Invasibility and Effects of Amur Honeysuckle in Southwestern Ohio Forests

TODD F. HUTCHINSON* AND JOHN L. VANKAT

*Department of Botany, Miami University, Oxford, OH 45056, U.S.A.

Abstract: *The Asian exotic Amur honeysuckle (*Lonicera maackii *[Rupr.] Herder) has become the dominant shrub in many forests in southwestern Ohio and in some other locations in the eastern United States. Our research focused on the invasibility of forest communities and relationships of* L. maackii *to the abundance of tree seedlings and herbs. We surveyed 93 forest stands near Oxford, Ohio (USA) to determine* L. maackii *cover, time since invasion, tree canopy cover, tree basal area, and a shade tolerance index. Stepwise multiple regression indicated that greater than one-half of the variation (*$r^2 = 0.550$*) in* Lonicera *cover was correlated to five variables (in descending order of importance): tree canopy cover, distance from Oxford, shade tolerance index, tree basal area, and time since invasion. The results suggest that high light levels and proximity to an abundant seed source increase forest invasibility. Tree seedling density, species richness of seedlings, and herb cover were all inversely related to* L. maackii *cover.* When Lonicera *becomes abundant, future structure and composition of forests could be affected and local populations of herbs threatened.*

Invasibilidad y Efectos de la Madreselva de Amur en Bosques del Sudoeste de Ohio

Resumen: *La madreselva de Amur (*Lonicera maackii *[Rupr.] Herder), originaria de Asia, se ha vuelto el arbusto dominante en muchos bosques del sudoeste de Ohio y en algunas otras locaciones en este de Estados Unidos. Nuestra investigación se enfocó en la invasibilidad de* L. maackii *en comunidades forestales y su relación con la abundancia de plántulas de árboles y arbustos. Muestreamos 93 bosques cerca de Oxford, Ohio (E.U.A.) para determinar la cobertura de* L. maackii*, tiempo desde la invasión, cobertura del dosel arbóreo, área basal de árboles y un índice de tolerancia de sombra. El análisis de regresión múltiple por pasos indicó que más de la mitad de la variación (*$r^2 = 0.550$*) en la cobertura de* Lonicera *se correlacionó con cino variables (en orden descendente de importancia): cobertura del dosel arbóreo, distancia de Oxford; índice de tolerancia de sombra, área basal de árboles y tiempo desde la invasión. Los resultados sugieren que la invasibilidad se incrementa debido a niveles altos de luz y la cercanía a una fuente abundante de semillas. La densidad de plántulas de árboles, la riqueza de especies de plántulas y la cobertura herbácea estuvieron inversamente, correlacionados con la cobertura de* L. maackii*. Cuando* Lonicera *es abundante, la estructura y composición de bosques podrían verse afectadas y poblaciones locales de hierbas estarían amenazadas.*

Introduction

Human population growth has favored the spread of exotic species through increased transportation (dispersal) of species and expansion of disturbed habitats (Elton

1958; Mooney & Drake 1986; Drake et al. 1989). Eurasian species have been especially successful, accounting for 80% of the invading species worldwide (di Castri 1989). One common mode of introduction of Eurasian plant species to the New World has been their use in ornamental planting (Heywood 1989; Mack 1991).

What makes natural or seminatural plant communities susceptible to invasion and colonization (hereafter referred to collectively as invasibility) by a particular exotic species? General observations have been reported

1117

in the literature, but community invasibility rarely has been studied quantitatively (Crawley 1987; Rejmanek 1989; Lodge 1993; but see Burke & Grime 1996). Most invasions have occurred more readily in areas modified by humans (Elton 1958), and disturbance has been positively correlated to invasibility in many studies (Mack 1981; Ewel 1986; Hobbs 1989; Bossard 1991; Richardson & Bond 1991; D'Antonio 1993; Parker et al. 1993; Burke & Grime 1996). Hobbs (1989) suggested that disturbance increases invasibility by increasing a limiting resource (e.g., light) or by reducing competition from the existing species. Given that disturbance initiates succession, early to mid-successional communities have been considered more invasible than late-successional communities (Rejmanek 1989). Brothers and Spingarn (1992) found that old-growth forest remnants in Indiana were resistant to exotic plant invasion; they speculated that light was limiting.

Invasive plants can modify community structure and function (Bazzaz 1986) and alter ecosystem-level processes (Vitousek 1990). Although most research has been on herbaceous species, exotic trees (Ewel 1986; Richardson & Bond 1991) and shrubs (Barnes 1972; Cross 1981; Hobbs & Mooney 1986; Luken 1988; Lonsdale & Abrect 1989; Woods 1993) also have invaded a variety of communities. Several studies have reported a correlation between dense thickets of exotic shrubs and reduced regeneration of native woody species (Barnes 1972; Cross 1981; Braithwaite et al. 1989; Yost et al. 1991; Woods 1993). Also, herb abundance and diversity have been found to be inversely related to exotic shrub cover (Woods 1993).

The shrub *Lonicera maackii* (Rupr.) Herder is native to northeastern Asia, where it occurs in a variety of forest types (Luken & Thieret 1995). It was first introduced to North America in 1896 as an ornamental (Luken & Thieret 1995). *Lonicera maackii* has escaped cultivation in at least 23 states east of the Rocky Mountains (Trisel & Gorchov 1994). *Lonicera maackii* was originally planted in the Oxford, Ohio area around 1960 (T. J. Cobbe, personal communication). It has spread outside of the city and has become the dominant shrub in many forested and some more open habitats.

The ability of *L. maackii* to invade communities may be related to several physiological traits. Bazzaz (1986) predicted that the success of invading species should relate to high allocation to reproduction, plastic responses to the environment, and high net primary productivity. *Lonicera maackii* does produce large quantities of fruit, and these are dispersed primarily by birds (cf. Ingold & Craycraft 1983). Also, its branch architecture is plastic in forest versus open habitats (Luken et al. 1995b), and its net primary productivity is high when light levels are high (Luken 1988; Luken et al. 1995c). Moreover, *Lonicera maackii* expands its leaves earlier in the spring and retains its leaves later in the fall than native shrubs and

trees (D. E. Trisel, unpublished data). Such extended leaf display has been shown to increase carbon gain in other invasive *Lonicera* taxa (i.e., *L.* × *bella* [Harrington et al. 1989] and *L. japonica* [Schierenbeck & Marshall 1993]). In addition, the lack of coevolved biological control agents (e.g., herbivory is uncommon) is undoubtedly important, as Schierenbeck (1994) demonstrated for *Lonicera japonica*, an invasive Asian vine.

Lonicera maackii has become abundant in forests that exhibit significant canopy disturbance (Yost et al. 1991; DeMars & Runkle 1992). In these forests it is possible that tree seedlings and herbs are adversely affected, as Woods (1993) reported for the exotic shrub *Lonicera tatarica* in several New England forests and Gould (1996) documented for three annual species in southwestern Ohio. Tree seedlings are an important component of these forest stands because current seedling stocks will contribute to future structure, composition, and economic value. Herbaceous plant species make up a major portion of the biodiversity of these communities.

Although numerous studies have examined exotic plant invasions at the community-level, few (if any) have sampled many stands in a landscape. Our objective was to examine a biological invasion by studying a wide variety of forest stands within the same landscape. Specifically, we focused on determining (1) factors affecting forest community invasibility by *L. maackii* and (2) relationships of *L. maackii* cover to the abundance of tree seedlings and herbs. Given our intent to study forest invasibility at the community level, we chose to examine patterns primarily at the level of forest stands rather than individuals of *Lonicera*.

Methods

Study Area

The study area was in the glaciated region of southwestern Ohio near the town of Oxford (39°30′N, 84°45′W). Topography is generally flat to rolling. The climate is continental humid with mean annual temperature and precipitation of 12.3°C and 930 mm, respectively. Most of the upland forests sampled were on the Russell-Miamian-Wynn soil series. These soils were formed in loess, glacial till, and shale and limestone residuum. They are deep to moderately deep, well-drained, and have moderately fine to fine textured subsoil. Forests on stream floodplains were in the Genesee-Ross series. They were formed in recent alluvium and are deep, well-drained, and have a medium textured subsoil (Lerch et al. 1980). The area is located in the southern portion of Braun's (1950) Beech-Maple deciduous forest region. The landscape pattern is an agricultural matrix with isolated forest patches and forest corridors associated with streams. Forest cover in Butler and Preble Counties is 10–24% (Griffith 1993).

Field Procedures

U. S. Geological Survey topographic maps and aerial photographs were used to select 93 forest stands of at least 1 ha and within the known distribution of *L. maackii*. All forest stands presumably had been cut-over or selectively harvested (several times in some cases) since European settlement and were chosen to represent a range of canopy cover (75–100%). Sixty-two stands were located on private property, and 31 stands were in nature preserves and parks. Therefore, a range of disturbance and protection histories is represented. Although none of the stands studied was currently being grazed, it is likely that some were grazed in the past. However, we were unable to quantify past grazing or logging disturbance. Most stands had generally flat topography, with slopes <10%.

Community invasibility was defined by degree of *L. maackii* cover, not by seedling establishment. *Lonicera* cover was estimated in the interior (>25 m from edge) of each stand by the line intercept method (Barbour et al. 1987) along a 50-m transect, which was placed randomly, avoiding particularly large, recent, treefall gaps. Herbaceous cover was visually estimated within 10, 0.5 × 1 m quadrats placed equidistantly beginning at 5 m and centered on the transect. Herb cover classes were 0, 1–2, 3–10, 11–20, and each subsequent 10% interval. Mean herb cover per stand was calculated using cover class midpoints. Tree seedlings of 0.5 to 2.5 m height were counted by species in a 2-m wide belt transect centered on the 50-m line transect.

The species and diameter at breast height (dbh) were recorded for tree saplings (>2.5 m height, but <10 cm dbh), subcanopy/canopy trees (10–<25 cm dbh), and canopy trees (≥25 cm dbh) in 2, 4, and 10 m wide belt transects, respectively. Tree canopy cover (percent) was measured at 10, 25, and 40 m along the transect with a spherical crown densiometer, a gridded concave mirror that allows estimation of percent open sky (Lemmon 1956). Four measurements facing the cardinal directions were taken at each of these points.

Time of initial invasion by *L. maackii* was estimated for each stand by counting the annual rings of the largest *L. maackii* stem in the 10 × 50 m belt transect. Ring data were not collected in eight stands because of technical problems. Stand distances from central Oxford were determined from U.S. Geological Survey topographic maps. All stands were sampled between 19 May and 3 August 1993.

Data Analysis

To infer light regimes of the recent past, a shade tolerance index was calculated for each stand based on data from the sapling size class. An importance percentage was obtained for each sapling species by averaging its relative values for density and basal area. The importance percentage for each species was then multiplied by the following shade tolerance values based on information from Burns and Honkala (1990): 1, very intolerant (e.g., *Juniperus virginiana*); 2, intolerant (e.g., *Fraxinus americana*); 3, intermediate (e.g., *Quercus rubra*); 4, tolerant (e.g., *Ulmus rubra*); and 5, very tolerant (e.g., *Acer saccharum*). Therefore, stands dominated by shade-tolerant saplings had high index values. Six stands were omitted from this analysis because ≤5 tree saplings were sampled.

Simple linear regression and stepwise multiple regression (SAS procedure REG; SAS 1990) were used to determine relationships between the dependent variable, *L. maackii* cover, and the following stand parameters: (1) tree basal area, (2) tree canopy cover, (3) shade tolerance index, (4) time since invasion, and (5) distance from Oxford. Simple regression analysis was also used to analyze relationships between basal area values for individual tree species and *L. maackii* cover.

To further test the relationship of inferred light regimes to *Lonicera* cover, stepwise multiple regression analysis was performed separately on stands invaded 1–15 and 16–30 years ago, using *L. maackii* cover as the dependent variable and (1) tree basal area, (2) tree canopy cover, (3) shade tolerance index, and (4) distance from Oxford as the independent variables.

Relationships between *L. maackii* cover and (1) seedling density of all tree species, (2) seedling density of individual tree species, (3) species richness of tree seedlings, and (4) mean herb cover were also analyzed with simple linear regression. To better understand the small-scale relationship of herb cover to *Lonicera* cover, analysis of covariance (ANCOVA; SAS procedure GLM; SAS 1990) was used. Here, the sampling units analzyed were the 0.5 × 1.0 m quadrats in the 39 stands in which *L. maackii* cover was ≥20%. The dependent variable was herb cover, and the independent variables were *L. maackii* cover and stand, with stand treated as a class variable. The analysis performed 39 separate regressions to obtain an overall r^2 value and p-value.

Results

Overall, the dominant tree taxa by basal area were *Fraxinus* spp. and *Acer saccharum*. Tree canopy cover and tree basal area ranged from 77% to 99% (mean = 94) and from 10.8 to 46.4 m²/ha (mean = 28.8), respectively. Shrub species other than *L. maackii* were uncommon. Mean herb cover was highly variable, ranging from 1% to 85% (mean = 17%), whereas tree seedling density ranged from 0 to 2.8 seedlings/m² (mean = 0.44).

Lonicera maackii cover along the transects in the 93 stands ranged from 0% to 96% (mean = 25%). Eighty-two stands had some *L. maackii* along the 50-m line

transect; the other 11 stands contained at least several individuals (personal observation).

Forest Invasibility

Lonicera maackii cover was inversely related to total tree basal area ($r^2 = 0.151$, $p < 0.0001$; Fig. 1a). Its cover commonly exceeded 50% only in stands with basal area <30 m²/ha. *Lonicera* cover was inversely related to the basal area of *Acer saccharum* ($r^2 = 0.182$, $p < 0.0001$; Fig. 1b), a highly shade tolerant species.
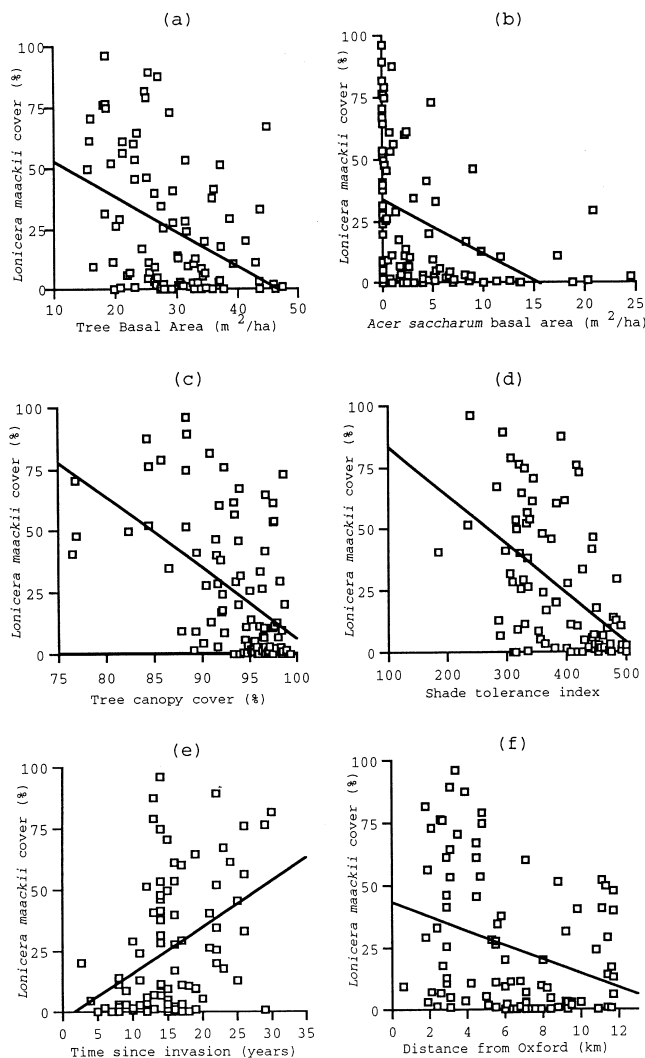
However, *Lonicera* cover was unrelated to the basal area of other common tree taxa (*Carya cordiformis*, *Fraxinus* spp., *Gleditsia triancanthos*, *Juglans nigra*, *Quercus muehlenbergia*, *Quercus rubra*, and *Robinia pseudoacacia*). There also was no relationship to the basal area of *Fagus grandifolia* (also highly shade tolerant), but *L. maackii* was ≤5% in 10 of the 12 stands where *Fagus* was present.

Lonicera maackii cover was inversely related to tree canopy cover ($r^2 = 0.292$, $p < 0.0001$; Fig. 1c). *Lonicera* cover was rarely <50% when tree canopy cover was <85%; but was highly variable when canopy cover was higher. *Lonicera maackii* cover was inversely related to shade tolerance index ($r^2 = 0.226$, $p < 0.0001$; Fig. 1d). Its cover was rarely >50% when index values were >400 (i.e., when most saplings were shade tolerant).

Lonicera maackii cover was positively related to estimated time since invasion ($r^2 = 0.172$, $p < 0.0001$; Fig. 1e). Its cover was >50% only in stands invaded ≥12 years ago.

Lonicera cover was inversely related to stand distance from Oxford ($r^2 = 0.133$, $p < 0.0006$; Fig. 1f). Its cover was >50% mostly in stands ≤5 km from Oxford.

Stepwise multiple regression analysis for all stands indicated that greater than one-half of the variation ($r^2 = 0.550$, $p < 0.0001$; Table 1) in *L. maackii* cover was explained by the five variables (in descending order of importance): tree canopy cover, distance from Oxford, shade tolerance index, tree basal area, and estimated time since invasion. Tree canopy cover and distance from Oxford were not correlated ($p = 0.142$). Shade tolerance index was added at step 3 and was correlated with tree canopy cover, ($r^2 = 0.272$, $p < 0.0001$), but the mean square error (MSE) decreased and r^2 increased when this factor was added. The r^2 value continued to increase and mean square error decreased in steps 4 and 5 (addition of tree basal area and time since invasion, respectively).

In stands invaded 1–15 years ago, tree canopy cover had the greatest influence on *L. maackii* cover ($r^2 = $

Figure 1. Linear regressions of Lonicera maackii *cover (dependent variable), which was used to define the degree of community invasibility and tree basal area (a,* $r^2 = 0.151$, p < 0.0001); Acer saccharum *basal area (b,* $r^2 = 0.182$, p < 0.0001); tree canopy cover (c, $r^2 = 0.292$, p < 0.0001); shade tolerance index (d, $r^2 = 0.226$, p < 0.001); estimated time since invasion (e, $r^2 = 0.172$, p < 0.0001); and distance from Oxford (f, $r^2 = 0.133$, p < 0.0006), (n = 93 stands).*

Table 1.   Stepwise multiple regression using *L. maackii* cover as the dependent variable.*

Independent variables	r²	p-value
Step 1		
Canopy cover	0.292	0.0001
Step 2		
Distance from Oxford	0.453	0.0001
Step 3		
Shade tolerance index	0.513	0.0001
Step 4		
Tree basal area	0.536	0.0001
Step 5		
Time since invasion	0.550	0.0001

At each step the independent variable that yields the highest r² value for that step is added to the model, (n = 93 stands).

Table 2. Stepwise multiple regression for stands invaded 1–15 and 16–30 years ago, using *Lonicera maackii* cover as the dependent variable.

Independent variables	r^2	p-value
Stands invaded 1-15 years ago (n = 44):[a]		
Step 1		
Canopy cover	0.484	0.0001
Step 2		
Distance from Oxford	0.589	0.0001
Step 3		
Shade tolerance index	0.691	0.0001
Stands invaded 16–30 years ago (n = 35):[b]		
Step 1		
Shade tolerance index	0.300	0.001
Step 2		
Distance from Oxford	0.424	0.0001
Step 3		
Tree basal area	0.532	0.0001

[a] *Tree basal area did not increase the r^2 value so is not included in the model.*
[b] *Tree canopy cover did not increase the r^2 value so is not included in the model.*

0.484, $p < 0.0001$; Table 2). Distance from Oxford and shade tolerance index were added at steps 2 ($r^2 = 0.589$) and 3 ($r^2 = 0.691$), respectively. For stands invaded 16-30 years ago, the multiple regression model explained less of the variation in *Lonicera* cover (Table 2). Shade tolerance index was most important ($r^2 = 0.300$, $p < 0.0001$), and distance from Oxford and tree basal area were added at steps 2 ($r^2 = 0.424$) and 3 ($r^2 = 0.532$), respectively.

Tree Seedling and Herb Abundance

Tree seedling density was inversely related to *L. maackii* cover ($r^2 = 0.118$, $p < 0.001$; Fig. 2a). When *L. maackii* cover was ≥15%, seedling densities were nearly always <0.5/m², but when *L. maackii* cover was <15%, seedling densities varied greatly. Of the five most common species, *Acer saccharum* seedling density was inversely related to *Lonicera* cover ($r^2 = 0.119$; $p < 0.001$; Fig. 2b) but *Fraxinus americana*, *Fraxinus pennsylvanica*, *Fraxinus quadrangulata*, and *Prunus serotina* seedling densities were unrelated to *Lonicera* cover.

The species richness of tree seedlings was also inversely related to *L. maackii* cover ($r^2 = 0.152$, $p < 0.0001$; Fig. 2c). When *L. maackii* cover was >50%, the number of species was usually ≤8, but richness was highly variable, ranging from 0 to 15 species, when *L. maackii* cover was <50%.

Mean herb cover per stand was unrelated to *Lonicera* cover ($r^2 = 0.007$, $p = 0.410$; Fig. 2d). However, when ANCOVA was used to analyze the quadrat data in stands with ≥20% *L. maackii* cover, herb cover proved to be
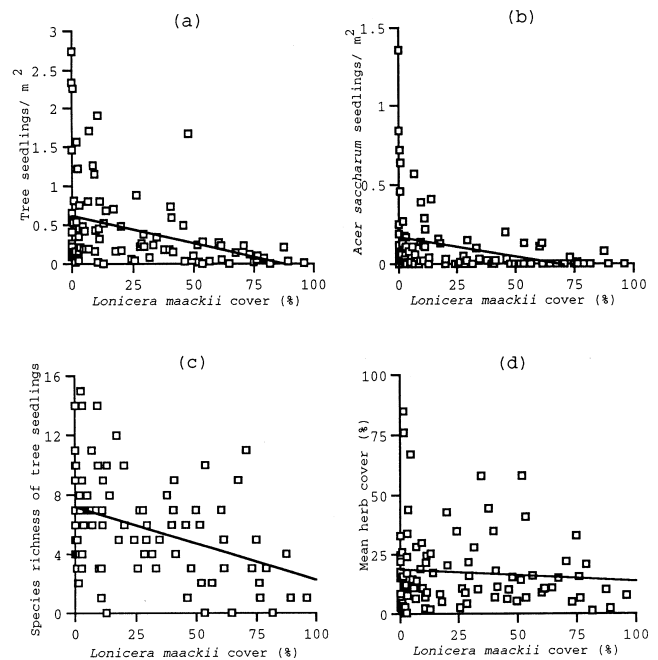

Figure 2. Linear regressions of Lonicera maackii *cover (independent variable) and tree seedling density (a, $r^2 = 0.118$, p < 0.001);* Acer saccharum *seedling density (b, $r^2 = 0.119$, p < 0.001); species richness of tree seedlings (c, $r^2 = 0.152$, p < 0.0001); and mean herb cover (d, $r^2 = 0.007$, p = 0.410), (n = 93 stands).*

inversely related to *L. maackii* cover ($r^2 = 0.494$, $p < 0.0001$; Table 3).

Discussion

Forest Invasibility

Light appears to be an important factor related to the invasibility of forests by *L. maackii*, as suggested by the importance of the inverse relationships of *L. maackii* cover to canopy cover and shade tolerance index in the multiple regression for all stands. More specifically, the light regime at the time of initial invasion appears to be a key factor correlated with current *Lonicera* cover, as suggested by the importance of canopy cover in stands

Table 3. Analysis of covariance (SAS, PROC GLM) with herb cover as the dependent variable and *Lonicera maackii* cover and stand (class variable) as the independent variables.*

Variables	df	F-value	p > F	r^2
Model	39	8.62	0.0001	0.494
Stand	38	7.04	0.0001	
L. maackii	38	68.72	0.0001	

**n* = 390 plots (0.5 × 1 m) in the 39 stands where* L. maackii *cover was ≥20%.*

recently invaded and shade tolerance index of saplings (which estimates the light regime of the recent past) in stands invaded 16–30 years ago.

The significance of light is demonstrated by Luken's (1995*c*) finding that biomass and leaf area of *L. maackii* seedlings increased with increasing light availability. A relationship of forest invasibility to light is consistent with Brothers and Spingarn's (1992) finding that the abundance of exotic species decreased from forest edge to interior. Also, increased light is likely related to canopy disturbance, and disturbance has been linked with increased invasibility in a variety of plant communities (Mack 1981; Ewel 1986; Hobbs 1989; Bosard 1991; Richardson & Bond 1991; D'Antonio 1993; Parker et al. 1993; Burke & Grime 1996).

In the Oxford area the late-successional forest communities are traditionally considered *Fagus-Acer* (Braun 1950), and these two species are highly shade tolerant (Burns & Honkala 1990). The inverse relationship of *L. maackii* cover to *A. saccharum* basal area and the low cover of *L. maackii* in stands with *F. grandifolia* further indicate that late-successional forests are more resistant to invasion than younger forests, presumably because of less light reaching the forest floor.

The importance of distance from Oxford reflects the original introduction of *L. maackii* in the Oxford area and subsequent spread. With one possible exception (see below), no clear evidence of invasion from populations established outside of the Oxford area was evident. The occurrence of stands with low *L. maackii* cover near Oxford supports the finding that light regimes are related to invasibility.

Tree basal area, which was included at the fourth step of the multiple regression for all stands, may be only a weak surrogate for light regimes because large trees of some species (e.g., *Fraxinus* spp., *Gleditsia triacanthos*, *Juglans nigra*, and *Robinia pseudoacacia*) provide thin canopy coverage. *L. maackii* cover is unrelated to the basal area of these species.

Given that *Lonicera maackii* was introduced into the Oxford area fairly recently, it is not surprising that *L. maackii* cover was positively related to estimated time since invasion. However, assuming that the estimates of time since invasion were accurate, the variability of *Lonicera* cover in stands invaded concurrently suggests that after establishment *Lonicera* cover increases at different rates, presumably related to the light regimes of the stands invaded.

One unexpected finding was that *L. maackii* cover was generally higher in stands >10 km south of Oxford than in stands 6–10 km distant (Fig. 1*f*). Age data suggest an additional small-scale invasion occurred from a cluster of homes 12 km south of Oxford.

Because the multiple regression model for all stands accounts for only about half of the variation in *L. maackii* cover, other factors must be important. Present

and past light regimes were only inferred, not measured directly. Inferences based on generalized shade tolerance codings are especially likely to be imprecise. For example, some species considered shade tolerant may also establish under high light conditions (e.g., *Cercis canadensis*, *Fraxinus pennsylvanica*, and *Ulmus rubra* [Burns & Honkala 1990]).

Also, some possibly important factors were not examined in this study. Anecdotal evidence suggests that disturbances to the forest floor (e.g., livestock grazing and water-scouring) that decrease herbaceous cover and leaf litter may be significant to *L. maackii* invasion. For example, despite high net productivity in open habitats, *L. maackii* is often less abundant in old fields, where dense herbaceous cover is present, than in forests (personal observation).

Another factor not studied was stand isolation. Dispersal of *L. maackii* seeds into a forest stand probably decreases as isolation from other *L. maackii* populations increases (van Ruremonde & Kalkhoven 1991; Matlock 1994; Hutchinson 1995).

Tree Seedling and Herb Abundance

Results suggest that when *L. maackii* becomes abundant, tree seedlings and herbs are negatively affected. If this is true, possible causes include reduced light under *L. maackii* canopies, reduced nutrients and moisture due to *L. maackii's* extensive shallow root system, and allelopathy.

Braithwaite et al. (1989) and Woods (1993) also found that tree seedlings were consistently sparse when exotic shrubs were abundant. Other studies have reported reduced tree regeneration under dense thickets of native shrubs (Huenneke 1983; Sakai & Sulak 1985; Niering et al. 1986).

Although the inverse relationships between *L. maackii* cover and tree seedling density and richness were significant, there was great variability in the data. The sampling design examined *L. maackii* cover versus tree seedling density and richness in relatively large areas (50 × 2 m belt transects), often with high intraplot variation of *L. maackii* cover (personal observation). A stronger relationship may have been apparent if small plots had been used, as was the case for the relationship between *L. maackii* cover and herb cover at the quadrat level (ANCOVA; Table 3). Also, tree seedlings that overtopped *L. maackii* shrubs presumably were not affected by light competition, possibly weakening the relationship between *L. maackii* cover and tree seedlings. Lastly, when *L. maackii* was present but not abundant, microsite conditions (e.g., high light, soil moisture, or soil nutrients) may have favored the establishment and growth of both *L. maackii* and tree seedlings.

The finding of a significant inverse relationship between *L. maackii* cover and herb cover with the small-

plot data but not with the stand data implies that *L. maackii* directly affected the underlying herbs, as Gould (1996) showed experimentally for three annual species. An alternative interpretation is that low herb cover facilitated *L. maackii* invasion, whereas high herb cover restricted invasion. Reduction in herb cover beneath invading shrubs also has been demonstrated in California grasslands (Hobbs & Mooney 1986) and New England forests (Woods 1993). Light reduction was implicated in both studies.

Conclusions

Canopy disturbance apparently facilitates invasion of *L. maackii* into deciduous forests in southwestern Ohio. Younger successional forests and forests that are thinned by cutting (such as private woodlots) are likely to be invaded. Where *L. maackii* has become abundant, tree regeneration appears to have been inhibited and tree seedling abundance and richness are low. This has the potential to alter future structure and composition of forests. Indeed, early- to mid-successional forests possibly may exhibit arrested development or eventual loss of a tree canopy. Continued dominance by early-successional tree species or conversion to stable shrublands (cf. Sakai & Sulak 1985; Niering et al. 1986) would have enormous ecological and economic impacts on southwestern Ohio forests.

Lonicera maackii cover also appears to have negatively affected herbaceous plants. Spring ephemerals and spring-summer herbs that require high light levels may be affected by *L. maackii's* early leaf expansion. Shade-tolerant summer herbs may be affected more by lower nutrient and moisture availability due to root competition. Decreases in herb cover could produce cascading trophic effects in the forest ecosystem (Braithwaite et al. 1989). Also, high *L. maackii* abundance has the potential to reduce herb diversity (cf. Woods 1993) and may threaten local herb populations. Studies focusing on individual shrubs are needed to more thoroughly understand the direct effects of *L. maackii* on herb layer species.

In regions where *L. maackii* is present, forests should be managed to reduce invasion by minimizing tree canopy disturbance. Where this is not possible, forests should be monitored for *L. maackii* invasion following disturbance. In forests where *Lonicera* is already established, management to reduce its cover is strongly recommended (see Luken & Mattimiro 1991; Nyboer 1992).

Acknowledgments

Literature Cited

Barbour, M. G., J. H. Burk, and W. D. Pitts. 1987. Terrestrial plant ecology. 2nd edition. Benjamin/Cummings, Menlo Park, California.

Barnes, W. J. 1972. The autecology of the *Lonicera × bella* complex. Ph.D. thesis. University of Wisconsin, Madison.

Bazzaz, F. A. 1986. Life history of colonizing plants: some demographic, genetic, and physiological features. Pages 96–110 in H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York.

Bossard, C. C. 1991. The role of habitat disturbance, seed predation and ant dispersal on establishment of the exotic shrub *Cytisus scoparius* in California. American Midland Naturalist **126:**1–13.

Braithwaite, R. W., W. M. Lonsdale, and J. A. Estbergs. 1989. Alien vegetation and native biota in tropical Australia: the impact of *Mimosa pigra*. Biological Conservation **48:**189–210.

Braun, E. L. 1950. Deciduous forests of eastern North America. Hafner, New York.

Brothers, T. S., and A. Spingarn. 1992. Forest fragmentation and alien plant invasion of central Indiana old-growth forests. Conservation Biology **6:**91–100.

Burke, M. J. W., and J. P. Grime. 1996. An experimental study of plant community invasibility. Ecology **77:**776–790.

Burns, R. M., and B. H. Honkala. 1990. Silvics of North America: 2. Hardwoods. Handbook 654. U. S. Forest Service, Washington, D.C.

Crawley, M. J. 1987. What makes a community invasible? Pages 629–654 in A. J. Gray, M. J. Crawley and P. J. Edwards, editors. Colonization, succession and stability. Blackwell, Oxford, United Kingdom.

Cross, J. R. 1981. The establishment of *Rhododendron ponticum* in the Killarney oakwoods, S. W. Ireland. Journal of Ecology **69:**807–824.

D'Antonio, C. M. 1993. Mechanisms controlling invasion of coastal plant communities by the alien succulent *Carpobrotus edulis*. Ecology **74:**83–95.

Demars, B. G., and J. R. Runkle. 1992. Groundlayer vegetation ordination and site-factor analysis of the Wright State University Woods (Greene County, OH). Ohio Journal of Science **92:**98–106.

di Castri, F. 1989. History of biological invasions with special emphasis on the old world. Pages 1–30 in J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, M. Williamson, editors. Biological invasions: a global perspective. Scope 37. John Wiley and Sons, New York.

Drake, J. A., H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. 1989. Biological invasions: a global perspective. Scope 37. John Wiley and Sons, Chichester, United Kingdom.

Elton, C. S. 1958. The ecology of invasions by animals and plants. Methuen, London.

Ewel, J. J. 1986. Invasibility: lessons from South Florida. Pages 114–130 in H. A. Mooney and J. A. Drake, editors. Ecology of biological invasions in North America and Hawaii. Springer-Verlag, New York.

Gould, A. M. A. 1996. Effects of the exotic invasive shrub *Lonicera maackii*, Amur honeysuckle, on native forest annual herbs. M.S. thesis. Miami University, Oxford, Ohio.

Griffith, D. M., D. DiGiovanni, T. L. Witzel, and E. H. Wharton. 1993. Forest Statistics for Ohio, 1991. Resource bulletin NE-128. U. S. Forest Service, Northeastern Forest Experiment Station, Radnor, Pennsylvania.

Harrington, R. A., B. J. Brown, and P. B. Reich. 1989. Ecophysiology of exotic and native shrubs in southern Wisconsin I. Relationship of leaf characteristics, resource availability, and phenology to seasonal patterns of carbon gain. Oecologia **80:**356–367.

Heywood, V. H. 1989. Patterns, extents and modes of invasions by terrestrial plants. Pages 31–55 in J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. Scope 37. John Wiley and Sons, Chichester, United Kingdom.

Hobbs, R. J. 1989. The nature and effects of disturbance relative to in-

vasions. Pages 389–405 in J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. Scope 37. John Wiley and Sons, Chichester, United Kingdom.

Hobbs, R. J., and H. A. Mooney. 1986. Community changes following shrub invasion of grassland. Oecologia **70:**508–513.

Huenneke, L. F. 1983. Understory response to gaps caused by the death of *Ulmus americana* in central New York. Bulletin of the Torrey Botanical Club **110:**170–175.

Hutchinson, T. F. 1995. Invasion of deciduous forests in southwestern Ohio by the exotic shrub *Lonicera maackii*: community and landscape studies. M.S. thesis. Miami University, Oxford, Ohio.

Ingold, J. L., and M. J. Craycraft. 1983. Avian frugivory on honeysuckle (*Lonicera*) in southwestern Ohio in fall. Ohio Journal of Science **83:**256–258.

Lemmon, P. E. 1956. A spherical densiometer for estimating forest density. Forest Science **2:**314–320.

Lerch, N. K., W. F. Hale, and D. D. Lemaster. 1980. Soil survey of Butler County. United States Department of Agriculture in cooperation with the Ohio Department of Natural Resources, Division of Lands and Soils, and the Ohio Agricultural Research and Development Center, Washington, D.C.

Lodge, D. M. 1993. Biological invasions: lessons for ecology. Trends in Ecology and Evolution **8:**133–137.

Lonsdale, W. M., and D. G. Abrect. 1989. Seedling mortality in *Mimosa pigra*, an invasive tropical shrub. Journal of Ecology **77:**371–385.

Luken, J. O. 1988. Population structure and biomass allocation of the naturalized shrub *Lonicera maackii* (Rupr.) Maxim. in forest and open habitats. American Midland Naturalist **119:**258–267.

Luken, J. O., and D. T. Mattimiro. 1991. Habitat-specific resilience of the invasive shrub Amur honeysuckle (*Lonicera maackii*) during repeated clipping. Ecological Applications **1:**104–109.

Luken, J. O., and J. W. Thieret. 1995*a*. Amur honeysuckle (*Lonicera maackii*; Caprifoliaceae): its ascent, decline, and fall. Sida **16:** 479–503.

Luken, J. O., T. C. Tholemeier, B. A. Kunkel, and L. M. Kuddes. 1995*b*. Branch architecture plasticity of Amur honeysuckle (*Lonicera maackii* (Rupr.) Herder): initial response in extreme light environments. Bulletin of the Torrey Botanical Club **122:**190–195

Luken, J. O., T. C. Tholemeier, L. M. Kuddes, and B. A. Kunkel. 1995*c*. Performance, plasticity, and acclimation of the nonindigenous shrub *Lonicera maackii* (Caprifoliaceae) in contrasting light environments. Canadian Journal of Botany **73:**1953–1961.

Mack, R. N. 1981. Invasion of *Bromus tectorum* L. into Western North America: an ecological chronicle. Agro-Ecosystems **7:**145–165.

Mack, R. N. 1991. The commercial seed trade: an early disperser of weeds in the United States. Economic Botany **45:**257–273.

Matlack, G. R. 1994. Plant species migrations in a mixed-history forest landscape in eastern North America. Ecology **75:**1491–1502.

Mooney, H. A., and J. A. Drake, editors. 1986. Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York.

Niering, W. A., G. D. Dreyer, F. E. Egler, and J. P. Anderson, Jr. 1986. Stability of a *Viburnum lentago* shrub community after 30 years. Bulletin of the Torrey Botanical Club **113:**23–27.

Nyboer, R. 1992. Vegetation management guideline: bush honeysuckles-tatartian, Morrow's, Belle, and Amur honeysuckle (*Lonicera tatarica* L., *L. morrowii* Gray, *L.* x *bella* Zabel, and *L. maackii* [Rupr.] Maxim.). Natural Areas Journal **12:**218–219.

Parker, I. M., S. K. Mertens, and D. W. Schemske. 1993. Distribution of seven native and two exotic plants in tallgrass prairie in southeastern Wisconsin: the importance of human disturbance. American Midland Naturalist **130:**43–55.

Rejmanek, M. 1989. Invasibility of plant communities. Pages 369–388 in J. A. Drake, H. A. Mooney, F. di Castri, R. H. Groves, F. J. Kruger, M. Rejmanek, and M. Williamson, editors. Biological invasions: a global perspective. Scope 37. John Wiley and Sons, Chichester, United Kingdom.

Richardson, D. M., and W. J. Bond. 1991. Determinants of plant distribution: evidence from pine invasions. American Naturalist **137:** 639–668.

Sakai, A. K., and J. H. Sulak. 1985. Four decades of secondary succession in two lowland permanent plots in northern lower Michigan. American Midland Naturalist **113:**146–157.

SAS (Statistical Analysis System). 1990. User's guide: statistics. Version 6. SAS, Cary, North Carolina.

Schierenbeck, K. A., and J. D. Marshall. 1993. Seasonal and diurnal patterns of photosynthetic gas exchange for *Lonicera sempervirens* and *L. japonica* (Caprifoliaceae). American Journal of Botany **80:** 1292–1299.

Schierenbeck, K. A., R. N. Mack, and R. R. Sharitz. 1994. Effects of herbivory on growth and biomass allocation in native and introduced species of *Lonicera*. Ecology **75:**1661–1672.

Trisel, D. E., and D. L. Gorchov. 1994. Regional distribution, ecological impact, and leaf phenology of the invasive shrub *Lonicera maackii*. Abstract. Bulletin of the Ecological Society of America **75**(Supplement):231.

van Ruremonde, R. H. A. C., and J. T. R. Kalkhoven. 1991. Effects of woodlot isolation on the dispersion of plants with fleshy fruits. Journal of Vegetation Science **2:**377–384.

Vitousek, P. M. 1990. Biological invasions and ecosystem processes: toward an integration of population biology and ecosystem studies. Oikos **57:**7–13.

Woods, K. D. 1993. Effects of invasion by *Lonicera tatarica* L. on herbs and tree seedlings in four New England forests. American Midland Naturalist **130:**62–74.

Yost, S. E., S. Antenen, and G. Hartvigsen. 1991. The vegetation of the Wave Hill natural area, Bronx, New York. Bulletin of the Torrey Botanical Club **118:**312–325.