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## Colonization dynamics of four exotic plants in a northern Piedmont natural area<sup>1</sup>

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### ABSTRACT

ROBERTSON, D. J., M. C. ROBERTSON AND T. TAGUE (Pennypack Ecological Restoration Trust, 2955 Edge Hill Road, Huntingdon Valley, PA 19006-5099). Colonization dynamics of four exotic plants in a northern Piedmont natural area. Bull. Torrey Bot. Club 121: 107-118. 1994. — Frequency and density of four invasive non-native plants (*Lonicera japonica* [L.] Thunb., *Ampelopsis brevipedunculata* [Maxim.] Trautv., *Celastrus orbiculatus* Thunb. and *Rosa multiflora* [L.] Thunb.) were measured in the Pennypack Wilderness, a 324 ha natural preserve located in a southeastern Pennsylvania suburban landscape. Stem frequency and density of each species were measured during 1988 and 1989 in 163 plots of 20 m<sup>2</sup> each located randomly and distributed proportionally among the 10 successional plant communities comprising the preserve. *Lonicera japonica* was the most frequently encountered and densely growing plant; frequency and density of the other three species appeared to be related to autecological characteristics of the species. Analysis of colonization and density patterns revealed that mature forest generally supported the fewest and least dense colonies, a result of complete shading and limited colonization sites. Frequency and density were also lower in successional plant communities comprising a Mixed Oak forest sere than they were in communities comprising a Mixed Mesophytic forest sere, probably a result of edaphic characteristics or vagaries of the location of introduction.

Key words: Piedmont, southeastern Pennsylvania, *Lonicera japonica*, *Ampelopsis brevipedunculata*, *Celastrus orbiculatus*, *Rosa multiflora*, non-native species, colonization.

Most of the Piedmont north of the Potomac River has been settled by European immigrants and their descendants for nearly three centuries. Therefore, it is not surprising that at the end of the twentieth century the vast majority of the province is directly controlled by man for urban and agricultural uses. Godfrey (1980) estimates that only about 30% of the land is wooded or in some stage of succession. This long history of settlement and use also means that natural areas in the northern Piedmont have a history of heavy and repeated disturbance resulting from timber and firewood harvest, fire, disease, grazing, and insect infestations. Disturbance continues into the present as a result of encroaching urbanization, air pollution, lowered water tables, surface water pollution, and altered hydrographs (Murphy 1988).

Larger natural preserves in the northern Piedmont generally have been assembled by aggregating numerous abandoned agricultural fields, woodlots, and streamside corridors. The juxtaposition of meadows and forest produces an

“edge” at which the forest abruptly stops and gives way to fields dominated by low-growing, short-lived herbaceous species. Prior to the wholesale dominance of the region by European colonists, disturbances in the forest such as fire, a gap in the canopy resulting from the death of a large tree, or severe storm damage also produced edge habitat, but the openings, gaps and windthrows quickly regrew to thickets, young woodland and, in less than a century, to forest (Marks 1974). In the pre-colonial forest, canopy gaps and the corresponding edge habitat were small in relation to the surrounding forest. Seed “rain” and the soil seed bank consisted largely of seeds generated by the forest trees surrounding the gap. In addition, large expanses of unbroken forest physically inhibited invasion by wind and animal dispersed herbaceous colonizers (Marks 1983). In contemporary fragmented forests, in contrast, vast numbers of prolifically seeding native and non-native ruderals and exotic tree species surround and isolate the woodlands. Instead of the pre-colonial condition of treeless areas occurring as relatively small communities dominated by short-lived herbaceous species interrupting a substantially forested landscape, the contemporary northern Piedmont is largely de-

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forested and the woodland remnants are embedded in an agricultural and suburban matrix (Burgess and Sharpe 1981; Hill 1985).

The preponderance of edge habitat in northern Piedmont preserves has now set the stage for two serious problems challenging the ecological integrity of native forested natural areas. The first of these is a high density of white-tailed deer. Deer are reaching historically high densities in many areas on the East Coast (Whittington 1984; Storm et al. 1989). Numerous studies have demonstrated that deer browsing and grazing can have profound impacts on regeneration, abundance and distribution of plants, especially if deer populations are dense (Hough and Forbes 1943; Graham 1954; Hough 1965; Bratton 1979; Marquis 1981; Redding 1987; Tilghman 1989; USDA-FS 1988; Brush and Ehrenfeld 1991; Miller et al. 1992; Strole and Anderson 1992).

The second threat to native plant communities in the northern Piedmont and elsewhere in the East is the overwhelming abundance of introduced plants (Overlease 1978, 1987; Bratton 1979; Thomas 1980; Whigham 1984; Decker and Enck 1987; Guldin et al. 1990; Yost et al. 1991; Brothers and Spingarn 1992). The plants that are proving to be most problematic in the northern Piedmont were imported from eastern Asia. Climatic similarities between the two regions may contribute to the successful establishment of these species (Baker 1974).

Alien plants can produce problems both at the edge of the forest and deep within the woodland (Saunders et al. 1991). Those plants that invade the edge of the forest typically are species that require high light intensities to prosper (Ranney et al. 1981; Saunders et al. 1991; Brothers and Spingarn 1992). Multiflora rose (*Rosa multiflora* [L.] Thunb.), Oriental bittersweet (*Celastrus orbiculatus* Thunb.), porcelainberry (*Ampelopsis brevipedunculata* [Maxim.] Trautv.), Japanese honeysuckle (*Lonicera japonica* [L.] Thunb.), akebia (*Akebia quinata* Dcne.) and kudzu (*Pueraria lobata* [Willd.] Ohwi) can quickly overwhelm and destroy a forest edge once they become established (Lutz 1943; Thomas 1980; Jackson 1987; Yost et al. 1991). Deeper within the forest, the herbaceous layer and the spring ephemeral flora are endangered by species adapted to low light intensities. Garlic mustard (*Alliaria petiolata* [Bieb.] Cavara & Grande) is a Eurasian biennial herb that spreads rapidly and limits space for native vegetation through crowding (Cavers et al. 1979; Baskin and Baskin 1992). While Japanese honeysuckle and Oriental bit-

tersweet grow most profusely in the sun, they are able to invade disturbed woodlands and exclude desirable plants (Patterson 1974; Slezak 1976; Hardt 1986; Dryer et al. 1987; Dryer 1988). *Microstegium vimineum* (Trin.) A. Camus, an annual grass with a dense growth habit, has the unusual ability to grow as well as full sun as it does with 82% shading thereby allowing it to invade woodlands with incomplete canopy closure (Winter et al. 1982).

We evaluated the colonization frequency and stem density of four of the most widespread exotic species in the Piedmont as independent functions of seral stage and forest association. The species of interest were Japanese honeysuckle (hereafter *L. japonica*), Oriental bittersweet (*C. orbiculatus*), porcelainberry (*A. brevipedunculata*), and multiflora rose (*R. multiflora*). Specifically, we sought answers to two questions: (1) do the exotic species occur as frequently and grow as densely in seral stages that have a history of limited disturbance as they do in seral stages that are subject to recent or frequent disturbance, and (2) do the exotic species occur more frequently and grow more densely in a Mixed Oak or a Mixed Mesophytic forest sere?

**STUDY SITE.** The Pennypack Wilderness is a private, 324 ha natural preserve surrounded by the northern suburbs of Philadelphia in Upper and Lower Moreland Townships and Bryn Athyn Borough, Montgomery County, Pennsylvania (40°08'39"N; 75°04'28"W). The preserve is located in the central portion of the 145 km<sup>2</sup> watershed of Pennypack Creek, a 35 km-long tributary of the Delaware River (Fig. 1).

The Wilderness straddles both of the two major geologic divisions of the northern Piedmont (Pennsylvania Bureau of Topographic and Geologic Survey 1960). The southern two-thirds of the preserve are underlain by Baltimore Gneiss, the crystalline Precambrian granitic bedrock that forms the basement of the entire province. The northern third of the Wilderness extends onto the Stockton Formation of the Newark Basin, one of six East Coast lowlands comprised of much less resistant Triassic sedimentary rocks.

We have surveyed extensively the arboreal vegetation of the mature forest stands comprising the Wilderness using the quarter-point method (Cottam and Curtis 1956). The forest vegetation can be organized into two associations related to soil type. In the northern third of the Wilderness, the relatively droughty soils derived from the Triassic sandstones support a Mixed

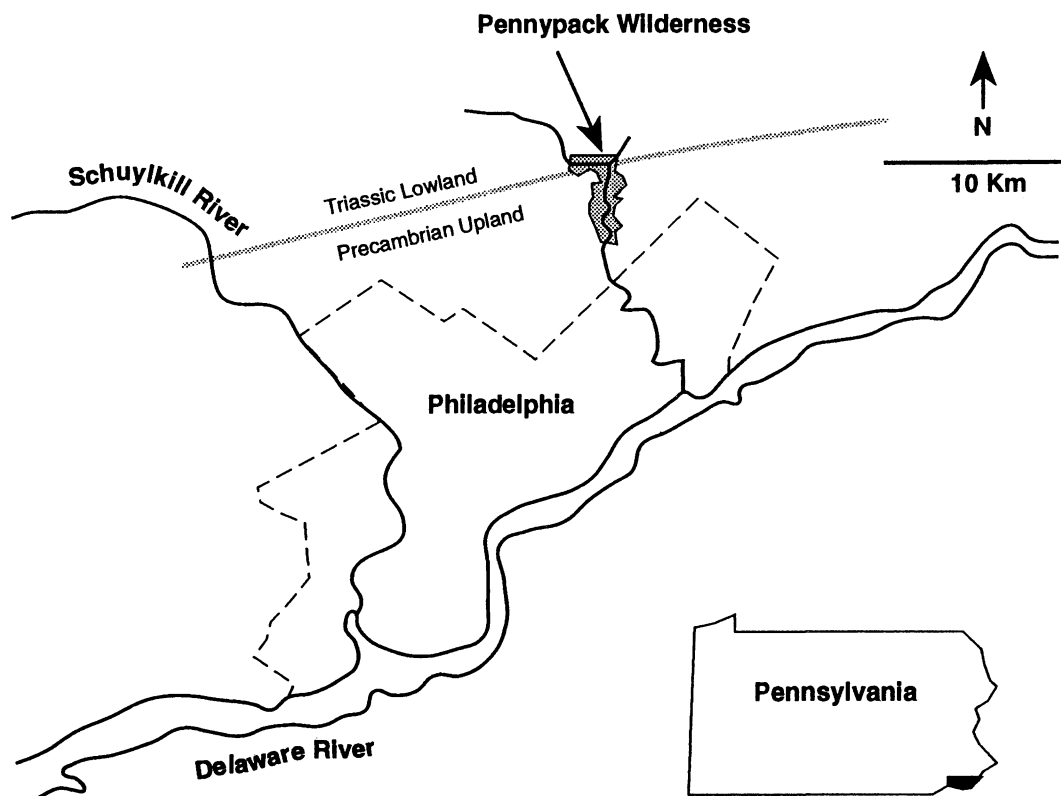


Fig. 1. Location of the Pennypack Wilderness preserve in southeastern Pennsylvania.

Oak association. The Mixed Oak forest in the Pennypack Wilderness is characterized by American beech (*Fagus grandifolia* Ehrh.) [relative dominance (r.d.) 0.58], chestnut oak (*Quercus prinus* L.) [r.d. 0.16], black oak (*Quercus velutina* Lam.) [r.d. 0.16], northern red oak (*Quercus rubra* L.) [r.d. 0.05], white oak (*Quercus alba* L.) [r.d. 0.03], tuliptree (*Liriodendron tulipifera* L.) [r.d. 0.03], shellbark hickory (*Carya lacinosa* Michx. f.) [r.d. 0.03], and five other species [cumulative r.d. 0.06]. American chestnut (*Castanea dentata* [Marsh.] Borkhr) was also formerly a co-dominant component of the mature forest, hence the characterization of this forest association as "Oak-Chestnut" by Keever (1973). Frequency of occurrence surveys of understory, shrub and herbaceous species conducted concomitantly with this study revealed a shrub flora dominated by low thickets of heaths (*Vaccinium* spp. L.) and viburnums (especially *Viburnum acerifolium* L. and *V. dentatum* L.).

In the southern two-thirds of the preserve, in contrast, the deep, silty soils derived from weathering of the ancient granitic and hornblende gneisses support a diverse Mixed Mesophytic as-

sociation of tuliptrees [r.d. 0.55], American beech [r.d. 0.24], northern red oak [r.d. 0.05], white oak [r.d. 0.04], white ash (*Fraxinus americana* L.) [r.d. 0.03], hickories (*Carya* spp.) [r.d. 0.02], bird cherry (*Prunus avium* [L.] L.) [r.d. 0.02], and nine other species [cumulative r.d. 0.05]. Flowering dogwood (*Cornus florida* L.) and sourgum (*Nyssa sylvatica* Marsh.) are abundant in the subcanopy. The shrub layer is dominated by spicebush (*Lindera benzoin* [L.] Blume), blackhaw (*Viburnum prunifolium* L.), downy arrow-wood (*Viburnum rafinesquianum* Schultes), arrow-wood (*Viburnum dentatum* L.), witch hazel (*Hamamelis virginiana* L.), and shadbush (*Amelanchier arborea* [Michx. f.] Fern.).

In the Wilderness each of the two forest associations, in turn, is comprised of four seral stages: mature forest, woodlands, thickets, and old fields. In the Mixed Oak association, the even-aged 60–70 year old woodlands contain especially large numbers of red maples and white ashes in addition to the species that characterize the forest association in general. Thickets which have recently regrown from abandoned fields in the Mixed Oak association are characterized by ex-

remely dense stands of red maple, black cherry (*Prunus serotina* Ehrh.), bird cherry, dogwood and sassafras (*Sassafras albidum* [Nutt.] Nees) saplings. Scattered throughout are larger specimens of red cedars (*Juniperus virginiana* L.), crab apples (*Malus* spp.), and hawthorns (*Crataegus* spp.). Red-ossier dogwood (*Cornus sericea* [Michx.] L.) and withered (*Viburnum cassinoides* L.) are common shrubs. Mixed Oak old fields contain typical herbaceous vegetation dominated by goldenrods (*Solidago* spp.). However, as in the mature forest, ericaceous shrubs (e.g., *Vaccinium* spp.) are abundant in the best-drained and least disturbed of the Mixed Oak old fields.

Mixed Mesophytic woodlands are nearly uniform stands of tuliptrees, white ashes and red maples. Dogwoods and cherries are the principal understory trees, although red maples, sourgums and occasional oaks occur. The Mixed Mesophytic thickets are dominated by red maple saplings, though black walnuts (*Juglans nigra* L.) and white ash saplings are also commonly encountered. The extremely densely shaded thickets in the Pennypack Wilderness support little understory vegetation, but goldenrods, *Microstegium vimineum*, ferns, wood nettles (*Laportea canadensis* [L.] Wedd.) and poison ivy (*Toxicodendron radicans* [L.] Kuntze) are the most common plants where light is sufficient to support herbaceous plants. In the Mixed Mesophytic old fields, goldenrods and brambles (*Rubus* spp. L.) predominate, often joined by grasses such as little bluestem (*Schizachyrium scoparium* Michx.) and herbs such as milkweed (*Asclepias* spp. L.), Indian hemp (*Apocynum cannabinum* L.) and poison ivy. Woody invaders include red cedar, flowering dogwood, sassafras, white oak, red maple, and Tree-of-Heaven (*Ailanthus altissima* [Mill.] Swingle).

Threading through all of the communities is riparian forest along the main stem of Pennypack Creek and its larger tributaries. Box-elder (*Acer negundo* L.) and sycamore (*Platanus occidentalis* L.) are important components of the flora on all of the flood plains. In the northern third of the preserve, silver maple (*Acer saccharinum* L.) and green ash (*Fraxinus pennsylvanica* Marsh.) share dominance on soils derived from Triassic sandstones. Downstream on the granitic soils, butternut (*Juglans cinerea* L.), black walnut, red maple, white ash, sycamore, and the naturalized Southern catalpa (*Catalpa bignonioides* Watt.) are important components. Because the forest composition of riparian areas is strongly related to the high-energy, unpredictable environment

of the flood plain, we consider the riparian areas as a fifth "seral stage" in subsequent analyses of the relationship between seral stage and exotic species.

**Methods.** The Wilderness was assembled from over 100 parcels. Historical land use within each tract tended to be homogeneous and changed abruptly at discrete, usually fenced, boundaries. Often, we could date with some precision when agriculture on individual tracts was abandoned. Therefore, we were able to trace the boundaries of the vegetation communities comprising the preserve onto a 1:200 scale map of the Wilderness and measure the size of each of the communities using a polar planimeter. We then located 163 circular plots of 20 m<sup>2</sup> each throughout the preserve. The number of plots located in each of the vegetative communities was proportional to the representation of the communities within the whole of the preserve. In the Mixed Oak association, 7 (4.3%) of the plots were assigned to mature forest stands, 2 (1.2%) to woodlands, 12 (7.4%) to thickets, 0 (0.0%) to old fields, and 6 (3.7%) to riparian forests. In the Mixed Mesophytic association, 18 (11.0%) of the plots were located in mature forest, 57 (35.0%) in woodlands, 4 (2.5%) in thickets, 21 (11.7%) in old fields, and 36 (22.1%) in riparian forest. The plots were located randomly within each seral stage of placing a numbered grid over the map and selecting coordinates on the grid from a random numbers table.

In the field we located the plots at the positions charted on the map, marking the center of the plot with a steel stake. We delimited the plot margins by tracing a circle with a radius of 2.5 m around the center. Within each plot, we counted all rooted stems of *L. japonica*, *C. orbiculatus*, *A. brevipedunculata*, and *R. multiflora*. In plots in which we judged *L. japonica* coverage to be nearly continuous and uniform, we counted stems in randomly selected portions of the plot to save time and extrapolated the total number of *L. japonica* stems to the entire plot. Field work was completed during the months of September and October in 1988 and 1989.

To determine if the frequency of occurrence of individual exotic species was related to seral stage, we performed R × C tests of independence (Sokal and Rohlf 1969) using the presence of a specimen in a plot as a measure of frequency. If a plot contained the species of interest (regardless of the number of individuals), we recorded the plot as an occurrence. Each of the four exotic

Table 1. Frequency of occurrence of four exotic species by seral stage (regardless of forest association): mature forest, woodland, thicket, old field, and riparian. R  $\times$  C test significance values: \* 0.05 > P > 0.01; N.S. not significant (P > 0.05).

Taxon	Serai stage					P-value
	Forest	Woodland	Thicket	Old Field	Riparian	
<i>Lonicera japonica</i>	0.48	0.91	0.71	0.76	0.71	*
<i>Ampelopsis brevipedunculata</i>	0.04	0.37	0.06	0.12	0.45	*
<i>Celastrus orbiculatus</i>	0.39	0.26	0.37	0.41	0.24	N.S.
<i>Rosa multiflora</i>	0.17	0.50	0.56	0.38	0.57	*

species was evaluated independently of the other species. To determine if frequency of occurrence was related to forest association, we compared the number of colonized plots in the Mixed Oak and Mixed Mesophytic associations using a  $\chi^2$  analysis (Sokal and Rohlf 1969).

Another aspect of exotic species colonization, density of exotic species both as a function of seral stage as well as a function of forest association, was evaluated using one-way analyses of variance (ANOVA; Sokal and Rohlf 1969). Each plant species was evaluated individually. Only plots containing the exotic species were included in the density analyses. In the cases in which ANOVA indicated significant differences in density, the data were evaluated further using the Student-Newman-Kuels a posteriori test (SNK; Sokal and Rohlf 1969) to identify the sources of the variability.

**Results. FREQUENCY OF OCCURRENCE BY SERAL STAGE.** *Lonicera japonica*, *A. brevipedunculata*, and *R. multiflora* occurred with greater frequency in some seral stages than in others (R  $\times$  C test, 0.05 > P > 0.01). In contrast, an R  $\times$  C analysis revealed that the presence of *C. orbiculatus* did not appear to be related to seral stage (P > 0.05). Frequency data and results of the seral stage analyses are summarized in Table 1.

In the mature forest, the number of plots containing *L. japonica* and the number of plots without *L. japonica* were virtually identical. In all four other seral stages, a large majority of the plots had been invaded by *L. japonica*. Three-quarters of the plots sampled in the thickets, old fields and riparian zones contained *L. japonica*. In the woodlands, fully 90% of the plots had been invaded, the highest frequency of invasion observed for any species in any seral stage. Overall, *L. japonica* was, by far, the most pervasive of exotics, occurring in three-quarters of all plots sampled.

*Ampelopsis brevipedunculata* was far less widespread than *L. japonica*, occurring on average in

only 29% of all plots. The differences we observed among seral stages ranged from a low of almost no occurrence (4%) in mature forest plots to riparian areas in which nearly half (45%) of the plots had been invaded. Considerably less than half of the woodland, thicket and old field plots contained *A. brevipedunculata*.

*Rosa multiflora* had successfully invaded a majority of riparian areas (57%) and thickets (56%), but had been less successful in mature forest and old fields where far less than half the plots supported *R. multiflora* bushes. In woodlands, half the plots contained *R. multiflora* and half did not. Nearly half (45%) of all plots sampled contained at least one *R. multiflora* stem, making it the second most frequent exotic after *L. japonica*.

*Celastrus orbiculatus* is the only species of the four in which differences in colonization were not significant among seral stages. Variability in colonization was low among seral stages, ranging from about 25% in riparian and woodland areas to about 40% in all three other stages. In all cases, the number of plots that had been invaded was smaller than the number of plots that remained free of the species. Overall, *C. orbiculatus* occurred in 30% of all plots.

**FREQUENCY OF OCCURRENCE BY FOREST ASSOCIATION.** We did not observe significant differences in the frequency of colonization between the Mixed Oak and Mixed Mesophytic forest associations by *L. japonica* and *R. multiflora* ( $\chi^2$ , P > 0.05). Fully 70% of the Mixed Oak plots and 78% of the Mixed Mesophytic plots had been colonized by *L. japonica*. Colonization rates were even more similar, though lower, for *R. multiflora*; 41% of Mixed Oak plots and 44% of Mixed Mesophytic plots contained *R. multiflora* bushes.

In contrast, *A. brevipedunculata* and *C. orbiculatus* both occurred with greater frequency in the Mixed Mesophytic than in the Mixed Oak association ( $\chi^2$ , *A. brevipedunculata* P < 0.001; *C. orbiculatus* 0.05 > P > 0.01). *Ampelopsis*

Table 2. Frequency of occurrence of four exotic species by forest association: Mixed Oak vs. Mixed Mesophytic.  $\chi^2$  test significance values: \*  $0.05 > P > 0.01$ ; \*\*\*  $P < 0.005$ ; N.S. not significant ( $P > 0.05$ ).

Taxon	Forest association		P-value
	Mixed Oak	Mixed Mesophytic	
<i>Lonicera japonica</i>	0.70	0.78	N.S.
<i>Ampelopsis brevipedunculata</i>	0.00	0.30	***
<i>Celastrus orbiculatus</i>	0.22	0.32	*
<i>Rosa multiflora</i>	0.41	0.44	N.S.

*brevipedunculata* did not occur in any Mixed Oak plots but was observed in 30% of Mixed Mesophytic samples. The disparity between associations was not as great for *C. orbiculatus*, although the difference between the 22% colonization rate in the Mixed Oak and 32% in the Mixed Mesophytic plots was significant. Results of the analyses are included in Table 2.

**DENSITY BY SERAL STAGE.** Like the  $R \times C$  analyses of differences in frequency between seral stages, ANOVA revealed significant differences in density among seral stages for all species but *R. multiflora* (Table 3). For *L. japonica*, the difference was especially striking (ANOVA,  $P < 0.001$ ). Results of SNK analysis indicated that there were no significant differences in density among forest, woodland, and riparian areas. However, average *L. japonica* density in forests, woodlands, and riparian areas was significantly lower than the average density recorded in thickets and old fields. Average densities in thickets and old fields were not significantly different from one another. *Lonicera japonica* grew most densely in old fields and thickets, and least densely in mature forest. Density in woodlands was between the two extremes. The density of riparian areas was low, only slightly greater than the density in the mature forest.

As noted previously, *L. japonica* was the most frequently encountered of the four exotic species we evaluated. *Lonicera japonica* was also, by far, the most densely growing of all four species. With the exception of *C. orbiculatus*, which grew as densely in old fields as did *L. japonica* in the shadier communities, *L. japonica* grew at least five times as densely as the next most densely-growing species (*A. brevipedunculata*) in riparian areas.

*Celastrus orbiculatus* had a density distribution pattern much like that of *L. japonica* with

significant differences among seral stages (ANOVA,  $0.05 > P > 0.01$ ). SNK analysis revealed that *C. orbiculatus* grew significantly more densely in old fields than it did in all other seral stages; differences among the remaining four seral stages were not significant. *Celastrus orbiculatus* grew least densely in thickets, slightly more densely in riparian areas, mature forest and woodlands, and much more densely in old fields. In old fields, *C. orbiculatus* grew twenty times as densely as in thickets, and nearly 16 times as densely as in riparian tracts.

*Ampelopsis brevipedunculata* density exhibited a pattern opposite that observed for *L. japonica* and *C. orbiculatus*, though differences among seral stages were significant nonetheless (ANOVA,  $0.05 > P > 0.01$ ). SNK analysis indicated that average *A. brevipedunculata* densities were the same in woodlands, thickets and old fields, which, in turn, were significantly lower than the density in riparian areas. The analysis also indicated, however, that *A. brevipedunculata* densities in old fields and riparian areas were not significantly different from one another. We observed the species so rarely in plots located within mature forest stands (frequency: 0.04) that we were unable to include mature forest in the analysis.

**DENSITY BY FOREST ASSOCIATION.** The density of three of the species was evaluated by ANOVA to determine if there were differences in density related to the major forest associations (Table 4). Only plots that contained the exotic species of interest were included in the evaluation (i.e., "zero" density plots were excluded from the analyses). *Ampelopsis brevipedunculata* was not included because it was not observed in any of the Mixed Oak plots.

There were no significant differences in the densities of *L. japonica* and *C. orbiculatus* between plots sampled in the Mixed Oak and the Mixed Mesophytic associations (ANOVA,  $P > 0.05$ ). In contrast, there was a very significant difference (ANOVA,  $P < 0.001$ ) in the density of *R. multiflora* stems between associations, with the Mixed Oak association supporting an average of 0.40 stems/m<sup>2</sup> compared to an average of 1.15 stems/m<sup>2</sup> in Mixed Mesophytic plots.

**Discussion.** Our analyses of the distributions and densities of four introduced species in the Pennypack Wilderness preserve revealed that: (1) each species occurred least frequently in the mature forest; (2) stem densities were lowest in the

mature forest; and (3) overall, regardless of seral stage, average stem densities were lower in the Mixed Oak association than in the Mixed Mesophytic association. Because unique characteristics of mature forest are probably responsible for producing the first two observations, we treat them together. Other, probably unrelated characteristics, led to the third observation, which we discuss separately.

**LOW FREQUENCY AND DENSITY IN MATURE FOREST.** In contrast to all of the other seral stages that we evaluated, mature forest possesses characteristics that work synergistically to produce low exotic plant frequencies and densities. The first and most important of these is low light levels on the forest floor. In the Mixed Mesophytic forests, in particular, light intensities on the forest floor (where seeds germinate and seedlings compete for light) are especially low because a very dense cover of shade-tolerant spicebush has developed which creates a secondary closed shrub canopy. In the Mixed Oak forest, shrub vegetation is less dense and as a result the forest floor receives more light, but the mature forest, nevertheless, is characterized by a complete and closed overstory tree canopy.

At least three of the four species of problematic exotics in the Pennypack Wilderness have difficulty becoming established in mature forest. In contrast to the deep shade offered by the forest, these exotics germinate and prosper best in full sunlight. The light required for germination and vigor of seedlings varies among species. *Rosa multiflora*, like all roses, grows best in full sunlight and is usually shaded out by more aggressive and shade-tolerant shrubs and trees in forests (Jackson 1987). Although no specific information is available on the light requirements of *A. brevipedunculata*, the species appears to be shade-intolerant (Yost et al. 1991). Species of the closely related native genus *Vitis* (grape) are very intolerant of shade and require nearly full sun to grow (Smith 1984). Gallace (1990) reported that grape seedlings will die within three years of germinating under a complete forest canopy. *Lonicera japonica* is more tolerant of shading. *Lonicera japonica* seeds will germinate in low light and are able to survive under considerably shaded conditions (Sather 1992). Anecdotal evidence and conventional wisdom suggest that there is a negative correlation between vigor of *L. japonica* and shading (e.g., Andrews 1919; Handley 1945; Slezak 1976; Barden and Matthews 1980; Cain 1984; Hardt 1986), but only

Table 3. Mean stem density (with standard deviation) of four exotic species per 20 m<sup>2</sup> plot by seral stage (regardless of forest association): mature forest, woodland, thicket, old field, and riparian. ANOVA significance values: \* 0.05 > P > 0.01; \*\*\* P < 0.001; N.S. not significant (P > 0.05). Mean densities followed by the same letter in italics are not significantly different from one another as indicated by SNK analysis.

Taxon	Serial stage					P-value
	Mature	Woodland	Thicket	Old Field	Riparian	
<i>Lonicera japonica</i>	158.9 ± 135.2a	267.9 ± 290.1a	295.0 ± 238.8b	497.9 ± 440.1b	168.4 ± 178.0a	***
<i>Ampelopsis brevipedunculata</i>	2.0 ± 0.0c	5.5 ± 4.3d	3.0 ± 0.0d	2.5 ± 0.6d,e	33.3 ± 55.6e	*
<i>Celastrus orbiculatus</i>	25.6 ± 42.3f	25.9 ± 61.7f	13.3 ± 24.9f	260.5 ± 265.7g	16.1 ± 28.5f	*
<i>Rosa multiflora</i>	9.5 ± 8.1h	21.8 ± 47.2h	27.2 ± 52.4h	23.6 ± 22.7h	24.8 ± 33.2h	N.S.



Table 4. Mean stem density (with standard deviation) of four exotic species per 20 m<sup>2</sup> plot by forest association (Mixed Oak, Mixed Mesophytic) regardless of seral stage. ANOVA significance values: \* 0.05 > P > 0.01; \*\* 0.01 > P > 0.001; \*\*\* P < 0.001; N.S. not significant (P > 0.05).

Taxon	Forest association		P-value
	Mixed Oak	Mixed Mesophytic	
<i>Lonicera japonica</i>	253.8 ± 246.3	274.6 ± 297.6	N.S.
<i>Ampelopsis brevipedunculata</i>	0	16.2 ± 37.3	—
<i>Celastrus orbiculatus</i>	10.0 ± 21.9	68.4 ± 149.5	N.S.
<i>Rosa multiflora</i>	8.0 ± 8.7	22.9 ± 41.3	***

two quantitative studies have demonstrated a link. Leatherman (1955), relying largely on cuttings exposed to varying shading regimes in field and greenhouse experiments, demonstrated inverse relationships between survival, productivity and growth vs. degree of shading, but the relationships were not straightforward and unequivocal. Studies by Thomas (1980) on an island in the Potomac River that had been invaded by several exotics including *L. japonica* clearly demonstrated that the intensity of light has a direct effect on productivity and vigor. Although *L. japonica* may persist and even spread in dense shade, it rarely flowers or produces fruit under these conditions.

*Celastrus orbiculatus* is probably the most shade-tolerant of all four species. In fact, best germination occurs under low light intensities (Dryer et al. 1987; Dryer 1988), and Patterson (1974) observed numerous seedlings growing in the shade of dense parent thickets. *Celastrus orbiculatus* is able to acclimate to low light levels and persist for long periods under heavy shading, then grow explosively if shading is reduced through creation of a gap in the canopy (Patterson 1974; Dryer et al. 1987; Dryer 1988). Despite its ability to survive under shaded conditions, however, *C. orbiculatus* is most abundant in stands representing early stages of succession, in understocked stands, and at forest edges. As tree density increases, the number and vigor of individual *C. orbiculatus* vines tends to decrease (Lutz 1943).

While low light intensity is probably the most important factor limiting colonization by exotics, the fact that mature forests enjoy a long period relatively free of landscape-scale physical disturbance also helps these forests resist invasion (Auclair and Cottam 1971). A history of soil disturbance is an important factor in the invasion of plant communities by exotics (Crawley 1986; Hobbs and Huenneke 1992). In the Pennypack Creek valley, the forested stands have been mostly undisturbed for over 130 years which has al-

lowed the canopy to close over the forest floor and has permitted organic matter to accumulate. In addition, except where animal digging activity has disturbed the soil or fallen trees have created massive tip-up root mounds, a layer of humus overlies the mineral soil in mature forests.

In temperate woodlands, seedling establishment of relatively small-seeded genera is adversely affected by a continuous cover of litter, and there is a strong tendency for seedling survival in such species to be restricted to local areas where mineral soil is exposed or to sites such as rotting logs or trees stumps (Keever 1973; Marks 1983). Such seedbed conditions, coincidentally, often occur in areas of recent disturbances that also produce high light levels such as blowdowns, death of a canopy tree, or human disturbance. In contrast, large-seeded species such as oaks, chestnuts, hickories and beech are capable of emerging from beneath litter and appear to experience lower rates of seed predation in such circumstances (Grime 1979).

Many of the small-seeded native genera such as *Betula*, *Pinus*, *Salix*, *Tsuga*, *Liquidambar*, *Rhus* and *Liriodendron* require exposed, disturbed sites to become established and grow rapidly. Like these native pioneers, the problematic exotics in the northern Piedmont produce seeds of approximately the same size (USDA-FS 1974). In addition to producing small seeds with minimal energy stores and seedlings with limited ability to penetrate organic litter, native and exotic colonizing species share several characteristics that make them successful competitors including rapid generation of biomass, continuous stem elongation and leaf production during the growing season, rapid physical adjustment to shading, reproduction after relatively few growing seasons, and production of large numbers of seeds (Bormann 1953; Grime 1979; Christiansen and Peet 1981; Holland and Olson 1989).

Other seral stages besides mature forest possess some of the characteristics that make the mature forests resistant to invasion, but none to

the same extent as the forest. For example, riparian areas are equally, if not more, shady than the mature forest (Thomas 1980). However, flooding represents a high-frequency disturbance regime that allows little humus to accumulate on the forest floor, restores fertility, and periodically replenishes the seed bank, incorporating seeds of exotics if the plants are growing upstream (Grime 1979; Van Cleve and Viereck 1981; Gosselink and Lee 1989; Williams 1993). Woodlands are also shaded, but the canopy is not as complete, disturbance is more recent, and humus is still in the process of aggrading (Bormann and Likens 1979). Thickets are characterized by even lower levels of organic matter and disturbance that occurred within two decades.

It is not a straightforward matter to continue to project seral processes "backward" in time to old fields. The characteristics that make each successively earlier seral stage more vulnerable to invasion, especially with respect to light, may not be applicable in old fields. For example, although the amount of light intercepted above the soil surface by dense herbaceous growth in old fields may be comparable to that intercepted by forest (Grime 1979), there is a major difference with respect to the height of the shading vegetation; because all of the plants that we investigated grow very rapidly, they can easily overtop field grasses and native herbs in one growing season. In addition, *L. japonica* and *R. multiflora* are semi-evergreen which allows them to photosynthesize unimpeded by shade during parts of the winter. Finally, disturbance in old fields is very recent; most old field communities have developed within a decade of abandonment.

**LOWER FREQUENCIES AND DENSITIES IN THE MIXED OAK ASSOCIATION.** Comparisons of the frequencies and densities of the exotic species between Mixed Oak and Mixed Mesophytic associations (regardless of seral stage) revealed that colonization frequencies and plant densities were consistently lower in the Mixed Oak association. The lower frequencies of *L. japonica* and *R. multiflora* recorded in the Mixed Oak plots were not significantly different from those recorded in the Mixed Mesophytic plots, but *C. orbiculatus* occurred significantly less frequently. The lower average densities of *L. japonica* and *C. orbiculatus* recorded in the Mixed Oak plots were not significantly different from those in the Mixed Mesophytic plots, but *R. multiflora* grew significantly less densely. *Ampelopsis brevipedunculata*

was not observed in any of the Mixed Oak association plots at all.

Forest composition differs dramatically between the Mixed Oak association growing on sedimentary-derived soils and the Mixed Mesophytic forest growing on metamorphic-derived soils, yet the soil supporting both these associations are very similar in pH, fertility, and suitability for supporting hardwood forest (USDA-SCS 1967). The Mixed Oak soils are slightly better drained, more acidic, and less fertile as a result of their origin on sandstones. These edaphic characteristics are expressed in the vegetation by the large number of drought-tolerant chestnut oaks in the canopy, the prominent ericaceous shrub layer (especially *Vaccinium stamineum* and *V. vacillans*), and the occurrence of colonies of ground pine (*Lycopodium clavatum* L. and *L. obscurum* L.). Chestnut oaks, blueberries, and ground pine are never found in association with the Mixed Mesophytic forests of the Wilderness. However, other not as yet identified, site-specific characteristics may be more important than soils in determining forest composition and invasibility in the Mixed Oak sere.

Despite its prominent absence, the lack of *A. brevipedunculata* in the Mixed Oak plot may not be indicative of differences between conditions regulating exotic species frequency or diversity. Though present in 1975 when a thorough vegetation inventory of the Wilderness preserve was completed, *A. brevipedunculata* was not perceived to be a significant problem by the stewardship staff. More than likely, *A. brevipedunculata* had recently invaded the Wilderness preserve in the early 1970's and had not yet spread widely. Based on current frequency and density patterns, we believe that *A. brevipedunculata* was probably introduced into the southern third of the preserve and is gradually expanding its range. The frequency of occurrence of *A. brevipedunculata* declines quickly north of the locus of highest frequency and density, but thins more gradually southward, the direction of flow of Pennypack Creek. It is likely that the *A. brevipedunculata* fruits fall into the creek and are carried downstream to colonize new areas. The presence of riparian colonies several kilometers downstream supports this contention. In contrast, the Mixed Oak association is located in the northern third of the preserve, upstream of the largest infestation. The absence of *A. brevipedunculata* may reflect true differences that make the Mixed Oak plots resistant to invasion, or it

Table 5. Comparison of frequencies of occurrence of three exotic species in forests and old fields in Wave Hill (Bronx, NY) and Pennypack Wilderness (Huntingdon Valley, PA).

	Forests		Old Fields	
	Wave Hill	Pennypack	Wave Hill	Pennypack
<i>Ampelopsis brevipedunculata</i>	0.70	0.23	0.88	0.12
<i>Lonicera japonica</i>	0.69	0.71	0.50	0.76
<i>Rosa multiflora</i>	0.49	0.45	0.46	0.38

may reflect the rather short interval since introduction of the species, a time too short to have allowed the *A. brevipedunculata* to spread into the Mixed Oak region.

**CORROBORATING OBSERVATIONS.** In a study similar to ours conducted at the northern edge of the Piedmont, Yost et al. (1991) documented the importance of exotic species in a small, highly-disturbed forest in the Wave Hill Garden in Bronx, New York. We compared the frequency of occurrence of three of the exotic species (*A. brevipedunculata*, *L. japonica*, and *R. multiflora*) in forested tracts and in old fields in the Pennypack Wilderness and at Wave Hill (Table 5). In half the comparisons, the frequency of occurrence between the two sites was remarkably similar. In the forested tracts, *L. japonica* and *R. multiflora* occurred at virtually identical frequencies. *Lonicera japonica* was more common in Pennypack's old fields (0.76 vs. 0.50), but the frequencies were high in both locations. *Rosa multiflora* was only slightly more common in the Wave Hill old fields than in the Wilderness old fields. *Ampelopsis brevipedunculata* exhibited the greatest disparity in occurrence between Pennypack and Wave Hill, with the likelihood of encountering the vine in Wave Hill's forests more than four times greater than at Pennypack (0.70 vs. 0.23), and six times more likely in Wave Hill's old fields (0.88 vs. 0.12).

The difference in *L. japonica* between the old fields at Pennypack and Wave Hill is difficult to explain because the species has been pervasive on the East Coast for nearly two centuries (Hardt 1986). The large difference in *A. brevipedunculata* frequencies between the two sites, however, can probably be attributed to the fact that the Pennypack Wilderness is 40 times larger than Wave Hill and *A. brevipedunculata* was most

likely introduced fairly recently at Pennypack at a location near one end of the preserve.

#### Literature Cited

- ANDREWS, E. F. 1919. The Japanese honeysuckle of the eastern United States. *Torreyia* 19: 37-43.
- AUCLAIR, A. N. AND G. COTTAM. 1971. Dynamics of black cherry (*Prunus serotina*) in southern Wisconsin oak forests. *Ecol. Monogr.* 41: 153-177.
- BAKER, H. G. 1974. The evolution of weeds. *Ann. Rev. Ecol. Syst.* 5: 1-24.
- BARDEN, L. S. AND J. F. MATTHEWS. 1980. Change in abundance of honeysuckle (*Lonicera japonica*) and other ground flora after prescribed burning of a Piedmont pine forest. *Castanea* 45: 257-260.
- BASKIN, J. M. AND C. C. BASKIN. 1992. Seed germination biology of the weedy biennial *Alliaria petiolata*. *Natural Areas J.* 12: 191-197.
- BORMANN, F. H. 1953. Factors determining the role of loblolly pine and sweetgum in early old field succession in the Piedmont of North Carolina. *Ecol. Monogr.* 23: 339-358.
- AND G. E. LIKENS. 1979. Patterns and process in a forested ecosystem. Springer-Verlag, New York.
- BRATTON, S. P. 1979. Impacts of white-tailed deer on the vegetation of Cades Cove, Great Smoky Mountains National Park. *Proceedings of the Annual Conference of the Southeastern Association of Game and Fish Commissioners* 33: 305-312.
- BROTHERS, T. S. AND A. SPINGARN. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. *Cons. Biol.* 6: 91-100.
- BRUSH, C. C. AND D. W. EHRENFELD. 1991. Control of white-tailed deer in non-hunted reserves and urban fringe areas, pp. 59-66. *In* L. W. Adams and D. L. Ledy [eds.], *Wildlife conservation in metropolitan environments. Symposium Series 2, National Institute for Urban Wildlife*, Columbia, MD.
- BURGESS, R. L. AND D. M. SHARPE. 1981. *Forest island dynamics in man-dominated landscapes*. Springer-Verlag, New York.
- CAIN, M. D. 1984. Japanese honeysuckle and associated ground cover inhibit establishment and growth of pine seedlings in all-aged stands. *Third Biennial Southern Silvicultural Research Conference*, Atlanta, GA.
- CAVERS, P. B., M. I. HEAGY AND R. F. KOKRON. 1979. The biology of Canadian weeds. 35. *Alliaria petiolata* (M. Bieb.) Cavara and Grande. *Can. J. Plant Sci.* 59: 217-229.
- CHRISTIANSEN, N. L. AND R. K. PEET. 1981. Secondary forest succession on the North Carolina Piedmont, pp. 230-245. *In* D. C. West, H. H. Shugart and D. B. Botkin [eds.], *Forest succession: Concepts and application*. Springer-Verlag, New York.
- COTTAM, G. AND J. T. CURTIS. 1956. The use of distance measures in phytosociological sampling. *Ecology* 37: 451-460.
- CRAWLEY, M. J. 1986. What makes a community invulnerable?, pp. 429-453. *In* A. J. Gray, M. J. Crawley and P. J. Edwards [eds.], *Colonization, succession and stability*. Blackwell Scientific Publications, Oxford, England.
- DECKER, D. J. AND J. W. ENCK. 1987. Exotic plants with identified detrimental impacts on wildlife hab-

- itats in New York State. Cornell Univ. Ag. Exp. Stn., Natural Resources Res. and Ext. Ser. No. 29, Ithaca, NY.
- DRYER, G. D. 1988. Efficacy of triclopyr in rootkilling Oriental bittersweet (*Celastrus orbiculatus* Thunb.) and certain other woody weeds. Proc. Northeastern Weed Sci. Soc. 42: 120-121.
- , L. M. BAIRD AND C. FICKLER. 1987. *Celastrus scandens* and *Celastrus orbiculatus*: Comparisons of reproductive potential between a native and introduced woody vine. Bull. Torrey Bot. Club 114(3): 260-264.
- GALLACE, B. 1990. Do you know how to combat the wrath of grapes? Pennsylvania Woodlands News 6(1): 5, Pennsylvania State University Forest Resources Extension, University Park, PA.
- GODFREY, M. A. 1980. A Sierra Club naturalists' guide to the Piedmont. Sierra Club Books, San Francisco, CA.
- GOSSELINK, J. G. AND L. C. LEE. 1989. Cumulative impact assessment in bottomland hardwood forests. Wetlands 9: 89-174.
- GRAHAM, S. A. 1954. Changes in northern Michigan forests from browsing by deer. Transactions of the Nineteenth North American Wildlife Conference 19: 526-533.
- GRIME, J. P. 1979. Plant strategies and vegetation processes. John Wiley and Sons, New York.
- GULDIN, J. M., J. R. SMITH AND L. THOMPSON. 1990. Stand structure of an old-growth upland hardwood forest in Overton Park, Memphis, Tennessee, pp. 61-66. In R. J. Mitchell, C. J. Shevait and D. J. Leopold [eds.], Ecosystem management: Rare species and significant habitats. N.Y. State Museum Bull. 471.
- HANDLEY, C. O. 1945. Japanese honeysuckle in wildlife management. J. Wildl. Mgt. 9: 261-264.
- HARDT, R. A. 1986. Japanese honeysuckle: From "one of the best" to ruthless pest. *Arnoldia* 46(2): 27-34.
- HILL, D. B. 1985. Forest fragmentation and its implications in central New York. Forest Ecology and Mgt. 12: 113-128.
- HOBBS, R. J., AND L. F. HUENNEKE. 1992. Disturbance, diversity and invasion: Implications for conservation. *Cons. Biol.* 6: 324-337.
- HOLLAND, P. AND S. OLSON. 1989. Introduced versus native plants in austral forests. *Prog. Phys. Geog.* 13: 260-293.
- HOUGH, A. F. 1965. A twenty-year record of understory vegetational change in a virgin Pennsylvania forest. *Ecology* 46: 370-373.
- AND R. D. FORBES. 1943. The ecology and silvics of forests in the high plateaus of Pennsylvania. *Ecol. Monogr.* 13: 299-320.
- JACKSON, L. 1987. Japanese or multiflora rose (*Rosa multiflora*), pp. 6-13. In D. J. Decker and J. W. Enck [eds.], Exotic plants with identified detrimental impacts on wildlife habitats in New York State. Exotic Plant Committee of The Wildlife Society (New York Chapter), Cornell Cooperative Extension, Cornell University, Ithaca, NY.
- KEEVER, C. 1973. Distribution of major forest species in southeastern Pennsylvania. *Ecol. Monogr.* 43: 303-327.
- LEATHERMAN, A. D. 1955. Ecological life-history of *Lonicera japonica* Thunb. Ph.D. Dissertation, University of Tennessee.
- LUTZ, H. J. 1943. Injuries to trees caused by *Celastrus* and *Vitis*. *Bull. Torrey Bot. Club* 70: 436-439.
- MARKS, P. L. 1974. The role of pin cherry (*Prunus pensylvanica* L.) in the maintenance of stability in northern hardwood ecosystems. *Ecol. Monogr.* 44: 73-88.
- . 1983. On the origin of the field plants of the northeastern United States. *Am. Nat.* 122: 210-228.
- MARQUIS, D. A. 1981. Effect of deer browsing on timber production in Allegheny hardwood forests in northwestern Pennsylvania. USDA Forest Service, Northeast Forest Experiment Station Research Paper NE-475, Radnor, PA.
- MILLER, S. G., S. P. BRATTON AND J. HADIDIAN. 1992. Impacts of white-tailed deer on endangered and threatened vascular plants. *Natural Area J.* 12: 67-74.
- MURPHY, D. D. 1988. Challenges to biological diversity in urban areas, pp. 71-76. In E. O. Wilson [ed.], Biodiversity. National Academy Press, Washington, DC.
- OVERLEASE, W. R. 1978. A study of forest communities in southern Chester County, Pennsylvania. *Proc. Pa. Acad. Sci.* 52: 37-44.
- . 1987. One hundred and fifty years of vegetation change in Chester County, Pennsylvania. *Bartonia* 53: 1-12.
- PATTERSON, D. T. 1974. The ecology of Oriental bittersweet, *Celastrus orbiculatus*, a weedy introduced ornamental vine. Ph.D. Dissertation, Duke University, Durham, NC.
- PENNSYLVANIA BUREAU OF TOPOGRAPHIC AND GEOLOGIC SURVEY. 1960. Geologic map of Pennsylvania. Pennsylvania Department of Environmental Resources, Harrisburg, PA.
- RANNEY, J. W., M. C. BRUNER AND J. B. LEVENSON. 1981. The importance of edge and the structure and dynamics of forest islands, pp. 67-95. In R. L. Burgess and D. M. Sharpe [eds.], Forest island dynamics in man-dominated landscapes. Springer-Verlag, New York.
- REDDING, J. C. 1987. Impact of deer on forest vegetation and timber in northern Pennsylvania, pp. 23-32. In R. LaBar [ed.], Proceedings of the symposium on deer, forestry, and agriculture: Interactions and strategies for management. Allegheny Society of American Foresters, Warren, PA.
- SATHER, N. 1992. Element stewardship abstract for *Lonicera japonica* (Japanese honeysuckle). The Nature Conservancy, Arlington, VA.
- SAUNDERS, D. A., R. J. HOBBS AND C. R. MARGULES. 1991. Biological consequences of ecosystem fragmentation. *Cons. Biol.* 5: 18-32.
- SLEZAK, W. F. 1976. *Lonicera japonica* Thunb., an aggressive introduced species in a mature forest ecosystem. Master of Science Thesis, Rutgers University, New Brunswick, NJ.
- SMITH, H. C. 1984. Forest management guidelines for controlling wild grapevines. United States Department of Agriculture, Forest Service, Northeast Forest Experiment Station Research Paper NE-548, Radnor, PA.

- SOKAL, R. R. AND F. J. ROHLF. 1969. Biometry. W. H. Freeman and Co., San Francisco, CA.
- STORM, G. L., R. H. YANNER, D. F. COTTAM AND G. M. VECELLIO. 1989. Population status, movements, habitat use and impact of white-tailed deer at Gettysburg National Military Park and Eisenhower National Historic Site, Pennsylvania. U.S. National Park Service Technical Report NPS/MAR/NRTR-89/043.
- STROLE, T. A. AND R. C. ANDERSON. 1992. White-tailed deer browsing: Species preferences and implications for central Illinois forests. *Natural Areas J.* 12: 139-144.
- THOMAS, L. K., JR. 1980. The impact of three exotic plant species on a Potomac island. United States National Park Service Scientific Monograph No. 13, Washington, DC.
- TILGHMAN, N. G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *J. Wildlife Mgt.* 53: 524-532.
- USDA-FS (UNITED STATES DEPARTMENT OF AGRICULTURE, FOREST SERVICE). 1974. Seeds of woody plants in the United States. U.S. Department of Agriculture Agricultural Handbook No. 450, U.S. Government Printing Office, Washington, DC.
- . 1988. Forest research, Warren, Pennsylvania. Northeast Forest Exp. Stn. Bull. NE-INF-81-88, Radnor, PA.
- USDA-SCS (UNITED STATES DEPARTMENT OF AGRICULTURE, SOIL CONSERVATION SERVICE). 1967. Soil survey of Montgomery County, Pennsylvania. U.S. Government Printing Office Pub. No. 1967 0-217-083, Washington, DC.
- VAN CLEVE, K. AND L. A. VIERECK. 1981. Forest succession in relation to nutrient cycling in the boreal forest of Alaska, pp. 185-211. In D. C. West, H. H. Shugart and D. B. Botkin [eds.], *Forest succession: Concepts and application*. Springer-Verlag, New York.
- WHIGHAM, D. 1984. The influence of vines on the growth of *Liquidambar styraciflua* L. (sweetgum). *Can. J. For. Res.* 14: 37-39.
- WHITTINGTON, R. W. 1984. Piedmont Plateau, pp. 355-366. In L. K. Halls [ed.], *White-tailed deer: Ecology and management*. Stackpole Books, Harrisburg, PA.
- WILLIAMS, C. E. 1993. The exotic Empress Tree, *Pau-*lownia tomentosa*: An invasive pest of forests? *Natural Areas J.* 13: 221-222.*
- WINTER, K., M. R. SCHMITT AND G. E. EDWARDS. 1982. *Microstegium vimineum*, a shade adapted C4 grass. *Plant Sci. Lett.* 24: 311-318.
- YOST, S. E., S. ANTENEN AND G. HARTVIGSEN. 1991. The vegetation of the Wave Hill natural area, Bronx, New York. *Bull. Torrey Bot. Club* 118: 312-325.