CASTANEA 68(1): 1–14. MARCH 2003

Vulnerability of Oak-Dominated Forests in West Virginia to Invasive Exotic Plants: Temporal and Spatial Patterns of Nine Exotic Species Using Herbarium Records and Land Classification Data

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ABSTRACT

Are oak-dominated forests immune to invasive exotic plants? Herbarium and land classification data were used to evaluate the extent of spread of nine invasive exotic plants and to relate their distributions to remotely-sensed land use types in West Virginia. Collector-defined habitats indicated that the most common habitat was roadsides, but seven of the nine species were found in forests. Regression analyses indicated that the most significant variables were urban land use and population per km^2, but these were only significant for three of the species. Detrended correspondence analysis showed a forest to urban gradient and that one of the species, *Rosa multiflora*, was significantly correlated to heavily forested counties while *Ailanthus altissima* was significantly correlated with more urbanized counties. Although forests clearly are not immune to invasion, the lack of spatial and temporal patterns among the species support the need for intensive plot-level monitoring before predictions of spread can be made.

INTRODUCTION

Many invasive plant species share characteristics of native early-successional plant species, such as abundant seed production, small seed size, rapid establishment, vegetative reproduction, and positive growth and reproductive response to relatively high light levels (Rajmanek and Richardson 1996, Gordon 1998). Native early-successional species are not typically found in forested areas except as part of the seed bank or in response to an opening. Once these openings close, the ruderal species disappear. Consequently, forests may be less vulnerable to invasion by exotics compared to open disturbed areas. While disturbed areas in and surrounding forests are subject to invasion by nonnative plants (Anderson 1999, Debinski and Holt 2000, Mack et al. 2000), it is not understood how infested openings, corridors, and surrounding matrices affect the adjacent forest. Forests are thought to regenerate in part using natural openings (gap-phase dynamics), and oak-dominated forests, in particular, are thought to be dependent on disturbance and are often maintained with fire or harvesting methods used to open the understory, sub-canopy, and canopy (Loftis 1983, Bartuska 1994, Cook 1998). Natural or managed regeneration of forests could promote invasion of exotic plant species (Orwig and Foster 1998, Knapp and Canham 2000). Oak-dominated forests are also susceptible to exotic insect infestations, including the gypsy moth (*Lymantria dispar*), which may increase exotic plant invasion (Liebhold et al. 1995).

Some exotic plants with evident potential for invasion grow and reproduce in variable environments, including low-light environments (pers. obs., Dreyer et al. 1987, Ingo 1995, Luken and Goessling 1995, Luken et al. 1995, Redman 1995, Luken et al. 1997, Byers and Quinn 1998, Horton and Neufeld 1998, Susko and Lovett-Doust 1998, Schweitzer and Larson 1999, Meekins and McCarthy 1999, Susko and Lovett-Doust 2000). This plastic behavior may

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improve the ability of such plants to move from the forest gaps and edges into the forest interior. If some exotic plant species have a plastic response to a wide range of environments, they may also exhibit different ecosystem functions in such environments. Varied function may enable such species to change typical successional pathways for forests, resulting in different species compositions that always include the exotic or other exotics (Gordon 1998, Myster and Pickett 1992, Robertson et al. 1994, Udvardy 1998, Fike and Niering 1999). It is this potential insidious replacement of multiple native species by functionally similar non-natives that may be of most concern, because prevention of exotic-species establishment and restoration of degraded sites will be much more difficult.

This paper focuses on nine exotic species: *Alliaria petiolata* (Bieb.) Cavara & Grande, *Microstegium vimineum* (Trin.) A. Camus, *Lonicera japonica* Thunb., *Celastrus orbiculatus* Thunb., *Lonicera maackii* (Rupr.) Maxim., *Lonicera morrowii* A. Gray, *Lonicera tatarica* L., *Rosa multiflora* Thunb., and *Ailanthus altissima* (Miller) Swingle (Gleason and Cronquist 1991). These species are chosen because an adequate sample size (at least 20 specimens) is available in the West Virginia University Herbarium, each species has been found in both high light and shade environments (pers. obs., Winter et al. 1982, Nuzzo 1993, Ingo 1995, Luken et al. 1995, Hutchinson and Vankat 1998), and they produce abundant seed (with the possible exception of *L. japonica*) that are viable for one to four years and often require cold stratification (Fairbrothers and Gray 1972, Schopmeyer 1974, Halls 1977, Dreyer et al. 1987, Graves 1990, Hutchinson and Vankat 1997, Byers and Quinn 1998, Nuzzo 1999, Baskin and Baskin 2001). These species also represent a spectrum of varied characteristics in terms of growth form, reproductive system, allelopathic properties, and known pathogens. Some of these differences may help explain any distribution or temporal patterns noted in this evaluation.

Alliaria petiolata is an overwintering biennial herb (Meekins and McCarthy 1999), while *M. vimineum* is an annual grass (Barden 1987). *Lonicera japonica* and *C. orbiculatus* are perennial vines, the three bush honeysuckles and *R. multiflora* are all perennial shrubs, and *A. altissima* is a perennial tree (Gleason and Cronquist 1991). Both *L. japonica* and *R. multiflora* have documented varieties (Paris and Maney 1939, Coombes 1991), which may explain some of their plastic growth behavior. It is probable that varieties exist for most, if not all, the other seven species, given their horticultural history. *Rosa multiflora* is the only species of the nine that is currently listed on West Virginia's noxious weed list (Laycock 1985). Some nurseries still use its root stock for other cultivated roses (Derr and Hagwood 1992), which may continue to promote *R. multiflora*'s spread.

Alliaria petiolata, *M. microstegium*, *L. japonica*, *L. maackii*, *L. morrowii*, and *R. multiflora* are hermaphroditic. *Alliaria petiolata* is facultatively xenogamous, but will self; it, however, cannot spread vegetatively (Cruden et al. 1996, McCarthy and Hanson 1998, Meekins and McCarthy 1999). *Microstegium vimineum*, possessing both cleistogamous and chasmogamous flowers, may reproduce apomictically, self and outcross, and will spread vegetatively by rooting at the nodes (pers. obs., Barden 1987). *Alliaria petiolata* flowers early (like a spring ephemeral), while *M. vimineum* does not flower until late summer or early fall (Gleason and Cronquist 1991). *Lonicera japonica* must outcross and spreads primarily by vegetative reproduction, which is bolstered by an extended growing period due to being semi-evergreen (Larson 2001). It is not known whether or not the bush honeysuckles self or facultatively outcross. While these species may sprout at the base, they do not spread rhizomatously, so vegetative spread is limited. However, they all leaf out and produce fruit early compared to most native shrubs and stay in leaf and fruit well into October in some cases (pers. obs., Hutchinson and Vankat 1997). *Rosa multiflora*, like the bush honeysuckles, sprouts at the base and may spread by root stock. Whether or not it is an obligate outcrosser has not been determined (Gleason and Cronquist 1991). Being dioecious, both *C. orbiculatus* and *A. altissima* are obligate outcrossers (Feret 1973, Dreyer et al. 1987, Gleason and Cronquist 1991). However, monoecious individuals of *C. orbiculatus* (Dreyer et al. 1987) and hermaphroditic flowers of *A. altissima* (Feret 1973) have been found on rare occasions. *Celastrus orbiculatus* can spread vegetatively by root suckering (Dreyer et al. 1987), and *A. altissima* spreads rhizomatously, forming extensive clones (Ingo 1995).

Alliaria petiolata, *L. maackii*, and *A. altissima* have allelopathic properties (Heisey 1990, Lawrence et al. 1991, Lin et al. 1995, Cruden et al. 1996, Heisey 1996, Hutchinson and Vankat 1997, McCarthy and Hanson 1998, Deering and Vankat 1999, Vaughn and Berhow 1999, Gould and Gorchov 2000). While it may make sense for allelopathic properties to be present for the other bush honeysuckles, none have been documented.

Alliaria petiolata, *R. muliflora*, and *L. tatarica* have known pathogens that could slow their spread. A European turnip mosaic virus has been isolated from *A. petiolata* plants in Ontario, Canada. However, it does not appear to affect populations of *A. petiolata* in a significant way, possibly because the plant does not serve as a reservoir of the virus, and seeds of infected plants do not carry the virus (Stobbs and Van Schagen 1987). Rose rosette disease, which is an eriophyid mite-transmitted disease, is endemic to North America and can be lethal to *R. multiflora*. Spread of the disease is dependent upon increasing the mite populations. Native roses are also susceptible (Hindel and Wong 1987, Epstein et al. 1997, Epstein and Hill 1999). *Lonicera tatarica* is susceptible to a western and central Russian aphid (*Hyadaphis tataricae*) that has spread over much of Canada and northern parts of the United States (Mahr and Dittl 1986, Tegel 1987, Voegtlin 1988). Because *L. tatarica* may be limited to colder latitudes and may be more susceptible to a pathogen, spread of this species may be less of a threat in West Virginia. Nonetheless, it is considered a problem species in the northeastern United States (Woods 1993).

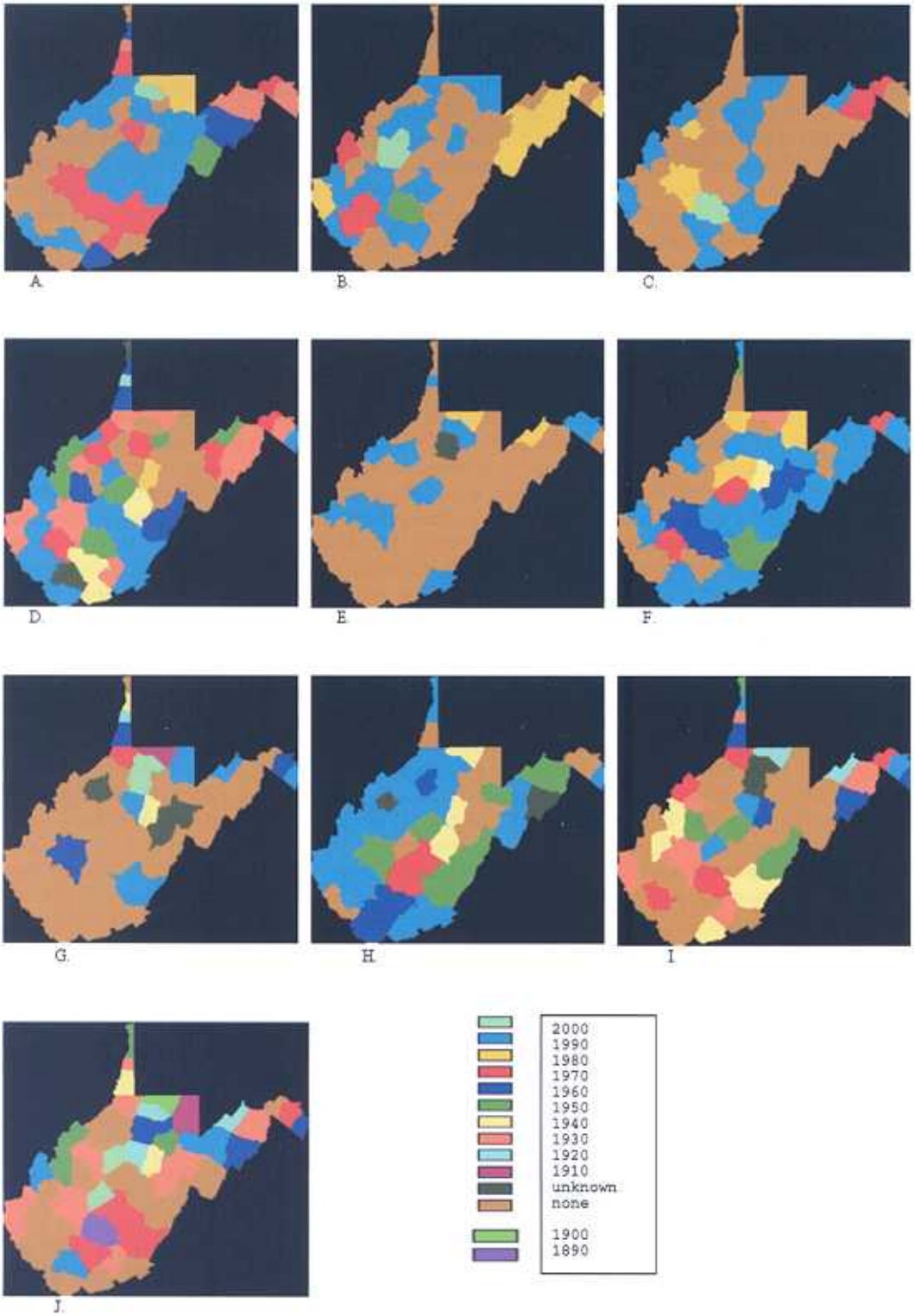
Herbarium data are currently used to determine the distribution and predict the spread of individual plant species; most of these data are at the county scale (e.g. www.invasivespecies.gov and www.plants.usda.gov; Flora of West Virginia Committee et al. 2001). There are several inherent problems associated with herbarium data including collection biases, potential misidentifications, and inaccurate locations and dates. Examples of collection biases include more collections near colleges, cities, accessible roadsides, and pristine natural areas that are of interest to botanists. There also may be an evident avoidance of undesirable species such as weedy exotics as well as collection intensities over a relatively short time period (T. Block, D. Ford-Werntz, M. Ortt, and M. Vincent, pers. comm.).

Despite all these flaws, more reliable plant distribution data over a regional scale are usually not available and, consequently, many land managers currently depend on herbarium data in developing their management plans. The purpose of this paper is to estimate the extent of spread of these nine invasive exotic plants in the forested areas of West Virginia, which are primarily oak-dominated, using herbarium and remotely sensed land use data. Herbarium data currently are not being related to coarse land-use cover types, which may enable more rapid predictions of spread. Nor, to my knowledge, are herbarium data being used to decipher both spatial and temporal patterns among several species. I view this analysis as a necessary first step to understanding and documenting the vulnerability of forests to invasion. I ask the following questions:

1. Is there a relationship between land-use cover types and the distribution of these exotic species?
2. Are there spatial and temporal patterns shared by these exotic species?
3. If so, are these patterns related to any species characteristics?
4. Can we reliably use herbarium and remotely-sensed land classification data to predict the spread of these invasive exotic plants into forested areas?

METHODS

Specimens from the West Virginia University Herbarium and the Draft Preliminary Atlas of the Vascular Plants of West Virginia, Curatorial Database System (Flora of West Virginia Committee et al. 2001) were used for this project. A total of 423 West Virginia specimens were examined; there are currently 41,850 specimens housed in the herbarium of which 29% are non-native to West Virginia. Information about county location, general habitat description, and collection date was available for most specimens. I also compared these specimens to a widespread, early-successional native species, *Solidago canadensis* L. (70 specimens). Color-coded county maps showing the county distribution of each species by decade were made to help


A
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2000
1990
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1950
1940
1930
1920
1910
unknown
none
1900
1890

Table 1. Land-use cover categories and their definitions for the 1:250,000 (US GeoData of the National Cartographic Information Center, USGS, 1986 version) and the 30 m × 30 m pixel (West Virginia Land Cover Data Set, USGS, 1999 version) scales

Category	Definition
Urban	Residential, commercial, industrial, transportation, mixed urban
Agricultural	Cropland, pasture, orchards, groves, vineyards, nurseries, confined feeding operations, herbaceous rangeland, shrub and brush rangeland, mixed rangeland
Forest	Deciduous forest, evergreen forest, mixed forest
Water	Streams, canals, lakes, reservoirs
Wetland	Forested wetland, non-forested wetland
Disturbed	Bare exposed rock, strip mines, quarries, gravel pits, transitional areas, mixed barren land

determine if there were any spatial and temporal patterns by species or shared by any of the species (Figure 1).

Both USGS 1:250,000 GeoData and 30 m pixel National Land Classification Data were used to determine land-use cover classes for each of the 55 counties (USGS 1986, USGS 1999; Table 1). Forest cover data from the 1:250,000 scale were then used to estimate forest fragmentation using an IDRISI for Windows, version 2, algorithm (Eastman 1997). Population per km^2 was determined from 1990 United States census data (GeoLytics, Inc. 1998) and related to land use and species distributions. Data were analyzed using both simple regression analysis (SYSTAT v. 9 1999) and detrended correspondence analysis (DCA; MjM Software Design 1999), using each county as the equivalent of a sample.

Time span was defined as the number of years from the year 2001 each species was found in each county. It was assumed that once a species was found in a county it remained there. Time span for each species was the dependent variable of the regression analyses and the six land use categories (Table 1) as well as county population per km^2 and forest fragmentation were separate independent variables. This resulted in a total of 72 separate linear regression analyses. The DCA used species time span in each county of all species together in a matrix and the land use categories plus fragmentation and population estimates by county in another matrix. Regression and DCA analyses using species counts (rather than time span) gave similar results. Multiple linear regression analysis was not possible due to multi-collinearity among several of the land use categories. The DCA provided different information about the data than the regression analyses, because all species data were analyzed together. Simple linear regressions were used to relate each of the land use variables as well as fragmentation and population per km^2 to the ordination axes. Thus, multi-collinearity was not a concern. In all analyses, both spatial scales gave similar results; only those for the 1:250,000 scale are presented in this paper.

RESULTS

A review of the West Virginia Curatorial Database Sysem (Flora of West Virginia Committee et al. 2001) revealed a collection bias. Most collections occurred in the 1930s and 1940s for the pteridophytes and gymnosperms (33% and 16%, respectively; Ford-Werntz 1997; Figure 2). All dicotyledons and members of the Asteraceae family (chosen as a representative

← Figure 1. Color-coded county-level distributions for each of the nine exotic species and *Solidago canadensis*. Each color represents a decade as defined in the legend. A = *Alliaria petiolata*; B = *Microstegium vimineum*; C = *Celastrus orbiculatus*; D = *Lonicera japonica*; E = *Lonicera maackii*; F = *Lonicera morrowii*; G = *Lonicera tatarica*; H = *Rosa multiflora*; I = *Ailanthus altissima*; J = *Solidago canadensis*. The colors for the 1890 and 1900 decades are separated in the legend because only collections of *Solidago canadensis* exist for these decades.

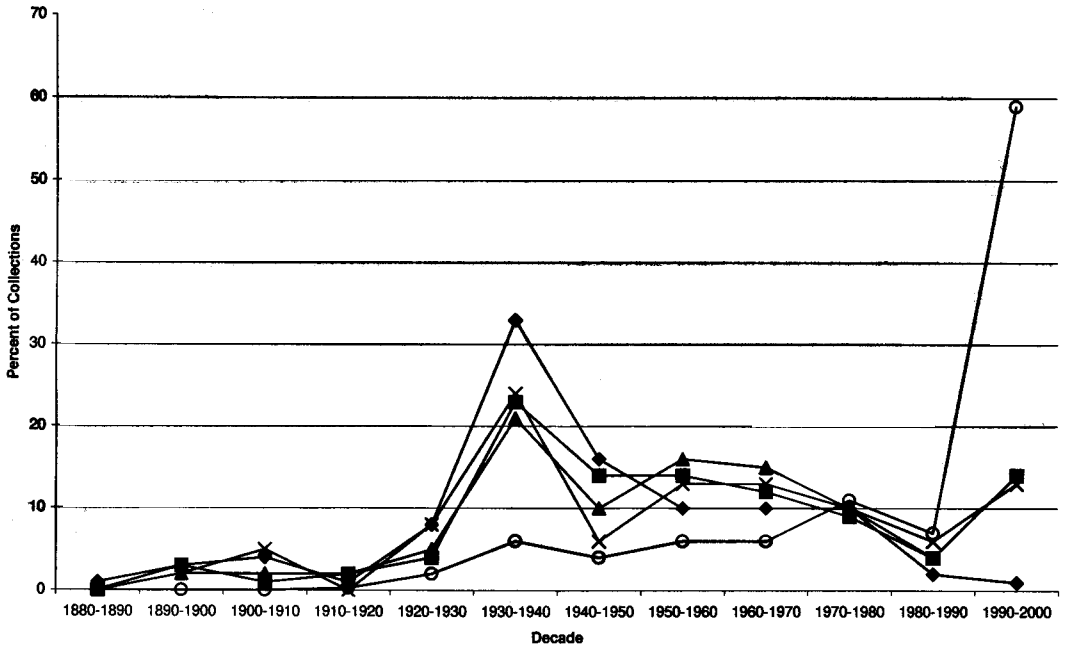

Figure 2. West Virginia University Herbarium collection distribution (percent of total in each category) by decade for the pteridophytes and gymnosperms (diamond), dicotyledons (square), members of the Asteraceae family (triangle), *Solidago canadensis* (×), and the nine exotics (○).

large family) showed a similar collection pattern as did the native early-successional species, *Solidago canadensis*. However, my nine exotic species did not share this collection intensity pattern, but instead showed that most collections occurred in the 1990s (Figure 2). In 1998, *A. petiolata*, *L. japonica*, *L. maackii*, *L. morrowii*, *L. tatarica*, and *R. multiflora* were deliberately sought in an organized collection program; these collections comprised 45% of that decade's collections for these six species. However, both *M. vimineum* and *C. orbiculatus* had their highest collection numbers in the 1990s and were not a part of this collection program. Moreover, subtracting out the 'deliberate' collections (80 specimens) still resulted in 36% of all the collections of the nine exotics occurring in the 1990 decade, compared to 10% in the 1970 decade (the decade with the next highest collection count).

Overall, the nine exotic species were most likely to be collected near roads (Table 2). However, *M. vimineum* was more commonly found near streams, *C. orbiculatus* was more commonly found in open forests, and *A. altissima* was more commonly found in residential areas. *Lonicera maacki*, *L. morrowii* and *A. petiolata* all had a relatively high percentage of their collections (18%, 10%, and 13%, respectively) found in closed-canopy forest habitats. *Microstegium vimineum* and *C. orbiculatus* had relatively high percentages (23% and 31% of their totals, respectively) in open forests. All nine species were found at least once in an open or closed forest habitat, and seven of the nine were found at least once in closed canopy forests. As with the exotic species, *S. canadensis* was most commonly found along roadsides. However, unlike the exotics, this native species was never recorded as being in a closed-canopy or open-canopy forest (Table 2).

The county-level species distributions showed the 1990s as the most important decade of spread for all but *A. altissima* and *L. tatarica* (Table 3, Figure 1). Also *A. altissima* appeared to be distributed along the major highways (I-79 and I-68) of West Virginia, forming a 'T,' and *L. tatarica* appeared to be located more often in northern counties. Unfortunately, no other definable patterns were detected. There was no trend in date of first arrival and the number of counties in which any particular species was found or the estimated spread rate (county per

Table 2. Percent of the specimens of each species found in collector-defined habitat types based on herbarium records. 'RR' refers to railroad. 'Other' refers to habitats that were not easily categorized or that were comparatively rare, such as 'hillside,' 'rocky slope,' or 'right of way.' 'Missing' refers to collections where no habitat type was indicated. 'Total' is the total number of specimens per species. The percentages are based on all habitat types noted; in some cases more than one habitat was noted per specimen. Information is also given for a common native early-successional species, *Solidago canadensis*

Species	Roads	Stream	Forest	Open Forest	RR	Trails	Old Field	Residential	Other	Missing	Total
Alliaria petiolata	26	19	13	7	6	3	0	6	11	9	58
Microstegium vimineum	26	27	3	23	10	1	3	0	6	1	48
Lonicera japonica	34	21	0	1	4	1	4	5	15	15	64
Celastrus orbiculatus	23	3	6	31	11	6	3	3	14	0	26
Lonicera maackii	33	6	18	6	12	0	9	3	13	0	27
Lonicera morrowii	50	7	10	6	1	4	6	4	11	1	77
Lonicera tatarica	24	14	5	5	5	5	0	24	0	19	21
Rosa multiflora	31	8	6	9	6	1	12	2	21	4	67
Ailanthus altissima	22	9	0	3	6	3	3	23	5	26	35
All 9 species	32	14	7	10	6	3	5	6	9	8	423
Solidago canadensis	28	8	0	0	3	4	24	13	6	14	70

Table 3. Species distribution data, based on herbarium records. There are a total of 55 counties in West Virginia. Data are also given for a common native early-successional species, *Solidago canadensis*

Species	First Record in WV	First County	# of Counties	# of Points of Entry	Rate of Spread Average (counties/year)	Rate of Spread in the 1990s (counties/year)
Alliaria petiolata	1933	Mineral	36	6	0.54	1.6
Microstegium vimineum	1956	Fayette	27	8	0.61	0.71
Lonicera japonica	1929	Ohio	46	8	0.66	1.3
Celastrus orbiculatus	1977	Hampshire	18	3	0.78	1.3
Lonicera maackii	1981	Monongalia	27	8	0.83	1.2
Lonicera morrowii	1938	Monongalia	39	5	0.65	2.5
Lonicera tatarica	1912	Monongalia	17	7	0.19	0.5
Rosa multiflora	1940	Webster	46	7	0.78	2.8
Ailanthus altissima	1921	Mineral	31	11	0.40	0.40
Solidago canadensis	1891	Fayette	38	6	0.34	0.30

year). Nor were there any patterns associated with estimated number of points of entry (possible starting points of spread within the state over time) and spread rate or number of counties or date of first arrival. For example, both *C. orbiculatus* and *L. tatarica* were located in approximately the same number of counties, but the county per year spread rate of *C. orbiculatus* was a little over four times higher than that of *L. tatarica*. Moreover, the fact that all three of the bush honeysuckles had their start in one county had no effect on their spread rate or spatial or temporal patterns. Also, species sharing plant characteristics, such as growth form, reproductive system, or allelopathic properties did not share an apparent spatial or temporal pattern. However, *L. tatarica*, despite having an early arrival date, showed a lack a spread and a slow spread rate, which may be due to its being successfully affected by a pathogen or having a limited range. In contrast, even though planting of *R. multiflora* is illegal and it may currently suffer from rose rosette disease, its spread rate increased in the 1990s (Table 3, Figure 1).

Based on the regression analyses, population per km^2 was a significantly important variable for *L. maackii*, *L. tatarica*, and *A. altissima*, as well as for the native species (Table 4). *Alliaria petiolata* and *L. tatarica* both showed a significant negative correlation with counties with a high percentage of forest cover, and *L. tatarica* and *A. altissima* showed a significant positive correlation with counties defined by a high percentage of urban land use. *Lonicera tatarica* was also positively correlated with counties with a large percentage of water cover, possibly because the water and urban land use categories were positively correlated with each other ($r = +0.741$). *Alliaria petiolata* showed a significant positive correlation with counties with high agricultural land cover; the agricultural and forest land types showed a significant negative correlation ($r = -0.940$). There were no other significant relationships for any other species. The relationship between species distribution and land use does not appear to be associated with invasion history (Table 3) or plant characteristics, except that three of the four species showing a significant relationship with a land use category are allelopathic.

The counties, as defined by all ten species in the DCA, were arranged horizontally in ordination space, indicating that axis 1 may represent an important environmental or disturbance gradient. Linear regression showed that population per km^2 ($r = -0.407$) was the most important variable correlated with axis 1 (Table 5, Figure 3). The land use categories 'urban,' ($r = -0.317$) 'wetland,' ($r = +0.320$) and 'forest,' ($r = +0.287$) ranked next in importance and were significantly correlated with axis 1. Thus, axis 1 represents a weak urban to forest/natural area gradient. However, only *S. canadensis*, *A. altissima*, and *R. multiflora* were significantly correlated with axis 1. *Rosa multiflora* appears to be more closely associated with counties with high forest cover, whereas *S. canadensis* and *A. altissima* were more closely associated with counties with high urban land use cover and population per km^2 values. All other species were more strongly correlated with axis 2 or 3, but these axes were not

Table 4. Linear regression results using remotely-sensed landscape categories (1:250,000 scale) as separate independent variables and each species as the dependent variable. See Table 1 for definitions of the landscape categories. Only landscape categories that were significant for at least one species are shown; all others were not significant for all species. Pearson correlation coefficients (r) are listed; * denotes p-value ≤0.05 and ** denotes p-value ≤0.01. NS represents 'no significance.' Data for *Solidago canadensis*, a native early-successional species, are also presented

Species	Urban	Forest	Water	Agriculture	Pop/km^2
Alliaria petiolata	NS	−0.481**	NS	+0.477**	NS
Microstegium vimineum	NS	NS	NS	NS	NS
Lonicera japonica	NS	NS	NS	NS	NS
Celastrus orbiculatus	NS	NS	NS	NS	NS
Lonicera maackii	NS	NS	NS	NS	+0.292*
Lonicera morrowii	NS	NS	NS	NS	NS
Lonicera tatarica	+0.514**	−0.369*	+0.389**	NS	+0.574**
Rosa multiflora	NS	NS	NS	NS	NS
Ailanthus altissima	+0.261*	NS	NS	NS	+0.290*
Solidago canadensis	NS	NS	NS	NS	+0.108*

significantly correlated with any of the land use variables (Table 5). None of these patterns appear related to invasion history (Table 3) or shared plant characteristics.

DISCUSSION

Question 1. Is there a relationship between land-use cover types and the distribution of these exotic species?

The habitat data indicate that many of the species are defined by urbanized areas. The regression analyses show that population per km^2 and urban land use are the most important variables in defining the distribution of some of these species. However, these urban or disturbance type land uses do not explain the distribution of all the exotic species and actually better explain the distribution of the one weedy native species. Both the habitat data and the ordination analysis indicate that many of these exotic species are found in forested areas. *Lonicera tatarica*, *A. petiolata*, and *A. altissima* are significantly more likely to be found in highly urbanized or disturbed counties rather than well-forested counties. *Rosa multiflora* is significantly more likely to be found in highly forested counties. The expected land use type distribution for the remaining exotic species remains unclear. *Microstegium vimineum*, *C. orbiculatus*, and *L. morrowii* show a trend of being found in well-forested counties or forested habitats and *L. japonica* shows a trend of being found in urbanized counties or more-urban habitat types. However, these trends are not significant. Moreover, contradictions in the results call to question the expected habitat or land use type of *A. petiolata*, *L. maackii*, and *R. multiflora*. Thus, though some land use and habitat types are clearly more important for some species, the variation among the species weakens any general conclusions that can be made about distribution and land use relationships of invasive exotic plants. Nonetheless, it is clear that the nine species are not behaving like a typical early-successional species (e.g., *Solidago canadensis*), which is significantly correlated with more urbanized counties and habitats and is never found in a forested area. Consequently, these results do support the assertion that our oak-dominated forests are not immune to invasion by these nine exotic species.

Question 2. Are there spatial and temporal patterns shared by these exotic species?

Depending on the analysis, some species do appear to be similar in their distribution. For instance, *C. orbiculatus*, *M. vimineum*, *L. morrowii*, and *R. multiflora* may be more likely to be found in forested areas or counties with a high percentage of forest cover. In contrast, *A. altissima*, *L. tatarica*, *A. petiolata*, *L. japonica*, and *S. canadensis* may be more likely to be

Table 5. Pearson's correlation coefficients (r) of each species and land use category with the DCA ordination axes. * denotes p-value ≤0.05 and ** denotes p-values ≤0.01

Species/Land Use	Axis 1	Axis 2	Axis 3
Alliaria petiolata	−0.200	+0.162	−0.295*
Microstegium vimineum	+0.109	+0.508**	−0.062
Lonicera japonica	−0.156	−0.166	−0.399**
Celastrus orbiculatus	+0.078	+0.117	−0.193
Lonicera maackii	−0.255	−0.410	−0.050
Lonicera morrowii	−0.043	−0.188	+0.286*
Lonicera tatarica	−0.147	−0.142**	−0.030
Rosa multiflora	+0.459**	−0.497**	+0.082
Ailanthus altissima	−0.277*	−0.214	−0.590**
Solidago canadensis	−0.664**	+0.081	+0.238
Fragmentation	−0.073	+0.012	+0.083
Pop/km^2	−0.407**	−0.145	−0.093
Urban	−0.317*	−0.152	−0.135
Agricultural	−0.219	+0.014	−0.118
Forest	+0.287*	+0.041	+0.130
Water	−0.165	−0.190	−0.148
Wetland	+0.320*	−0.250	+0.125
Disturbed	−0.041	+0.109	+0.253

found in urbanized/agricultural/disturbed areas. However, none of these similarities are evident in the color-coded county diagrams, meaning there appear to be no shared county-level spatial or temporal patterns among these species. It is possible that we are missing crucial environmental variables, such as soil type and topography. These environmental variables may be more important than land use categories or the synergy of the two may be the key in revealing patterns (Bossard 1991, Burke and Grime 1996).

Question 3. Are these patterns related to any species characteristics?

None of these distributions appear to be related to shared invasion history or plant characteristics. This finding is disappointing given past research focus on shared plant characteristics that may predict invasive potential (Rajmanek and Richardson 1996, Reichard and Hamilton 1997, Kolar and Lodge 2001). Invasive plant characteristics combined with invasion history of each plant do not lead to predictable distribution patterns.

Question 4. Can we reliably use herbarium and remotely-sensed land classification data to predict the spread of these invasive exotic plants into forested areas?

Contradictions in our data and the lack of patterns could be due to weaknesses in both the herbarium and remotely-sensed data. For instance, the habitat data indicates that *A. petiolata* and *L. maackii* are likely to be found in forested areas, but the regression and ordination results both indicate that these species are more likely to be found in non-forested areas. *Alliaria petiolata* and *L. maackii* may be good examples of species found in forested areas but located in non-forested counties, possibly in small fragmented forest patches. This possibility is supported by Hutchinson and Vankat's (1998) landscape-level research on *L. maackii* in Ohio. The converse is also possible; *R. multiflora* specimens in a given county still may have been found more commonly near roads or in old fields (as our habitat data indicate), but in highly forested counties (ordination results). *Rosa multiflora* may have been restricted somewhat to smaller, abandoned farms where it was historically planted as a hedgerow species (Laycock 1985). Many of these smaller farms were likely located in well-forested counties or counties that have since reverted to forests.

Because of these contradictions and a lack of patterns, I conclude that both herbarium and coarse land use data are currently inadequate in predicting the spread and distribution of exotic

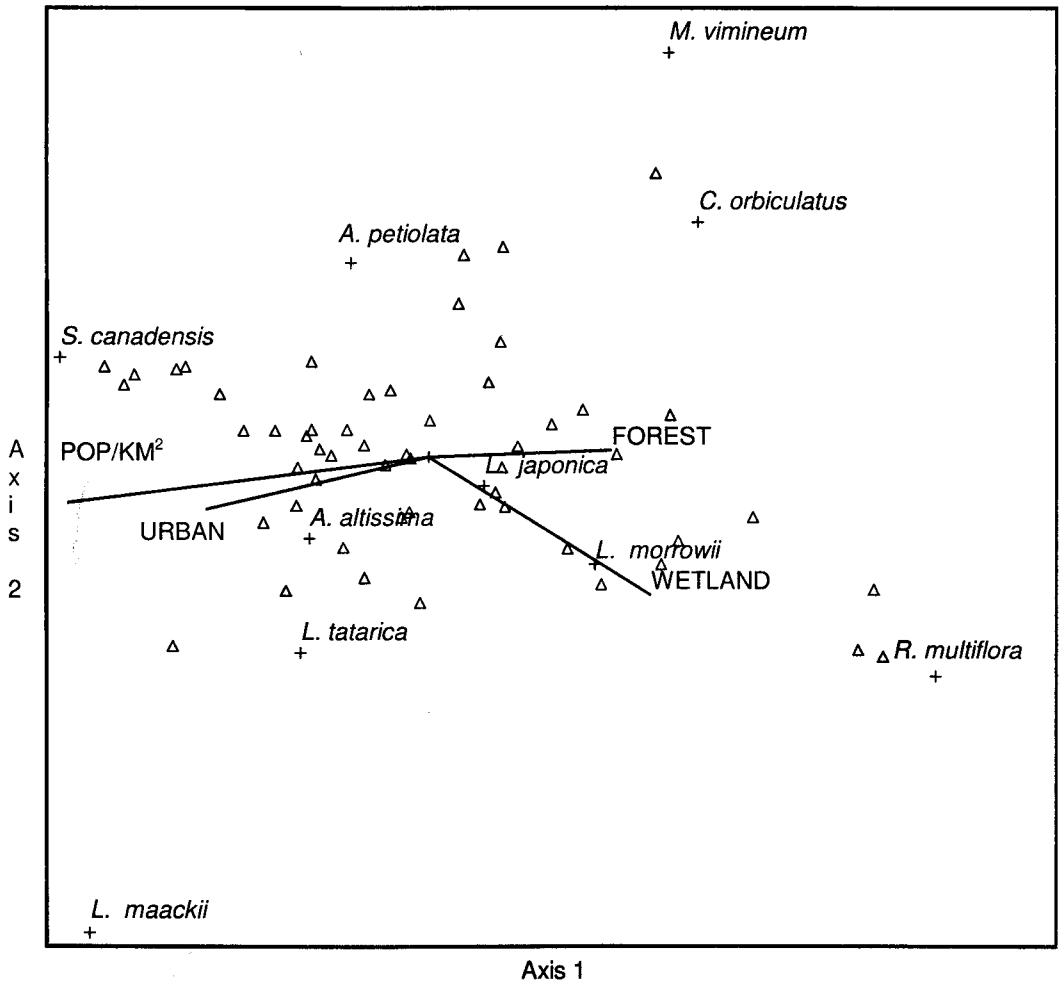

Figure 3. Detrended correspondence analysis (DCA) relating length of time (time span) each species has been in each county and the land use categories as defined by USGS 1:250,000 land classification data (Table 1), showing only significant variables (Table 5). The ordination scores defined by the ten species for each county, are represented by diamonds in the diagram. The eigenvalues for axis 1, 2, and 3 are 0.267, 0.184, and 0.114, respectively.

invasive plants. However, this weakness does not appear to be due to collection patterns or biases; the nine species did not have the same collection pattern bias as the other species in the West Virginia Herbarium (Figure 2). Instead, I argue that it is due to insufficient herbarium data. A lack of collections is evident when a very common native weed is not recorded for several West Virginia counties.

Based on these findings, it is unlikely if similar 'Slow The Spread' programs, as developed for the gypsy moth and other exotic insects making their way across the United States (http://www.ento.vt.edu./STS/), can be developed for invasive exotic plants. Invasion fronts for plants may not be easily delineated due to incomplete herbarium collections. However, an indistinct front may also be due to lack of quarantines on the transport and sale of the invasive exotic plant as well as characteristics unique to plants, such as long-lived seeds in the seed bank and vegetative growth (Liebhold et al. 1995, Mack et al. 2000). Moreover, our data indicate that susceptible land use types are not easily defined for each exotic species, whereas susceptible forest types and host species are more easily defined for exotic insect pests.

The search for exotic plant invasion patterns may be a misguided effort given the complexity of the systems and the interacting mechanisms behind invasion, making invasibility and its impact entirely site-specific (Bossard 1991, Burke and Grime 1996, Lambrinos 2002). Indeed, the latter may explain why the invasive nature of my nine species appears so idiopathic. Nonetheless, a better understanding of the strengths and weaknesses of herbarium data and their potential use and misuse, which this paper hopefully provides, may encourage voucher collections and subsequent herbarium deposits from more detailed plot data. Permanent monitoring plots that are widespread and include detailed environmental and disturbance measurements may be the best way to track invasive plant species, if voucher specimens are diligently collected and deposited in accessible herbaria over time. This information, coupled with studies on the underlying mechanisms of invasion, may help identify patterns of invasibility and any associated exotic plant species guilds (Lavoral et al. 1999).

ACKNOWLEDGMENTS

I thank Donna Ford-Werntz of the West Virginia University Herbarium for her guidance, Gino Luzader for help in obtaining the USGS data, and the United States Forest Service for funding this project.

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Received October 4, 2001; Accepted April 29, 2002.