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Effects of Invasion by *Lonicera tatarica* L. on Herbs and Tree Seedlings in Four New England Forests

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ABSTRACT.—A shrubby, exotic honeysuckle, *Lonicera tatarica* L., has aggressively invaded woodlands throughout the northeastern United States. This paper explores its effects on herbaceous species and tree regeneration in three stands in southwestern Vermont and one in northwestern Massachusetts. In mesic stands with relatively rich soil, total herbaceous cover, herb species richness and density of tree seedlings were substantially depressed when *L. tatarica* cover exceeded ca. 30%, a relationship not observed at a dry poor site. Ordination indicates that evergreen herbaceous species and sprawling or vining understory species may be more tolerant of *L. tatarica*, suggesting that its effects on the community may be related to seasonal competition for light.

INTRODUCTION

Ecological questions about invasion may concern life-history attributes that typify invasive species, ecosystem or community characteristics that allow invasion and effects of invasion on the pre-existing community and ecosystem. Classical and recent studies have addressed various of these aspects of biological invasion (Elton, 1958; Baker and Stebbins, 1965; Mooney and Drake, 1986; Groves and Burdon, 1986; Diamond and Case, 1986; Mack, 1985; Drake *et al.*, 1989). Probably most attention has been focused on understanding life histories of invasive species (Ehrlich, 1986; Bazzaz, 1986; Baker, 1974; Mack, 1981, 1986; Martins and Jain, 1979; Mooney *et al.*, 1986; Knight, 1986; Simberloff, 1981, 1986).

Nearly all discussions of invasion since Elton (1958) emphasize the importance of external disturbance in opening a community to invasion, and this has been generally upheld empirically. Relatively species-poor communities may be more easily invasible, presumably because such communities use available resources less efficiently (Elton, 1958; Diamond and Case, 1986). Introductions may, therefore, be more likely to succeed if the invader has a life-form or life-history absent or rare in the flora of the new community.

Ecosystem effects of invading plants, on net production and biomass and on mineral cycling, have also been demonstrated (Vitousek, 1986), most frequently in successional or island habitats. Although it has been suggested that invaders might cause changes in abundance or extinction of other species through competition, predation or parasitism (Simberloff, 1986; Diamond and Case, 1986), competitive effects of invading plants on the rest of the plant community, particularly in relatively undisturbed communities, are not well-documented (*see* Davis, 1981; Woods and Davis, 1989; Walker and Vitousek, 1991).

I report, here, a study of effects of *Lonicera tatarica* L. (Tatarian honeysuckle) on understory communities in four forest communities near Bennington, Vermont. Because this exotic is a successful invader of intact, late-successional forests, it provides a particularly appropriate case for study of effects of an invader on the pre-existing community.

Study system.—*Lonicera tatarica* L. is a Eurasian shrub native to forests of W-central Eurasia. There it grows in communities similar in generic composition to those of north-eastern U.S. (Bozoyan, 1981; Zolotukhin, 1980). Introduced to North America before 1800 (Rehder, 1927) as an ornamental, it has been used extensively in shelter belts and wildlife

plantings (U.S. For. Serv., 1974). It has also become an aggressive invader of lower elevation forests throughout northeastern U.S., growing most densely along forest edges and in clearings, but also invading the interior of intact forests. In many forests, previously open understories are now near-impenetrable masses of honeysuckle. [In this study, *L. tatarica* is not distinguished from *L. ×bella*, a hybrid of *L. tatarica* and *L. morrowi*. Barnes (1972) concludes that the hybrid swarm is extensively distributed in the northeastern U.S., so the populations studied here may be taxonomically complex.]

Lonicera tatarica has some characteristics considered “typical” of successful invaders; it grows rapidly and produces large quantities of showy, bird-dispersed berries. However, its breeding system and demographic characteristics are not documented. The native flora of the Northeast includes shrubby *Lonicera* species which appear similar in life history but are not particularly aggressive. It is unclear why *L. tatarica* has been so much more aggressive in forests than native or other introduced shrubs. There is some suggestion that it has been released from natural enemies in its native habitat (Baloch *et al.*, 1985; Mahr and Dittl, 1986). It is also possible that *L. tatarica* is filling a vacant “resource niche” (Vitousek, 1986; Givnish, 1982); northeastern forests with closed canopies do not naturally have a strongly developed shrub canopy.

There is little documentation of effects of *Lonicera tatarica* invasion on community structure or composition, although some evidence suggests that it may chemically suppress some other species (Uesato *et al.*, 1986; Zolotukhin, 1980). It appears, however, to negatively affect herbaceous plants and tree seedlings, and foresters have undertaken control efforts (Kline, 1981; Ahrens and Pill, 1985). There have been some experiments with chemical control in nature preserves (M. DesMeules, Vermont Nature Conservancy, pers. comm.; Kline, 1981; Kline *et al.*, 1982). Horticulturalists have worked to control pests of *L. tatarica* (Mahr and Dittl, 1986).

METHODS

Research was conducted at four field sites:

1. *McCullough Woods* is a mature, relatively undisturbed forest of about 50 ha, owned by The Nature Conservancy, in the Town of Bennington, Vermont. It is a rich, dry-mesic forest, at ca. 250 m elevation, dominated by *Acer saccharum* Marsh. (sugar maple), *Quercus rubra* L. (red oak) and *Fraxinus americana* L. (white ash), with a very diverse herbaceous flora. This study was conducted in an area of about 2 ha in a particularly mesic part of the reserve with a primarily NW aspect and at least 100 m from the edge of the mature forest stand. Parts of McCullough Woods were heavily damaged by a major snowstorm on 4 October 1987, but damage was not extensive in the study area. *Lonicera tatarica* was present in the study area in patches of various sizes occupying somewhat less than half of the forest floor. Soils are circumneutral to limey, with high nutrient availability.

2. *Sugar Bush* is a stand of ca. 10 ha on the Bennington College campus. This stand probably was never fully cleared, but was managed as a sugar bush before 1930. The presence of a few large *Picea abies* (L.) Karst. (Norway spruce) and *Acer saccharinum* L. (silver maple) indicates some disturbance more than 50 years ago, but the stand has suffered no significant disturbance since. The canopy, dominated by sugar maple, is closed except in gaps caused by recent natural treefalls. Part of the stand is level, part has a moderate slope with westerly aspect. Soils are circumneutral, with high nutrient availability. Sampling was primarily on the sloping portion of the stand.

3. *Jennings Woods* is also on the college campus. It is an even-age stand (ca. 75 yr old) of about 5 ha, strongly dominated by *Acer saccharum*. Microtopography, location and soil profile suggest that the area was previously cultivated. The stand is level, and characterized

by a relatively impoverished herb stratum. *Lonicera tatarica* is quite abundant in this stand, constituting a nearly continuous stratum in some areas.

4. *Hopkins Forest* is a research and natural area of several hundred hectares belonging to Williams College in Williamstown, Massachusetts. Hopkins Forest is diverse in soil, topography and vegetation. Generally, the soils are more acidic and lower in nutrient availability than those of the other stands studied, and *Lonicera tatarica* is apparently more restricted in distribution to wetter soils. Sampling was confined to a single stand, ca. 70 yr old, on a gentle E-facing slope where *L. tatarica* occurrence is extensive and generally associated with seepage.

Field procedures.—In each of the four stands, two 50-m transects were established. Transects were placed parallel to contour (except at Hopkins Forest, where honeysuckle distribution mandated transects perpendicular to contour) in areas containing sufficient *Lonicera tatarica* to ensure transects would intersect *Lonicera* patches. Sample plots (2 × 2 m), subdivided into four 1-m² quadrats, were located at 10-m intervals along each transect. The following data were recorded in each quadrat: basal diameter for all *L. tatarica* stems rooted in the plot (the layering habit of *L. tatarica* sometimes required arbitrary judgments as to which stems were independently rooted); total cover of *L. tatarica*; total cover by species for all herb species and tree seedlings <1 m tall (cover classes used were <1%, 1–5%, 5–10%, and subsequent increments of 10%); cover of nonsoil surface area (rocks, wood, tree trunk); number of seedlings by species for all woody plants <1 m tall (tree seedlings <1 m tall were aged by counting terminal bud scars) and basal diameter for woody stems 1–2 m tall.

At each 2 × 2 m sample plot, tree canopy cover was estimated to the nearest 10%. All trees over 5 cm diam and within 8 m of each sample plot center were identified, measured (diameter at breast height) and their distance to plot center measured. Soil texture was described and pH measured for 2–4 points on each transect.

An additional seven sets of plots (two sets each at Jennings and McCullough Woods, and three in Sugar Bush), each consisting of three 2 × 2 m plots, divided into four 1 × 1 m quadrats (as for transect sample points) were located in areas of high and low *Lonicera tatarica* cover. Data were recorded as for transect samples described above. In analyses described here, these data are combined with those from transects.

In total, 44 m² quadrats were sampled at Hopkins Forest, 84 at McCullough Woods, 84 at Jennings Woods, and 92 at Sugar Bush.

At five transect points at McCullough Woods and Sugar Bush, the two or three largest tree seedlings (typically 1–3 m tall) and the two largest *Lonicera tatarica* stems in honeysuckle patches near sample plots were cut and basal sections collected for aging by ring-count. Measurements of photosynthetically active radiation were made immediately above the *L. tatarica* canopy and at ground level at 5-m intervals on transects in McCullough Woods and Sugar Bush, yielding light data for 50 points in each stand.

Data analysis.—Basal area for canopy stems was calculated and summed by species for all plots. For each sample point, correlations were calculated between basal area for each canopy species and *Lonicera tatarica* cover and basal area. Canopy composition for each stand was obtained by averaging basal area measurements for 8-m radius plots (Table 1).

Total herb cover was obtained by summing cover estimates for all species in 1-m² plots (allowing total cover >100%). Species richness per plot was used as a diversity measure for herbaceous communities.

Since stands differed floristically and ecologically, analyses of variance were used to examine effects, at the plot level, of *Lonicera tatarica* cover, *L. tatarica* basal area, and stand (as a categorical variable) on herb species richness, total herb cover, and tree seedling density. The three independent variables showed significant main effects ($P < 0.01$) on all three

TABLE 1.—Average basal area (m²/ha) by species for all stands

	Sugar Bush	McCullough Woods	Jennings Woods	Hopkins Forest
<i>Acer rubrum</i>				18.0
<i>A. saccharinum</i>	7.2		2.0	
<i>A. saccharum</i>	34.0	19.3	27.0	1.2
<i>Betula lenta</i>	0.0			
<i>Carya cordiformis</i>		1.1		
<i>C. ovata</i>		0.8		
<i>Fraxinus americana</i>	1.1	3.8	1.1	4.6
<i>Picea abies</i>				
<i>Pinus strobus</i>			0.6	
<i>Prunus serotina</i>	0.1		0.1	5.7
<i>Quercus borealis</i>		2.7		0.2
<i>Tilia americana</i>		0.7		
<i>Ulmus americana</i>		1.0		0.1
Other species*	0.1	0.2	0.5	0.4
Total basal area	42.4	29.6	31.2	30.2

* Species included here did not reach basal areas greater than 0.50 m²/ha in any stand. They are: *Carpinus caroliniana*, *Fagus grandifolia*, *Rhamnus cathartica*, *Ostrya virginiana*, *Cornus alternifolia*, *Betula lenta* and *Crataegus* sp.

dependent variables, so in subsequent analyses and results stands are treated separately. *Lonicera tatarica* cover effects were, in all tests, significant at lower P values than those associated with *L. tatarica* basal area, so remaining analyses and discussion concern cover only.

Relationships between *Lonicera tatarica* cover (independent variable) and total herb cover, herb species richness, and tree seedling density were examined using linear, least-squares

TABLE 2.—Herb cover and species richness and seedling density (mean \pm 1 SD) with respect to honeysuckle cover (n = number of 1 m² plots)

Stand	Honeysuckle cover	Herb stratum		Seedling number	n
		Total cover	Richness		
McCullough	0–30%	79.4 \pm 39.3	6.5 \pm 1.8	5.7 \pm 3.2	37
	40–70%	33.0 \pm 23.8	6.3 \pm 1.5	2.8 \pm 1.9	6
	80–100%	17.0 \pm 22.7	4.2 \pm 2.0	0.8 \pm 1.3	25
Sugar Bush	0–30%	96.6 \pm 48.0	3.7 \pm 1.6	3.9 \pm 3.6	43
	40–70%	87.0 \pm 43.3	3.2 \pm 1.5	2.0 \pm 1.7	5
	80–100%	41.6 \pm 34.6	3.2 \pm 1.7	0.2 \pm 0.5	24
Jennings	0–30%	20.8 \pm 33.8	1.2 \pm 1.1	7.6 \pm 6.1	23
	40–70%	33.2 \pm 50.7	3.0 \pm 2.9	5.5 \pm 3.5	4
	80–100%	2.8 \pm 6.3	0.9 \pm 1.0	1.9 \pm 2.4	35
Hopkins	0–30%	12.1 \pm 15.5	2.7 \pm 2.2	4.3 \pm 3.5	25
	40–70%	49.5 \pm 34.4	5.8 \pm 2.3	1.2 \pm 0.8	4
	80–100%	31.9 \pm 29.6	5.8 \pm 2.4	0.4 \pm 0.6	35

TABLE 3.—Cover for understory herbs with occurrence in more than 10 quadrats. (* indicates difference between low and high honeysuckle quadrats, Mann-Whitney U Test, P = 0.05)

Honeysuckle cover: n =	McCullough Woods				Sugar Bush			
	<30%		>30%		<30%		>30%	
	38		30		46		26	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
<i>Alliaria officinalis</i>					1.9*	11.8	0.0	0.0
<i>Amphicarpa bracteata</i>	4.8	17.4	0.5	1.8				
<i>Arisaema triphyllum</i>					2.7*	9.6	0.3	0.8
<i>Athyrium filix-femina</i>					6.3	17.0	3.0	8.6
<i>Chelidonium majus</i>					0.2*	0.8	0.0	0.0
<i>Carex rosea</i>					8.9*	18.2	0.4	1.9
<i>C. plantaginea</i>	1.0*	1.7	0.2	0.4				
<i>C. hitchcockiana</i>	9.5*	21.7	0.1	0.3				
<i>C. albursina</i>	1.6*	5.1	0.1	0.3				
<i>C. annectens</i>	0.7*	1.1	0.0	0.1				
<i>Caulophyllum thalictroides</i>	0.3*	0.8	0.0	0.1				
<i>Circaea quadrisulcata</i>	0.4*	0.9	0.0	0.2				
<i>Dryopteris intermedia</i>	0.3	1.0	0.3	1.5	3.7	14.5	4.6	13.6
<i>Hepatica nobilis</i>	1.3	1.9	1.6	1.8				
<i>Hydrophyllum virginianum</i>	37.0*	8.2	8.2	17.8				
<i>Impatiens biflora</i>					60.8*	36.2	14.5	19.9
<i>Mitella diphylla</i>	0.2	0.9	0.4	1.0				
Mosses	1.4	2.7	2.4	4.4	7.0	15.3	5.3	11.9
<i>Parthenocissus quinquefolia</i>	2.2	6.2	0.9	2.1				
<i>Polygonatum pubescens</i>	0.8*	1.1	0.4	0.9				
<i>Polystichum acrostichoides</i>					1.8	8.9	0.6	2.2
<i>Rubus</i> sp.					0.3	1.1	1.2	3.2
<i>Trillium erectum</i>	0.9	2.3	0.4	1.0				
<i>Viola canadensis</i>	2.4	8.2	0.8	1.2	1.1*	0.2	0.0	0.0

regression analysis (although large numbers of 0% herb cover points at Jennings Woods make that regression suspect).

Compositional patterns in herb communities were examined using detrended correspondence analysis (DECORANA) (Hill, 1979) and multidimensional scaling (MDS) (Minchin, 1987). Ordinations were based on herb species only.

RESULTS AND DISCUSSION

Canopy effects.—*Lonicera tatarica* cover was not significantly correlated with either total canopy basal area or basal area for any single species, except at Hopkins Forest where there was a positive association between *L. tatarica* cover and basal area of *Fraxinus americana*. *Fraxinus* was found primarily on the moist soils also favored by *L. tatarica*.

Herb communities.—McCullough Woods had the highest average and total herb species richness per sq-m plot (Tables 2, 3). Nearly all species were native and typical of rich mesic forests. Sugar Bush and Jennings Woods had progressively lower herb species richness, increasing proportions of alien and weedy species and more quadrats with no herbs. This pattern appeared to be independent of *Lonicera tatarica* cover, but may be related to successional status; McCullough Woods is thought to approximate old-growth forest, while Sugar Bush is of intermediate successional status, and Jennings Woods is even-aged and

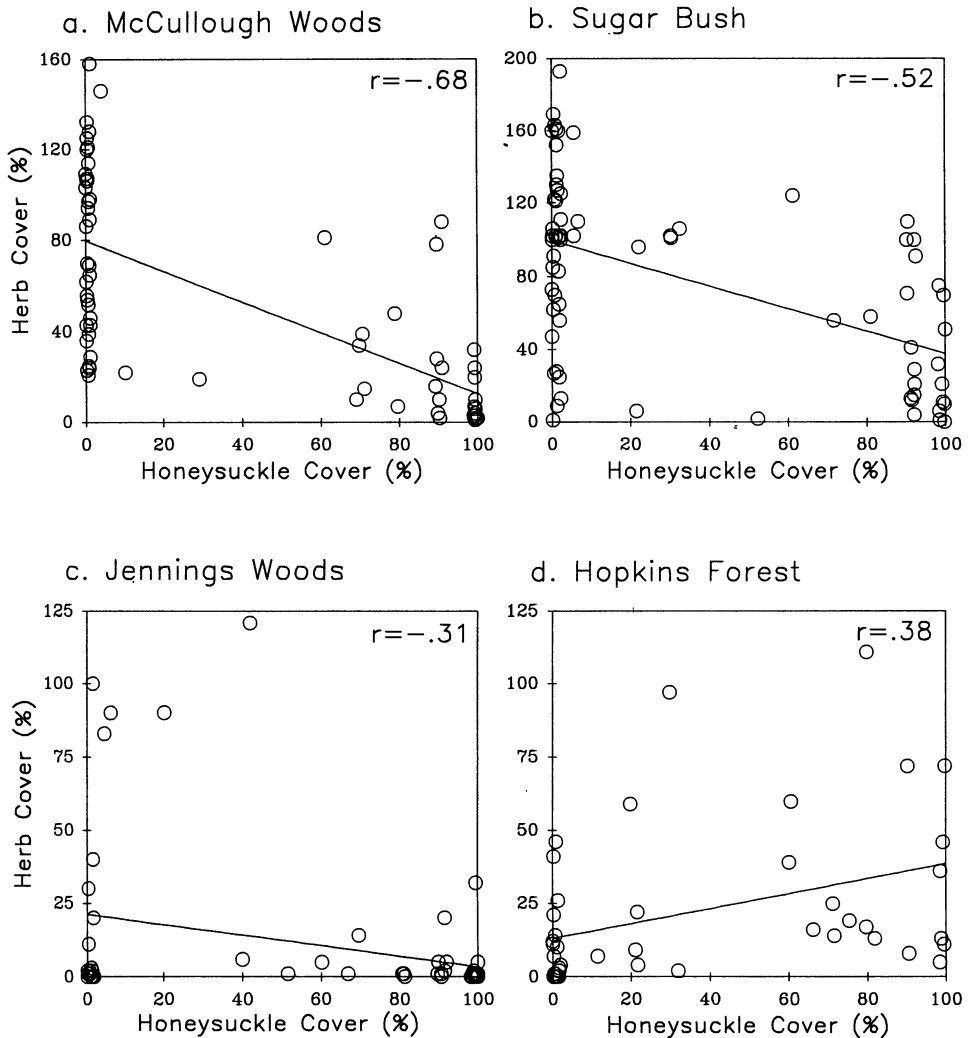


FIG. 1.—Plots of total herb cover (summation of cover estimates for all species) against percent honeysuckle cover for (a) McCullough Woods; (b) Sugar Bush; (c) Jennings Woods, and (d) Hopkins Forest. Points represent single 1-m² quadrats. Honeysuckle cover was estimated to nearest 10% (or as 1% or 5% when less than 10%); values were randomly displaced slightly (“fuzzed”) for better visibility of individual points. Linear, least-squares regression lines are shown. All slopes and correlation coefficients differ significantly from 0

young. Hopkins Forest had intermediate herb diversity and cover, with mostly native species, but the species assemblage was distinct in being dominated by successional species and species typical of poor soils, presumably reflecting different soil and historical situations.

In the three Vermont stands, both herb richness and cover declined with increasing *Lonicera tatarica* cover (Figs. 1a–1c, 2a–2c), but the effects were greatest at McCullough Woods and least at Jennings Woods. Correlations were significant at $P < 0.01$ except for

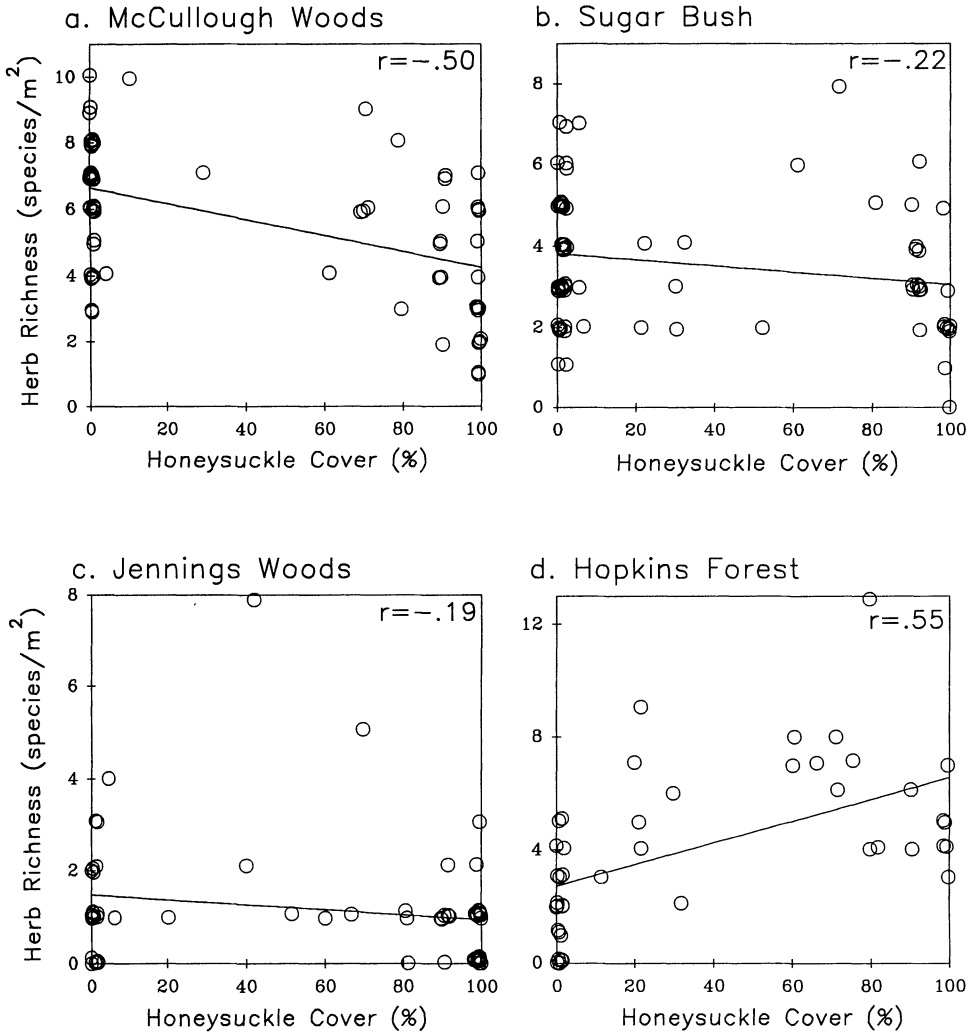


FIG. 2.—Plots of herb species richness against percent honeysuckle cover for (a) McCullough Woods; (b) Sugar Bush; (c) Jennings Woods, and (d) Hopkins Forest. Format as for Figure 1. Points are “fuzzed” on both axes for visibility

species richness at Sugar Bush and Jennings Woods where $P < 0.05$. The appearance of little effect at Jennings Woods is, in part, a consequence of low herb diversity. The differences among stands may also reflect greater sensitivity to effects of *L. tatarica* invasion of late-successional communities of native forest herbs, as the only apparent differences in stand characteristics concern successional status.

At Hopkins Forest in Massachusetts the relationships between *Lonicera tatarica* cover and herb cover and diversity are positive, a reversal of trends in other stands (Figs. 1d, 2d), but this change probably should not be interpreted as a positive effect of *L. tatarica* on herb communities. At the other stands, there were no detectable substrate differences between

sample plots with and without *L. tatarica*. At Hopkins, *L. tatarica* was concentrated on microsites that were distinctly more moist due to seepage. Herb communities and *L. tatarica* may both be responding positively to this variable, obscuring herb response to *L. tatarica* density.

Hopkins Forest also differed from the other three stands with respect to the relationship between basal area of canopy stems and *Lonicera tatarica* cover. In the other three stands there was no significant correlation between canopy basal area (total or for any single tree species) and *L. tatarica* cover. At Hopkins Forest, there was a positive correlation ($P < 0.05$). Again, the correlation could be due to positive response of both trees and *L. tatarica* to areas of moister soils within the stand.

Herb community ordinations were not useful for all stands. Neither technique produced interpretable patterns for Jennings Woods, apparently due to low diversity, uniformity of composition and large number of quadrats with no herbs. Ordinations for Hopkins Forest were also not informative. DECORANA was unsuccessful in extracting a first axis, while the first two axes in MDS separated two distinct groups reflecting the distinct composition of moist and dry quadrats. Moist quadrats were also higher in *L. tatarica* cover, but the direct effects of soil differences and *Lonicera tatarica* cover on herb communities cannot be separated.

For both McCullough Woods (Fig. 3) and Sugar Bush (Fig. 4), ordinations show a strong association between herb community structure and *L. tatarica* cover. In both MDS ordinations, *Lonicera tatarica* cover and first axis scores are highly correlated ($P < 0.01$), but *L. tatarica* cover is not significantly correlated with scores on subsequent axes. In both cases, most low honeysuckle-cover quadrats that fall in the “high honeysuckle” regions of the ordinations were quadrats with exposed rock, tree bases, or high cover by dead wood, and, consequently, with reduced herb cover and diversity for reasons other than *L. tatarica* cover.

The DECORANA ordinations also showed strong *Lonicera tatarica* effects. However, the strongest correlations with *L. tatarica* cover were for the second (Sugar Bush) or third (McCullough Woods) axes. This may be a consequence of variation in the data set being too great for successful treatment in DECORANA (Minchin, 1987).

The effects of *Lonicera tatarica* cover appeared to vary, however, among herbaceous species (Table 3). This variation may be accounted for, in part, by differences in life histories. With very few exceptions, frequently occurring herbs that were not apparently suppressed by *L. tatarica* were either at least partly evergreen (e.g., *Hepatica nobilis*, *Dryopteris intermedia*, *Mitella diphylla*, *Polystichum acrostichoides*, mosses) or sprawling or vining in habit (*Rubus* sp., *Parthenocissus quinquefolia*, *Amphicarpa bracteata*). In the DECORANA ordinations of herb species, these species were also centered nearer the “high honeysuckle” region of the ordination. On the other hand, suppression was particularly marked for the few annual species (all in Sugar Bush). This pattern suggests correlation between tolerance of *L. tatarica* cover and life-history traits.

Tree seedlings.—In all stands, tree seedling density (seedlings < 1 m tall) declined significantly ($P < 0.01$) with increasing *Lonicera tatarica* cover (Fig. 5). Although stand effect on seedling density was significant, there is much less variation among sites than in herb community characteristics. All sites showed average seedling density $> 5/m^2$ without *L. tatarica*, but less than $1/m^2$ when *L. tatarica* cover exceeded 90%. This effect was not significant ($P > 0.05$) for seedlings 1–2 m tall; these frequently overtopped *L. tatarica*. Ring counts of basal sections of seedlings and *L. tatarica* stems confirmed that the larger seedlings were older than any current *L. tatarica* stems. These data suggest that seedlings which predate *L. tatarica* establishment are more tolerant of its presence, but establishment of new seedlings is prevented.

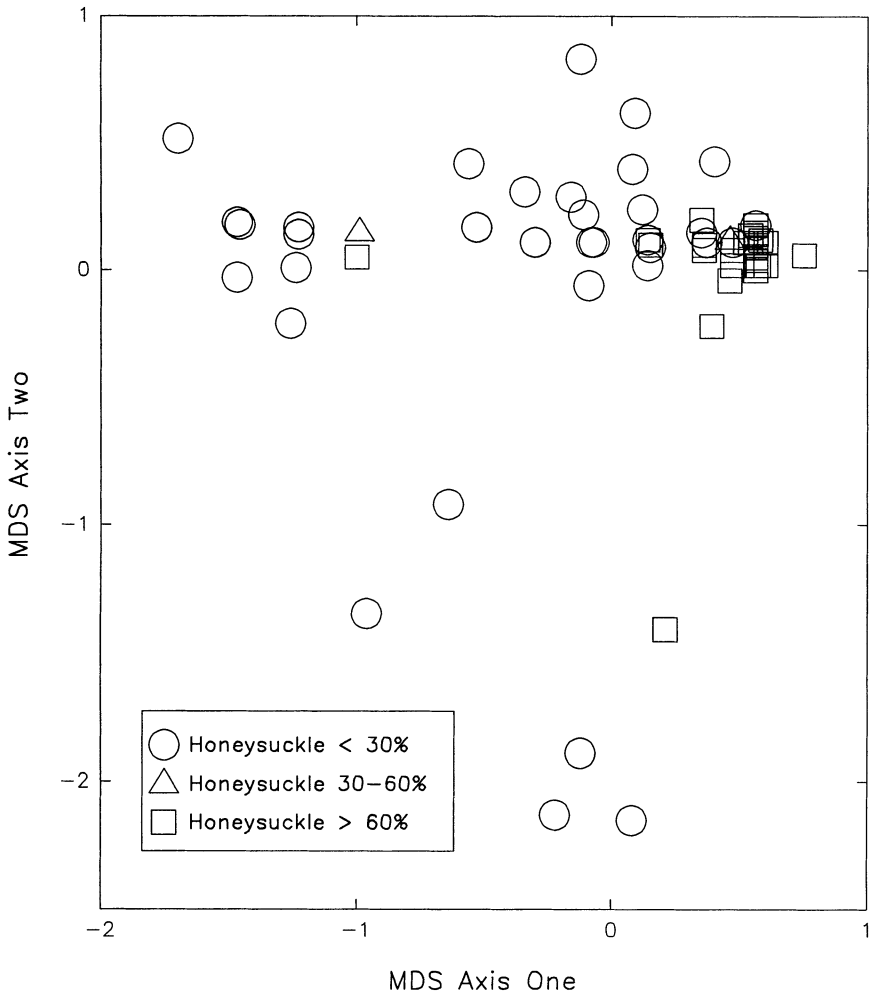


FIG. 3.—Multidimensional scaling ordination of herb sample quadrats for McCullough Woods. Symbols show position of 1-m² quadrats on first two axes of ordination. Symbol shape indicates honeysuckle cover as indicated

Mechanisms and consequences of honeysuckle effects.—This study does not allow direct tests of hypotheses concerning mechanisms by which *Lonicera tatarica* affects herb and seedling communities, nor even whether *L. tatarica* causes the patterns observed. Effects of soil differences at Hopkins Forest appear to mask or override effects of *L. tatarica*. However, in the three Vermont stands on soils that are relatively uniform in moisture conditions and of higher pH, there was no observed association between any physical or biological condition and *L. tatarica* cover. In these stands, correlations of *L. tatarica* cover with community characteristics are more likely to reflect causal relationships.

Although chemical interactions are possible causes of these patterns (Uesato *et al.*, 1986; Zolotukhin, 1980), some observations are consistent with the hypothesis that *Lonicera tatarica* suppresses other species through competition for light (Barnes, 1972; Harrington *et al.*,

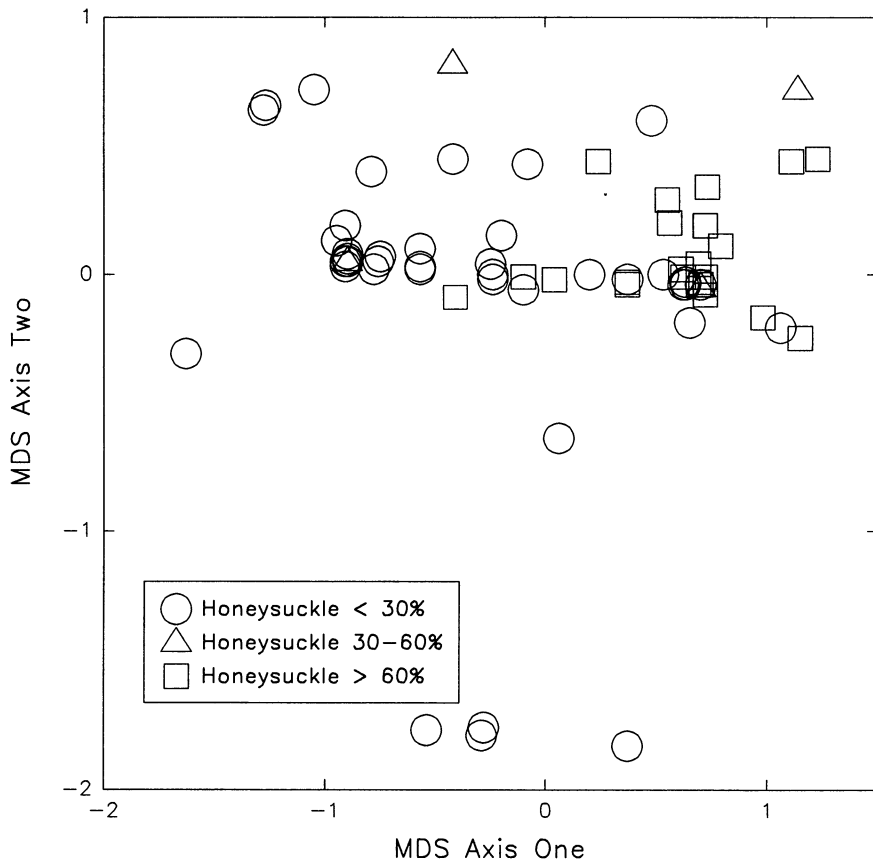


FIG. 4.—Ordination of herb sample quadrats for Sugar Bush. See Figure 3 for explanation

1989a, b). Tatarian honeysuckle is the earliest deciduous woody plant to leaf out in these stands, with leaf expansion beginning ca. 2 wk earlier than for trees in the same stands. *Lonicera tatarica* also retains green leaves longer than other woody species. Consequently, it casts shade at the forest floor at a time critical for carbon gain for many herbs, particularly the spring ephemerals. Measurements of light above and below heavy *L. tatarica* canopy at midsummer showed reductions of ca. 60% in light reaching the forest floor. The relative dominance, under *L. tatarica*, of evergreen species and sprawling species with the potential for subsidy from leaves outside of *L. tatarica* canopy is consistent with postulated light limitation. Further understanding of mechanisms, however, will require experimental work.

The consequences of *Lonicera tatarica* invasion for community structure and dynamics appear important, reducing richness and cover of herb communities. Reduction of populations of some herb species may increase the likelihood of local extinction. Over the long term, additional major consequences may result from *L. tatarica*'s effects on tree seedlings. With *L. tatarica* cover, it is possible that suppression of advance regeneration could lead to changes in canopy composition or even failure of canopy tree replacement and conversion of forests to more open canopies or shrublands. Egler (1954) has also suggested that shrub

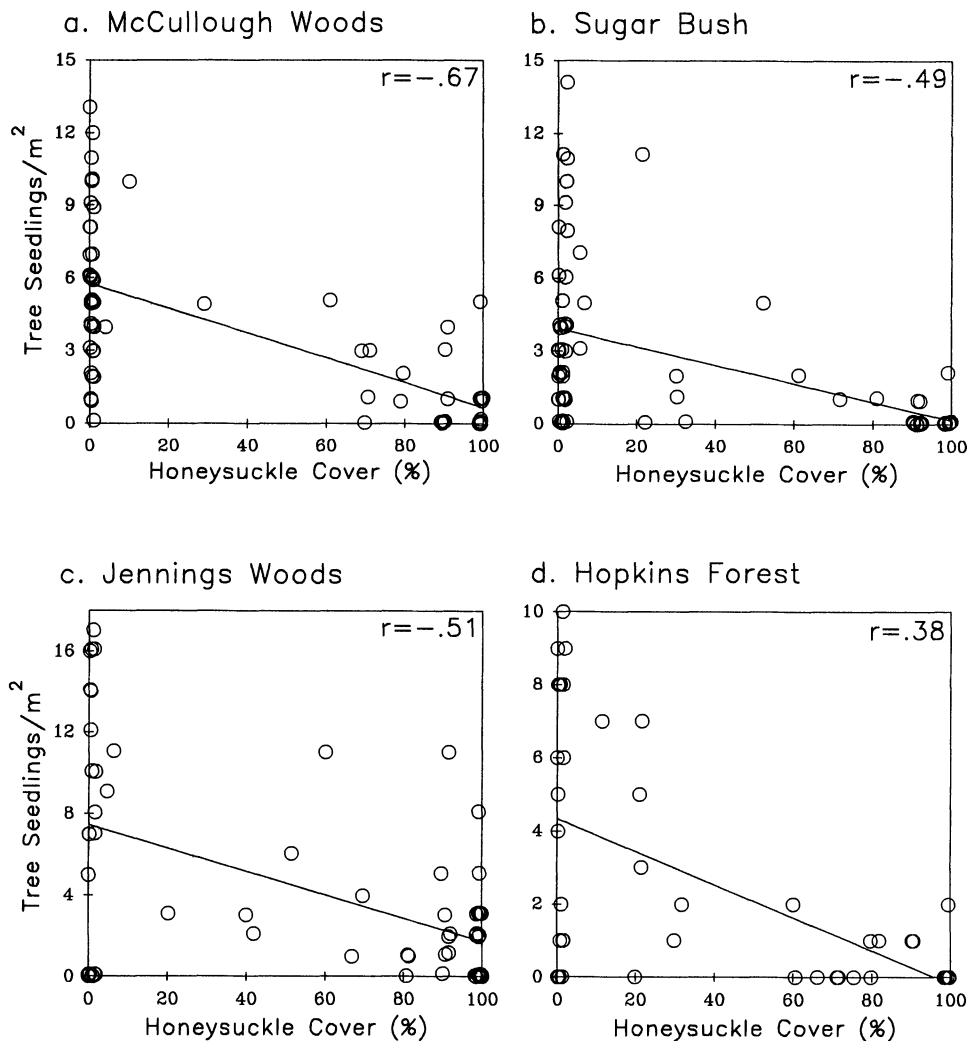


FIG. 5.—Plots of seedling density against percent honeysuckle cover for (a) McCullough Woods; (b) Sugar Bush; (c) Jennings Woods, and (d) Hopkins Forest. Format as for Figure 1. Points are “fuzzed” on both axes for visibility

communities may resist tree invasion, but it is not clear whether a pure *L. tatarica* community could completely suppress tree reproduction.

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