

# Spatial patterns of female *Ailanthus altissima* across an urban-to-rural land use gradient

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Published online: 20 March 2009  
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**Abstract** *Ailanthus altissima* is an invasive, dioecious deciduous tree common at the interface between urban and rural areas in the mid-Atlantic region, U.S.A. To examine spatial patterns of abundance and associations with land use type, we mapped all mature female trees in nine 89.5 ha plots (805.5 ha total area) across a typical urban-to-rural land use gradient using aerial images obtained via remote sensing supplemented by detailed ground referencing. Rural plots were dominated by forest and had the lowest density of mature females (0.007 females ha<sup>-1</sup>); urban and suburban plots did not differ significantly in mean density (0.37 females ha<sup>-1</sup> vs. 0.34 females ha<sup>-1</sup>, respectively). Individuals in urban plots were more evenly distributed, but were not associated with a wider variety of land uses and were closer to roads or openings than those in suburban plots. Given less available habitat per unit area in urban than in suburban environments, these patterns suggest that *Ailanthus* fits the profile of an invasive species that may be proliferating outward from urban centers. With continued disturbances associated with development in the suburban areas, and timber harvesting in the rural areas, further spread of *Ailanthus* seems likely.

**Keywords** Invasion · Dispersion · *Ailanthus* · Land use · Environmental gradient

## Introduction

Invasive species impose high socioeconomic, cultural, and environmental costs on society (Pimental et al. 2000, 2005). There is growing recognition of the problem by scientists,

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policymakers, and land managers, yet the impacts will continue unless sufficient resources are committed to combat invasive species. The problem is worldwide, and is likely to intensify with increasing human travel and global trade.

Ecologists recognize invasives as one of the most serious and challenging global environmental threats (Millennium Ecosystem Assessment 2005) and have devoted significant energy to improving the understanding of the causes and consequences of successful invasions of exotic species. Using both theoretical models and experimental studies, research has addressed demographic and ecological attributes of species that confer invasiveness (Daehler 2003; Hastings et al. 2005), ecosystem attributes that enhance the success of invaders (Davis et al. 2000, Shea and Chesson 2002, Hansen and Cleverger 2005), and the role of chance and timing in invasion dynamics (Crawley 1989).

The most efficient, cost effective approach to managing an invasion event is to understand species-habitat relationships and contain the population before it proliferates beyond control (Moody and Mack 1988). Once the species reaches a high density or occupies a large area, it is very difficult and costly to eliminate. Geographic analysis consisting of detailed description of the spatial distribution of reproductive individuals is the first step toward describing the species' habitat relationships. The second component needed is an accurate description of land cover—habitat types where the species is both present and absent. Such descriptive data can be acquired using GPS-supported field surveys, supplemented by current and historical aerial photographs (Herben et al. 2006). By understanding the spatial patterns of distribution and abundance of reproductive members of the invasive population, insight into the ecological processes that drive the demographic patterns of invasion become possible (Guisan and Zimmerman 2000; Pysek and Hulme 2005).

The urban-rural land use gradient (McDonnell et al. 1997; Lockaby et al. 2005) provides a broad array of habitats that potentially can be exploited by invasive species (Burton et al. 2005). Characterized by a highly urbanized core of industrial development and commercial services surrounded by intermediate density industry, services, and residential areas, this gradient terminates at the suburban—rural interface where land use patterns can be characterized as a heterogeneous mix of low-density residential, light industrial-commercial, agricultural, and natural land cover types. Because of its characteristic spatial pattern of land cover types, the urban-rural gradient offers a useful domain for describing and assessing spatial patterns of invasive plants and their associations with land use (Porter et al. 2001; Burton et al. 2005). This pattern of development might also offer a useful setting for “natural experiments” for studying ongoing land use change impacts and as it may represent a “space-for-time substitution experiment” whereby urban, suburban, and rural forest fragments serve as analogs of future conditions over broader areas (Carreiro and Tripler 2005).

*Ailanthus altissima* (Mill.) Swingle was introduced into the eastern U.S. in the late 18th century and was quickly adopted throughout the U.S. as a desirable urban tree because of its rapid growth, showy appearance, and tolerance of stressful environmental conditions (Hu 1979). Confined primarily to urban and other highly localized disturbed areas in the 19<sup>th</sup> and early 20<sup>th</sup> centuries, it is rapidly becoming a noxious pest in a variety of relatively productive, natural ecosystem types throughout the mid-Atlantic region of the U.S. and elsewhere. Because it is a rapidly maturing dioecious species, and because mature females are easily identifiable and capable of producing as many as 300,000 wind-dispersed seeds annually (Bory and Clair-Maczulajtys 1980), a description of the distribution of reproductive females across a representative urban-to-rural land use gradient will provide information on habitat associations (Kota et al. 2007; Landenberger et al. 2007), potential environmental limitations, and possible future abundance and distribution, information that is critically important in the early stages of an effective management strategy.

*Ailanthus* appears to be spreading from metropolitan areas into surrounding suburban and rural landscapes. While *Ailanthus* is frequently observed along roadsides, we wanted to determine actual distributions across this gradient in order to characterize the habitat associations of core populations and ‘nascent focus’ populations (Moody and Mack 1988) across the landscape. Specifically, we examined the spatial association between female (seed-bearing) trees and land use type, slope, aspect, distance to road edges and other openings to determine 1) whether female *Ailanthus* density differed between urban, suburban, and rural land use classes; 2) whether females were more aggregated in urban vs. suburban and rural areas; 3) whether females were closer to road edges and other openings in urban vs. suburban and rural areas; 4) whether females were associated with a higher diversity of land use types in urban than in suburban and rural areas and to what degree the amount of habitat varied between land use classes; and 5) whether there were significant relationships between female *Ailanthus* and slope or aspect.

## Methods

### Study area and sampling

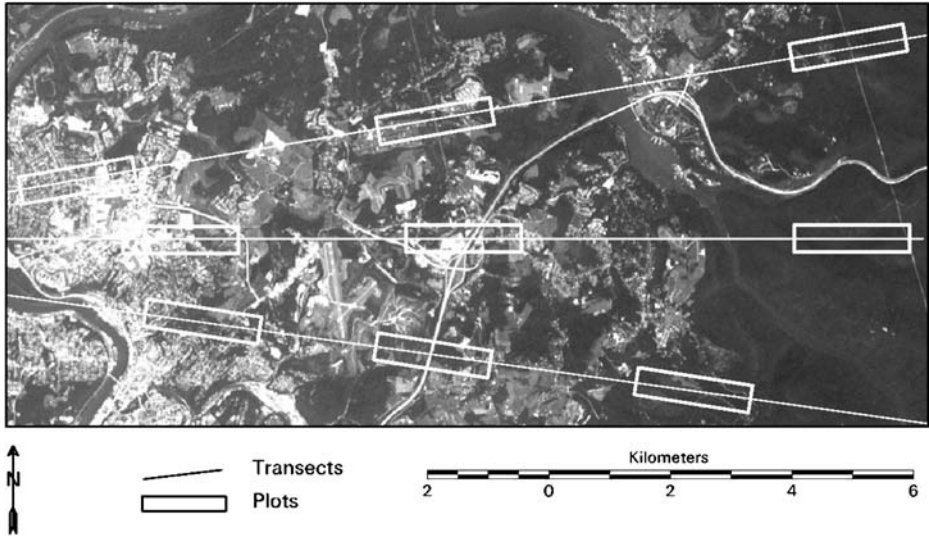
The study was conducted within Monongalia County, West Virginia, extending from Morgantown east to Chestnut Ridge (Nellis et al. 2000). Morgantown is a rapidly growing area that gained metropolitan status in 2002 and has a current population of approximately 28,000 (U.S. Census 2004). It continues to grow in population and along the margins growth can be characterized as ‘urban sprawl’ development, providing a strong gradient of land use development for ecological study of invasive species. Farmlands and forested areas are being converted to housing and commercial space both within city limits and in the suburbs.

Nine plots, each encompassing 89.5 ha (450 m × 1,990 m) were sampled; three in urban, three in suburban, and three in rural habitats (Fig. 1). To obtain high resolution imagery of these plots (Dean et al. 2000), three transects were flown in mid-May and early September, 2004. Each plot was imaged with a Sigma D9 SLR digital camera outfitted with a 50 mm lens, requiring eight images per plot to cover the area at a spatial resolution of 25 cm per pixel.

In January and February 2005 all reproductive female *Ailanthus* on each of the nine plots were mapped using GPS during complete ground surveys. Ground surveys involved searching the entire extent of each plot when all deciduous trees had shed their leaves, allowing identification of reproductive female *Ailanthus* by their characteristic, easily identifiable seed clusters. Land cover types were adapted from the U S Geological Survey’s National Land Cover Data classification system (Vogelmann et al. 1998) (Table 1), with a minimum mapping unit of 5 m<sup>2</sup>. The land cover map was generated using a supervised classification of a 2000 2.8 m resolution 3-band color-infrared QuickBird image (Space Imaging Corporation) acquired in September 2002, assessed for accuracy against our high resolution aerial photos and ground referenced at *Ailanthus* sampling locations during the field survey (Myeong et al. 2001). Ancillary digital environmental data included a roads vector layer and a digital elevation model (10 m postings). These were used to determine distance from female *Ailanthus* to roads and other openings, as well as slope, aspect, and elevation positions of the trees.

### Analysis

The difference in mean density between urban and suburban land use classes was tested using a t-test on the mean number of female *Ailanthus* per plot ( $n=3$  plots). The spatial dispersion



**Fig. 1** Grey-scale satellite image of Morgantown, WV (39 °39' N, 79 °57' W) and surrounding area acquired September, 2002 showing the three transects, nine plots, and three land use classes. Urban plots are western-most and occur over the Morgantown metropolitan area, suburban plots are central, and rural plots are eastern-most. Each 89.5 ha plot was thoroughly searched for female *Ailanthus altissima* in December–February, 2004–05

pattern of females within urban and suburban land use classes was estimated using Diggle’s (1983) Index of Dispersion, ‘I’, the variance to mean ratio. ‘I’ was computed from counts of female trees within 1 ha (100 m×100 m) grid cells created within each plot. The test statistic,  $(n-1)*I$  [where n is the number of cells per plot;  $n=89$  in our case], is distributed as Chi-square with  $n-1$  degrees of freedom. Statistical significance ( $p<0.05$ ) of the test statistic indicates significant deviation from a random distribution (Kathirgamatamby 1953; Diggle 1983); if  $I>1$ , then the distribution is clumped and if  $I<1$ , the distribution is spaced.

*Ailanthus* is thought to be a ‘shade-intolerant’ species, so another index of the stage of invasion is the degree to which individual trees are found in close proximity to existing

**Table 1** Percent of land cover type by land use class in each 89.5 ha plot

Land use class	Land cover type						
	Developed	High density	Inter. density	Low density	Shrubland	Forest	Agriculture <sup>a</sup>
		Residential	Residential	Residential			
Urban (plot 1, 2, 3)	20, 26, 6	23, 22, 8	41, 14, 21	2, 4, 23	6, 9, 9	5, 7, 27	3, 18, 6
Suburban (plot 1, 2, 3)	4, 7, 5	3, 5, 4	7, 15, 13	47, 31, 18	18, 9, 14	10, 10, 36	11, 13, 10
Rural (plot 1, 2, 3)	2, 1, 3	0, 0, 0	2, 0, 4	3, 0, 7	9, 4, 3	79, 95, 83	6, 0, 0

Land Use Classes were developed using the U S Geological Survey’s National Land Cover Data. We excluded those classes that were represented by less than 2% cover on our plots (wetlands, barren) and created three residential classes from the NLCD ‘Developed’ class

<sup>a</sup> Includes maintained grassland (parks, golf courses)

canopy openings or open areas. Therefore, we determined the distance of female trees to roads and other large openings by plotting the point locations on our high resolution aerial imagery and measuring the distance between trees and roads, and trees and openings, using a GIS.

Mean distances between individual *Ailanthus* trees and nearest roads as well as nearest openings were determined for each plot. Then using plot as the replicate within land use classes, we performed a one-way nested ANOVA to compare land use classes in terms of mean tree positions with respect to road and openings.

We were also interested in determining whether female *Ailanthus* showed different affinities for land cover types in urban versus suburban environments. By determining the proportion of land area occupied by each cover class within the two environments, and knowing the total *Ailanthus* count in each land use class, we calculated an ‘expected’ number of *Ailanthus* to be found in each cover class (assuming no affinity, the null hypothesis). Then, for each land cover class, we analyzed the difference in the number of expected *Ailanthus* in each cover class using a mixed model two-way ANOVA allowing examination of the land use (environment) by land cover class interaction. This model also permitted pair-wise comparisons of individual land cover classes between the two land use classes (Sokal and Rohlf 1995).

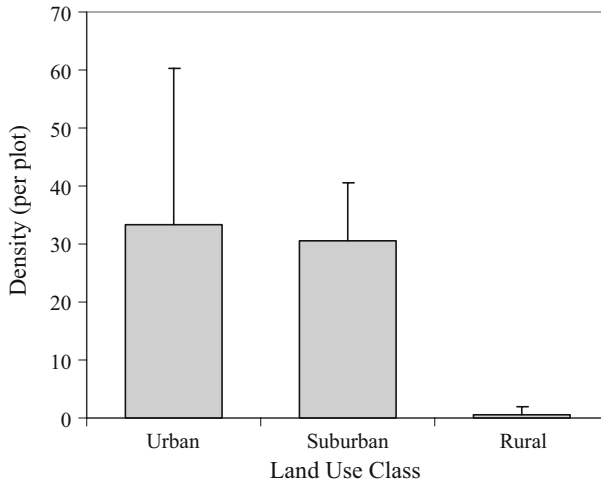
To estimate the amount of potential habitat in urban, suburban, and rural plots, we calculated *Ailanthus* “Habitable Area” (HA) by discriminating between pervious and impervious surfaces in the 2002 QuickBird image (Arnold and Gibbons 1996). HA was defined as all pixels that contained a pervious surface, defined as all forest, agriculture, parkland, lawn, and undeveloped classes including old-fields and timber harvest areas. All remaining pixels, including those that contained roads, highways, structures, exposed bedrock, and water were considered ‘impervious’, non-habitable land use classes. Because distributions of slope and aspect were unique for each plot, association of female trees with these two variables was determined by comparing the actual distribution against a spatially random distribution of 32 points per plot using a G-test (Sokal and Rohlf 1995).

## Results

Within the nine plots, 195 reproductive female trees were found. All three suburban plots contained reproductive trees whereas only two of the urban plots and one rural plot had such trees. There was no difference in mean density of *Ailanthus* between the urban and suburban land use classes ( $p=0.93$ ) (Fig. 2, Table 2).

In the urban environment, the comparison of actual *Ailanthus* positions on the landscape with random points showed that *Ailanthus* was significantly more likely to be found on steeper slopes than the random positions in the landscape ( $G=30.14$ ,  $p<0.0001$ ). In the suburban environment, there was no such bias in the slopes of sites where *Ailanthus* was found ( $G=3.82$ ,  $p>0.05$ ). In terms of aspect, in the urban environment *Ailanthus* was found with equal probability on all aspects ( $G=3.12$ ,  $p>0.05$ ). In suburban environments, there was a statistical trend toward lower probabilities of encountering *Ailanthus* on east and south aspects and greater probabilities than expected on north and west aspects ( $G=7.32$ ,  $.05 < p < 0.10$ ). With respect to elevation, a  $t$ -test showed that in urban areas *Ailanthus* tended to be found on higher elevation sites ( $t=4.60$ ,  $p<0.0001$ ) but the opposite tendency occurred in suburban sites ( $t=2.00$ ,  $p=0.047$ ). The elevation differences between *Ailanthus* trees and random points were small (14 m and 11 m, respectively), and probably not biologically meaningful.

Within urban and suburban plots that contained female trees, individuals were clumped at the 1 ha scale ( $p<0.001$ ), with suburban trees tending to be more clumped than urban



**Fig. 2** Mean density of female *Ailanthus altissima* in 89.5 ha sample plots in urban, suburban, and rural land use classes in north central West Virginia. Error bars are plus one standard error of the mean

trees (Fig. 3). Suburban trees were no closer in proximity to openings ( $F=5.25$ ;  $p=0.16$ ; Fig. 4) or roads ( $F=2.04$ ;  $p=0.25$ , Fig. 5) than urban trees. Within cover classes in urban and suburban areas, tree density varied dramatically by plot. As a result, there was no difference in the expected number of trees in each environment ( $F=0.55$ ,  $p=0.46$ ) or in each land cover class ( $F=1.19$ ,  $p=0.35$ ), and trees showed no difference in affinity for certain land cover types in the two environments ( $F=0.34$ ,  $p=0.91$ ). The only two trees found in the rural plots were located within a power line right-of-way, thus no analysis of affinity by plot or between the three environments was possible (Fig. 6).

There is less Habitable Area available for *Ailanthus* on urban plots compared to suburban and rural plots, increasing the effective density of reproductive trees relative to suburban and rural areas where abundant, unoccupied habitat is available (Table 3).

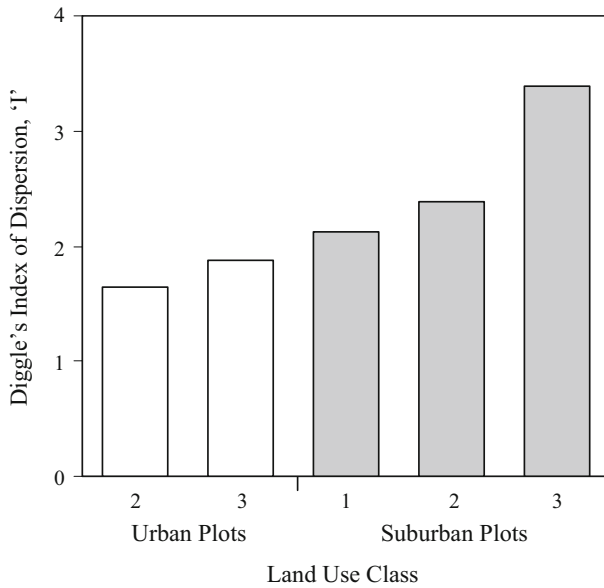
## Discussion

To spread across the landscape, a species must not only colonize new habitat, but must survive, reproduce, and successfully disperse. Because reproductive individuals drive population spread, identifying their location in the landscape is a first step in understanding

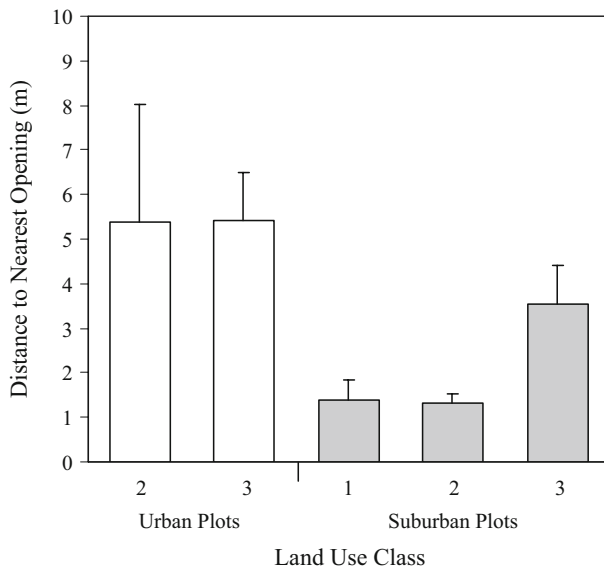
**Table 2** Total number and mean density of reproductive females *Ailanthus altissima*  $\text{ha}^{-1}$  found in Urban, Suburban, and Rural plots following complete searches

	Urban			Suburban			Rural		
	Plot-1	Plot-2	Plot-3	Plot-1	Plot-2	Plot-3	Plot-1	Plot-2	Plot-3
Total	0	14	87	10	43	39	2	0	0
Density	0	0.15	0.97	0.11	0.48	0.44	0.02	0	0
<b>Mean density</b>	<b>0.38</b>			<b>0.34</b>			<b>0.007</b>		

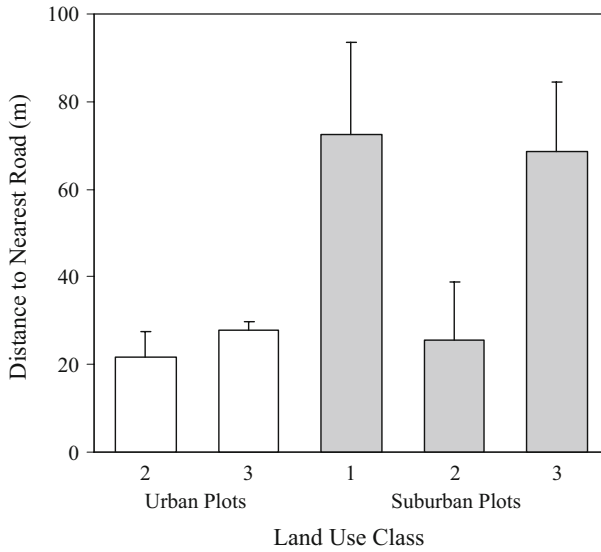
Each plot measured 89.5 ha (450 m  $\times$  1,990 m)



**Fig. 3** Diggle's Index of Dispersion, 'I', for each urban and rural plot where reproductive female *Ailanthus altissima* were found. The higher the index value, the more clumped individual trees are. An 'I' greater than 1.26 is significant at  $p=0.05$ . All values are significant at  $p<0.001$ , demonstrating a highly clumped spatial pattern

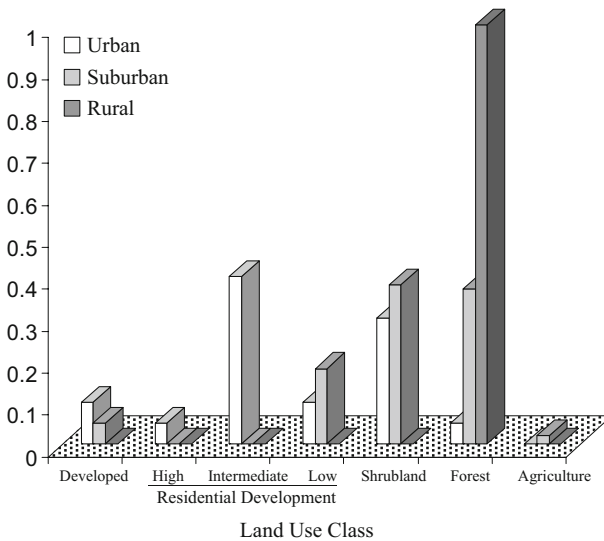


**Fig. 4** Distance of reproductive female *Ailanthus altissima* to the nearest opening. Openings were defined as areas of completely open sky greater than 25 m×25 m, and included roads, fields, lawns, undeveloped lots, and similar environments where the overhead sky was not occluded above 5 m. Partially harvested forest, mid-successional old-fields, and similar areas with residual trees > 5 m were not considered openings. Error bars are plus one standard error of the mean



**Fig. 5** Distance of reproductive female *Ailanthus altissima* trees to the nearest road. Roads included highways, state and county roads, and local roads of all surface types. Error bars are plus one standard error of the mean

the potential for further spread. Based on our census plots, we estimated that the Morgantown urban area had 987 reproductive females, or an average of 34.2 females per km<sup>2</sup>, compared to 1,694 females in the suburban area, or 33.8 females per km<sup>2</sup>. Presence of reproductive populations, however small, signifies both environmental tolerance and potential expansion. These populations may represent nascent foci that have high potential



**Fig. 6** Proportion of total reproductive female *Ailanthus altissima* on sample plots in each of five land use categories. urban plots; suburban plots; rural plots



**Table 3** Habitable area by land use class

	Urban			Suburban			Rural		
	plot-1	plot-2	plot-3	plot-1	plot-2	plot-3	plot-1	plot-2	plot-3
HA Plot <sup>-1</sup> (ha)	43.7	47.4	61.5	82.1	58.9	79.3	83.1	83.6	82.8
Mean HA plot <sup>-1</sup>		50.9			73.4			83.2	
Mean trees HA <sup>-1</sup>	<b>0.66</b> (0.37 <sup>a</sup> )			<b>0.42</b> (0.34 <sup>a</sup> )			<b>0.008</b> (0.007 <sup>a</sup> )		

Habitable Area (HA) was determined by classifying lands using a binary rule that distinguished between permeable land use types and impermeable land use types

<sup>a</sup> mean tree density ha<sup>-1</sup> without correcting for HA

contributions to future population growth through both local and long distance dispersal (Moody and Mack 1988; Clark 1998).

Our findings, given the limitation imposed by a single study area, indicate that reproductive females are found in a wide range of habitat types ranging from highly developed urban environments which are typically characterized by poor soils and extremes of both light and temperature (Gilbert 1989; Hamerlynck 2001) to highly disturbed, successional forest and mature forest edges. The species' ability to successfully colonize and survive in intermediate light conditions in old-growth forest gaps (Knapp and Canham 2000) is a recent finding, although earlier evidence exists of a similar population in late successional forest in West Virginia (Kowarik 1995). However we found no reproductive females in either forest edges or interior second-growth forest in rural areas around Morgantown, despite their low-level presence in the rural landscape. Given that the species is capable of dispersing from edges into interior forest (Landenberger et al. 2007), it is somewhat surprising that individuals were not found in interior forest gaps. This could be due to environmental limitations of intact mid-successional forest. Although *Ailanthus* is capable of germinating in eastern deciduous forest leaf litter (Kota 2004; Kota et al. 2007), seedling performance decreases with increasing litter depth (Kostel-Hughs et al. 2005). Seeds may arrive and germinate but don't survive to reproductive age in interior mixed-mesophytic and mixed-oak forest types characteristic of the study landscape. Alternatively, viable seed may not have reached many of these areas.

Reproductive trees were clumped at the 1-ha scale in both urban and suburban environments, and have similar density at larger ~100 ha scales. Adjusting for habitable area, *Ailanthus* had a higher reproductive population density in urban areas compared to suburban areas where abundant habitat exists, perhaps because of their historical presence in the city, or due to higher habitat quality. Given the broad observed niche of *Ailanthus*, there is evidently unoccupied habitat available for colonization in both urban and suburban areas throughout the study landscape. However the urban environment is not changing from one land use category to another as rapidly as suburban areas. Suburban forest patches and agricultural land are being converted to commercial and residential land around which *Ailanthus* seems to thrive. In addition, intact forest stands in both suburban and rural areas are being logged at fairly high rates. Although some of these areas are not converted to alternative land uses and remain in forest, the residual stands are often highly disturbed and susceptible to *Ailanthus* invasion (Kota et al. 2007).

*Ailanthus* is a serious competitor with native trees and shrubs in many habitat types throughout the eastern deciduous forest region, and appears to be increasing in both local

abundance and geographic extent as it disperses along highway corridors and other rights-of-way (Rentch et al. 2005). With the increase in timber harvest expected in the second-growth eastern deciduous forest over the next few decades, large-scale openings will be created for colonization by invasive species, including *Ailanthus*. If satellite populations of *Ailanthus* are allowed to persist and continue spreading from suburban into rural areas, a drastic expansion of this species can be expected in the coming century with dire effects on the forest resource. Some mid-Atlantic states (Maryland, Pennsylvania) have initiated control programs that focus on eliminating trees along interstate highways and rights-of-way. The present study, limited as such to a single study area, suggests that effective control aimed at destroying nascent focus populations will need to extend beyond roadways since *Ailanthus* is found in both urban and suburban zones well beyond the edges of roads. A rapid survey and response program that includes other likely areas, such as old-fields, edges of agricultural fields, and in highly disturbed forests near roadways, may be more effective.

## Conclusions

Despite a wealth of research over the past 30 years, a set of common principles of nonindigenous species ecology remain elusive. However for those nonindigenous species that become invasive, one pattern seems to have emerged—a small population is established, transitions over time to a phase of rapid expansion, and reaches dynamic equilibrium between density and habitat availability. This indicates that control of the species at points of nascent foci, at the leading edge(s) of the invasive front where control is most efficient and effective, can be successful in slowing further spread.

Invasive species management has benefited from this finding, and does not have to focus on idiosyncratic, species-specific approaches to limiting the spread of invasives across the landscape, but rather should focus on managing small outlying populations at the leading edge of the front. Such an approach requires that the species be easily identifiable, an attribute characteristic of reproductive female *Ailanthus* in winter when their large clusters of seeds are easily seen at a distance. Once identified, a map indicating representative density and distribution patterns of the populations, including outliers that may be in very low densities that are difficult to detect, can be generated. Early detection is one of the most challenging issues in invasive species management. Mapping and assessing density and abundance patterns is one step managers can use to prioritize their specific management strategies.

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