Effects of Below- and Aboveground Competition from the Vines Lonicera japonica and Parthenocissus quinquefolia on the Growth of the Tree Host Liquidambar styraciflua
Author(s): L. R. Dillenburg, D. F. Whigham, A. H. Teramura, I. N. Forseth
Reviewed work(s):
Source: *Oecologia*, Vol. 93, No. 1 (1993), pp. 48-54
Published by: Springer in cooperation with International Association for Ecology
Stable URL: http://www.jstor.org/stable/4220218
Accessed: 05/03/2012 07:50

Oecologia (1993) 93:48–54

Oecologia

Effects of below- and aboveground competition from the vines *Lonicera japonica* and *Parthenocissus quinquefolia* on the growth of the tree host *Liquidambar styraciflua*

L.R. Dillenburg[1,2], **D.F. Whigham**[2], **A.H. Teramura**[1], **I.N. Forseth**[1]

[1] Department of Botany, University of Maryland, College Park, MD 20742, USA
[2] Smithsonian Environmental Research Center, Edgewater, MD 21037, USA

Received: 20 February 1992 / Accepted: 12 August 1992

Abstract. Detrimental effects of vines on tree growth in successional environments have been frequently reported. Little is known, however, about the relative importance of below and aboveground competition from vines on tree growth. The objective of this study was to quantify and compare the growth responses of *Liquidambar styraciflua* saplings to below and/or aboveground competition with the exotic evergreen vine, *Lonicera japonica* (Japanese honeysuckle), and the native deciduous vine, *Parthenocissus quinquefolia* (Virginia creeper). Soil trenching and/or vine-trellising were used to control the type of vine competition experienced by trees. Comparisons among untrenched treatments tested for effects of belowground competition, singly or in combination with aboveground competition. Comparisons among trenched treatments tested for effects of aboveground competition. After two growing seasons, *Lonicera japonica* had a greater effect on the growth of *L. styraciflua* than did *P. quinquefolia*. This effect was largely due to root competition, as canopy competition only had a negative effect on tree growth when it occurred in combination with root competition. Leaf expansion was consistently and similarly affected by all treatments which involved belowground competition.

Key words: Vines – Aboveground and belowground competition – *Lonicera japonica* – *Parthenocissus quinquefolia* – *Liquidambar styraciflua*

Woody vines (lianas) are found in almost every climate and plant community where there are trees to support them (Richards 1952). In North America, woody vines can be found across a wide range of physiognomic regions, from open fields to climax forests (Teramura et al. 1991). They become particularly abundant when light availability is high, such as at forest edges, in tree gaps, and in early- to mid-successional forests (Penfound 1974; Boring et al. 1981; Putz 1984). Vines can greatly affect the growth of their hosts under these circumstances, and arrest the regeneration of both woody and herbaceous vegetation (Lutz 1943; Penfound 1974; Thomas 1980; Friedland and Smith 1982; Whigham 1984; Putz 1984).

Competition between woody vines and trees, similar to other plants, can occur at two different levels: belowground (roots), and aboveground (canopies). What makes competition between trees and vines unique is the close association between tree and vine canopies that results from the vine's dependence on the tree for external support. An architecture that emphasizes photosynthetic tissue over that of support structures enables vines to collect light efficiently (Monsi and Murata 1970). Aboveground competition thus appears to be the most obvious aspect of the interaction between vines and their tree hosts.

Wilson (1988) concluded that root competition between herbaceous species is generally more important than canopy competition, at least during the initial stages of interaction. Although there have been several studies which attempted to separate the effects of root and shoot competition (e.g., Donald 1958; Aspinall 1960; King 1971; Martin and Snaydon 1982; Wilson 1989), only a few have examined the competitive interactions between vines and other plants (Patterson 1973; Whigham 1984).

Most studies on competition between trees and vines are based on observations that plants not infested with vines grow better than vine-infested ones (Featherly 1941; Lutz 1943; Siccama et al. 1976; Thomas 1980; Putz 1984). Because vines may predominate in habitats where, for unrelated reasons, their hosts do not grow well, and because vines may spread more rapidly through hosts that have low vigor or are already competitively suppressed, studies based on observations of natural vine infestations do not allow us to separate vine from habitat effects on host plants (Stevens 1987). Manipulative experiments, like those conducted by Whigham (1984) and Stevens (1987), have helped to separate the effects of aboveground versus belowground competition.

Whigham (1984) performed a vine removal experiment in an abandoned field, and showed that the annual growth of sweetgum trees (*Liquidambar styraciflua*) was significantly affected by interaction with vines (mostly *Lonicera*

Correspondence to: D.F. Whigham

japonica and *Rhus radicans*). He speculated that the results were most likely due to belowground competition. These results were surprising, given the fact that the trees that Whigham studied were heavily infested with vines (Whigham, personal communication). The present study was undertaken to experimentally evaluate the relative effects of above- and belowground competition of two common woody vine species on saplings of *Liquidambar styraciflua* L., a common early successional hardwood tree. The vine species selected for this study were *Lonicera japonica* (L.) Thunb. (Japanese honeysuckle, an introduced, evergreen, twining vine), and *Parthenocissus quinquefolia* L. (Virginia creeper, a native, deciduous, tendriled vine). Although competition between paired plants should have an adverse effect on both individuals, compared to their performance under non-competitive conditions, we designed this study to examine competition from the "tree's point of view". Three specific questions were addressed: 1. is tree growth affected by the presence of vines?, 2. how do growth responses compare between trees interacting with vines below and aboveground?, and 3. is *L. styraciflua* affected differentially by competition with *L. japonica* compared to *P. quinquefolia*?

Materials and methods

Plant material

In March 1988, 1 year-old, commercially grown, *L. styraciflua* seedlings (15 to 25 cm tall) were transplanted into 35 cm long citrus tubes (2.4 l) with a 2:1:1 (v:v:v) mixture of peat, sand and compost. Rooted shoots of *L. japonica* and *P. quinquefolia* were collected from forest edges in Maryland in July of the same year, grown in 18 cm pots (2.7 l) with a commercial soil mixture (ProGro 300S). All plants were kept outdoors at the University of Maryland greenhouse, watered daily and fertilized biweekly with a full strength solution of 25-5-20, N-P-K. In October 1988 they were moved to the experimental garden.

The study site

This study was conducted at facilities of the Smithsonian Environmental Research Center (SERC), Edgewater, MD, on the inner coastal plain of the Chesapeake Bay (38°53'20"N, 76°33'20"W), where all three species are very common (Whigham 1984). Experimental plots were located in a 25 × 25 m site in an old field, from which all vegetation had been cleared by mowing, prior to tilling.

Experimental and treatment designs

The site was divided into 60 regularly spaced 1 × 1 m plots, the centers of each plot being 2.5 m apart. Plot treatment assignment followed a 2 × 2 × 3 incomplete factorial design. The 3 factors and their respective levels were: vine species (*L. japonica* or *P. quinquefolia*), soil trenching (trenched or not), and presence of vine on the host (on, off, or absent). Of the 12 possible treatment combinations, only 10 were used (Table 1). For treatments where vines were to be absent, the two vine species were not distinguished from each other. The different competition treatments are illustrated in Fig. 1. Plots and treatments were organized according to a randomized complete block design, with 6 replicates per treatment. Criteria for blocking included field location, and initial size of trees. Also, measurements were always taken a block at a time.

A single tree was planted at the center of each plot, and 2 vines of the same species were planted, one at the east and the other at the west side of the tree, either 30 cm away from the tree trunk (untrenched plots), or just outside each of the 2 trenches, which had been dug 30 cm away from the tree, at its east and west sides (trenched plots). All plots were covered with shredded hardwood mulch to reduce weed infestation and periodically weeded. There were no statistical differences in tree size among treatment means at the onset of the experiment. Means and standard errors across all 10 treatments ($n = 60$) were 65.3 ± 0.70 cm, 1.26 ± 0.013 cm, and 2.15 ± 0.063 m for height, diameter, and total stem length, respectively.

Soil trenching was used to exclude or minimize root competition. The trenches were 1 m long, 40 cm deep, and 15 cm wide, and were lined with a double layer of 4 mil black plastic before they were refilled with soil. For the trenched plots, we periodically uprooted any shoots that had rooted inside the area limited by the trenches. For treatments that excluded aboveground competition, vines were grown on 1 m tall wire trellises ("tomato cages") that were placed to the east and west sides of each tree, to minimize shading effects. There was little shading of trees by vines on trellises in the first year, because vines were still small. By the time the vines fully covered the trellises (second year), trees were twice the size of the trellised vines, and early morning and late afternoon shading of the trees was restricted to the lower part of the canopy.

Field and laboratory measurements

Height and diameter at 10 cm above the ground of all trees were recorded at the onset of the experiment, and then on a monthly basis during the 1989 and 1990 growing seasons. Trunk diameter was measured with an electronic digital caliper in 1989, and with a metal tape in 1990. In November of each year (including 1988), the height of the main stem of each tree and the length of all branches at least 1 cm long were measured. These measurements were used to compute the total stem length of each tree.

The expansion of 2 recently unfurled leaves per tree was monitored twice per week from 26 April to 25 May in 1989, and from 27 April to

Table 1. Factorial arrangement of treatments (for each factor combination, the level of competition and the treatment legend are indicated)

	L. japonica (LJ)		*P. quinquefolia* (PQ)	
	Not Trenched	Trenched	Not Trenched	Trenched
On Host	above + below (LJ A + B)	above (LJ A)	above + below (PQ A + B)	above (PQ A)
Off Host	below (LJ B)	"none"[a] (LJ OUT)	below (PQ B)	"none"[a] (PQ OUT)
Absent	none[b] (CONTROL # 1)	none[b] (CONTROL # 2)	none[b] (CONTROL # 1)	none[b] (CONTROL # 2)

[a] "none" indicates that no competition is expected because vines are rooted outside the trenches

[b] Because vines were not present, these treatments were represented only once for each level of trenching. Instead of 12, the number of treatments used was 10

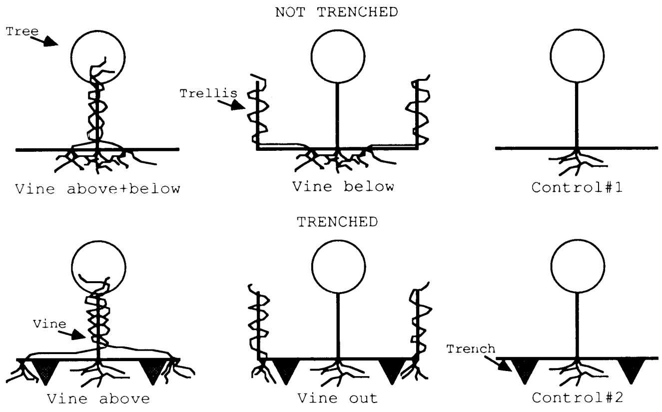

Fig. 1. Schematic representation of treatments. Diagrams represent the 6 different types of vine competition

14 May, and 12 June to 6 July in 1990. This was done by measuring leaf length and width with a flexible ruler and then using a linear regression equation to estimate leaf area. The regression was based on data collected from 50 leaves of trees from the same seedling source as those planted in the field. Each leaf was measured for length (l) (from base of mid-vein to tip of central lobe), width (w) (greatest distance between two opposite leaf lobes), and area (LI-COR model 3100 Area Meter). The regression equation used to estimate leaf area (y) was $y = 0.574 \times (w \times l) - 0.08$ ($r^2 = 0.96$).

Between 11 and 26 September 1990, all leaves from trees in 3 of the 6 replicates were harvested by breaking at the petiole base. Total leaf area (LI-COR model 3100 Area Meter) and total leaf dry weight for each tree were measured.

Data analysis

The analysis of treatment effects on tree growth was based on preplanned pairwise comparisons of individual treatment means (factorial simple effects). A two-way analysis of variance (block and treatment effects) was performed, followed by the least significant difference (LSD) mean separation technique. Homogeneity of variances of the residuals was tested using Hartley's F_{max} test, and nonhomogeneous data were transformed. Statistical significance was attributed to those differences which had a probability level equal to or less than 0.05 ($P \leq 0.05$).

Mean comparisons were separately made for trenched and untrenched treatments. Comparisons of means among untrenched treatments tested for effects of belowground competition, singly or in combination with aboveground competition. Comparisons among trenched treatments tested for effects of aboveground competition. For both trenched and untrenched trees, every treatment was compared to the control, and treatments involving the same vine species were compared to each other. A remark needs to be made for comparisons made between trenched treatments. Mean comparisons between treatments which had either *L. japonica* or *P. quinquefolia* planted outside the trench (LJ OUT and PQ OUT) and the trenched control (CONTROL#2) tested for the effects of vine presence outside the trenches on the tree. Because differences between those treatments and the control were never statistically significant, the comparisons LJ A vs. LJ OUT and PQ A vs. PQ OUT also tested for aboveground competition effects on tree growth.

Analysis of covariance (ANCOVA) was made when comparing competition effects on annual growth in height, diameter and total stem length. Values of those growth parameters at the beginning of each season were used as covariates. Besides block and treatment effects, the model used for ANCOVA included the effect of the covariate and its interaction with treatment effects. This interaction was never statistically significant ($P \leq 0.05$), so it was removed from the model. All statistical analyses were performed using SAS (SAS Institute Inc.)

Results

Vine cover in tree canopies was limited during the first year, but, by the end of the growing season, *L. japonica* had twined around the main stem and had reached the top of the trees in the below and aboveground competition treatment (LJ A + B). In most cases, *L. japonica* had not reached the top of the tree in the aboveground competition treatment (LJ A). *Parthenocissus quinquefolia* infestations on tree canopies were less than *L. japonica* in the first year, mostly due to herbivory by Japanese beetle (*Popillia japonica*). In the second year, *L. japonica* infestations had increased dramatically. All trees were overtopped and most leaves were either fully or partly shaded by the vines in the LJ A + B treatment. Vine cover was less dense in the LJ A treatment, with a greater percentage of tree leaves receiving direct sunlight than in the LJ A + B treatment. Light penetration through the tree canopies at mid-summer were reduced by 65 and 40% in the LJ A + B and LJ A treatments, respectively, compared to controls (unpublished data). Some of the shoots of *P. quinquefolia* that had reached the tops of trees in the first year had died-back or were detached from the tree branches by the second year. Infestations of *P. quinquefolia* leaves by powdery mildew and grazing by Japanese beetle also contributed to lower amounts of vine cover on tree canopies in the second year. Trees in the PQ A + B and PQ A treatments had a 35% reduction in light penetration compared to control trees during mid-summer (unpublished data), and a much more diffuse vine cover than trees in the LJ A + B and LJ A treatments.

By the end of the first growing season, there was no significant effect of vine competition on tree height, diameter, and total stem length (Fig. 2). Instead, trees competing below- and aboveground with *L. japonica* grew significantly taller than control trees. After two growing seasons, however, trees interacting below- and both below- and aboveground with *L. japonica* grew significantly less than control trees, but were not significantly different from each other (Fig. 2). Compared to controls, trees competing belowground with *L. japonica* grew 43, 36 and 53% less in diameter, height, and total stem length, respectively. Growth reductions for trees competing both below- and aboveground with *L. japonica* were only slightly greater for diameter (56%), height (61%), and total stem length (59%). This relatively greater reduction in height growth was, in part, due to the weight of the vines, which bent the main stem of the tree: the reduction in height would still be significant, however, had the length of the stems that had been bent been included in the height measurement. Belowground competition with *P. quinquefolia* resulted in significant reductions in tree height (37%) and diameter (27%) growth, after two years. Surprisingly, below- and aboveground competition together had no significant effect on tree growth.

No differences among treatments were found for trenched trees, demonstrating no detectable effects on tree growth from aboveground competition alone (Fig. 2).

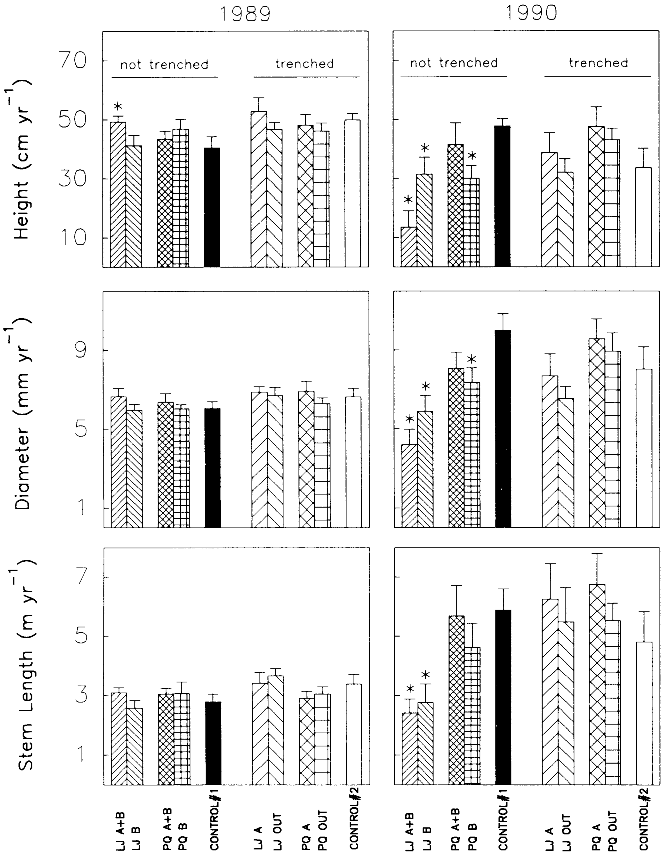

Fig. 2. Annual increases in height, diameter, and total stem length. Vertical bars are individual standard errors of the mean; $n=6$. Significant differences from the control within each trenching group are indicated by "*" ($P \leq 0.05$). No statistical differences were detected between paired treatments involving the same vine species. Pooled standard errors from ANOVA were height = 2.75, diameter = 0.38, and stem length = 0.27 in 1989, and height = 5.40, diameter = 0.84, and stem length = 0.86 in 1990. Treatment legends as in Table 1

In fact, trees with only aboveground competition grew more in height and total stem length than control trees (CONTROL#2) or trees that had vines growing on wire trellises outside the trenches (LJ OUT and PQ OUT) (Fig. 2).

By the end of the second growing season, total leaf area (50% reduction) and leaf biomass (48% reduction) were significantly reduced in trees competing with *L. japonica* belowground, compared to controls. Total leaf area (60% reduction) and leaf biomass (57% reduction) were also significantly reduced for trees competing both below and aboveground with *L. japonica* (Table 2). The two treatments were not statistically different from each other. Neither of the belowground competition treatments with *P. quinquefolia* had any significant effect on total leaf area and total leaf biomass of trees.

Total leaf area and leaf biomass were significantly greater for trees competing aboveground with *L. japonica* than for controls. Similarly, trees competing aboveground with *P. quinquefolia* had a greater total leaf area than control trees.

Table 2. Final leaf area and leaf biomass of *L. styraciflua*. Data are mean ± standard error (n = 3). Means are compared within each trenching group

Treatment	Leaf Area m^2	Leaf Biomass g
Not trenched		
LJ A+B	0.52 ± 0.09*	41.7 ± 9.12*
LJ B	0.63 ± 0.05*	51.6 ± 4.49*
PQ A+B	0.89 ± 0.13	74.3 ± 12.0
PQ B	0.80 ± 0.09	74.7 ± 16.9
CONTROL#1	1.22 ± 0.24	104.0 ± 15.8
Trenched		
LJ A	1.32 ± 0.05*	112.7 ± 8.14
LJ OUT	0.99 ± 0.07	80.0 ± 6.93
PQ A	1.51 ± 0.26*	128.2 ± 19.6*
PQ OUT	1.28 ± 0.07	105.5 ± 10.1
CONTROL#2	0.86 ± 0.25	70.9 ± 21.3
Pooled SEM[a]	0.16	14.2

[a] Standard error of the mean from ANOVA

* Significantly different from the control at $P \leq 0.05$; no statistical differences between paired treatments involving the same vine species were detected

Note: LJ – *L. japonica*, PQ – *P. quinquefolia*, A – aboveground competition, B – belowground competition, OUT – vine rooted outside trench

L. styraciflua produces about the same number of leaves later in the season as those preformed in the terminal bud in the spring (Zimmermann and Brown 1977). Measurements of leaf expansion taken in the spring were thus on leaves emerging from terminal buds. Leaf measurements made in early summer were made on leaves that developed from new leaf primordia. For measurements taken in the spring of 1989, leaves from trees competing with vines below and aboveground tended to attain a greater leaf size than leaves from controls, but differences in final size and expansion rate were not statistically significant. Independent measurements of leaf size done on 26 June 1989 in 5 representative leaves per tree also showed no effect of competition (data not shown). In the spring of 1990, there was again no competition effect on leaf expansion (Table 3). In contrast, significant treatment effects were found for leaf expansion rates and leaf size in early summer of 1990. Trees competing belowground with vines had significantly slower rates of expansion and smaller final leaf sizes than control trees (Table 3). Consistent with these results, leaf sizes measured independently on 6 July 1990 in 5 representative leaves per tree were also significantly smaller (22% reduction) than leaves on controls (data not shown). Aboveground competition alone had no effect on leaf expansion.

Discussion

Effects of vine competition on tree growth

Belowground and below- and aboveground competition with *L. japonica* led to a clear reduction in growth of *L. styraciflua* after two growing seasons. Tree growth was less

Table 3. Leaf expansion rates (LER) and final leaf size (LS) for *L. styraciflua*. Data are mean ± standard error (n = 6). Means are compared within each trenching group

Treatment	Spring 89		Spring 90		Summer 90	
	LER[a] cm^2/day	LS cm^2	LER cm^2/day	LS cm^2	LER cm^2/day	LS cm^2
Not trenched						
LJ A+B	1.68±0.15	38.7±3.15	1.43±0.30	23.5±1.98	1.97±0.09*	37.0±2.09*
LJ B	1.20±0.20	33.4±3.25	1.59±0.17	26.8±3.11	1.93±0.28*	36.1±4.45*
PQ A+B	1.65±0.16	41.1±4.65	2.21±0.33	35.4±4.29	2.02±0.23*	37.5±4.33*
PQ B	1.51±0.24	35.0±4.90	1.77±0.33	27.7±4.29	1.79±0.20*	33.0±3.47*
CONTROL #1	1.37±0.16	33.6±4.49	1.89±0.31	29.9±2.97	2.74±0.24	50.6±5.14
Trenched						
LJ A	1.04±0.14	28.5±2.25	1.57±0.22	27.2±2.79	–	–
LJ OUT	1.08±0.15	28.7±1.38	1.21±0.23	24.4±2.33	–	–
PQ A	1.12±0.16	27.3±2.82	1.66±0.19	29.8±2.22	–	–
PQ OUT	1.43±0.18	38.9±2.78	2.15±0.26	34.5±3.13	–	–
CONTROL #2	0.99±0.21	30.9±2.83	1.65±0.19	31.5±3.47	–	–
Pooled SEM[b]	0.18	3.2	0.27	3.1	0.21	3.7

[a] Calculated based on the linear portion of the expansion curve

[b] Standard error of the mean from ANOVA

* Significantly different from the control at $P \leq 0.05$; no statistical differences between paired treatments involving the same vine species were detected

Note: LJ – *L. japonica*, PQ – *P. quinquefolia*, A – aboveground competition, B – belowground competition, OUT – vine rooted outside trench

affected by competition with *P. quinquefolia*. A significant reduction in leaf expansion rates and final leaf size in the summer of 1990 suggests that this process is one of the first to be affected by belowground competition. The responsiveness of leaf expansion even to incipient water and nitrogen stress has been reported (Radin and Boyer 1982; Boyer 1988; Roden et al. 1990; Steinberg et al. 1990; Wullschleger and Oosterhuis 1990), and Chapin (1991) suggested that a fast leaf growth response may be an early warning system that enables plants to reduce growth and change allocation patterns before a severe imbalance of carbon and nitrogen-containing metabolites develops. The lack of a negative effect on leaf expansion in the spring of 1990 could relate to those leaves being pre-formed in the fall of the previous year.

Comparative effects of the two vine species

The greater competitive effect of *L. japonica*, compared to *P. quinquefolia*, was not surprising, considering its well-documented weediness and identification as one of the worst pest species in managed forests (Bruner 1967; Brown and Brown 1972; Slezak 1976). *P. quinquefolia*, in comparison, only occasionally outcompetes supporting vegetation in disturbed sites and woodland borders (Bell et al. 1988; Boring et al. 1981; Brown and Brown 1972).

Comparative effects of below- and aboveground competition

The ability of *L. japonica* to heavily cover other plants (Leatherman 1955; Little 1961; Bruner 1967; Slezak 1976; Thomas 1980; Friedland and Smith 1982) suggests that aboveground competition should be very effective. The results of this study, however, indicated that belowground competition is more important than aboveground competition during early stages of vine-tree interactions.

Patterson (1973) found that root competition by the exotic weedy vine *Celastrus orbiculatus* had a negative impact on the growth of the herbaceous species *Amaranthus hybridus* and *Setaria lutescens*. Kennedy (1981) showed that the final height and diameter of 6 young hardwood species, including *L. styraciflua*, was substantially improved by eliminating competition from vines and other weeds by disking the soil for 4 consecutive years. When weeds were only mowed, there was no significant improvement on tree growth. Although disking may have affected tree growth through factors other than reduction of competition (changes in soil structure, aeration, water infiltration, etc.), these results suggest that root competition was more important than canopy competition in determining the growth of those trees. Whigham (1984) found that *L. japonica* had a negative effect on diameter growth of *L. styraciflua* trees (15 m tall) that were growing alone in an abandoned field. His results suggested that belowground competition was more important than aboveground competition, but his experimental design did not allow the two to be examined separately. The importance of belowground competition on tree growth has also been demonstrated for non-vine species (Jones et al. 1989; Jones and Sharitz 1990; Cogliastro et al. 1990; Kolb and Steiner 1990).

The trend toward increased growth in diameter, height and total stem length, and significant positive effects of aboveground competition on total tree leaf area and leaf biomass was surprising, considering the reported shade intolerance of *L. styraciflua* (Baker 1950; Borman 1953; Jackson 1967). A possible explanation for this result is that it took longer for vines that were rooted outside of the trenches to grow into the canopy of the host. As a result, negative effects of competition would have been slower to develop in the aboveground competition treatment. However, this does not explain the apparent positive effects of the aboveground interaction. The greater leaf area and biomass in trees that competed aboveground with vines in the absence of belowground competition may indicate an increased allocation to leaf production in response to the presence of vines. There are other studies suggesting that shading does not necessarily reduce the growth of sweetgum trees. Holbrook and Putz (1989) have found that, despite changes in canopy architecture, the final aboveground dry weight of 2-year old *L. styraciflua* was not significantly affected by uniform lateral shading with a 10% transmittance shade cloth. Bormann (1953) also called to attention the fact that, in upland forests of North Carolina, *L. styraciflua* grows mostly under the shade of pines. These conflicting observations can be resolved to some extent if one also accounts for belowground processes. Plants growing under the shade of a forest not only experience canopy competition for light, but also root competition (Horn 1985; Jones and Sharitz 1990; Jones et al. 1989). The expression "shade tolerance" accounts for only one of the environmental factors that plants experience in the understory, and may not be entirely appropriate. Horn (1971) concluded that the axiom that shade tolerance increases with successional status of trees can only be confirmed if tolerance is defined to include the effects of root competition as well as shade. The interaction of root competition and shading in determining the tolerance of this and other species to existence in the understory should be subject to experimental investigation.

Clements et al. (1929), Donald (1958) and Caldwell (1986) have suggested that the effects of root and shoot competition should interact synergistically. Despite the lack of effects of canopy competition alone, there was a consistent trend for trees competing both below and aboveground with *L. japonica* to grow even less than those competing only belowground. However, it is not possible to ascertain whether this resulted from interactive effects of root and canopy competition or from simple additive effects, since trees experiencing only aboveground competition with *L. japonica* were less accessible to the vine shoots than untrenched trees, due to the distance between the bases of trees and vines imposed by trenches. The consistent and strongly negative effect of root competition with *L. japonica*, however, provides strong evidence for the importance of root competition during the early stages of vine-tree interactions, and may provide an additional explanation for the lower vine infestations on trees which did not have their growth suppressed by vine root competition. Supporting the role of root competition in determining the degree of aboveground infestation is the similarity in vine infestation between trees competing aboveground and trees competing below- and aboveground with *P. quinquefolia*, and the reduced effect of root competition from this vine on tree growth.

The significance of vine competition in nature

The results of this study are most relevant to early stages of succession, where vine-tree interactions appear to be most intense. The results are also relevant to other highlight situations such as those that occur on forest edges and in large tree gaps. Clearly, there are differences in the competitive abilities of the two vines. Trees in areas infested with *L. Japonica* are more likely to have lower growth rates than trees growing in areas infested with *P. quinquefolia*. The results presented by Whigham (1984) also suggest that the effects of root competition observed in the study might be long-lasting and that they may affect trees long after they have grown tall enough to grow beyond the influence of the vine canopy. Particularly in the case of *L. japonica*, our results suggest that the ultimate fate of a tree that is experiencing vine competition can be greatly affected by the intensity of belowground competition. If the negative effects of root competition develop quickly, trees are likely to have a smaller chance of "outgrowing" the vines. Since *L. japonica* often forms dense and extensive mats in the forest floor, belowground competition is likely to be an important mechanism by which this weedy vine affects the structure and dynamics of successional forests.

Acknowledgements. We sincerely thank Luis Mauro Rosa, John O'Neill, Darcy Dillenburg, and Cicilia Dillenburg for field and lab assistance. We also thank David Challinor and Arvydas Grybauskas for helpful suggestions to this study and to earlier versions of this manuscript, Francis Gouin for helpful information on the growth requirements of sweetgum trees, and Edward Whereat and Francis Putz for suggestions to this manuscript. We further acknowledge David Challinor for helping provide financial support for this research. Support for this research was provided by the Brazilian National Council for Scientific and Technological Development (CNPq), and the Smithsonian Institution (Office of Fellowships and Grants, Smithsonian Environmental Sciences Program, and Smithsonian Environmental Research Center).

References

Aspinall D (1960) An analysis of competition between barley and white persicaria. Ann Appl Biol 48: 637–654

Baker FS (1950) Principles of silviculture. McGraw Hill, New York

Bell DJ, Forseth IN, Teramura AH (1988) Field water relations of three temperate vines. Oecologia 74: 537–545

Boring LR, Monk CD, Swank WT (1981) Early regeneration of a clear-cut southern Appalachian forest. Ecology 62: 1244–1253

Bormann FH (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

Boyer JS (1988) Cell enlargement and growth-induced water potentials. Physiol Plant 73: 311–316

Brown RG, Brown ML (1972) Woody plants of Maryland. Port City Press, Baltimore

Bruner MH (1967) Honeysuckle – a bold competitor on bottomland hardwood sites. For Farmer 26: 9–17

Caldwell MM (1986) Root system competition in natural communities. In: Gregory PJ (ed) Root development and function, effects of the physical environment. Cambridge University Press, Cambridge, pp 162–185

Chapin FS III (1991) Integrated responses of plants to stress. Bioscience 41: 29–36

Clements FE, Weaver JE, Hanson HC (1929) Plant competition: an analysis of community functions. Carnegie Institute, Washington

Cogliastro A, Gagnon D, Coderre D, Bhereur P (1990) Response of seven hardwood tree species to herbicide, rototilling, and legume cover at two southern Quebec plantation sites. Can J For Res 20: 1172–1182

Donald CM (1958) The interaction of competition for light and for nutrients. Aust J Agric Res 9: 421–35

Featherly HI (1941) The effect of grapevines on trees. Proc Oklahoma Acad Sci 21: 61-62

Friedland AJ, Smith AP (1982) Effects of vines on successional herbs. Am Midl Nat 108: 402-403

Holbrook NM, Putz F (1989) Influence of neighbors on tree form: effects of lateral shade and prevention of sway on the allometry of *Liquidambar styraciflua* (sweet gum). Am J Bot 76: 1704-1749

Horn HS (1971) The adaptive geometry of trees. Princeton University Press, Princeton

Horn JC (1985) Responses of understory tree seedlings to trenching. Am Midl Nat 114: 252-258

Jackson LWR (1967) Effect of shade on leaf structure of deciduous tree species. Ecology 48: 498-499

Jones RH, Sharitz RR (1990) Effects of root competition and flooding on growth of chinese tallow seedlings. Can J For Res 20: 573-578

Jones RH, Sharitz RR, McLeod MKW (1989) Effects of flooding and root competition on growth of shaded bottomland hardwood seedlings. Am Midl Nat 121: 165-175

Kennedy HE Jr (1981) Foliar nutrient concentrations and hardwood growth influenced by cultural treatments. Plant Soil 63: 307-316

King J (1971) Competition between established and newly sown grass species. J Br Grassld Soc 26: 221-229

Kolb TE, Steiner KC (1990) Growth and biomass partitioning of northern red-oak and yellow poplar seedlings: effects of shading and grass root competition. For Sci 36: 34-44

Leatherman AD (1955) Ecological life history of *Lonicera japonica* Thunb. Ph D Dissertation, University of Tennessee, Knoxville

Little S (1961) Recent results of tests in controlling Japanese honeysuckle. Hormolog 3: 8-10

Lutz HJ (1943) Injuries to trees caused by *Celastrus* and *Vitis*. Bull Torrey Bot Club 70: 436-439

Martin MPLD, Snaydon RW (1982) Root and shoot interactions between barley and field beans when intercropped. J Appl Ecol 19: 263-272

Monsi M, Murata Y (1970) Development of photosynthetic systems as influenced by distribution in matter. In: Prediction and measurements of photosynthetic productivity. PUDOC, Wageningen, pp 115-130

Patterson DT (1973) The ecology of oriental bittersweet, Celastrus orbiculatus, a weedy introduced ornamental vine. Ph D Dissertation, Duke University, Durham, NC

Penfound WT (1974) The role of vines in plant communities. Adv Frontiers Plant Sci 17: 187-192

Putz FE (1984) The natural history of lianas on Barro Colorado Island, Panama. Ecology 68: 1713-1724

Radin JW, Boyer JS (1982) Control of leaf expansion by nitrogen nutrition in sunflower plants. Role of hydraulic conductivity and turgor. Plant Physiol 69: 771-775

Richards PW (1952) The tropical rain forest; an ecological study. Cambridge University Press, London

Roden J, Van Volkenburgh E, Hinckley TM (1990) Cellular basis for limitation of poplar leaf growth by water deficit. Tree Physiol 6: 211-219

Siccama TG, Weir G, Wallace K (1976) Ice damage in a mixed hardwood forest in Connecticut in relation to *Vitis* infestation. Bull Torrey Bot Club 103: 180-183

Slezak WF (1976) *Lonicera japonica* Thumb., an aggressive introduced species in a mature forest ecosystem. MS Thesis, Rutgers University, New Brunswick, NJ

Steinberg SL, Miller JC Jr, McFarland MJ (1990) Dry matter partitioning and vegetative growth of young peach trees under water stress. Aust J Plant Physiol 17: 23-36

Stevens GC (1987) Lianas as structural parasites: the *Bursera simaruba* example. Ecology 68: 77-81

Teramura AH, Forseth IN, Gold W (1991) Physiological ecology of mesic, temperate vines. In: Mooney H, Putz FE (eds) Biology of Vines. Cambridge University Press, Cambridge, pp 237-277

Thomas LK Jr (1980) The impact of three exotic plant species on a Potomac island. National Park Service Scientific Monograph Service, No. 13. US Dept of Interior, Washington, DC

Whigham D (1984) The influence of vines on the growth of *Liquidambar styraciflua* L. (sweetgum). Can J For Res 14: 37-39

Wilson JB (1988) Shoot competition and root competition. J Appl Ecol 25: 279-296

Wilson JB (1989) Root competition between three upland grasses. Funct Ecol 3: 447-451

Wullschleger SD, Oosterhuis DM (1990) Canopy development and photosynthesis of cotton as influenced by nitrogen nutrition. J Plant Nutr 13: 1141-1154

Zimmermann MH, Brown CL (1977) Trees, structure and function. Springer, New York