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Author(s): Thomas J. McAvoy , Amy L. Snyder , Nels Johnson , Scott M. Salom , and Loke T. Kok
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Thomas J. McAvoy, Amy L. Snyder, Nels Johnson, Scott M. Salom, and Loke T. Kok*

Tree-of-heaven is an invasive, nonnative species that invades newly disturbed areas and forms large monospecific stands. It was surveyed from a vehicle along 5,175 km of roads in Virginia in 2004, 2005, 2010, and 2011. Fifty-eight percent of every 1.6-km road segment had at least one tree-of-heaven. Mean density of tree-of-heaven throughout the roads surveyed in Virginia was 39 km^{-1}. The interaction between road classification (interstate, primary, and secondary) and physiographic region (mountain, piedmont, and tidewater) was significant; consequently, the density of tree-of-heaven along the different road classifications depended on the effect of the physiographic region and vice versa. Tree-of-heaven was fairly evenly distributed throughout Virginia ranging from 39 to 78% of 1.6-km road segments infested, but had a greater variation in density. Current areas with low densities could increase in density in the future. The highest density of tree-of-heaven was along interstate highways in the mountains (85 km^{-1}), followed by the tidewater (63 km^{-1}), and piedmont (46 km^{-1}) regions. Primary roads had a moderate density of tree-of-heaven with a range of 24 to 36 km^{-1}. Secondary roads had lower densities with 12 km^{-1} and 41 km^{-1} in the tidewater and mountain regions, respectively. Tree-of-heaven spreads primarily by wind-dispersed seeds from female trees, and populations bordering roadsides could serve as seed sources for further local and landscape spread.

Nomenclature: Tree-of-heaven; *Ailanthus altissima* (P. Mill.) Swingle.

Key words: Invasive tree, physiographic region, road survey, Virginia.

Ailanthus altissima (P. Mill.) Swingle (Simaroubaceae) (tree-of-heaven) was first introduced as an ornamental into North America in Philadelphia, PA, in 1784 (Feret 1985; Tellman 1997). A second introduction occurred in 1820 in New York (Davies 1942). Both introductions were for ornamental purposes and originated from English root stock imported from China. Another route of introduction occurred in California during the gold rush in the mid-1800s. Chinese laborers brought tree-of-heaven from China for its medicinal and cultural value (Tellman 1998). Currently tree-of-heaven has been recorded in all of the lower 48 states except Montana, North and South Dakota, New Hampshire, Vermont, and Wyoming (USDA, NRCS 2012). A Bayesian model developed by Albright et al. (2010) showed that tree-of-heaven has the potential to spread substantially beyond its current distribution. Kowarik and Säumel (2007) provided an extensive review of tree-of-heaven in Europe where it is an invasive species mostly in urban areas and along transportation corridors.

Seeds are normally broken loose in high turbulent winds and can be blown over 450 m (1,476 ft) (Kowarik and von der Lippe 2011; Landenberger et al. 2007). Tree-of-heaven forms large monospecific stands due to the production of vegetative root suckers and allelopathic compounds (Gómez-Aparicio and Canham 2008; Heisey 1996; Lawrence et al. 1991; Lin et al. 1995). It is an early-succession, shade-intolerant species with a high germination rate in disturbed sites that can out-compete native plant species (Call and Nilsen 2005; Hull and Scott 1982; Kostel-Hughes et al. 2005; Kota et al. 2007; Martin et al. 2010; Motard et al. 2011). Kok et al. (2008) identified 17 associated tree species that may be displaced by monospecific stands of tree-of-heaven in Virginia. While the ailanthus webworm moth, *Atteva aurea* (Fitch) (Lepidoptera: Yponomeutidae) was the most commonly found herbivore during a survey in Virginia, its impact was minimal on large trees (Kok et al. 2008).

Impact. The impact of tree-of-heaven is both economic and ecological (Kok et al. 2008; Motard et al. 2011; Vilà

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* First, second, fourth, and fifth authors: Laboratory Specialist, Research and Laboratory Specialist, Professor, and Professor, respectively, Department of Entomology, Virginia Tech, 216A Price Hall, Blacksburg, VA 24061; third author: Ph.D candidate, Department of Statistics, Laboratory for Interdisciplinary Statistical Analysis, 406-A Hutcheson Hall, Virginia Tech, Blacksburg, VA 24061. Corresponding author's E-mail: tmcavoy@vt.edu

Management Implications

The invasive nonnative tree-of-heaven invades newly disturbed areas and forms large monospecific stands. The mean density of tree-of-heaven throughout the 5,175 km of roads surveyed in Virginia was 39 km^{-1} with mean infestation of 58% of 1.6-km road segments. Interstate highways had the highest tree-of-heaven densities and high infestation frequencies. Populations bordering the roads serve as seed sources for further dispersal along roads and into open and forested areas. Efforts to minimize the impact and spread of tree-of-heaven should be concentrated along the leading edge of infestations. Chemical applications and felling of mature female trees would reduce seed dispersal along roads and into adjacent forests. Reducing the amount of disturbed soil and quickly reseeding with native seeds would help in reducing new invasions of tree-of-heaven.

et al. 2006). This species is tolerant of urban conditions, poor soils, and air pollution (Davis et al. 1978; Kim 1975). Celesti-Grapow and Blasi (2004) reported that tree-of-heaven was present and may become more widespread and harmful to archaeological sites in Italy. In rural areas it is common in fields, along roads, fencerows, woodland edges, and forest openings (Knapp and Canham 2000; Kostel-Hughes et al. 2005; Kowarik 1995; Patterson 1976). It has also been reported in gaps in old-growth forests (Knapp and Canham 2000) and is frequently found spreading into forests (Espenschied-Reilly and Runkle 2008; Martin et al. 2010).

Forty-nine counties in Virginia have measureable quantities of tree-of-heaven based on the U.S. Forest Service's Southern Research Station Forest Inventory and Analysis (Asaro et al. 2009). Statewide, the volume of tree-of-heaven is estimated to be 1.9 million m^3 which is 0.2% of the live volume of trees in Virginia and is 42nd in abundance of 128 tree species. Tree-of-heaven is widespread in the Shenandoah National Park (Marler 2000) and is the second most abundant nonnative tree species in the southern United States, occupying 86,781 ha (216,953 ac) (Ridley et al. 2011). Stipes (1995) indicated 30% of southwest Virginia interstate highways are infested with tree-of-heaven.

Tree-of-heaven has been reported to be commonly spread along transportation corridors (Gelbard and Belnap 2003; Kowarik and von der Lippe 2011; Tyser and Worely 2003; von der Lippe and Kowarik 2007). Merriam (2003) conducted a survey of roads, railroads and other edges and reported that tree-of-heaven occupied 1.7% of edges and was most abundant in the piedmont of North Carolina. Due to its rapid growth it can obstruct vistas and block drivers' views along transportation corridors (Burch and Zedaker 2003).

Management. Chemical control has been found to be the most effective management tool (Asaro et al. 2009; Burch and Zedaker 2003; Constán-Nava et al. 2010; DiTomaso and Kyser 2007; Lewis and McCarthy 2006, 2008; Meloche and Murphy 2006). Because of the abundance and invasiveness of this species, and the expense in controlling it with chemical and mechanical methods, biological control of tree-of-heaven may be an additional tool to control tree-of-heaven. *Eucryptorrhynchus brandti* (Harold), a weevil native to China, was recommended by Ding et al. (2006) as a potential biological control agent. Host feeding studies of *E. brandti* have been completed (Herrick et al. 2012) and a petition for field release of *E. brandti* has been submitted to the U.S. Department of Agriculture, Animal and Plant Health Inspection Service. An additional potential biological control agent, the fungus *Verticillium albo-atrum* sensu lato Reinke and Berthold, has been observed in Pennsylvania, and has weakened and killed thousands of tree-of-heaven trees (Schall and Davis 2009). Snyder et al. (2012) found that *E. brandti* has potential to act as a vector for this fungus.

The purpose of this study was to establish baseline distributions and densities of tree-of-heaven along roads in Virginia and determine the effect of road classifications as well as different physiographic regions on the density of roadside populations. This may help to determine whether additional road and forest management tools and biological control are justified and where control measures should be concentrated. If biological control agents are released in the future these data could be used to identify release sites and measure their impact in a pre- and postrelease study.

Materials and Methods

This study was conducted from May to September in 2004, 2005, 2010, and 2011. A windshield survey was performed along the secondary, primary, and interstate roads in Virginia. To maintain consistent counts the majority of observations were made by the first author; a few observations were performed by three others in the vehicle with the first author and 12% of the observations were done by the second author after extensive travel with the first author. Young tree-of-heaven stems quickly exceed heights over 1 m and are easily identified by their long compound leaves. The number of living tree-of-heaven stems up to 25 m from the edge of both sides of the road and in the median, if present, were counted and recorded in 1.6-km road segments. At the end of each 1.6-km road segment the total number of tree-of-heaven was recorded and a new count was begun for the next 1.6-km road segment. Since vehicle odometers and roadside markers are in miles, the total number of tree-of-heaven seen every mile was tallied and then converted into number of tree-of-heaven km^{-1}. The windshield counts may not have provided exact counts of tree-of-heaven, but the purpose of the study was to perform an extensive baseline survey of Virginia. To determine the amount of error in the

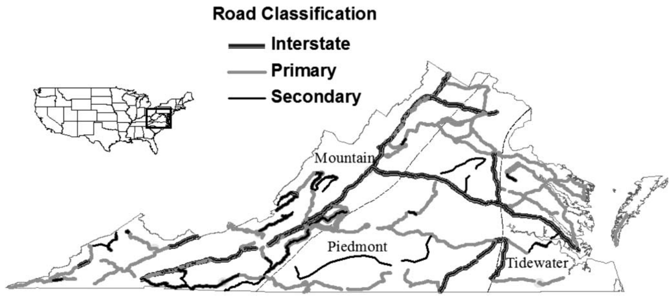

Figure 1. Classification of roads surveyed for tree-of-heaven in the three physiographic regions of Virginia.

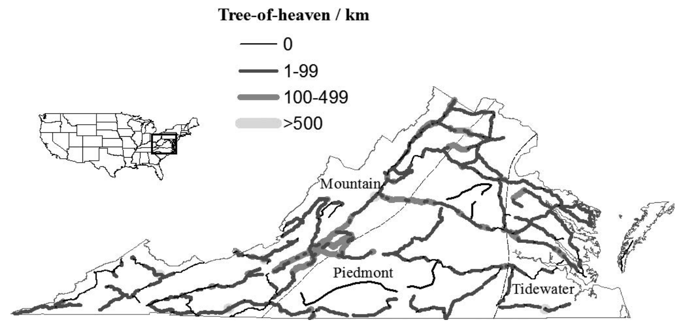

Figure 2. Population density of tree-of-heaven along the surveyed roads in the three physiographic regions in Virginia.

windshield counts 10 1.6-km road segments (five primary and five secondary) infested with tree-of-heaven were surveyed from the vehicle. At the end of each 1.6-km segment, both sides of the road were walked and the number of tree-of-heaven stems was counted. The difference between the windshield and walking counts was analyzed using linear regression.

To determine differences in tree-of-heaven density throughout the different climatic or physiographic regions of Virginia, each road segment was assigned to one of the three physiographic regions of Virginia: tidewater, piedmont, and mountain (Fenneman 1938; Hoffman 1969). These regions are dissimilar in topography, climate, and soil structure and may provide some indication as to where tree-of-heaven is more successful. Each road was classified as one of three road types: interstate roads were four-lane divided highways with limited access; primary roads were either divided or undivided two- or four-lane roads with many points of access; and secondary roads were two-lane, high-access roads frequently found in rural areas.

To determine if the prevalence of tree-of-heaven depended on road classification and physiographic region, a generalized linear model was fitted to the number of tree-of-heaven km^{-1}. The assumption was made that the number of tree of heaven km^{-1} could be modeled by a Tweedie distribution with parameter $p = 1.5$. This class of distributions was described by Jørgensen (1987) and named after Tweedie (1984). When $1 < p < 2$, this distribution is a good choice for modeling responses with a point mass at exactly zero, but is continuous and positive elsewhere. This model described the data well, where a large proportion of road sections had no observed tree-of-heaven. The following model was fitted to the data using quasi-likelihood in SAS 9.2 (2008) using PROC GLIMMIX where equation 1 describes the relationship between the linear predictor and the mean of the Tweedie distribution and equation 2 describes the variance function of the Tweedie distribution:

$$\log\left[E\left(Y_{ijk}\right)\right] = \mu + \alpha_i + \beta_j + (\alpha\beta)_{ij} \qquad [1]$$

$$\mathrm{var}(Y_{ijk}) = \varphi E\left(Y_{ijk}\right)^{1.5} \qquad [2]$$

where μ is the overall mean number of tree-of-heaven km^{-1}; α_i is the effect for road type i; β_j is effect for physiographic region j; $(\alpha\beta)_{ij}$ is the interaction effect for road type i and physiographic region j; and φ is the dispersion parameter; and k is 1,2, … , n_{ij}, where n_{ij} is the number of observations with road type i and physiographic region j. If the test of type III sums of squares for fixed effects was significant, post hoc tests were performed for pair-wise differences between the least square means for each level of road type and physiographic region. The percentage of 1.6-km road segments with or without tree-of-heaven along the three road types and physiographic regions were compared using logistic regression (PROC GLIMMIX) in SAS 9.2 (2008).

The ESRI geographic information system software suite (ArcGIS, ESRI, Redlands, CA) was used to create a map of the roads surveyed. The road data used in the software included a length attribute. To display the density distribution, each surveyed 1.6-km segment was associated to a road segment in ArcGIS. The sum of all the trees associated with that road segment divided by the length of that road segment was used to determine the number of tree-of-heaven km^{-1}. This value was used to symbolize density and distribution along the roads.

Results and Discussion

A total of 5,175 km of roads was surveyed in Virginia from 2004 to 2011. Tree-of-heaven was found across the state, from the far southwest corner of Virginia at Cumberland Gap, east to Virginia Beach and north to Winchester (Figures 1 and 2). The mean density of tree-of-heaven was 39 ± 2 km^{-1} throughout Virginia. Fifty-eight percent of each 1.6-km of road segment surveyed had at least one tree-of-heaven.

Based on the walking survey done to account for errors in counting from the vehicle, the vehicle counts were underestimated by 10% based on the slope (0.90) of the liner regression model, plus an additional underestimation of 39.0 trees km^{-1} based on the intercept and slope (39.0 trees km^{-1} = 35.0/0.90) of the same model, y = −35.0 +

Table 1. Density of tree-of-heaven and frequency of infested 1.6-km road segments along different road types in different physiographic regions in Virginia.

Road classification	Physiographic region	Total surveyed km	Mean (± SE) tree-of-heaven 1.6 km^{-1}	% of 1.6-km road segments with tree-of-heaven
Interstate	Mountain	684	85.3 ± 6.3 a[a]	68 b
	Piedmont	416	46.2 ± 6.6 b	58 b
	Tidewater	105	63.3 ± 11.8 ab	63 ab
Primary	Mountain	1,189	30.0 ± 2.5 bc	46 cd
	Piedmont	882	36.0 ± 2.2 bc	78 a
	Tidewater	626	24.3 ± 3.5 cd	62 b
Secondary	Mountain	684	41.0 ± 6.2 b	39 d
	Piedmont	371	13.3 ± 1.1 d	64 ab
	Tidewater	218	11.6 ± 2.7 d	46 cd

[a] Means in the same column followed by the same letter are not significantly different at $P < 0.05$, Tukey-Kramer Honestly Significant Difference test.

(0.90×). This walking survey represents 10 1.6-km road segments, which is 0.3% of the total roads survey and since only road segments that were infested with tree-of-heaven were surveyed in the walking survey, the model may not perform well when tree-of-heaven was absent. Therefore, the data were not transformed. However, this survey gave an indication as to how accurate the survey was along road segments that were infested with tree-of-heaven and that the windshield survey underestimated the actual count by 10% and was reasonably close to the number of tree-of-heaven km^{-1}.

The type III test for fixed effects for the interaction between road type and physiographic region for tree-of-heaven density ($F = 9.97$, 4 num df, 3,065 den df, $P < 0.001$) and frequency ($F = 20.27$, 4 num df, 3,065 den df, $P < 0.001$) was significant; consequently, density and frequency of tree-of-heaven along the different road classifications depended on the effect of the physiographic region and vice versa. The results of the post hoc analysis comparing the least square means for the road type and physiographic region interaction are presented in Table 1.

The highest density of tree-of-heaven was found along interstate highways in the mountains (85 km^{-1}), followed by the tidewater (63 km^{-1}) and the piedmont interstates (46 km^{-1}) (Table 1). The primary roads had a moderate density of tree-of-heaven and ranged from 24 to 36 km^{-1}. The lowest densities of tree-of-heaven were found along the secondary roads ranging from 11 to 41 km^{-1} from the tidewater to the mountain region, respectively. In the mountain region the interstates (85 km^{-1}) had higher densities than the primary (30 km^{-1}) and secondary (41 km^{-1}) roads. In the piedmont there was a higher density along the interstates (46 km^{-1}) and primaries (36 km^{-1}) than along the secondary roads (13 km^{-1}). In the tidewater region a higher density was found along the interstates (63 km^{-1}) compared with the primary (24 km^{-1}) and secondary (12 km^{-1}) roads.

Differences in frequency of infested road segments ranged from 39 to 78% infested, and did not vary as much or as consistently as density of tree-of-heaven (Table 1). Current areas with low densities could increase in density in the future. Frequency of infested 1.6-km road segments along the interstates was similar in all three regions ranging from 58 to 68%, whereas primary roads in all three regions had different frequency of infested roads with 46, 78, and 62% infested in the mountain, piedmont, and tidewater regions, respectively. The road segments with the lowest percentage of infestation were found along secondary roads in the mountains (39%). The predominance of extensive forest may have reduced the frequency of infestations in these areas but once established tree-of-heaven reached moderate densities (41 km^{-1}).

Interstate highways provide an ideal habitat for the establishment of tree-of-heaven. Landenberger et al. (2009) reported that tree-of-heaven was often found on steep slopes exposed by road construction creating extensive areas of open soil, ideal for its germination (Greenberg et al. 1997; Trombulak and Frissell 2000). These areas are similar to what was found along the interstates, especially in the mountains. In addition, the movement of tree-of-heaven roots and seeds from grass-mowing and maintenance equipment may also help its establishment in new locations. The volume of high-speed vehicles, especially large trucks, acts as a corridor along interstate highways (Gelbard and Belnap 2003; Tyser and Worely 2003; von der Lippe and Kowarik 2007) and hard, impervious surfaces increase wind-mediated long-distance seed dispersal (Kowarik and von der Lippe 2011). Interstates also have a wider right-of-way providing a much wider open area than primary and secondary roads and would contribute to a comparatively higher density of tree-of-heaven. However, Sullivan et al. (2009) reported little evidence for roads acting as linear dispersal corridors and suggested that plant diversity is more reflective of what grows on the neighboring land. These studies suggest that road corridors and adjoining land can act as sources for new plant invasions.

Water also provides a pathway for tree-of-heaven dispersal. Kaproth and McGraw (2008) and Kowarik and Säumel (2008) reported tree-of-heaven seeds and stem fragments that had floated in water had an increase in seed germination and shoot growth. High density of tree-of-heaven along roads that are in close proximity to waterways may be a secondary source of dispersal.

Tree-of-heaven was most frequently found in clusters and isolated single trees were rarely observed along the roads surveyed. Size of tree clusters varied greatly and ranged from several trees to well over 100 trees. These clusters may have been composed of one or more genets. We also observed high densities of tree-of-heaven along railroad tracks but these were not documented in this study. Railroad tracks can provide another corridor for tree-of-heaven dispersal that warrants more study. Merriam (2003) found an unusually high association of tree-of-heaven with railroad rights-of-way. During the survey, tree-of-heaven was occasionally seen farther than 25 m from the road growing in large populations along the edge of forests and fields. McDonald and Urban (2006) found tree-of-heaven to be indicative of edge communities in the North Carolina piedmont.

Our study demonstrates that many of the major roadways in Virginia are heavily infested with tree-of-heaven. Prevention of new introductions of tree-of-heaven as well as other invasive species should be a high priority for future road construction and maintenance of roadside verges (Hobbs and Humphries 1995; Mack et al. 2000). Actions such as minimizing soil depth disturbances and reestablishing native vegetation (Bugg et al. 1997) can be useful in reducing new invasion sites. Moore and Lacey (2009) reported that sweetgum (*Liquidambar styraciflua* L.) and sycamore (*Platanus occidentalis* L.) germinated more quickly than tree-of-heaven in a greenhouse study and may be useful in reclaiming disturbed areas with native species. Gómez-Aparicio and Canham (2008) found red maple (*Acer rubrum* L.) to be resistant to ailanthone, an allelopathic compound produced by tree-of-heaven. However, Burch and Zedaker (2003) reported an increase in native species after removal of tree-of-heaven without reseeding. Grading, mowing, and herbicide application should be performed to maximize the control of invasive species while minimizing the impact on native species. Good forest management practices can also reduce invasion by tree-of-heaven into forests by felling mature female trees within 200 m of forests (Kota 2005). As recommended by Landenberger et al. (2009), efforts to minimize the impact should be concentrated along the leading edge of infestations, by targeting and chemically treating or felling mature female trees to reduce or eliminate the dispersal of tree-of-heaven seeds.

Although the roadways of Virginia are extensively infested with tree-of-heaven, the one area that has a low density and frequency is the eastern shore of Virginia, on the Delmarva Peninsula (Figure 2). This is an area that would warrant intensive management to reduce further dispersal.

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Literature Cited

Albright, T. P., H. Chen, L. Chen, and Q. Guo. 2010. The ecological niche and reciprocal prediction of the disjunct distribution of an invasive species: the example of *Ailanthus altissima*. Biol. Invasions 12: 2413–2427.

Asaro, C., C. Becker, and J. Creighton. 2009. Control and Utilization of Tree-of-Heaven: A Guide for Virginia Landowners. Charlottesville, VA: Department of Forestry Publication No. P00144. 15 p.

Bugg, R. L., C. S. Brown, and J. H. Anderson. 1997. Restoring native perennial grasses to rural roadsides in the Sacramento Valley of California: establishment and evaluation. Restor. Ecol. 5:214–228.

Burch, P. L. and S. M. Zedaker. 2003. Removing the invasive tree *Ailanthus altissima* and restoring natural cover. J. Arboric. 29:18–24.

Call, L. J. and E. T. Nilsen. 2005. Analysis of interaction between the invasive tree-of-heaven (*Ailanthus altissima*) and the native black locust (*Robinia pseudoacacia*). Plant Ecol. 176:275–285.

Celesti-Grapow, L. and C. Blasi. 2004. The role of alien and native weeds in the deterioration of archaeological remains in Italy. Weed Technol. 18:1508–1513.

Constán-Nava, S., A. Bonet, E. Pastor, and M. J. Lledó. 2010. Long-term control of the invasive tree *Ailanthus altissima*: Insights from Mediterranean protected forests. Forest Ecol. Manag. 260: 1058–1064.

Davies, P. A. 1942. The history, distribution, and value of Ailanthus in North America. Trans. Ky. Acad. Sci. 9:12–14.

Davis, D. D., C. A. Miller, and J. B. Coppolino. 1978. Foliar response of 11 woody species to ozone with emphasis on black cherry. Proc. Am. Phytopathol. Soc. 4:185.

Ding, J., Y. Wu, H. Zheng, W. Fu, R. Reardon, and M. Liu. 2006. Assessing potential biological control of the invasive plant, tree-of-heaven, *Ailanthus altissima*. Biocontrol Sci. Technol. 16:547–566.

DiTomaso, J. M. and G. B. Kyser. 2007. Control of *Ailanthus altissima* using stem herbicide application techniques. Arboric. Urban For. 33: 55–63.

Espenschied-Reilly, A. L. and J. R. Runkle. 2008. Distribution and changes in abundance of *Ailanthus altissima* (Miller) Swingle in a southwest Ohio woodlot. Ohio J. Sci. 108:16–22.

Fenneman, N. N. 1938. Physiography of Eastern United States. New York: McGraw-Hill. 714 p.

Feret, P. P. 1985. *Ailanthus*: variation, cultivation, and frustration. J. Arboric. 11:361–368.

Gelbard, J. L. and J. Belnap. 2003. Roads as conduits for exotic plant invasions in a semiarid landscape. Conserv. Biol. 17:420–432.

Gómez-Aparicio, L. and C. D. Canham. 2008. Neighborhood analyses of the allelopathic effects of the invasive tree *Ailanthus altissima* in temperate forests. J. Ecol. 96:447–458.

Greenberg, C. H., S. H. Crownover, and D. R. Gordon. 1997. Roadside soils: a corridor for invasion of xeric shrub by nonindigenous plants. Nat. Areas J. 17:99–109.

Heisey, R. M. 1996. Identification of an allelopathic compound from *Ailanthus altissima* (Simaroubaceae) and characteristics of its herbicidal activity. Am. J. Bot. 83:192–200.

Herrick, N. J., T. J. McAvoy, A. L. Snyder, S. M. Salom, and L. T. Kok. 2012. Host-range testing of *Eucryptorrhynchus brandti* (Coleoptera: Curculionidae), a candidate for biological control of tree-of-heaven, *Ailanthus altissima*. Environ. Entomol. 41:118–124.

Hobbs, R. J. and S. E. Humphries. 1995. An integrated approach to the ecology and management of plant invasions. Conserv. Biol. 9:761–770.

Hoffman, R. 1969. The biotic regions of Virginia. Pages 23–62, The Insects of Virginia: No. 1. Blacksburg, VA: Virginia Polytechnic Institute Research Division B. 48.

Hull, J. C. and R. C. Scott. 1982. Plant succession on debris avalanches of Nelson County, Virginia. Castanea 47:158–176.

Jørgensen, B. 1987. Exponential dispersion models (with discussion). J. R. Stat. Soc. B. 49:127–162.

Kaproth, M. A. and J. B. McGraw. 2008. Seed viability and dispersal of the wind-dispersed invasive *Ailanthus altissima* in aqueous environments. Forest Sci. 54:490–496.

Kim, M. H. 1975. Studies on the effect of sulfur dioxide gas on tree leaves. Res. Rep. For. Res. Inst. Korea. 22:31–36.

Knapp, L. B. and C. D. Canham. 2000. Invasion of an old-growth forest in New York by *Ailanthus altissima*: sapling growth and recruitment in canopy gaps. J. Torrey Bot. Soc. 127:307–315.

Kok, L. T., S. M. Salom, S. Yan, N. J. Herrick, and T. J. McAvoy. 2008. Quarantine evaluation of *Eucryptorrhynchus brandti* (Harold) (Coleoptera: Curculionidae), a potential biological control agent of tree of heaven, *Ailanthus altissima*, in Virginia, USA. Pages 293–299 *in* Proceedings of the XII International Symposium on Biological of Weeds. Wallingford, UK: CAB International.

Kostel-Hughes, F., T. P. Young, and J. D. Wehr. 2005. Effects of leaf litter depth on the emergence and seedling growth of deciduous forest tree species in relation to seed size. J. Torrey Bot. Soc. 132:50–61.

Kota, N. L. 2005. Comparative seed dispersal, seedling establishment and growth of exotic, invasive *Ailanthus altissima* (Mill.) Swingle and native *Liriodendron tulipifera* (L.). M.S. thesis. Morgantown, WV: West Virginia University. 108 p.

Kota, N. L., R. E. Landenberger, and J. B. McGraw. 2007. Germination and early growth of *Ailanthus* and tulip poplar in three levels of forest disturbance. Biol. Invasions 9:197–211.

Kowarik, I. 1995. Clonal growth in *Ailanthus altissima* on a natural site in West Virginia. J. Veg. Sci. 6:853–856.

Kowarik, I. and I. Säumel. 2007. Biological flora of central Europe: *Ailanthus altissima* (Mill.) Swingle. Perspect. Plant Ecol. 8:207–237.

Kowarik, I. and I. Säumel. 2008. Water dispersal as an additional pathway to invasions by the primarily wind-dispersed tree *Ailanthus altissima*. Plant Ecol. 198:241–252.

Kowarik, I. and M. von der Lippe. 2011. Secondary wind dispersal enhances long-distance dispersal of an invasive species in urban road corridors. NeoBiota 9:49–70.

Landenberger, R. E., N. L. Kota, and J. B. McGraw. 2007. Seed dispersal of the non-native tree *Ailanthus altissima* into contrasting environments. Plant Ecol. 192:55–70.

Landenberger, R. E., T. A. Warner, and J. B. McGraw. 2009. Spatial patterns of female *Ailanthus altissima* across an urban-to-rural land use gradient. Urban Ecosyst. 12:437–448.

Lawrence, J. G., A. Colwell, and O. J. Sexton. 1991. The ecological impact of allelopathy in *Ailanthus altissima* (Simaroubaceae). Am. J. Bot. 78:948–958.

Lewis, K. C. and B. C. McCarthy. 2006. Tree-of-heaven control using herbicide injection (Ohio). Ecol. Rest. 24:54–56.

Lewis, K. and B. McCarthy. 2008. Nontarget tree mortality after tree-of-heaven (*Ailanthus altissima*) injection with imazapyr. North. J. Appl. For. 25:66–72.

Lin, L. J., G. Peiser, B. P. Ying, K. Mathias, F. Karasina, Z. Wang, J. Itatani, L. Green, and S. Hwang. 1995. Identification of plant growth inhibitory principles in *Ailanthus altissima* and *Castela tortuosa*. J. Agr. Food Chem. 43:1708–1711.

Mack, R. N., D. Simberloff, W. M. Lonsdale, H. Evans, M. Clout, and F. A. Bazzaz. 2000. Biotic invasions: causes, epidemiology, global consequences, and control. Ecol. Appl. 10:689–710.

Marler, M. 2000. A survey of exotic plants in federal wilderness areas. Pages 318–327 *in* Wilderness Science in a Time of Change Conference—Volume 5: Wilderness Ecosystems, Threats, and Management. Missoula, MT: Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Martin, P., C. D. Canham, and R. K. Kobe. 2010. Divergence from the growth–survival trade-off and extreme high growth rates drive patterns of exotic tree invasions in closed-canopy forests. J. Ecol. 98:778–789.

McDonald, R. I. and D. L. Urban. 2006. Edge effects on species composition and exotic species abundance in the North Carolina Piedmont. Biol. Invasions 8:1049–1060.

Meloche, C. and S. D. Murphy. 2006. Managing tree-of-heaven (*Ailanthus altissima*) in parks and protected areas: a case study of Rondeau Provincial Park (Ontario, Canada). Environ. Manag. 37:764–772.

Merriam, R. W. 2003. The abundance, distribution and edge associations of six non-indigenous, harmful plants across North Carolina. J. Torrey Bot. Soc. 130:283–291.

Moore, J. E. and E. P. Lacey. 2009. A comparison of germination and early growth of four early successional tree species of the southeastern United States in different soil and water regimes. Am. Midl. Nat. 162: 388–394.

Motard, E., A. Muratet, D. Clair-Maczulajtys, and N. Machon. 2011. Does the invasive species *Ailanthus altissima* threaten floristic diversity of temperate peri-urban forests? C. R. Biologies 334:872–879.

Patterson, D. T. 1976. The history and distribution of five exotic weeds in North Carolina. Castanea 41:177–180.

Ridley, T., V. A. Rudis, and H. Beresford. 2011. Forest Inventory Nonnative Invasive Plant Web-Application, Version 1.0. http://srsfia2.fs.fed.us/nonnative_invasive/Southern_Nonnative_Invasives.html. Accessed: March 5, 2011.

SAS. 2008. User's Guide. Release 9.2. Cary, NC: SAS Institute.

Schall, M. J. and D. D. Davis. 2009. Verticillium wilt of *Ailanthus altissima*: susceptibility of associated tree species. Plant Dis. 93: 1158–1162.

Snyder, A. L., S. M. Salom, L. T. Kok, G. J. Griffin, and D. D. Davis. 2012. Assessing *Eucryptorrhynchus brandti* (Coleoptera: Curculionidae) as a potential carrier for *Verticillium nonalfalfae* (Phyllachorales) from infected *Ailanthus altissima*. Biocontrol Sci. Technol. 22:1005–1019.

Stipes, R. J. 1995. A tree grows in Virginia. Va. J. Sci. 46:105.

Sullivan, J. J., P. A. Williams, S. M. Timmins, and M. C. Smale. 2009. Distribution and spread of environmental weeds along New Zealand roadsides. N. Z. J. Ecol. 33:190–204.

Tellman, B. 1997. Exotic pest plant introduction in the American Southwest. Desert Plants 13:3–10.

Tellman, B. 1998. Stowaways and invited guests: how some exotic plant species reached the American Southwest. Pages 144–149 *in* The

Future of Arid Grasslands: Identifying Issues, Seeking Solutions. Tucson, AZ: Department of Agriculture, Forest Service, Rocky Mountain Research Station.
Trombulak, S. C. and C. A. Frissell. 2000. Review of ecological effects of roads on terrestrial and aquatic communities. Conserv. Biol. 14:18–30.
Tweedie, M.C.K. 1984. An index which distinguishes between some important exponential families. Pages 579–604 *in* Statistics: Applications and New Directions. Proceedings of the Indian Statistical Institute Golden Jubilee International Conference. Calcutta, India: Indian Statistical Institute.
Tyser, R. and C. A. Worley. 2003. Alien flora in grasslands adjacent to road and trail corridors in Glacier National Park, Montana. Conserv. Biol. 6:253–262.
[USDA, NRCS] U.S. Department of Agriculture, Natural Resources Conservation Service. 2012. The PLANTS Database, National Plant Data Team. http://plants.usda.gov. Accessed: July 30, 2012.
Vilà, M., M. Tessier, C. M. Suehs, G. Brundu, L. Carta, A. Galanidis, P. Lambdon, M. Manca, F. Médail, E. Moragues, A. Traveset, A. Y. Troumbis, and P. E. Hulme. 2006. Local and regional assessments of the impacts of plant invaders on vegetation structure and soil properties of Mediterranean islands. J. Biogeogr. 33:853–861.
von der Lippe, M. and I. Kowarik. 2007. Long-distance dispersal of plants by vehicles as a driver of plant invasions. Conserv. Biol. 21:986–996.

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