees with discolored foliage is useful for deciding which spots to ground check. During outbreaks, spots assigned a low priority by aerial observers may not warrant immediate ground checking. These spots, together with others that are not controlled promptly, should be reevaluated on a subsequent flight. At the time of the second visit, spots that may have enlarged since first detection can be assigned a higher ground-check priority and spot size estimate to reflect the need for immediate attention by ground crews. On the other hand, spots which no longer contain yellow-crowned trees can be designated as nonexpanding spots, requiring no control action during summer months (Billings 1979).

Improving Control Operations

Even with a multiple-tree reporting threshold, many newly detected spots will be inactive during summer months – approximately 30 to 40 percent during most years in Texas, for example. Efficiency of control operations could be improved by concentrating efforts only on those spots most likely to expand.

A recent study of spot growth (Hedden and Billings 1979) has provided useful information for establishing a more realistic control threshold. This team found that summer spots containing less than 10 active trees seldom became larger after detection. Ten-tree spots that did expand

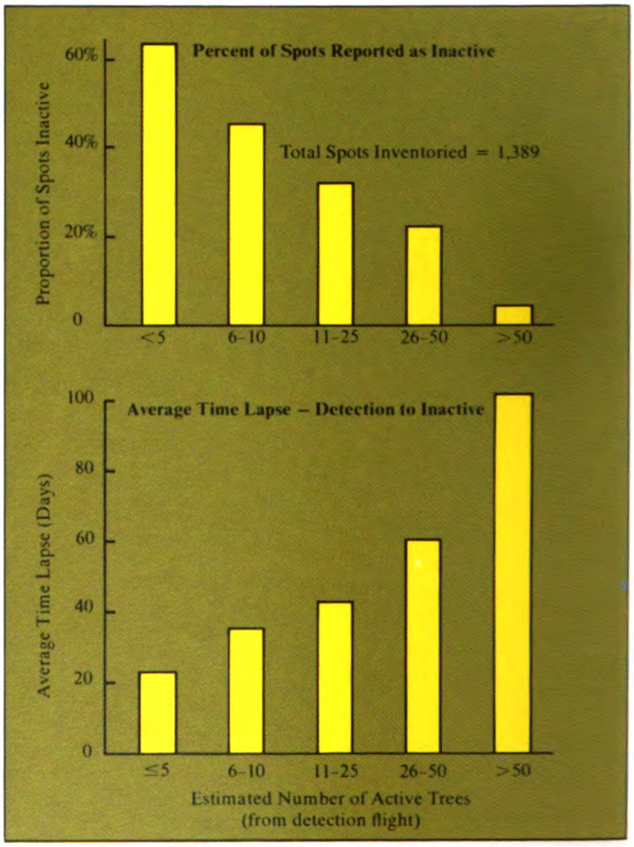
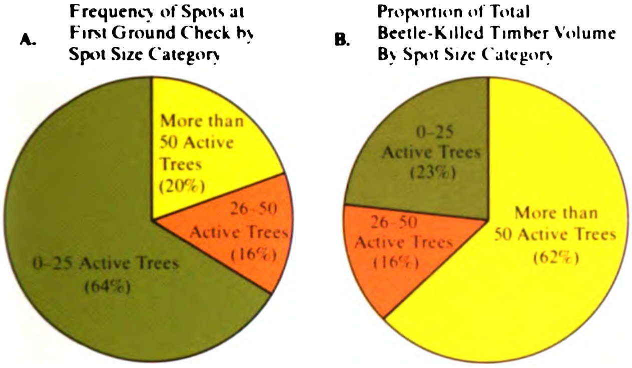


Figure 10-7. – Relationship of initial spot size as observed by survey crews and persistence of SPB infestations.

exhibited declining rates of growth (i.e., the number of active trees declined over time), and the spots soon went inactive. Additional timber losses in these spots were insufficient to justify immediate control.

In medium-sized spots (11 to 50 active trees) growth was largely dependent on prevailing stand conditions, with the number of active trees increasing only in stands of high basal area. A field guide illustrating how to evaluate the potential for spot growth as a basis for setting control priorities has been prepared (Billings and Pase 1979b).

Large spots (50 or more active trees) demand highest priority for control. Even though such spots are relatively uncommon, they account for over 60 percent of the timber volume killed each year (fig. 10-8). Large spots almost invariably grow larger, with rates of spread increasing in direct relation to the initial number of active trees and density of host trees (fig. 10-9). If they are left unattended, excessive timber losses will accrue from both rapid spot growth and the eventual proliferation of new spots as winter approaches.


A. Frequency of Spots at First Ground Check by Spot Size Category

B. Proportion of Total Beetle-Killed Timber Volume By Spot Size Category

Figure 10-8. – Average spot size distributions during summer months in the Gulf Coast region, by frequency of occurrence (A) and by proportion of total timber volume killed (B). (Data derived from Texas Forest Service operational records 1974-1977.)

Studies in North and South Carolina (Moore 1978) suggest that attack:emergence ratio may be more reliable for summer predictions of spot growth in that region than criteria of number of active trees and stand density. Moore accurately predicted population trends of several spots in Atlantic Coast States over time periods of 8 to 12 months, using the attack:emergence ratio, plus five secondary factors to improve the accuracy of predictions on static spots. This method appears practical and simple enough to be used by trained personnel in Atlantic Coast and Piedmont States, where beetles have fewer generations per year and individual spots may persist from one summer to the next. The reliability of the attack:emergence ratio for prediction purposes has been questioned (*see* Chapter 5).

Selecting a Control Tactic

Among factors to be considered in selecting the control option best suited for a particular spot are the season of the year and the size of the spot.

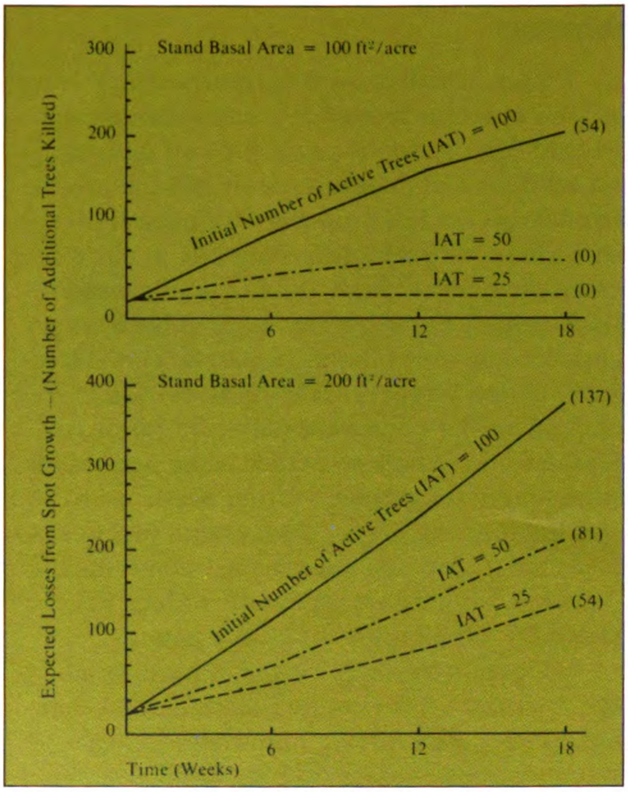


Figure 10-9. – Influence of initial number of active trees and stand basal area on expected losses from summer spot growth in the Gulf Coast region. Numbers in parentheses indicate estimated number of active trees after 18 weeks (derived from Hedden and Billings 1979).

Salvage remains the preferred choice at all seasons if the spot is accessible, sufficient timber volume is involved to cover costs, and there is a market for the beetle-killed trees. Cut-and-leave treatment to disrupt spot growth is recommended for use in summer and fall only – the seasons when spots are most likely to expand. Similarly, cut-and-leave or registered insecticides (lindane or chlorpyrifos) are most appropriate for medium-size spots that are a threat to enlarge but are not suited to prompt salvage. Small spots (< 10 active trees) may need no control during the summer. In the winter, insecticides may offer the best means to reduce overwintering beetle populations in spots not accessible or suitable for salvage. Cut-and-top and pile-and-burn remain of questionable value as control tactics, even during winter months.

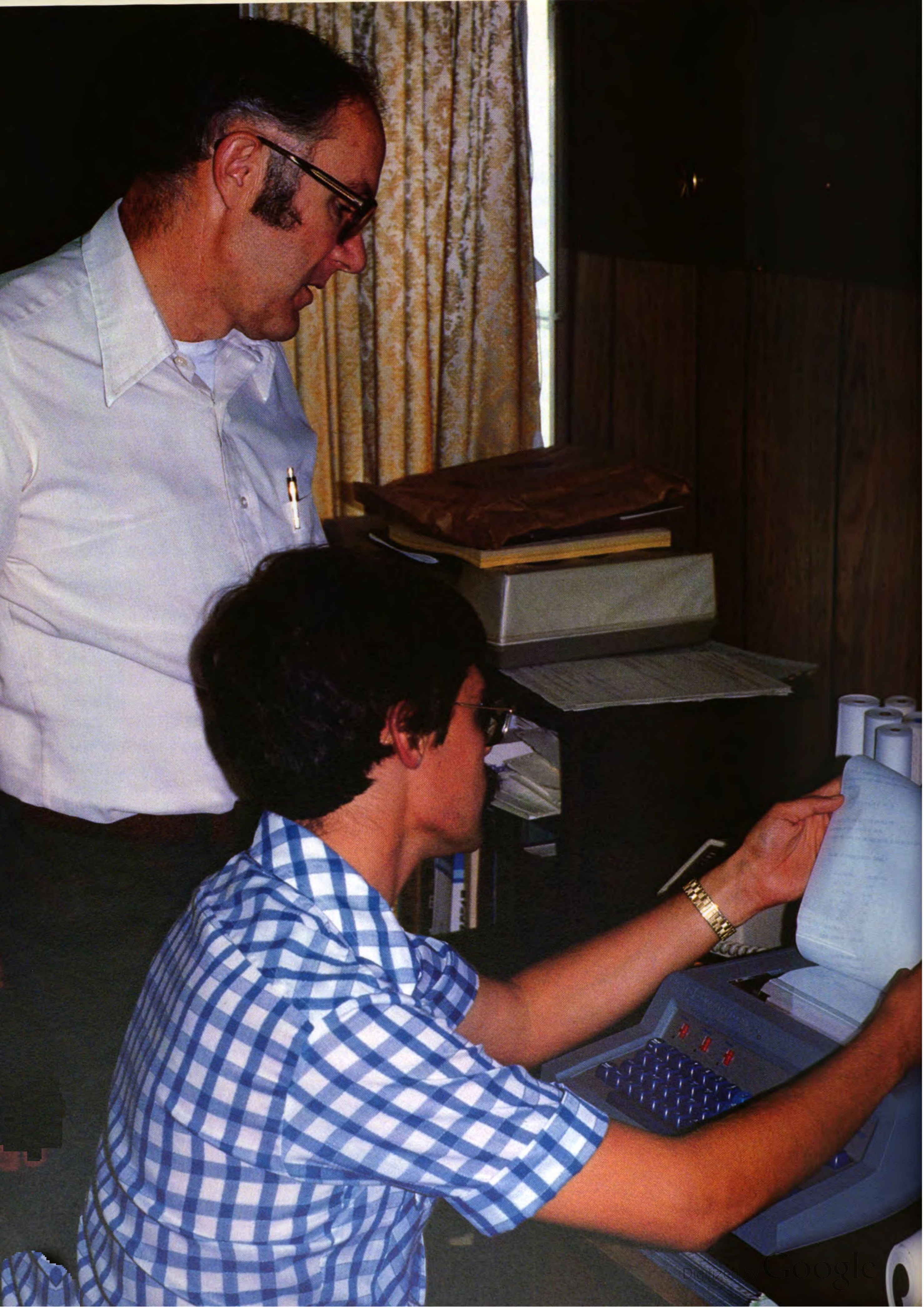
Summary

Direct control options currently available to the land manager remain few and relatively unchanged from previous years. Prompt salvage and utilization of infested trees is still the preferred direct control procedure for most spots. Yet we have progressed substantially in our understanding of the insect and in our approach to direct control. For example, the SPB is no longer considered an unavoidable pest to be eliminated wherever and whenever it appears. Foresters are recognizing that preventive (silvicultural) treatment to increase host resistance is the best way to assure long-term protection from beetle problems. By applying proper silvicultural practices to those unmanaged and overstocked stands most favored by SPB, we can markedly reduce both the occurrence and severity of infestations.

Once spots develop, however, prompt salvage or disruption by cut-and-leave assures that timber losses are kept to a minimum. In high-value situations, lindane and the newly registered insecticide chlorpyrifos are available for remedial control or prevention. A third chemical, fenitrothion, has proved effective against SPB but has yet to be registered.

Meanwhile, progress has been made toward the eventual application of synthetic pheromones for direct control. Once techniques are developed, the use of the bark beetle's own chemical attractants or inhibitors may eliminate the need to fell trees in order to disrupt spot expansion.

Perhaps most important, we now realize that all infestations need not be treated by direct control in order to cope with the beetle. Some infestations pose more of a threat than others. By considering the initial size of the spots, prevailing stand conditions, value of the timber, and season, pest managers can set realistic detection, ground-check, and control priorities. These procedures will optimize available manpower and equipment use during outbreak periods. In this manner, we make the best of a very complex pest problem while foresters strive to correct the stand conditions that predispose our forests to SPB outbreaks.



Developing Integrated Management Strategies

Jack E. Coster[1]

11

Introduction

The succssful management of southern pine forests requires a thorough knowledge of the biological and ecological factors regulating them. Insects are an important component of forest ecosystems; therefore, their ecological roles must be considered. And if forest resource management goals are to be optimized, then the negative economic and ecological effects of pests must be minimized, i.e., pests must be managed. In order to develop specific pest management practices that can be incorporated into total resource management, it is critical that the prerequisite research be properly conceived and carried out. A characteristic of integrated pest management (IPM) research programs is their system concept for structuring research and development activities (Waters and Stark 1980).

The systems framework of Waters and Ewing (1974) has been used to organize and plan ESPBRAP research (Coster 1978). This system has four research and development subsystems (fig. 11-1): insect population dynamics and epidemiology, plant population (forest stand) dynamics, impacts on resource values and management objectives, and treatment strategies. Each subsystem is complex and requires a coordinated research plan. The forest resource manager is less concerned with the research components and is primarily concerned with information and procedures to help him make proper decisions on SPB prevention and suppression. Research to develop decisionmaking models for the resource manager is termed benefits/cost integration. Primary linkages and information flows between the components are shown by the heavier arrows, and feedbacks are indicated by the lighter arrows.

Research and development activities provide input to an operational pest management system, which, in turn, is a part of overall forest resource management. An objective of ESPBRAP was to develop operational integrated management systems for SPB (Leuschner et al. 1977). The bottom

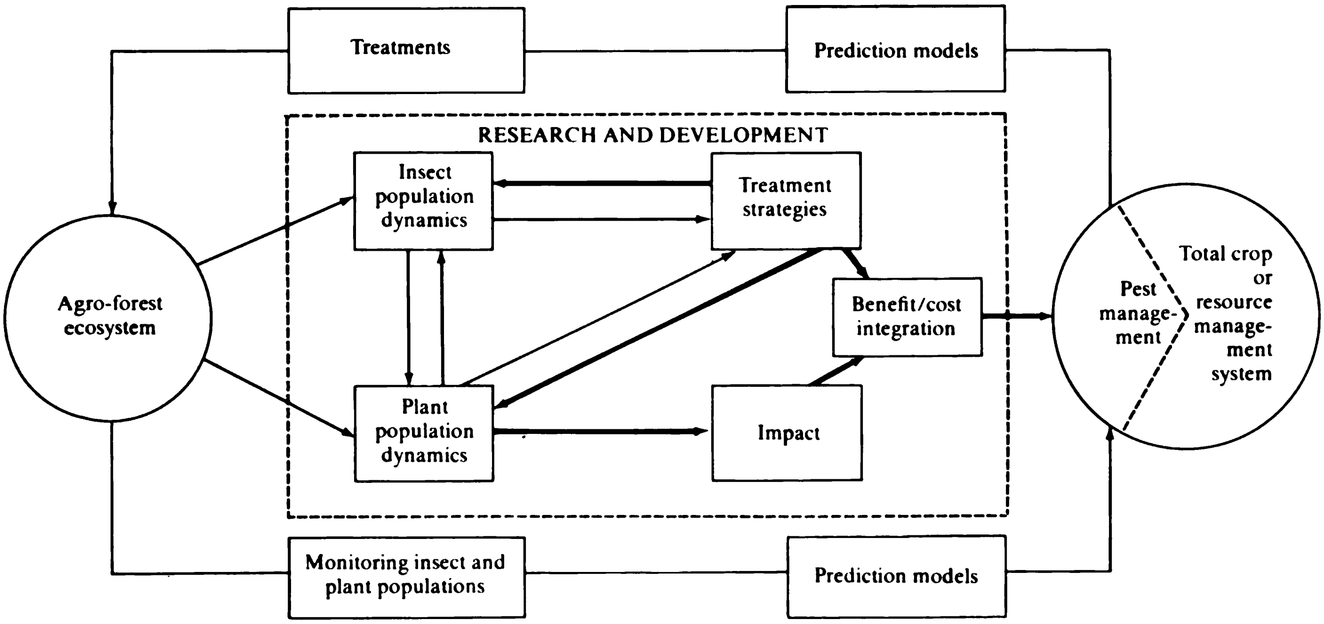


Figure 11-1—Model structure of an insect pest management system, with research and development components and the action sequence. (From Waters and Ewing 1974.)

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line of such programs, from the resource manager's viewpoint, is improvement in his decisionmaking capability. Benefits from improved decisionmaking include (1) more efficient and effective utilization of financial resources for SPB control, (2) less disruption of long-term management plans and activities through timely prevention or remedial control actions, (3) more sound management plans through inclusion of SPB considerations into proposed forest practices (thinning, harvesting, species conversion, etc.), (4) a more accurate description of SPB damages, and (5) a reduced need for costly, short-term crisis response activities that do not alter the basic causes of beetle outbreaks.

Summary of IPM Research Accomplishments

The preceding chapters have presented, in considerable detail, the status of southern pine beetle research as of 1980. This chapter briefly summarizes the results from ESPBRAP research as they relate to the four research and development components of an IPM system. Such a summary, along with an earlier one (Coster 1978) and Chapter 12 on recommendations for future research, is a status report on research and development that is the basis for integrated SPB management.

SPB Population Dynamics

Population dynamics is the study of changes in numbers of an organism in space and over time. Understanding the dynamics of both the SPB and its host trees is, therefore, the foundation of an integrated management system. Waters and Stark (1980) point out that "... whereas some immediate or short-term *control* decisions can be made on the basis of current pest population levels and damage, pest *management* encompasses a greater timespan, and more detailed knowledge of the factors affecting the dynamics of specific pest populations is needed to develop the interactive predictive models for input to the stand dynamics and treatment components."

Population dynamics of the southern pine beetle has been described at three levels: within individual trees, within individual spots, and throughout the forest (Chapter 5). Methods have been developed for sampling SPB populations at all three levels and for predicting population trends (Chapter 6). The Arkansas and TAMBEETLE population dynamics models are suitable for predicting timber loss and rate of development for individual spots. Two regression models for predicting spot growth have also been formulated. Predictions of longer-term, areawide populations and damage can be made with the DAMBUGS and FRONSIM simulators. The subject of modeling SPB populations has been discussed in detail in the proceedings of an ESPBRAP-supported symposium (Stephen, Searcy, and Hertel 1980).

Forest Stand Dynamics

Accurate descriptions of the dynamics of southern pine stands are necessary in pest management because management decisions are based on forecasts of the effects of SPB on growth, yield, and distribution of the stands. Stand dynamics models must operate within the framework of the pest management system and also be compatible with the overall forest management scheme in order to forecast effects of a variety of silvicultural practices.

Growth of loblolly pine stands may be simulated using PTAEDA (*see* Chapter 7). There are two variations of the model, one for plantations and another for naturally seeded stands. The models simulate stand growth with or without mortality and can also be used to estimate growth and yield in general. The several stand-rating systems (Chapter 8) relate soil, site, and stand conditions to relative hazard of stands to SPB attack. Some of the models also estimate the probability (incidence) of SPB outbreaks in given hazard types (*see* Chapter 6).

Treatment Strategies

This component of IPM is much more complex than a simple array of tactics that have been shown, at one time or another, to cause significant SPB mortality. In the first place, both direct and indirect control approaches are part of this component. And the pest manager needs the capability to predict the potential biological and ecological outcomes of treatment alternatives under a range of hypothetical conditions. He must also be able to assess the benefits and costs of each treatment. Cost includes not only the direct costs for applying the treatment, but also the costs of possible environmental effects on the resources. These costs may be very difficult to assess for preventive (long-term) treatments.

Direct controls for use against the beetle include lindane and chlorpyrifos insecticides, salvage removal of infested material, cut-and-leave, and pile-and-burn (*see* Chapter 10). In the forest, only salvage and cut-and-leave are currently used to an appreciable extent.

Silvicultural recommendations for reducing southern pine beetle losses have been developed from the site-stand data (*see* Chapter 4) and from experience in managing southern pines. Hazard ratings (Chapter 8) can be used to assign treatment priorities to stands highly susceptible to beetle attack. Recommendations for promoting tree and stand resistance and protecting sites in each of the major geographic subregions of the South are available (*see* Chapter 9). Because of the long timespan needed to evaluate their effectiveness, the efficacy of silvicultural approaches in preventing SPB losses is unknown.

Methodologies are available to assess efficacy of proposed treatments on southern pine beetle populations and on timber damages (Coster and Searcy 1979).

Impacts on Resources

Impact assessment gives the resource manager measures of values. Impact and damage (injury) should not be equated. Impact was defined in Chapter 7 as any change in the forest caused by an insect population. The impact may affect flora and/or fauna. SPB damage, therefore, may result in positive, negative, or no impact, depending on the conditions.

From an economic standpoint, the southern pine beetle most severely affects the timber resource. This impact can be simulated for wide areas by using FRONSIM (*see* Chapter 6). For individual spots, the spot-growth models previously mentioned under SPB population dynamics will provide estimates of timber loss. All of the spot and areawide models can give estimates of timber volume killed, number of spots, and number of dead trees. Economic guidelines (Chapter 7) also describe salvable values from beetle-killed timber. Economic impacts on timber for large areas can be calculated from the Timber Benefits Analysis Program (TBAP) using local volume tables, volume of trees affected, stumpage values, and acreages affected.

The economic impacts of infestations on recreation, hydrologic, and grazing resources can be measured, but impacts on wildlife populations and on wildfire occurrence can only be qualitatively estimated. Esthetic impacts can be quantified with a relative scale, but economic values for the impacts cannot be derived (*see* Chapter 7).

Combined aerial and ground sampling plans, an electronic radio navigation system, and a computer-aided infestation accounting system all materially improve the efficiency and effectiveness of gathering basic timber loss data (Chapter 6).

Benefit/Cost Integration

Before proper decisions can be made, alternative courses of action must be identified and their economic and environmental consequences spelled out. An areawide SPB outbreak, with all of its political, economic, and ecological complexities, requires thorough decision analyses. Benefit/cost analysis is essentially the process by which alternative actions and their consequences are presented for the resource manager's decision.

Factors Influencing Development Of SPB Management Systems

The foundations for an IPM system for the southern pine beetle are in place. And although most land managers and pest managers would agree that there is need both for refinement of existing information and for additional research, the existing information can be used to markedly improve current management decisions for SPB. This improved support information will enable resource managers to better plan SPB prevention and suppression activities to meet the overall objectives of forest resource management plans.

There are several characteristics of southern forests and forest management that influence development of SPB management systems. More than 70 percent of the southern forest lands belong to small, private, nonindustrial owners. Responsibilities for insect control and management activities reside in a variety of State, Federal, and private organizations. In many cases, there are inadequate numbers of properly trained personnel in these organizations to service integrated SPB management systems.

Southern pine stands are quite dynamic and site and stand conditions are highly variable. Growing seasons are long (220–270 days) and conditions are favorable for overlapping SPB generations each year. The insect itself has a high reproductive potential that results in rapid population buildups. This situation puts pressure on suppression operations to stay current with the outbreak.

These considerations have led to a general ESPBRAP management philosophy regarding the development and implementation of an integrated management system for SPB. The varied ownership and management objectives of southern pine forests; the range of Federal, State, and private policies with regard to pest control activities; the variation in capabilities of pest managers, landowners, and resource managers to gather technical input data; and the wide range of biological conditions in southern pine forests all indicate that *an integrated management system composed of tightly linked, computationally interdependent models and submodels would, at this time, be useful to only a limited number of landowners and managers concerned with the SPB problem.* Instead, the approach is to develop a series of more or less independent models that are suited to different-sized areas, timespans, and predictive uses (Leuschner 1979). The hierarchy of predictive models is shown in table 11-1.

Results of ESPBRAP research on the various components of an integrated system are still so new that time has not permitted the simulations, validations, and modeling efforts to be thoroughly carried out. These analyses are needed in order to enable proper integration of components into a practical system. But land managers and landowners have immediate needs and, in some areas, a new research finding can be put to use immediately to meet the need adequately.

Thus, the stepwise decision processes now used in forest pest management can be strengthened by indicating where new technology and methodology is appropriate for use by decisionmakers. Such an array of information, when related to the decisionmaking process, is called a decision support system. The general goal of such support systems is to provide resource managers and landowners with tools and information they need to consider alternative means of maintaining beetle-caused damage at tolerable levels, according to their management objectives, on a continuing, long-term basis.

Components of SPB Decision Support Systems

A southern pine beetle decision support system must address both long-term (preventive) and short-term (crisis response) control needs (Coster 1977). One of the real benefits of integrated SPB management will be to put crisis response actions in better perspective with regard to the overall management objectives of a resource manager or landowner. Long-term controls for SPB, primarily silvicultural manipulations, are thought to offer the best possibilities for lowering the incidence and severity of SPB infestations and for reducing the frequency of crisis response actions (Coster 1978). One of the hallmarks of implementation of integrated SPB management will be more emphasis on preventive

Table 11-1—Hierarchy of models developed in ESPBRAP, showing area coverage, length of predictions, and use of predictions.

Model number	Area covered	Information predicted	Use of prediction
I	Wide area[1]	Impact over next 5–50 years	Estimate benefits of long-term prevention programs
II	Wide area	Impact next year	Plan control activities for coming field season
III	Wide area	Impact next month	Plan field activities
IV	Specific spot	Spot growth if uncontrolled	Plan suppression activities on spot

[1] Wide areas are multicounty or forest survey unit-sized areas.

strategies and a concurrent shift in attention of landowners and resource managers from local (spot) populations to areawide populations.

It should be made clear that a decision support system is only an information-gathering and -collating system. The resource manager or landowner will bear the final responsibility for management decisions. The basic questions that he must answer are (1) Is the long-term and/or short-term level of damage detrimental to my management/ownership goals? (2) Of the long- and short-term SPB management options, which are most suitable for the current situation?

The components of a southern pine beetle decision support system will include

(1) Description of susceptible and/or attacked stands (species, age, projected growth, hazard ratings, and history of SPB occurrence).

(2) Evaluation of SPB activity (socioeconomic impacts, current distribution and abundance of SPB, prognosis for continued activity).

(3) Resource management considerations (end products, rotation lengths, multiple-use plans, silvicultural systems, esthetic factors).

(4) Environmental and social considerations of proposed SPB management options.

(5) Available SPB management options and their potential costs and benefits.

The landowner/resource manager would normally supply information on (1) and (3) while the pest management specialist would be primarily responsible for providing information on the other items. Both the manager and the specialist would contribute information on (4).

The importance of landowner/resource manager input to SPB management decisions should be emphasized. Managers bear responsibility for the final decisions and must, therefore, spell out clearly the time, space, and economic limitations that their overall resource management plans may place on SPB management actions. Failure to do so may result in either inadequate information for decisionmaking, or excessive costs in obtaining information.

Developing SPB Decision Support Systems

Implementation of a decision support system that is based on state-of-the-art ecological and economic data and that provides for modeling and simulation of management options, is the first step in putting into practice an integrated SPB management system. A functional decision support system must provide information to the forest manager at the proper junctures during deliberations on SPB control/management. In other words, the support information must be supplied in proper sequence – and in the proper format. The support system must also indicate who is responsible for information gathering, who is responsible for simulations and analyses, and, if all decisions are not made by the same manager, who is responsible for making the decisions.

The steps in developing SPB decision support systems are

(1) Collate information and technology on SPB suppression, prevention, and management.

(2) Define the probable utility and function of the information and technology.

(3) Define the resource management goals, constraints, and values for the affected area.

(4) Array a range of short-term and long-term actions (options) that are consistent with goals, constraints, and values.

(5) Prescribe computer-based and/or noncomputer-based models that will simulate consequences of alternative actions.

An outline of a rather complete SPB decision support system is shown in figure 11-2. To the left is the landowner/resource manager's decisionmaking process as presented by Freeman (1978). It serves as the template against which the decision support system is juxtaposed. The support system includes both support persons and support tools (information, models, procedures, guidelines, etc.). Decision support persons are the "keepers" of the system, responsible for its "care and feeding."

Decisions are reached at three places in the process. At any decision level, further deliberation and input from the decision support system may be terminated. Decision *A* often is made by field or survey personnel when they assess spot sizes and spot activity. The decision may simply be to ignore the beetle activity. Early decisions also may concern the need to evaluate site and stand conditions for purposes of improving surveillance and monitoring activities or for selecting areas in which to concentrate preventive practices.

Decision *B* is reached after considerable input from the decision support system along with careful consideration of management objectives. If at this juncture the manager/landowner decides that his objectives are being, or will be, significantly affected by the beetle activity, then a great deal more information will subsequently be required from the decision support system. The importance of accurate evaluations (step 3) and of accurate statements of land management goals (step 4) is apparent. Any error at juncture *B* can be costly.

Considerable information support is also needed for decision *C*. The decision at this point may be to defer action. Perhaps, under the conditions, none of the controls is cost effective, or perhaps the environmental/social consequences of all actions are untenable. A decision to undertake preventive or suppressive actions may carry with it the selection of more than one option. For example, salvage along with the initiation of stand thinnings may be selected in order to simultaneously control existing infestations, recover some of the loss, and minimize future outbreaks.

At step 12, the resource manager reexamines forest management plans for the affected unit(s) and makes adjustments in view of the preceding decisions. Perhaps the selection of a silvicultural option shifts age class distributions, species composition, and product mix. If so, inventories and harvest schedules must be revised. And all of these changes could, in turn, have future effects on wildlife habitat, esthetics, and other resources.

And finally, the decision process culminates with implementation of suppression tactics and/or preventive strategies. Implementation leads to an entire new set of logistical decisions. Evaluation of the actions taken, and the decisions that led to them, are also part of the pest management decisionmaking process (step 13). Posttreatment evaluations provide feedback for improvement of the decision support system and may be required where public funds are involved.

The decision process and support system in figure 11-2 is an outline and is not intended to apply to all management situations. With such an outline, however, pest management specialists and land managers can tailor a support system for specific management goals.

One of the important contributions of such data-based systems is that the simulations and guidelines can be used to examine combinations of prevention and suppression actions *before* SPB outbreaks occur in a forest. By varying such factors as level of beetle activity, hazard ratings, and resource values, the manager can better plan *where* preventive strategies may be most effective, *when* beetle activity has reached levels requiring suppression actions, and *what* suppression and prevention actions will be most appropriate. In other words, the resource manager can use the tools of the decision support system to arrive at an SPB prevention and suppression plan that is ecologically and economically rational. Such prevention and suppression plans clearly place SPB management within overall forest management planning, displacing the current "wait-and-see" policy toward SPB with a "look-ahead" policy.

Implementing SPB Decision Support Systems

Despite the advantages and benefits that will accrue from better management decisions concerning SPB control, we can expect problems in getting landowners and forest managers to adopt

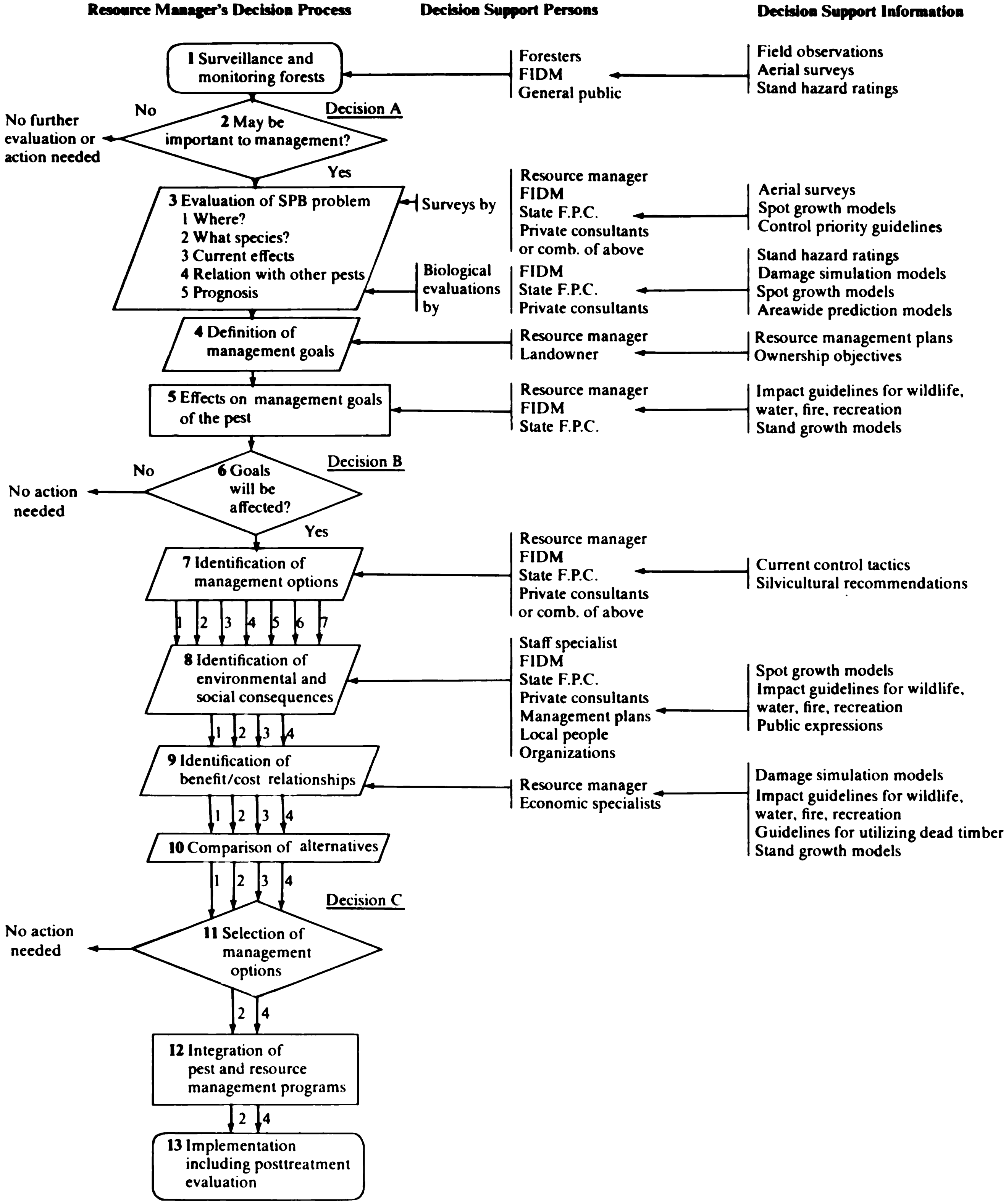

Figure 11-2—Decision process and decision support system for SPB management.

the new practices. The experience of technology transfer experts indicates that it often takes many years to incorporate new scientific developments and technology into practice. The distant planning horizons used in forest management suggest that incorporation of new SPB management options, especially long-term preventive actions, into forest management plans will occur slowly.

The challenge of implementing decision support systems comes down to the need for setting in motion an aggressive technology transfer process. During the final 2 years of ESPBRAP, a broad-based technology transfer (applications) effort was begun. An eight-step technology transfer process was defined (U.S. Department of Agriculture Forest Service 1979):

1. Identify the technology available.
2. Identify target user groups.
3. Develop an applications plan.
4. Package the technology for easy understanding.
5. Select the media to be used.
6. Involve researchers, specialists, users.
7. Provide for feedback and troubleshooting.
8. Evaluate process used and results obtained.

A task force of forest managers, pest managers, and researchers recommended priorities for allocation of ESPBRAP funds to support technology transfer (U.S. Department of Agriculture Forest Service 1979). Technology transfer teams were constituted for eight applications areas: silvicultural practices and stand-rating systems, utilization of SPB-killed timber, socioeconomic guidelines, insecticides and improved spray systems, sampling methods and predictive models, aerial survey and navigation systems, behavioral chemicals, and integrated management strategies.

The task force gave low priority to immediate need for technology transfer activities in the integrated management strategies area, reasoning that through the end of ESPBRAP there was greater need for continued research and development. The task force recognized that technology transfer activities in this area should begin to increase rapidly, however, in 1981.

Decision support systems, and the resulting prevention and suppression plans, will be developed for several classes of forests (e.g., industrial, private nonindustrial, high-use recreation, low-use recreation, urban, etc.). Technology transfer activities will be somewhat different for the several types of ownerships because of their different concerns and/or management objectives. Indeed, even the complexity of the decision support systems will be quite different for different classes of ownership.

Opportunities for reducing SPB impact by implementing SPB management appear to be best in those forests where the beetle is a chronic problem and where well-developed forest management plans have been implemented. These forests include those that are intensively managed for timber production and/or for multiple products, e.g., National Forests and industrial forests. Implementation of successful SPB management by several such innovative organizations would serve to demonstrate the effectiveness of the new methods to other forest landowners.

Who has the responsibility for encouraging forest landowners to implement new SPB management practices? Pest management specialists in State forestry organizations, cooperative extension services, the U.S. Forest Service, and the universities must take this leadership in technology transfer. The primary need of potential users is for technical assistance. Pest management specialists are in the best position to meet that need.

Conclusion

ESPBRAP has served as the vehicle to bring a diverse group of researchers and specialists from many disciplines together to work on a common problem—the southern pine beetle. As a consequence, existing information on SPB was reexamined, up-to-date methodology in biology, engineering, and mathematics was employed in new investigations, and a considerable amount of information was acquired for improving SPB management.

It would be remiss to leave the impression that the quality and quantity of existing information is adequate for all management situations. It is not. Chapter 12 points out future needs. Many of the decision support tools have not been validated and refined for use in other areas and/or under other conditions. Resource managers must provide feedback (step 13, fig. 11-2) to pest management specialists and researchers so that the models and guidelines can be improved.

Further analysis and synthesis of the large amount of knowledge on SPB is needed to properly design integrated SPB management and treatment strategies. But landowners and forest managers can incorporate the improved information that now exists into their pest management decision processes. These improved decision support systems, which might be called "first generation SPB management systems," can markedly improve today's pest management decisions.

Recommendations for Future Work[1]

12

Introduction

Making sure that the southern forestry community obtains maximum benefits from the 6-year Expanded Southern Pine Beetle Research and Applications Program is a job that will outlive the Program itself. In early 1979 the Southern Pine Beetle Task Force (Appendix, table 8) and eight SPB Technology Transfer Teams (Appendix, table 9) started working on this task. Their efforts (Belanger et al. 1979a) outline what must be done to derive the most from ESPBRAP research, now and into the future.

Through the Task Force effort, the Southeastern Area of State and Private Forestry took on the responsibility for coordinating all SPB technology transfer activities (Southeastern Area, State and Private Forestry 1979a). In order to accomplish this task, the position of implementation leader was created and filled. Writer/editor support was also provided as backup for this new position. State and Private Forestry continues to utilize selected Technology Transfer Teams to carry out certain activities. A regional planning group was brought together late in 1980 to set priorities and review accomplishments of integrated pest management (IPM) Program participants and Technology Transfer Teams.

In mid 1979, the team leaders for each Technology Transfer Team completed individual Activity Plans, which were combined into one Southwide plan (Belanger et al. 1979a). The accomplishment of the fiscal year 1980 tasks was impressive. Over 80 percent of all implementation activities identified in late 1979 were completed. That success provided the necessary momentum to encourage planning and implementing of followup activities in FY 1981.

The Activity Plan also served as a basis for the applications and research community to develop an applications program for the 1981-1985 period. The Activity Plan served as a basis for this chapter.

We will direct our attention to activities that should be considered in the next 5 years. The first section will identify technology ready for validation, pilot testing, or transfer to users. The next section will focus on critical new or additional research needs. We will conclude with some remarks on needs for southern forestry community involvement in getting these jobs completed.

New Technology Ready for Validation, Pilot Testing, and Transfer to Users

Integrated Management Strategies

Integrated pest management (IPM) can be defined as "the maintenance of destructive agents, including insects, at tolerable levels by the planned use of a variety of preventive, suppressive, or regulatory techniques and strategies that are ecologically and economically efficient" (Waters 1974). Actions taken must be fully integrated into the total resource management process – in both planning and operation. This means that pest management must be geared to the lifespan of a tree crop as a minimum and to a longer span where the resource planning horizon so requires (Waters 1974). This definition contains four messages about the concept of IPM. First, the foundation of IPM rests on the principles of ecology. Second, the methodology involves a combination of tactics. Third, the functional goal is to reduce or maintain pest populations at tolerable levels (both economic and social values). Fourth, IPM is simply a component of total resource management.

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[1] This chapter was compiled by **Gerard D. Hertel**, Research Coordinator, Expanded Southern Pine Beetle Research and Applications Program, USDA Forest Service, with assistance from the Technology Transfer Team Leaders: **Roger P. Belanger**, Principal Silviculturist, USDA Forest Service, Southeastern Forest Experiment Station, Athens, Ga.; **Robert N. Coulson**, Professor, Dept. of Entomology, Texas A. & M. University, College Station, Tex.; **Joe Lewis**, Economist, USDA Forest Service, Southeastern Area, State and Private Forestry, Atlanta, Ga.; **Thomas L. Payne**, Professor, Dept. of Entomology, Texas A. & M. University, College Station, Tex.; **Frederick M. Stephen**, Associate Professor, Dept. of Entomology, University of Arkansas, Fayetteville, Ark.; **John W. Taylor**, Chemical Coordinator, USDA Forest Service, Southeastern Area, State and Private Forestry, Atlanta, Ga.; **James G. D. Ward**, Supervisory Entomologist, USDA Forest Service, Southeastern Area, State and Private Forestry, Doraville, Ga.; and **Robert F. Westbrook**, Sawmill Specialist, USDA Forest Service, Southeastern Area, State and Private Forestry, Pineville, La.

During the last decade considerable thought has been given to defining the research components required to develop operational IPM systems. Although classified in various ways, information on the following four subjects is generally considered to be necessary: pest population dynamics, host population dynamics, impact assessment, and treatment tactics. Interactions between these components are extremely important (Waters and Stark 1980).

The ESPBRAP supported research on each of the components (*see* Chapter 11). A tremendous volume of information and new technology pertinent to development of integrated management strategies for the SPB has been accumulated. The organization of this information and technology has been a funcion of the Technology Transfer Teams.

The expectations and needs of the various user groups for information on SPB are obviously quite different (*see* Chapter 11). Basic technology and information for development of a decision-support system for SPB are available as result of the research provided by ESPBRAP. An outline for such a system is presented in Chapter 11.

Implementation –

- Identify opportunities for integrating pest management approaches into
  - forest management planning
  - forest inventory systems
  - operational programs, including scheduling and harvesting activities.
- Prepare and release a handbook on how to apply direct suppression tactics to control SPB populations.

Aerial Survey and Navigation Systems

The first step in determining that there may be a problem that requires control is the detection of pest activity. For SPB, detection is usually accomplished from the air by locating groups of dead or dying trees (Chapter 10). To determine the size and potential of the problem, survey crews must accurately survey that portion of forested areas currently infested or most likely to suffer further losses. Aerial survey results can be used both to guide ground control operations and to quantify and predict future losses.

Accurate, low-cost methods for determining the status of SPB outbreaks have been developed. Using a digital computer-aided system, DeMars (1979) monitored spots on sequential photographs of a large ownership over time. Clerke and Ward (1979) reported on aerial sampling techniques to determine impacts of SPB at one point in time or over a year's time. The Loran-C radio navigation system improved the accuracy and repeatability of the aerial survey flights in the latter study. Setting ground-check priorities following aerial surveys (Billings and Doggett 1980) and setting control priorities for spots having different characteristics (Billings and Pase 1979b) have helped the southern forestry community deal with SPB outbreaks.

Implementation –

- Provide field training, demonstrations, and workshops on the use of the Loran-C and digital computer systems for quantifying timber mortality over time.
- Develop a users' guide for the digital computer-based system.
- Prepare and release a handbook on how to determine SPB impacts with aerial photography and digitized, computer-aided accounting system.
- Conduct symposium on new or improved aerial survey techniques.

Sampling Methods and Predictive Models

Lack of adequate sampling methods has hindered the development of successful control procedures for the southern pine beetle. The lack of sampling methods can be related to several problems. Evaluation of control tactics is dependent on reliable estimates of pre- and post-treatment measurements of beetle populations. Without good sampling methods we cannot fully understand the dynamics of beetle populations and their interactions with their immediate environment, i.e., their host trees. Without understanding insect population dynamics, we cannot develop reliable predictive capabilities that enable us to focus control on those spots most likely to grow at the fastest rate.

Sampling studies have provided us with a Southwide series of large data bases on southern pine beetle populations. These data have, in turn, provided some of the information needed to develop mathematical models that mimic beetle population dynamics. As with sampling methods, the spatial and temporal characteristics of models built during the ESPBRAP vary widely. By relating beetle numbers to numbers or characteristics of infested trees, predictions can be made not only of population trends over time but also of the amount of tree mortality that could be expected from growth. Thus damage can be predicted in terms of number of infested trees and expected volume loss as a function of beetle population trend over time (*see* Chapter 6).

Input and output for these models have purposely been made flexible to permit different levels of accuracy at different costs. Thus, the models can accept precise estimates of initial beetle numbers within a spot, and produce estimates of how these numbers will change as the infestation grows or declines. The population dynamics researcher may need such information. Using the same model but with less sophisticated input, the pest control specialist can obtain an estimate of expected damage in terms of infested trees and volume lost in a given area after some length of time. To calculate these outputs, he needs to input only numbers of infested trees and stand condition associated with a particular spot. Thus these models can be adapted to meet the needs of researchers or field practitioners.

Although much progress has been made in the area of population sampling and model construction, we are far from finished. (Stephen, Searcy, and Hertel 1980). Mathematical modeling abstracts pertinent information about complex systems. Therefore, a particular model can always be considered incomplete, since our abstract only approximates the information contained therein. However, the modeling approach forces the scientist to conceptualize and define objectively the system being modeled. As he gains additional experience and data, there may be good reason to reexamine the assumptions, logic, and techniques used in developing, validating, and implementing the models.

Users should be made aware of the potential applications for predictive techniques. Therefore, users should be included in the testing and improvement of the models. This is particularly important, as models must have input and output formats that the intended users can understand, accept, and use. For example, expressing loss in terms of cubic feet versus dollar value may be important to the potential user, and easily accommodated by simple programming changes within the model structure.

Validation –

- Validate spot growth models in Alabama, Georgia, Mississippi, and South Carolina.
- Refine and update the population models as time, data, and experience permit.

Implementation –

- Pilot test computer-based spot growth models, which determine population/damage trends and the need for action.
- Translate into FORTRAN and install insect population models on Forest Service computer or maintain on university computer.
- Develop user manuals for computer-based models.
- Integrate model components into forest pest management guidelines.
- Continue to refine and update computerized models as new information becomes available.
- Conduct workshops on the use of predictive models for forecasting population/damage trends.
- Use models for selecting and evaluating proposed control tactics and strategies that will provide optimum results in operational control programs.

Socioeconomic Guidelines

In recent years, there have been increasing demands from all segments of society for government-provided goods and services. Yet public agencies have come under intense pressure to reduce spending or, at the very least, limit the use of taxpayers' dollars to those activities that demonstrate a favorable return on investment. In competing for funds, it is imperative that forest resource managers make a critical economic analysis of all proposed project costs and benefits.

To provide resource managers with the tools for making sound economic analyses, ESPBRAP has developed methods for measuring and/or analyzing the physical and economic impacts of SPB on various forest resources (e.g., timber, recreation, wildlife, grazing, water, and esthetics). Results from such analyses are needed to quantify the SPB's impacts over time.

Several analytical procedures have been developed for use in making control decisions. These include the computer-based models FRONSIM, PTAEDA, TBAP, and DAMBUGS (*see* Chapter 7). Also available are the procedures for evaluating esthetic and recreation impacts.

Validation –

- Validate or refine socioeconomic models.

Implementation –

- Implement the DAMBUGS model on the Forest Service computer to simulate damage levels over large areas in future years. Prepare and release user's guide for the model.
- Incorporate models in integrated forest pest management guidelines.

Silvicultural Practices and Stand Rating Systems

Promotion of stand resistance through improved forest management is our best approach to preventing SPB infestation incidence and to minimizing losses should outbreaks occur. Research efforts of the ESPBRAP regional site-stand project were directed toward developing effective prevention strategies. Findings identified stand, site, host tree, and climatic conditions associated with SPB attack *(see* Chapter 4). Systems were developed to rank the susceptibility of stands to beetle infestations (Chapter 8). Overstocking and poor growth were common characteristics of high-risk stands. Silvicultural and management recommendations were developed to prevent or remedy these conditions (Chapter 9).

Several stand hazard-ranking systems have been implemented. Their uses vary with land management objectives and forest conditions. To identify current silvicultural treatment needs, one can rank stands that are already susceptible in order of priority. And knowing a stand's likelihood of sustaining SPB damage facilitates surveillance and planning of control activities. As a result, the forest manager can anticipate where infestations are most likely to occur and undertake the most appropriate cultural measures on a timely basis.

The southern forestry community has demonstrated enthusiastic support for the development of hazard-ranking systems and management practices to reduce losses from the southern pine beetle. The assistance, suggestions, and constructive criticisms of interested persons and organizations have greatly benefited the research process. The involvement of user groups with technology transfer and implementation has also helped Program management identify additional work that remains to be done:

Validation –

- Validate stand hazard rating system
  - on National Forests in the South
  - in three States on State-owned and private lands
  - on the lands of two forest industries.

Implementation –

- Conduct awareness workshops on stand hazard-ranking systems.
- Prepare and release "How-to" handbooks and fact sheets on stand rating systems for natural stands in the Gulf Coastal, Piedmont (Georgia), and southern Appalachian regions.

- Where appropriate, incorporate ranking systems into management guidelines for National Forests, industry, States, Soil Conservation Service, National Park Service, Corps of Engineers, and the Department of Defense.
- Establish demonstration areas to illustrate
  - conditions favoring SPB infestations
  - the field application of stand-ranking systems
  - cultural treatments recommended to reduce losses from the SPB.
- Incorporate silvicultural practices and stand rating system(s) into integrated forest pest management guidelines.
- Implement, maintain, and monitor a Southwide evaluation of the effects of thinning in preventing or reducing SPB damage in plantations and natural stands.

Guidelines for Utilizing SPB-Killed Timber

Proper utilization of America's timber resources is one of the most important endeavors of State and Federal resource agencies and the forest products industry. Over the years approximately one-half of all the SPB-killed wood has not been utilized. ESPBRAP-supported research has given us just about all the existing information on utilization of beetle-killed wood (Chapter 7). Possible uses include lumber, particle board, hardboard, pulp, blue-stained paneling, and plywood.

Contrary to popular opinion, wood from beetle-killed trees can be used even after the bark is loose and begins to slip off (Levi 1980). These trees are usable for pulpwood for at least 2 years in the northern part of the region. The effects of beetle damage on the properties of wood from these trees, presented in Levi's handbook, can be determined by external appearance class of the tree on the stump.

Attempts are being made to get this information to loggers, wood dealers, and mill operators. Popular articles (Sinclair 1978, Sinclair and Ifju 1977), fact sheets (Southeastern Area, State and Private Forestry 1979b and c), and Agriculture Handbooks (Levi 1980, Sinclair 1979) have been used along with awareness workshops and training sessions. Technology transfer in the wood utilization area should continue to have a high priority.

Validation –

- Validate cruising guidelines (uniform appearance classes) for determining state of deterioration of beetle-killed timber in several geographic subregions.
- Validate for the western Gulf States the mill operators' guide (Sinclair 1979) that was developed in Virginia to determine the profitability of processing beetle-killed timber.

Implementation –

- Conduct workshops on utilization of SPB-killed wood.
- Present a symposium on utilization of beetle-killed timber at a forest products association meeting.
- Incorporate utilization results into integrated forest pest management guidelines.

Behavioral Chemicals

Historically, efforts to control the southern pine beetle have been primarily remedial in nature and principally involved the use of insecticides and salvage. These methods have only been partially successful in large areas, as evidenced by continuing epidemics of the pest. Salvage has become the principal approach in the last decade since cost and environmental concerns have all but eliminated the operational use of insecticides in the forest. As a result, the forest manager has few alternatives for dealing with the beetle.

Remedial control techniques are still urgently needed, and over the past 15 years, researchers have investigated behavioral chemicals for their potential use in filling that need. Several chemicals, including attractants and inhibitors, play a role in SPB landing and attack behavior (*see* Chapter 2). Attractants cause enough flying beetles to congregate on a common host tree over a relatively short period of time so that they are able to overcome the natural resistance of the tree and successfully colonize it.

Research on attractants and inhibitors is now at a point where they should be considered as potential control agents for suppressing southern pine beetle infestations. The attractants will likely be most practical for use in smaller infestations and will give foresters and/or pest management specialists the potential for reducing or halting spot growth where salvage is impractical. The inhibitors, on the other hand, could be applied to larger, unmanageable infestations. More work is needed in this area before use of behavioral chemicals can be recommended.

Validation –

- Pilot test area permeation with inhibitors applied from the ground and air in slow-release devices.
- Pilot test frontalure alone and in combination with other treatments for disrupting spot growth or suppressing beetle populations.

Implementation –

- Register a behavioral chemical for SPB spot disruption.
- Prepare and release a handbook on the use of behavioral chemicals for disrupting SPB spots and in combination with other suppression approaches.
- Organize and conduct workshops on the use and evaluation of behavioral chemical treatments.
- Hold a symposium on the use of behavioral chemicals in SPB surveys and suppresion.

New Insecticides and Improved Spray Systems

Except for treating small spots (< 25 trees) during the winter, insecticides are little used for operational control projects in the forest. However, they can be used to protect high-value trees in areas such as seed orchards, campgrounds, or urban situations. The use of spray systems that limit insecticide drift is of special concern in such areas. Billings has summarized the various aspects of using insecticides to control bark beetles in Chapter 10.

Lindane has long been the standard insecticide for controlling SPB infestations. However, recent concerns about the longevity of chlorinated hydrocarbon pesticides in the environment and the Rebuttable Presumption Against Registration issued against lindane have caused concern about its continued availability. This concern resulted in an ESPBRAP-funded effort to identify potential replacements for lindane in chemical control of SPB. Several compounds were screened and tested under both field and laboratory conditions. Two – chlorpyrifos and fenitrothion – proved particularly efficacious and did not present any unreasonable adverse environmental impacts when used in forest ecosystems. Chlorpyrifos (Dursban 4E®) has been registered for use against SPB.

Implementation –

- Write fact sheets summarizing insecticide research results.
- Determine cost/benefits and include chemical treatments in integrated pest management guidelines.

Continuing and New Research Needs

Population Dynamics

The understanding of southern pine beetle population dynamics in individual trees has blossomed during the ESPBRAP. We have accumulated a storehouse of information on the bark beetle, host tree, and associated microorganisms. Much of our understanding at the infestation level comes through extrapolation from the individual tree level. What goes on in the relationship between beetle numbers and the forest is not completely understood.

There are, however, many knowledge gaps left to be filled:

1. Interrelationships between bark beetle species

2. Role and interrelationships between biological control agents

3. Insect-host-climatic interactions
4. Completion and validation of biological/physical models
5. Nutritional and rearing requirements
6. Genetic characteristics of populations
7. Communication system of the SPB.

Stand Dynamics

Host-pest relationships are complex ecological phenomena that ultimately achieve a balance in undisturbed systems. The pest must be able to thrive and reproduce; but, equally important, it must permit the host to survive. Without a good understanding of host dynamics, the usefulness of the population dynamics information might never be realized. The following efforts should be undertaken.

1. Characterize the host factors or processes regulating tree and stand susceptibility.
2. Construct biological models of time, stand, site, and climatic interactions affecting tree and stand susceptibility to beetle attack.
3. Validate predictive models for forecasting tree and stand susceptibility as influenced by variations in age and size class of trees, stand density, growth rate, site factors, climatic events, tree disease incidence, beetle population densities, and forest management objective.
4. Simplify modeling inputs to encourage use by pest control specialists, analysts, and resource managers.

Treatments

The concern of most forest managers is "What can I do after the beetles are here?" The approach being taken today by integrated pest management specialists is to convince the land manager to "think insects" whenever he does anything. However, forest *pest* management can be accomplished only as part of the forest management process. Future research should consider the following items.

1. Modification or development of new forest management techniques to reduce damage to residual forests and prevent or reduce beetle loss. Areas of consideration include
    a. Logging practices and equipment
    b. Single- *v.* mixed-species management
    c. Silvicultural systems
    d. Rotation lengths
    e. Thinning priorities, precommercial and commercial
2. Development, testing, and validation of integrated management systems under varying management regimes.
3. Development and testing of techniques for evaluating treatment effects before and after control.

Other Research Activities

The technology transfer teams have identified the following items for new and continued research.

Silvicultural Practices and Stand Rating Systems

- Develop a stand ranking system for pine plantations.
- Determine inherent differences in susceptibility to SPB attack between and within the major southern pine species.
- Determine effects of other cutting and harvesting practices in preventing or reducing damage caused by SPB, and develop management guidelines.

Guidelines for Utilizing SPB-Killed Timber

- Identify harvesting problems associated with beetle-killed timber.
- Determine potential for using beetle-killed timber as an energy source.
- Identify mocroorganisms responsible for destruction of beetle-killed wood.
- Determine potential for using beetle-killed wood for crossties, shingles, and shakes.

Socioeconomic Guidelines

- Develop, refine, or validate socioeconomic models.

New Insecticides and Improved Spray Systems

- Continue field and laboratory screening of insecticides showing potential for controlling SPB.
- Evaluate feasibility of using combinations of insecticides and pheromones for SPB control.

Sampling Methods and Predicitive Models

- Determine relationship between spot growth and areawide damage trends.
- Continue to study low-level SPB populations in South Atlantic and Gulf Coastal States to determine factors regulating such populations.
- Develop input routine(s) for sampling and predicting population/damage that are more compatible with the needs and capabilities of pest management specialists and resource managers.

Aerial Survey and Navigation Systems

- Measure SPB impacts with small-scale photography.
- Test any new developments in previsual detection technology.
- Interface Loran-C system with digitizer and computer.

Behavorial Chemicals

- Develop deployment technology for attractants and inhibitors.
- Evaluate the use of inhibitors for protecting urban trees.
- Test spot disruption with frontalure applied from the air. Continue the isolation, identification, and synthesis of promising attractive and inhibitory compounds.

Integrated Management Strategies

- Develop decision support systems.
- Consolidate SPB findings into integrated pest management systems suited to local pest, forest, and environmental conditions.
- Refine, develop, and test integrated pest management systems for SPB in two geographic subregions.

How Do We Get This Job Done?

To complete the research and applications jobs outlined in this chapter, the forestry community in the South has made a commitment. Activity flows developed from the original action plan have been considered by State and Private Forestry, Southeastern Forest Experiment Station, Southern Forest Experiment Station, Southern Agricultural Experiment Station Directors, State Foresters in the South, and the Cooperative Extension Service. At this time the details of who will actually do the work and how they will be supported are being worked out. It has been made clear through this cooperative venture that SPB remains a high-priority pest problem.

The bottom line to all the work is the implementation of new results. To achieve this implementation, the information must be offered, received, and acted upon. The research community must offer the information that was originally sought by users. The linker groups must receive it, use it, and pass it on to other users.

The movement of information from the research community to the user community requires a process that many organizations cannot deal with. We have seen over the years a stockpiling of research results. To develop a more uniform approach to this problem, the U.S. Forest Service put together a National Action Plan for Technology Transfer (1979). This Plan follows the USDA Interagency Agreement on Forestry (1978), which spells out the responsibilities of the U.S. Forest Service, Soil Conservation Service, State Foresters, conservation districts, and the Agricultural Stabilization Commodity Service as far as technology transfer is concerned.

As an attainment process, technology transfer involves (1) users' perceiving a problem, need, or opportunity; (2) practitioners' inquiring for knowledge source; (3) analyzing available information; (4) checking costs and benefits; and (5) adopting new technology or knowledge.

The forestry community clearly has a big job ahead. Technology development, translation, distribution, and implementation is no easy matter. This book has brought us up to date on the technology relating to the southern pine beetle as of April 1980. This chapter should give readers a feeling for the work left to be done. The work should be accomplished with the assistance of the southern forestry community.

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Glossary

Acarology: the branch of zoology that treats of mites and ticks.

Aerotriangulation: a method by which aerial photographs are oriented and placed in proper relationship to one another.

Aggregation: the massing of populations of male and female adults on a tree about to be attacked.

Allocation: the combination of emerging and reemerging beetles from one tree going from source to sink trees, i.e., from trees that have been attacked to those being attacked.

***Alpha*-pinene:** the most significant host-tree odor in the behavioral complex of the SPB.

Arthropods: animals with segmented bodies and paired, jointed appendages – e.g., insects and spiders.

Attractant: a chemical or odor that affects SPB behavior by attracting beetles to a particular area.

Bark beetles: group of beetles, mainly of the family Scolytidae, whose adults bore through the bark of host trees to lay their eggs, and whose larvae tunnel and feed under the bark.

Biome: an ecological formation considered in terms of both plants and animals of the area concerned and usually identified in terms of characteristic vegetation forms.

Bole: the trunk or stem of a tree.

Cambium: the layer of cells that lies between, and gives rise by active division to, secondary xylem and secondary phloem, i.e., to wood and the innermost living bark.

Canadian Standard Freeness: a measure of the drainage characteristics of pulps.

Clearcutting: removal of the forest stand completely, in one cut.

Climax species: species capable of perpetuation under the prevailing climate and soil conditions.

Colonization: the phase of the SPB's life cycle that includes mating, egg laying, and gallery construction.

Cord: a unit of gross volume measurement for stacked round or cleft wood, based on external dimensions, e.g., a stack of wood 4 ft high, 4 ft thick, and 8 ft long.

Diameter at breast height (d.b.h.): diameter of a tree at 4.5 ft (1.37 m) above the ground, measured from the high side of slope.

Diapause: a condition of suspended animation, or resting period, during which development ceases, as during the egg overwintering period.

Diel: involving a 24-hour period that usually includes a day and its adjoining night.

Dispersal: the act or result of dispersing or scattering; usually refers to the redistribution of larvae after eggs have hatched – e.g., dispersal of first instars.

Ecology: the study of plants and animals in relation to their environment.

Ecosystem: an assemblage of living plants and animals and their environment.

Edge: the area where two types of vegetation meet and intermix.

Efficacy: effectiveness, as of an insecticide; a product's ability to control the specified target pest or to produce the specified action.

Electrophoresis: slow movement of colloidal particles in an electric field; a process used to separate and identify compounds.

***Endo*-brevicomin:** a pheromone, produced by male SPB, which inhibits the responses of both sexes to attractive host trees and thus facilitates attacks on other new trees.

Evapotranspiration: evaporation of transpired water from the surface and crown of plants.

Frass: solid insect excrement.

Frontalin: the primary aggregation pheromone of the SPB.

Frontalure: the synthetic SPB attractant, a mixture of frontalin and *alpha*-pinene.

Glue-line test: a test of the load carrying capacity (strength) of glued joints.

Histogram: a graph of a frequency distribution in which equal intervals of values are marked on a horizontal axis and the frequency corresponding to each interval is indicated by the height of a rectangle having the interval as its base.

Host: any organism upon or within which another organism lives.

Hydric: characterized by, relating to, or requiring an abundance of water.

Hyphae: the individual threads that make up the mycelium of a fungus.

Infestation geometry: spatial arrangement of trees and susceptibility factors.

Inhibitor (re behavioral chemicals): a chemical or odor that affects SPB behavior by repulsing beetles from a particular area.

Instar: period or stage between molts of an insect larva.

Isomer: one of two or more compounds composed of the same percentage of elements but differing in structure and properties.

Larva: immature form of an insect that undergoes complete metamorphosis; a caterpillar, maggot, or grub.

Life table: tabulation of mortality factors acting on an insect population, which displays the relative importance of each factor and permits estimation of survival; when coupled with a knowledge of fecundity, can be used to estimate the size of the succeeding generation.

Lipids: the class of substances including fats, waxes, phosphatides, cerebrosides, and some steroids and carotenoids.

Multivoltine: having many broods and generations in a year or season.

Mycangium: specialized body structures on the exterior of SPB, in which mites or fungi reside.

Myrtenol: a pheromone produced by both male and female SPB, which encourages males to stop near the source of the pheromones, esp. the entrance holes belonging to female SPB.

No. 1 structural (grade): the highest quality of softwood dimension lumber, graded for its load-carrying capacity according to the grading rules of the Southern Pine Inspection Bureau.

Nonlinear least-squares technique: method of fitting data to a nonlinear model by minimizing the sum of squares of the differences between the predicted (model) values and the actual values.

Oleoresin exudation pressure: pressure within resin ducts in some conifers.

Orthophotography: photographic reproduction of aerial photographs in which displacements of images due to tilt and relief have been removed.

Overwintering: the phenomenon of SPB larvae remaining in the tree through the winter months.

Oviposit: to lay eggs.

Parasitism: the mode of life of a parasite, i.e., as between it and its host.

Parasitoid: a life form that usually develops from egg to adult on a single host, using the host for food but not killing it until the parasitoid has fully matured.

Pheromone: substance released by one individual that modifies the behavior of another of the same species, e.g., the SPB pheromone is an odor released by females that attracts males.

Phloem: complex vascular tissue in higher plants, which functions in translocation, support, and storage.

Phoretic: exhibiting phoresy, the nonparasitic association of one kind of animal (as a larval insect) with another in order to obtain transportation.

Population dynamics: the study of changes and the reasons for changes in population size.

Predation: a form of life in which food is primarily obtained by killing and consuming animals.

Predator: a free-living organism that feeds on other organisms; as birds and other insects that feed on SPB.

Primary parasite: a parasite that establishes itself in or on a host that is not a parasite.

Pupa: the resting, intermediate stage of an insect between the larva and the adult.

Radially loaded: a term applied to toughness tests where a standard stick of wood is oriented in such a way that the breaking load is applied perpendicular to the grain and parallel to the annual rings.

Ratio of increase (R.I.): ratio of emerging brood adult SPB to original attacking (parent) adults.

Reemergence: the phase of SPB activity when adults come back out of the bark after ovipositing.

Resinosis: abnormal exudation of resin from conifers or abnormal impregnation of conifer tissue with resin.

Respiration: process in plants of absorbing oxygen from the air, oxidizing organic compounds to simpler compounds and carbon dioxide, and yielding energy.

Scribner rule: a diagram rule for estimating board-foot yields from timber (logs). It assumes 1-inch boards and ¼-inch kerf, makes a liberal allowance for slabs, and disregards taper.

Selection cutting: periodic harvest removal of trees (particularly mature trees), either singly or in small groups (as opposed to clearcutting, in which all trees are removed in a single operation).

Significance: when a statistical hypothesis is tested, it is declared true if a calculated probability exceeds a given value, referred to generally as the significance level.

Silviculture: theory and practice of controlling the establishment, composition, and growth of trees.

Socioeconomic model: a collection of computer programs used to translate the volume of timber, water, and other factors into dollar impacts of a particular simulated SPB outbreak.

Southern pine bark beetles: As a group, the major bark beetles attacking pines in the South – southern pine beetle, *Ips grandicollis, I. avulsus, I. calligraphus,* and *D. terebrans.*

Stand geometry: the spatial arrangement of trees.

Stemflow: water that is caught on leaves, needles, branches, and bole and eventually flows down the bole onto the forest floor.

Stochastic: random, as in processes or variables.

Stumpage: current value of standing timber, considered with reference to its quantity or marketable value.

Succession (forest): the establishment, development, and maturation of forest communities under the influence of site factors and reaction of vegetation upon them; the progressive development of vegetation on the same site resulting from the successive replacement of one community by another of different growth form, e.g., moss, weed-grass meadow, hardwood thicket, poplar forest, spruce-fir forest.

Survivorship: rate of survival or proportion of insects surviving over a specific period, e.g., a developmental stage or generation.

Symbiosis: the living together in more or less intimate association or even close union of two dissimilar organisms.

Synergist: an agent that increases the effectiveness of another agent when combined with it.

Tangentially loaded: a term applied to toughness tests where a standard stick of wood is oriented in such a way that the breaking load is applied perpendicular to the grain and the annual rings.

Terpene: general name of hydrocarbons having the formula $C_{10}H_{16}$, related to isoprene, commonly occurring in many species of wood, and generally having a fragrant odor.

Top-kill: for individual trees, some portion of the live crown and stem killed, from the top down, by any cause.

Toxicity: poisonous quality, especially its degree or strength.

Tracheids: water-conducting tissues in the xylem.

***Trans*-verbenol:** an odor produced by female SPB that can synergize the attractiveness of frontalin.

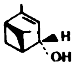
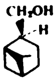
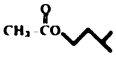
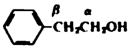
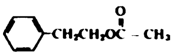
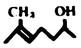
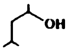
Verbenone: a pheromone produced mainly in male SPB which, when exuded, helps balance the sex ratio of attacking beetles.

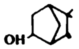
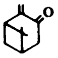
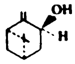
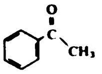
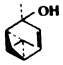
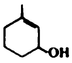
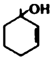
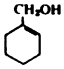
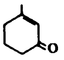
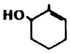
Volatiles: tree-produced or insect-produced odors that affect SPB behavior.

Xylem: woody tissue of higher plants, which functions in support and water conduction.

Appendix

Table 1. – Beetle- and host tree-associated compounds found to affect southern pine beetle behavior.

COMPOUND	REFERENCE	SOURCE	BEHAVIORAL EFFECT	METHOD OF INVESTIGATION
Frontalin (racemic) (+) (-)	1, 2	A, B, C, D	Attractant (1, 14, 15)	Field & laboratory bioassay
Endo-brevicomin 	3, 4	A, C, D	Inhibitor (14, 16, 17)	Field & laboratory bioassay
Trans-verbenol 	5, 2	A, B, C, D	Synergist	Field & laboratory bioassay
Cis-verbenol (racemic) (R) (S) 	6, 2	B, C, D		
Verbenone 	5, 2	A, B, C, D	Multifunction Inhibitor/Synergist (14, 15, 17, 18)	Field & laboratory bioassay
Alpha-pinene 	7, 2	C, D	Synergist (1, 7, 14, 15)	Field & laboratory bioassay
Myrcene 	2	C, D	Attractant (19)	Laboratory bioassay
Myrtenol 	8, 9	A, B, C, D	Synergist (20)	Laboratory bioassay
Cis-myrtanol 	2	B, D, C		
Isoamyl acetate 	10	E	Synergist (10)	Laboratory bioassay
Isoamyl alcohol 	10, 11	E, F	Synergist (10)	Laboratory bioassay
2-phenylethanol 	10	E	Synergist (10)	Laboratory bioassay
2-phenylethyl acetate 	10, 11	E	Synergist (10)	Laboratory bioassay
6-methyl-5-hepten-2-one 	11	F		
6-methyl-5-hepten-2-ol 	11	F		
4-methyl-2-pentanol 	9	A, B		

COMPOUND	REFERENCE	SOURCE	BEHAVIORAL EFFECT	METHOD OF INVESTIGATION
6-hydroxycamphene 	12, 2	A, B, C, D		
Pinocarvone 	9, 2	A, B, C, D		
Trans-pinocarveol 	9, 2	A, B, C, D		
Myrtenal 	9, 2	A, B, C, D		
Acetophenone 	2	A, C, D		
Chrysanthenone 	2	A, C, D		
4-Allylanisole 	2	C, D		
Cis-3-pinen-2-ol 	13	B		
3-methyl-2-cyclohexen-1-ol (seudenol) 	13	A, B		
1-methyl-2-cyclohexen-1-ol 	13	A, B		
1-cyclohexenemethanol 	13	A, B		
3-methyl-2-cyclohexen-1-one (MCH) 	13	A, B		
2-methyl-2-cyclohexen-1-ol 	13	A, B		

1 – Kinzer et al. 1969
2 – R. M. Silverstein and J. R. West, personal communication
3 – Silverstein et al. 1968
4 – Pitman et al. 1969
5 – Renwick 1967
6 – Silverstein et al. 1966
7 – Renwick and Vité 1969
8 – Hughes 1973
9 – Renwick et al. 1973
10 – Brand et al. 1977
11 – Brand and Barras 1977
12 – Renwick et al. 1976
13 – Renwick and Hughes 1975
14 – Payne et al. 1978a
15 – McCarty et al. 1980
16 – Vité and Renwick 1971
17 – Richerson and Payne 1979
18 – Rudinsky 1973
19 – P. D. Billings, personal communication
20 – Rudinsky et al. 1974

A – Male hindguts
B – Female hindguts
C – Beetle-infested tree parts
D – Female frass
E – Yeast metabolite
F – Basidiomycete

Table 2. – Arthropod predators in the southern pine beetle.[1] References designated by ( ).

- **Hemiptera**
  - Anthocoridae
    - *Lyctoris campestris* (Fab.) **(6)**
    - *Lyctoris elongatus* (Reuter) **(1)** **(2)** (3) **(5)** **(6)** **(7)** **(8)** **(9)**
    - *Scoloposcelis flavicornis* (Reuter) **(2)** **(9)**
    - *Scoloposcelis mississippensis* Drake & Harris **(1)** (3) **(5)** **(6)** **(7)** **(8)**
  - Aradidae
    - *Aradus cinnamomeus* (Panzer) (8)
  - Pentatomidae
    - *Diolcus chryssorhoesus* (Fab.) (8)

- **Coleoptera**
  - Carabidae
    - *Apristus subsulcatus* (Dejean) **(6)**
    - *Dromius piceus* Dejean **(6)**
    - *Pinacodera limbata* Dejean (3)
    - *Pinacodera platicollis* (Say) **(6)**
    - *Stenolophus lineola* (3?)
    - *Tachyta pavicornis* Notman (3)
  - Histeridae
    - *Abraeus* sp. (3)
    - *Cylistix attenuata* Lec. (3) (7)
    - *Cylistix cylindrica* (Payk.) **(1)** (3) **(5)** **(6)** (7)
    - *Epierus pulicarius* Erichson (7)
    - *Hister* sp. (3)
    - *Platysome parallelum* Say (3) **(5)** (7)
    - *Plegaderus pusillus* Lec. (7)
    - *Plegaderus transversus* Say (7)
    - *Plegaderus* sp. (2 spp.?) **(5)** **(6)**
  - Staphylinidae
    - Aleocharinae (3)
    - *Leptacinus paurumpunctatus* (Gyll.) (3?) **(6)**
    - *Nacaeus tenellus* Erichson (3?)
    - *Pseudolispinodes tenellus* Erichson (7)
    - *Silusa* sp. **(6)**
    - sp. (undetermined) (4 spp.?) (3) (7)
  - Orthoperidae
    - *Molamba* sp. (3)
    - *Sacium* sp. (7?)
  - Trogositidae
    - *Corticotomus parallelus* Melsh. (3)
    - *Temnochila virescens* (Fab.) **(1)** **(2)** (3) (6) (7) **(8)** **(9)**
    - *Tenebroides collaris* (Sturm) **(1)** **(2)** (3) (7) **(8)** **(9)**
    - *Tenebroides marginatus* (P. de B.) (3) (7)
    - *Tenebroides nanus* (Melsh.) (3)
    - *Tenebroides* sp. **(6)**
  - Cleridae
    - *Cregya oculata* (Say) (3?)
    - *Cymatodera undulata* (Say) (3)
    - *Enoclerus quadriguttatus* Oliv. **(2)** **(9)**
    - *Phyllobaenus pallipennis* Dejean (3?)
    - *Priocera castanea* (Newm.) **(2)** (3) **(9)**
    - *Thanasimus dubius* (Fab.) **(1)** **(2)** (3) **(5)** **(6)** (7) **(8)** **(9)**
    - *Tillus collaris* Spin. (3?)
  - Elateridae
    - *Anchasius signaticollis* (Germ.) (3)
    - *Athous* sp. (3)
    - *Elateridae* sp. **(9)**
    - *Glyphonyx* sp. (3)
    - *Lacon impressicollis* (Say) (3) (8)
    - *Melanotus* sp. (2 spp.?) (3) (8)
    - sp. (undetermined) (3)
  - Eucnemidae
    - *Dirhagus triangularis* (Say) (3)
    - *Dirhagus* sp. (3)
  - Throscidae
    - *Trixagus* sp. (3)
  - Cucujidae
    - *Ahasverus advena* (Waltl) (8)
    - *Carthartosilvanus imbellis* (Lec.) (3)
    - *Nausibus clavicornis* (Kug.) (3)
    - *Silvanus bidentatus* (Fab.) (7?)
    - *Silvanus muticus* Sharp (3)
    - sp. (unidentified) (2 spp.?) (3)
  - Colydiidae
    - *Aulonium ferrugineum* Zimm. (3) **(5)** **(6)** (7?)
    - *Aulonium tuberculatum* Lec. (3) **(5)** **(6)**
    - *Colydium lineola* Say (3?)
    - *Colydium nigripenne* Lec. (3)
    - *Lasconotus pusillus* Lec. (3) **(6)**
    - *Lasconotus referendarius* Zimm. (3) **(7)**
    - *Pycnomerus sulcicollis* Lec. (3)
  - Cerylonidae
    - *Cerylon castaneum* Say (3)
  - Mordellidae
    - sp. (unidentified) (2 spp.?) (3?)
  - Tenebrionidae
    - *Corticeus glaber* (Lec.) (3) (7)
    - *Corticeus parallelus* Melsh. (7) (**9** as *Hypophloeus parallelus*)
    - *Corticeus* sp. (2 spp.?) **(5)** **(6)**
  - Coccinelidae
    - *Nephus bioculatus* Mulsant (8)
  - Melyridae
    - *Melyrodes cribratus* Lec. **(7)**
  - Rhizophagidae
    - *Rhizophagus* sp. (7)

- **Diptera**
  - Stratiomyidae
    - *Zabrachia* sp. (3)
  - Empidae
    - *Euhybus* sp. near *gentivus* Melander (undescribed) (3)
    - *Syndas polita* (Loew) (3)
  - Dolichopodidae
    - *Medetera bistriata* Parent **(1)** **(5)** (7) (recorded as parasite in **6**)
    - *Medetera maura* Wheeler **(8)**
    - *Medetera* sp. (2 spp.?) (2) (recorded as parasite in **6**)

Phoridae
Dorniphora sp. (3?)
Lonchaeidae
Lonchaea auranticornis McAlpine (7?)
Lonchaea polita Say (7?)
Lonchaea sp. (3)

Hymenoptera
Formicidae
Camponotus clarus Mayr (7)
Camponotus nearcticus Emery (7)
Camponotus sayi Emery (3)
Crematogaster ashmeadi Mayr (3) (7)
Crematogaster sp. (3)
Cryptopone gilva (Roger) (3)
Dorymyrmex pyramicus (Roger) (7)
Hypoponera opacior (Forel) (3)
Leptothorax schaumi Roger (7)
Monomorium minimum (Buckley) (7)
Paratrechina parvula (Mayr) (7)
Pheidole metallescens metallescens Emery (7)
Pheidole sp. (3)
Proceratium croceum (Roger) (3)
Solenopsis picta Emery (3)
Solenopsis sp. (7)
Sp. (undetermined) **(6)**

[1] References indicated in bold type specify predatory role with the SPB. Others recorded only as predators of bark beetles or predators under bark. Unconfirmed predatory roles indicated by (?).

References for Table 2

(1) Coulson, R. N., T. L. Payne, J. E. Coster, and M. W. Houseweart. 1972. The southern pine beetle *Dendroctonus frontalis* Zimmerman (Coleoptera:Scolytidae) 1961-1971. Tex. For. Serv., Pub. 108. College Station, Tex.
(2) Dixon, J. C., and E. A. Osgood. 1961. Southern pine beetle: a review of present knowledge. U.S. Dep. Agric. For. Serv., Res. Pap. SE-128. Southeast For. Exp. Stn., Asheville, N.C.
(3) Dixon, W. N., and T. L. Payne. 1979. Sequence of arrival and spatial distribution of entomophagous and associated insects on southern pine beetle-infested trees. Tex. Agric. Exp. Stn., MP-1432. College Station, Tex.
(4) Lenhard, G. J., and R. A. Goyer. 1979. The relative abundance and seasonal distribution of the major predators of the southern pine beetle in loblolly pine. [Unpublished ms.]
(5) Moore, G. E. 1972. Southern pine beetle mortality in North Carolina caused by parasites and predators. Environ. Entomol. 1:58-65.
(6) Moser, J. C., R. C. Thatcher, and L. S. Pickard. 1971. Relative abundance of southern pine beetle associates in east Texas. Ann. Entomol. Soc. Am. 64:72-77.
(7) Overgaard, N. A. 1968. Insects associated with the southern pine beetle in Texas, Louisiana, and Mississippi. J. Econ. Entomol. 61:1197-1201.
(8) Thatcher, R. C. 1960. Bark beetles affecting southern pines: a review of current knowledge. U.S. Dep. Agric. For. Serv., South. For. Exp. Stn., Occas. Pap. 180. [Discontinued South. Stn. series.]

Table 3. – Arthropod parasitoids of the southern pine beetle.[1] References designated by ( ).

Hymenoptera
Braconidae
Atanycolus comosifrons Shenefelt **(6)** (7?)
Atanycolus ulmicola (Vier.) (3?)
Cenocoelius nigrisoma (Rohwer) **(1)** (3) (7)
Cenocoelius sp. **(6)**
Coeloides pissodis (Ashm.) **(1) (2)** (3) **(4) (6)** (7) **(9)**
Compyloneurus movoritus (Cress.) (2) (9)
Dendrosoter sulcatus Mues. (1) (2) (3) (4) (6) (7) (9)
Doryctes sp. **(1) (2)** (3) **(7) (9)**
Heterospilus sp. **(6)**
Meteorus hypophloei Cushman **(6)**
Spathius canadensis Ashm. **(1) (2) (9)**
Spathius pallidus Ashm. **(1)** (3) **(4) (6) (7) (9)**
Vipio rugator (Say) **(1)**
Ichneumonidae
Cremastus sp. **(6)**
sp. (undetermined) (3)
Eupelmidae
Arachnophaga sp. (3)
Eupelmus cyaniceps cyaniceps (Ashm.) (7)
Lutnes sp. (3) (7?)
Torymidae
Liodontomerus sp. **(1)**
Lochites sp. **(2) (9)**
Roptrocerus eccoptogastri (Ratz.) **(1) (2)** (3) **(8) (9)**
Roptrocerus xylophagorum Ratz. **(1) (4) (6) (7) (8)**
Roptrocerus sp. **(6)**
Pteromalidae
Dinotiscus (= *Cecidostiba*) *dendroctoni* (Ashm.) **(1) (2)** (3) **(4) (6) (9)**
Heydenia unica Cook & Davis **(1) (2)** (3) **(4) (6) (7)**
Rhopalicus pulchripennis (Crawford) (3) (7)
Eurytomidae
Eurytoma cleri (Ashm.) **(6)**
Eurytoma tomici Ashm. **(1)** (7)
Eurytoma sp. (3)
Scelionidae
Gyron sp. **(8)**
Idris sp. **(8)**
Leptoteleia sp. **(6)**
Probaryconus heidemanni Ashm. **(8)**
Telenonus podisi Ashm. (8)
Bethylidae
Parasierola sp. (3)

[1] References indicated in bold type specify parasitic role with the SPB. Others recorded only as parasitoids of bark beetles. Unconfirmed parasitic roles indicated by (?).

References for Table 3

(1) Coulson, R. N., T. L. Payne, J. E. Coster, and M. W. Houseweart. 1972. The southern pine beetle *Dendroctonus frontalis* Zimmerman (Coleoptera:Scolytidae) 1961-1971. Tex. For. Serv., Pub. 108. College Station, Tex.

(2) Dixon, J. C. and E. A. Osgood. 1961. Southern pine beetle: a review of present knowledge. U.S. Dep. Agric. For. Serv., Res. Pap. SE-128. Southeast. For. Exp. Stn., Asheville, N.C.
(3) Dixon, W. N., and T. L. Payne. 1979. Sequence of arrival and spatial distribution of entomophagous and associated insects on southern pine beetle-infested trees. Tex. Agric. Exp. Stn., MP-1432. College Station, Tex.
(4) Goyer, R. A., and C. K. Finger. 1980. The relative abundance and seasonal distribution of the major hymenopterous parasites of the southern pine beetle, *Dendroctonus frontalis* Zimmerman, on loblolly pine. Environ. Entomol. 9:97-100.
(5) Lenhard, G. J., and R. A. Goyer. 1979. The relative abundance and seasonal distribution of the major predators of the southern pine beetle in loblolly pine. [Unpublished ms.]
(6) Moore, G. E. 1972. Southern pine beetle mortality in North Carolina caused by parasites and predators. Environ. Entomol. 1:58-65.
(7) Moser, J. C., R. C. Thatcher, and L. S. Pickard. 1971. Relative abundance of southern pine beetle associates in east Texas. Ann. Entomol. Soc. Am. 64:72-77.
(8) Overgaard, N. A. 1968. Insects associated with the southern pine beetle in Texas, Louisiana, and Mississippi. J. Econ. Entomol. 61:1197-1201.
(9) Thatcher, R. C. 1960. Bark beetles affecting southern pines: a review of current knowledge. U.S. Dep. Agric. For. Serv., South. For. Exp. Stn., Occas. Pap. 180. [Discontinued South. Stn. series.]

Table 4. – Key to the final instar larvae of the major parasites of the southern pine beetle. (From Finger and Goyer 1978.)

1 Body covered with many microspines; head with many sclerites; spiracles on segments 1 and 4-11 2
1′ Body with some setae but without microspines; head with few if any sclerites; spiracles on segments 2-10 . . 4
2 Labial sclerite very thick and rounded, often with slight projection on ventral surface and flat on dorsal surface between arms; silk orifice on wide oval sclerite . . . . *Dendrosoter sulcatus* (figs. 1B, 2B, 3B)
2′ Labial sclerite not as above 3
3 Thickness of ventral part of labial sclerite about 2 times as wide as where dorsal arms start; area inside labial sclerite more circular than ovoid; silk orifice forming a straight line (figs. 1A, 2A, 3A) . . . . . . *Coeloides pissodis*
3′ Thickness of ventral part of labial sclerite at least 3 times as thick as where arms start; area inside labial sclerite more ovoid; silk orifice often with slight "V" in middle (figs. 1C, 2C, 3C) . . . . *Spathius pallidus*
4 Head with very long setae; stalk of spiracle with over 20 chambers (figs. 1D, 2E, 3D) . . . . *Heydenia unica*
4′ Head with short setae; stalk of spiracle with less than 20 chambers 5
5 Stalk of spiracle with less than 9 chambers, each decreasing in size from the atrium, forming a continuous funnel-shaped spiracle (figs. 2F, 3E) . . . . *Dinotiscus dendroctoni*
5′ Stalk of spiracle with more than 9 chambers, only first 3 chambers and atrium forming enlarged club-shaped structure (fig. 2G) . . . . *Roptrocerus eccoptogastri*

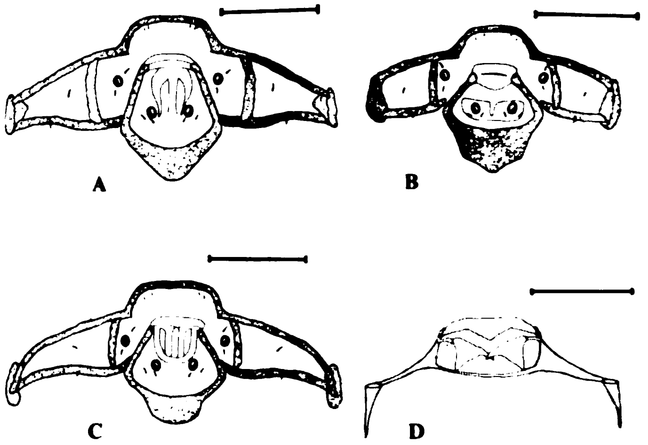


Figure 1.–Cephalic structure of final instar larvae (scale = 0.1 mm).
A. *Coeloides pissodis* B. *Dendrosoter sulcatus*
C. *Spathius pallidus* D. *Heydenia unica.*

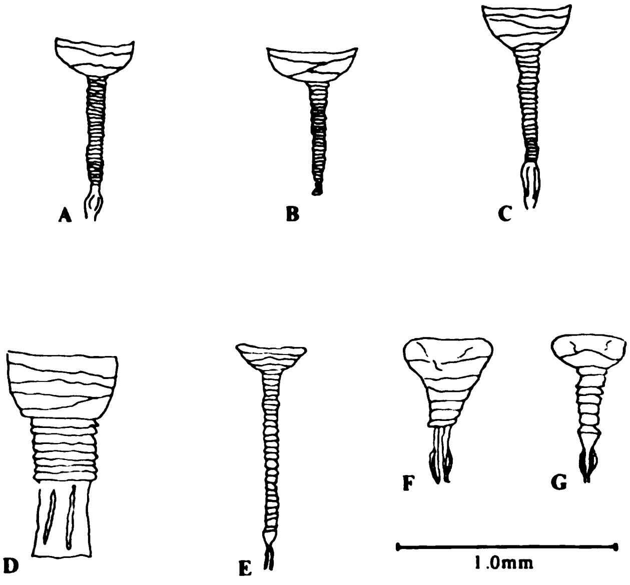


Figure 2.–Spiracles of final-instar larvae.
A. *Coeloides pissodis* B. *Dendrosoter sulcatus*
C. *Spathius pallidus* D. *Atanycolus comosifrons*
E. *Heydenia unica* F. *Dinotiscus dendroctoni*
G. *Roptrocerus eccoptogastri.*

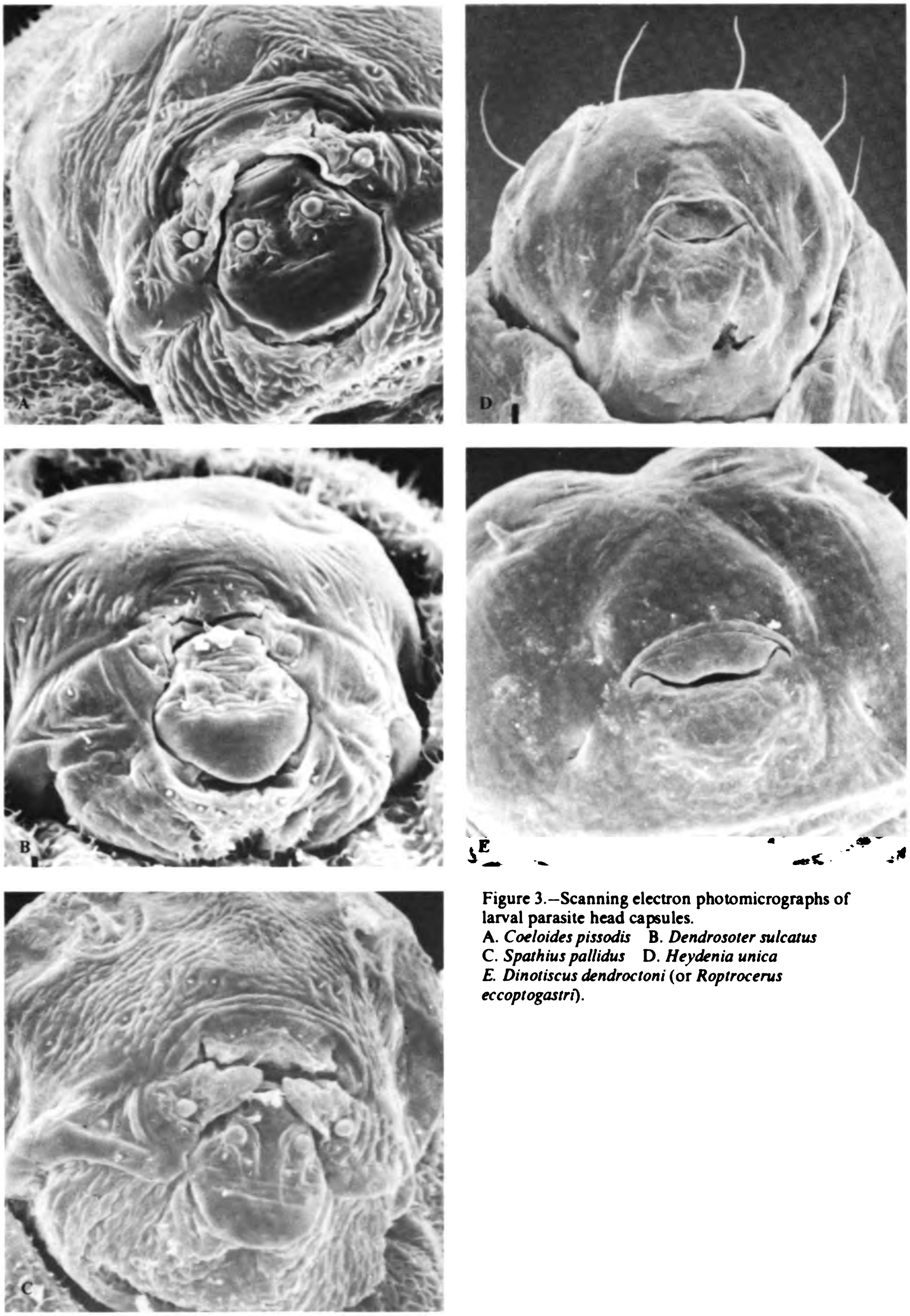


Figure 3.–Scanning electron photomicrographs of larval parasite head capsules.
A. *Coeloides pissodis* B. *Dendrosoter sulcatus*
C. *Spathius pallidus* D. *Heydenia unica*
E. *Dinotiscus dendroctoni* (or *Roptrocerus eccoptogastri*).

Table 5. – Mites that prey on the southern pine beetle

Kleemannia sp.
Lasioseius dentatus (Fox)
Lasioseius epicriodopsis DeLeon
Lasioseius tubiculiger (Berlese)
Proctolaelaps bickleyi (Bram)
Proctolaelaps dendroctoni Lindquist and Hunter
Proctolaelaps fiseri Samsinak
Proctolaelaps hystricoides Lindquist and Hunter
Proctolaelaps hystrix (Vitzthum)
Dendrolaelaps isodentatus Hurlbutt
Dendrolaelaps neocornutus Hurlbutt
Dendrolaelaps neodisetus Hurlbutt
Dendrolaelaps rotoni Hurlbutt
Dendrolaelaps varipunctatus Hurlbutt
Androlaelaps casalis (Berlese)
Hypoaspis sp. nr. *praesternalis* Willman
Hypoaspis vitzthumi (Womersley)
Pseudoparasitus thatcheri Hunter and Moser
Macrocheles boudreauxi Krantz
Macrocheles mammifer Berlese
Eugamasus lyriformis McGraw and Farrier
Gamasolaelaps subcorticalis McGraw and Farrier
Cercoleipus coelonotus Kinn
Pleuronectocelaeno drymoecetes Kinn
Trichouropoda lamellosa Hirschmann
Uroobovella americana Hirschmann
Histiogaster arborsignis Woodring
Histiogaster rotundus Woodring
Pyemotes parviscolyti Cross and Moser
Iponemus calligraphi calligraphi Lindquist
Iponemus confusus oriens Lindquist
Iponemus truncatus eurus Lindquist

Table 6. – Key to mites commonly associated with the southern pine beetle. (From D. N. Kinn 1976.)

1 Discernible without the aid of a lens; often red-brown in color; body hardened, with many shields or plates; stigmata (respiratory openings) located lateral to the bases of legs III and IV; tritosternum present; special sensory hairs not present on dorsal surface (fig. 1) . . . Order Parasitiformes – Suborder Mesostigmata 2

1′ Usually small and light in color; body without numerous plates, stigmata not located lateral to bases of legs III and IV; tritosternum absent; special sensory hairs may be present on the anterior dorsal surface (fig. 4) . . . Order Acariformes 8

2 Turtle shaped; leggs can be withdrawn into grooves (fig. 2); attached to beetle by anal pedicle . . . Superfamily Uropodoidea – Family Uropodiadae 3

2′ Not turtle shaped; leg grooves absent; attached to beetle by the mouthparts and/or leg claws . . . Superfamily Parasitoidea 4

3 Anal shield with 14 hairs (fig. 2A); length about one-tenth of host's length . . . . *Trichouropoda australis*

3′ Anal shield with 10 hairs (fig. 2B); length about one-third of host's length . . . . . *Trichouropoda hirsuta*

4 Large red-brown mite lacking claws on leg I; peritremes looped, joining stigmata posteriorly (fig. 1C) . . . Family Macrochelidae . . . . *Marocheles boudreauxi*

4′ Leg I with claws; peritremes not looped; joining stigmata anteriorly (fig. 1B) 5

5 Dorsal shield entire; posterior end rounded (fig. 3A) . . . Family Ascidae 6

5′ Dorsal shield divided into two plates; posterior end more or less truncated (fig. 3B) . . . . Family Digamasellidae 7

6 Ventral surface with four shields (sternal, genital, ventral, and anal) (fig. 1A) . . *Proctogastrolaelaps libris*

6′ Ventral surface with three shields (sternal, genital, and anal) (fig. 1B) . . . . *Proctolaelaps dendroctoni*

7 Body about two times longer than wide (fig. 3B) . . . . *Dendrolaelaps neodisetus*

7′ Body about four times longer than wide (fig. 3C) . . . . *Longoseius cuniculus*

8 Mouthparts functional; anal suckers absent; special sensory hairs present on anterior dorsal surface (fig. 4) . . . . Suborder Prostigmata 9

8′ Mouthparts vestigial; anal suckers present; special sensory hairs not present on anterior dorsal surface (fig. 5) . . . Suborder Astigmata 13

9 Small, slow-moving mites often found under the beetle's wing covers or around the leg bases; mouthparts indistinct; sensory hairs club-shaped; legs short in relation to body (figs. 4B and 6) . . . . Superfamily Tarsonemoidea 10

9′ Fast-moving, orange-colored mite; mouthparts distinct; sensory hairs long and barbed; legs long in relation to body (fig. 4A) . . . Superfamily Tydeoidae – Family Ereynetidae. . . . . *Ereynetoides scutulis*

10 Legs IV without claws and terminating with two whiplike hairs (fig. 6) . . . Family Tarsonemidae 11

10′ Legs II-IV terminating with two claws; legs I terminate with a single large claw (fig. 4B) . . . . Family Pyemotidae . . . . *Pygmephorus bennetti*

11 Legs II and III each with two claws; claw of leg I short, stout, and straight (fig. 6A) . . . . *Heterotarsonemus lindquisti*

11′ Legs II and III each with two claws; claw of leg I single, not modified (fig. 6B, C) 12

12 Cuticular thickenings anterior to bases of legs III extending laterally beyond bases of legs III; lobe between bases of legs IV not elongated (fig. 6B) . . . . *Tarsonemus krantzi*

12′ Cuticular thickenings anterior to bases of legs III not extending laterally beyond bases of legs III; lobe between bases of legs IV very elongated and extending behind bases of legs IV (fig. 6C) . . . . . *Tarsonemus ips*

13 All legs short and stout; legs III and IV often directed backward; distal segments of legs III and IV short (fig. 5A) . . . . Superfamily Acaroidea – Family Acaridae . . . . *Histiogaster arborsignis*

13′ Legs I and II stouter than legs III and IV; legs III and IV often directed forward and have long, slender distal segments (fig. 5B, C) . . . . Superfamily Anoetoidea – Family Anoetidae **14**

14 Entire dorsal surface always ornamented; fused mouthparts project well beyond body outline; dorsal hairs short and slender (fig. 5B) . . . . . *Anoetus sordida*

14′ Dorsal ornamentation variable; fused mouthparts do not usually project beyond anterior edge of body; dorsal hairs long and thick (fig. 5C) . . . . *Anoetus varia*

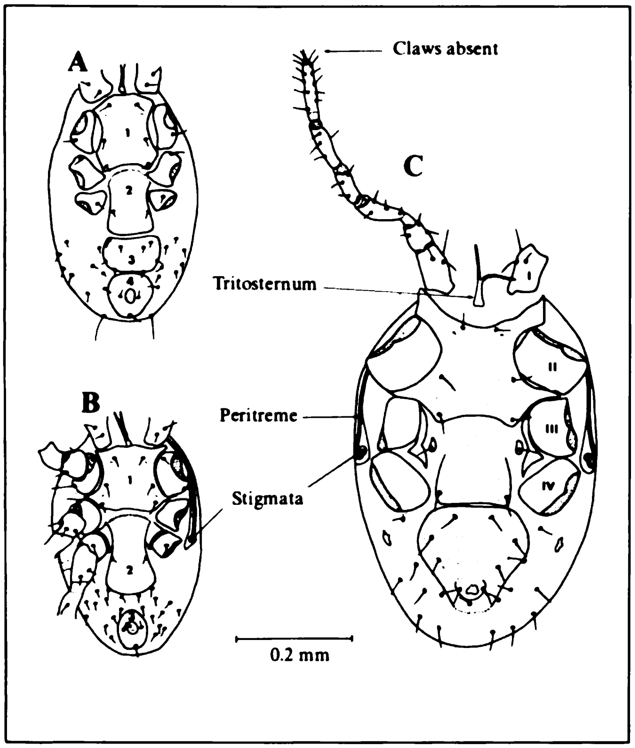


Figure 1.–Ventral aspect of (A) *Proctogastrolaelaps libris*, (B) female *Proctolaelaps dendroctoni*, (C) female *Macrocheles boudreauxi*.

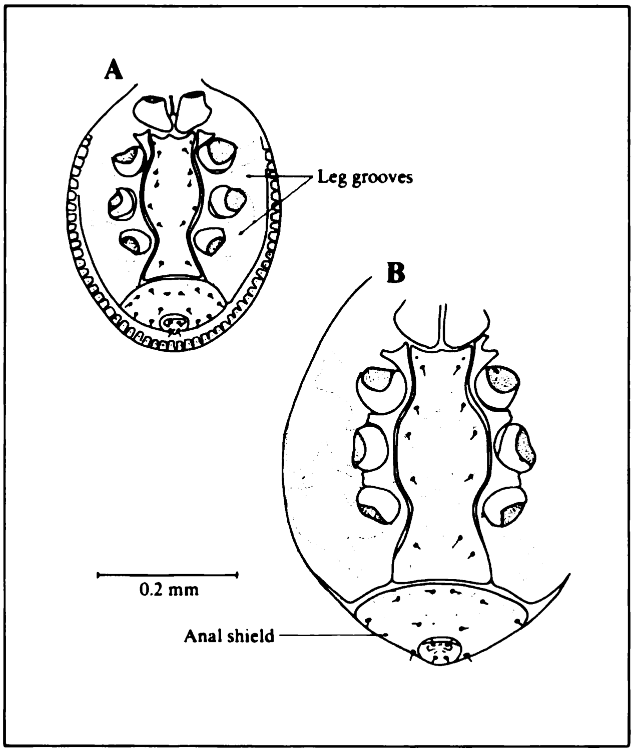


Figure 2.–Ventral aspect of (A) *Trichouropoda australis* deutonymph, (B) *T. hirsuta* deutonymph.

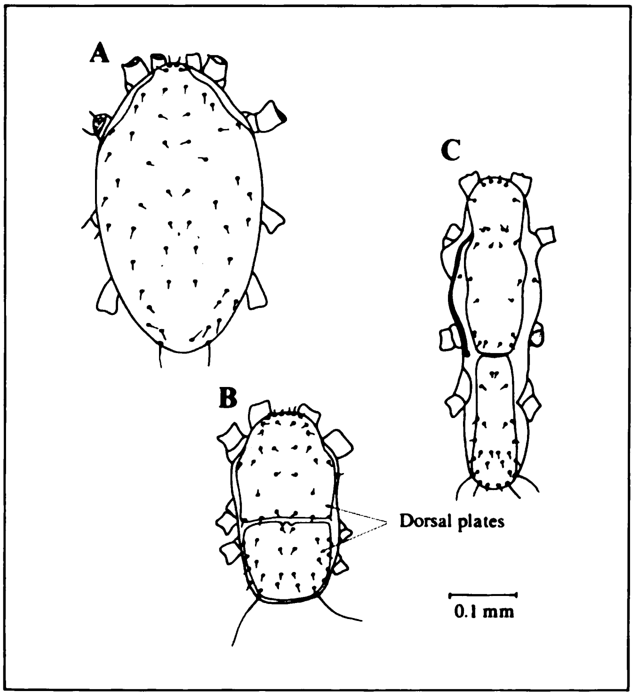


Figure 3.–Dorsal aspect of (A) *Proctolaelaps* sp., (B) *Dendrolaelaps neodisetus* deutonymph, (C) *Longoseius cuniculus* deutonymph.

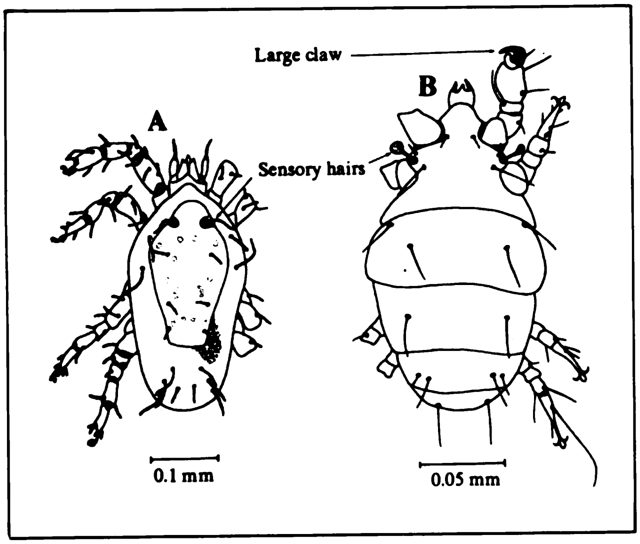


Figure 4.—Dorsal aspect of (A) *Ereynetoides scutulis*, (B) *Pygmephorus bennetti*.

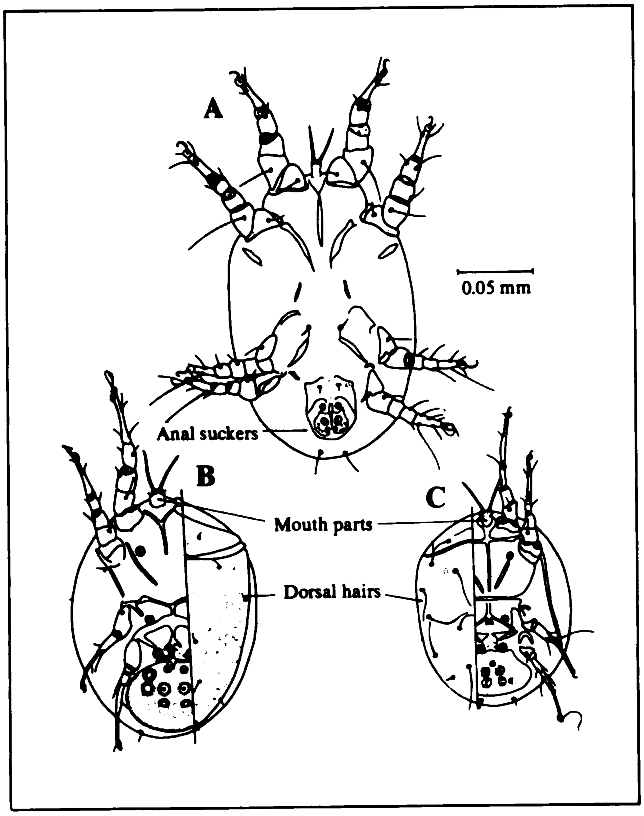


Figure 5.—Ventral aspect of (A) *Histiogaster arborsignis* hypopus, (B) *Anoetus sordida* hypopus, (C) *Anoetus varia* hypopus.

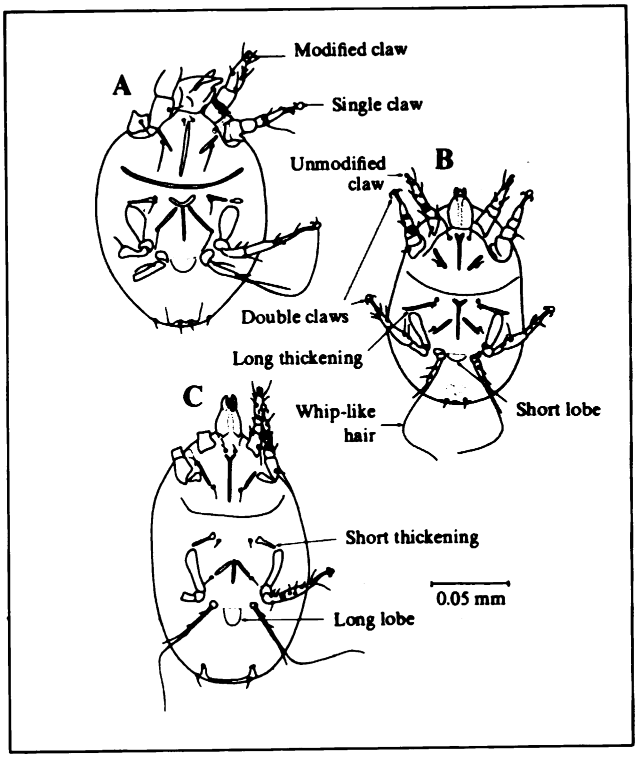


Figure 6.—Ventral aspect of (A) female *Heterotarsonemus lindquisti*, (B) female *Tarsonemus krantzi*, (C) female *Tarsonemus ips*.

Table 7. – Frequently encountered pathogens of southern pine beetle (total of 13,458 diseased specimens) in Mississippi and Alabama (1975-1977)

Pathogens	% Infected
Bacteria	
Pseudomonas spp.	1.5
Serratia marcescens	.2
Fungi	
Aspergillus flavus	.01
Beauveria bassiana	.6
Cephalosporium sp.	.3
Entomophthora sp.	4.0
Metharhizium anisophilae	1.5
Paecilomyces viridis	7.0
Paecilomyces sp.	7.5
Yeastlike organism	12.2
Nematodes	
Contortylenchus brevicomi	7.3
Contortylenchus sp.	
Protozoa	
Unikarion minutum	21.0
Microsporida (unknown)	9.2
Viruses	
Unknown (possibly virus)	12.42

Table 8. – Members of the Southern Pine Beetle Technology Transfer Task Force

Name	Title and Organization
Stan Adams	Director, Office of Information, USDA-Forest Service, R-8
Dick Fitzgerald	Group Leader, Silviculture, USDA-Forest Service, R-8
Thad Harrington	Assistant Director, USDA-Forest Service, Southern Forest Experiment Station
Jim Neal	Regional Extension Forester, Science and Education Administration, Cooperative Extension Service
Jim Tiner	Management Chief, Arkansas Forestry Commission
Harvey Toko	Staff Director, Forest Insect and Disease Management, USDA-Forest Service, State and Private Forestry, Southeastern Area
Fred Trew	Center Leader, Westvaco Corporation
Zeb White	Consulting Forester and President, Zebulon White and Co., Inc.
Dick Williams	Management Forester, Georgia Pacific Corporation
Jack Coster	Chairman; Applications Coordinator, Expanded Southern Pine Beetle Research and Applications Program

Table 9. – Members of the Southern Pine Beetle Technology Transfer Teams

Team and Membership

•Silvicultural Practices and Stand Rating Systems
- R. P. Belanger, Team Leader, SE For. Exp. Stn., Athens, GA
- H. L. Williston, S&PF, Jackson, MS
- T. Price, Ga. For. Commission, Macon
- B. Malac, Union Camp Corp., Rincon, GA
- J. R. McGraw, Coop. Ext. Service, Raleigh, NC
- K. M. Swain, S&PF Atlanta, GA
- J. E. Coster, SPB Program, Pineville, LA

•Guidelines for Utilizing SPB-Killed Timber
- R. F. Westbrook, Team Leader, S&PF, Pineville, LA
- D. Weldon, Texas Forest Service, Lufkin
- G. Ifju, VPI & SU, Blacksburg, VA
- J. L. Barrett, National Forests, R-8, Atlanta, GA
- M. P. Levi, Coop. Ext. Serv., Raleigh, NC
- B. Deless, Ga. Pac. Corp., Crossett, AR
- G. D. Hertel, SPB Program, Pineville, LA

•Socioeconomic Guidelines
- J. Lewis, Team Leader, S&PF, Atlanta, GA
- G. Dutrow, SE For. Exp. Stn., Durham, NC
- M. Vasievich, SE For. Exp. Stn., Durham, NC
- Sue Harper, S&PF, Atlanta, GA
- W. A. Leuschner, VPI & SU, Blacksburg, VA
- B. Schick, Westvaco Corp., Rupert, WV
- R. C. Thatcher, SPB Program, Pineville, LA

•New Insecticides and Improved Spray Systems
- J. W. Taylor, Team Leader, S&PF, Atlanta, GA
- C. W. Berisford, Univ. of Ga., Athens
- F. L. Hastings, S.E. For. Exp. Stn., Res. Tri. Pk., NC
- C. Fleming, National Park Serv., Beaumont, TX
- A. D. Dressen, Coop. Ext. Serv., Houston, TX
- J. Godbee, Union Camp Corp., Rincon, GA
- J. E. Coster, SPB Program, Pineville, LA

•Sampling Methods and Predictive Models
- F. M. Stephen, Team Leader, Univ. Ark., Fayetteville
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•Integrated Management Strategies
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- Team Leaders
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