

PHOTOSYNTHETIC AND BIOMASS ALLOCATION RESPONSES OF *LIQUIDAMBAR STYRACIFLUA* (HAMAMELIDACEAE) TO VINE COMPETITION¹

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This 2-year field study examined stomatal conductance, photosynthesis, and biomass allocation of *Liquidambar styraciflua* saplings in response to below- and aboveground competition with the vines *Lonicera japonica* and *Parthenocissus quinquefolia*. Vine competition did not affect stomatal conductance of the host trees. The leaf photosynthetic capacity and photosynthetic nitrogen-use efficiency were significantly reduced by root competition with vines, either singly or in combination with aboveground competition, early in the second growing season. However, such differences disappeared by the end of the second growing season. Trees competing below ground with vines also had lower allocation to leaves compared with stems. Aboveground competition with vines resulted in reduced photosynthetic capacity per unit leaf area, but not per unit leaf weight, in trees. No correlation was found between single leaf photosynthetic capacity and tree growth. In contrast, a high positive correlation existed between allocation to leaves and diameter growth. Results from this study suggest that allocation patterns are more affected than leaf photosynthesis in trees competing with vines.

Reduced availability of light, water, and nutrients due to competitive interactions can reduce plant growth through changes in both physiological and morphological attributes. Leaf photosynthesis has dominated causal explanation of plant growth for almost a century (Körner, 1991). More recent observations suggest that measurements of leaf-level photosynthesis contribute less than previously believed to an understanding of plant growth (Küppers, 1985; Küppers, Koch, and Mooney, 1988; Cromer and Jarvis, 1990; Poorter, Remkes, and Lambers, 1990; Chapin, 1991; Körner, 1991). Plants commonly respond to low resource levels by differential allocation to organs responsible for capturing the most limiting resource (Fitter, 1987; Küppers, Koch, and Mooney, 1988; Kolb et al., 1990; Ranney, Whitlow, and Bassuk, 1990; Aerts, Boot, and van der Aart, 1991; Fredeen, Gamon, and Field, 1991; Ingestad and Ågren, 1991). Variations in biomass allocation patterns can then obscure the relationships between the commonly measured leaf-level photosynthesis and growth (Küppers, Koch, and Mooney, 1988; Poorter, Remkes, and Lambers, 1990; Chapin, 1991).

Vines can greatly affect the growth of their hosts and arrest the regeneration of both woody and herbaceous vegetation, particularly under conditions of high light

availability (forest edges, tree gaps, and early- to mid-successional forests) (Penfound, 1974; Thomas, 1980; Friedland and Smith, 1982; Putz, 1984; Whigham, 1984). Dillenburg et al. (1993a) have examined the competitive effects of two common woody vine species in temperate forests of the eastern United States, *Lonicera japonica* (L.) Thunb. and *Parthenocissus quinquefolia* L., on the growth of the host tree *Liquidambar styraciflua* L., a common early successional hardwood tree often infested by these vine species. Significant reductions in tree growth were found after two growing seasons due to belowground competition with *L. japonica*, either singly or in combination with aboveground competition. Associated with reductions in growth were reductions in both light availability and leaf nitrogen (N) status, with N apparently affecting growth to a greater extent than light (Dillenburg et al., 1993b). The question then arises as to what physiological and morphological responses of trees to vine competition are most relevant in linking the previously reported effects of competition on resource availability (mostly light and nitrogen) to the effects on tree growth. The objectives of this study were twofold: 1) to describe the effects of vine competition on stomatal conductance, photosynthetic capacity, and allocation of a host tree; and 2) to explore the relationship between individual leaf photosynthesis and allocation responses and whole-plant growth.

¹ Manuscript received 27 December 1993; revision accepted 30 September 1994.

The authors thank Luis Mauro Rosa, John O'Neill, and Darcy and Cecilia Dillenburg for field and lab assistance; David Challinor for partial support for this study and helpful suggestions to earlier versions of this manuscript; and Francis Gouin for information on the growth requirements of sweetgum trees. 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).

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MATERIALS AND METHODS

Experimental and treatment designs—This study was conducted during 1989 and 1990, in an experimental garden at the Smithsonian Environmental Research Center, Edgewater, Maryland (39°53'N, 76°33'W). The site was located on a gently sloping Donlonton sandy loam soil, described as an Ultisol and having a high available moisture capacity (Kirby and Matthews, 1973). A 2 × 2 × 3 incomplete factorial design was used, with trees as the experimental units. The three factors and their levels

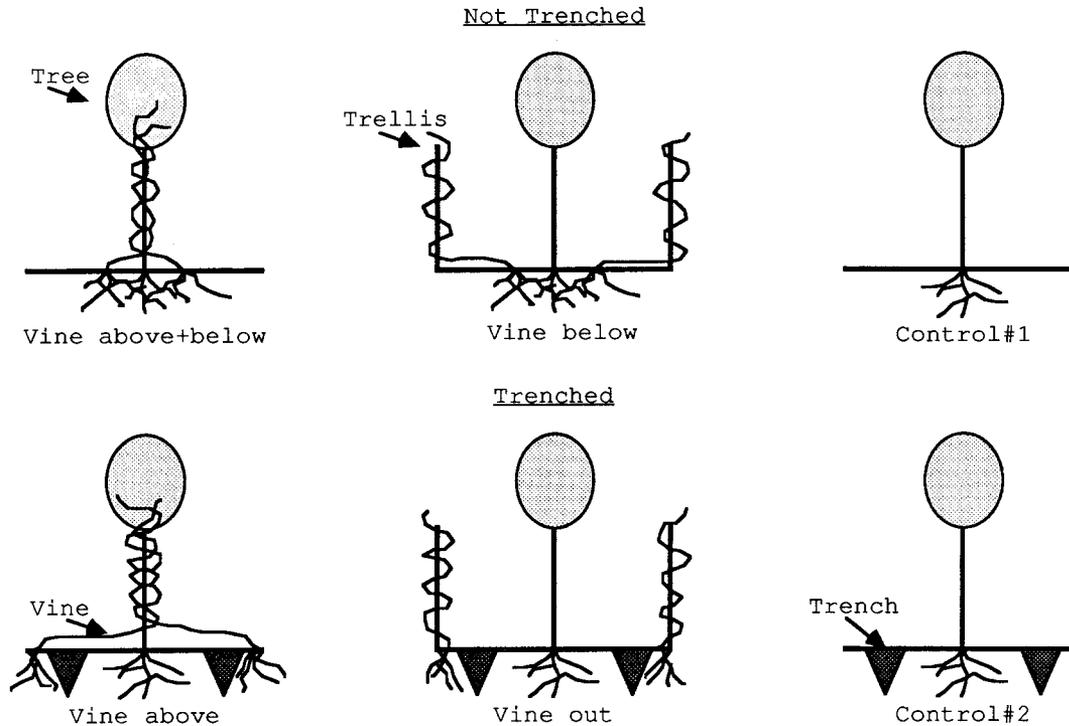


Fig. 1. Schematic representation of the six different types of vine competition treatments.

were: vine species (*L. japonica* or *P. quinquefolia*), soil trenching (trenched or not), and vine presence on the host (on, off, or absent). Ten of the 12 possible treatment combinations were represented in the study (the two vine species were not distinguished from each other in the "vines absent" treatments). The different competition treatments are illustrated in Fig. 1. The treatment legends to be used throughout this paper are as follows: 1) untrenched plots with above- and belowground competition with *L. japonica* = (LJ A + B) or *P. quinquefolia* = (PQ A + B); 2) untrenched plots with belowground competition with *L. japonica* (LJ B) or *P. quinquefolia* (PQ B); 3) untrenched plots with no vines present = (Control #1); 4) trenched plots with aboveground competition with *L. japonica* = (LJ A) or *P. quinquefolia* = (PQ A); 5) trenched plots with no aboveground competition but with *L. japonica* = (LJ Out) or *P. quinquefolia* = (PQ Out) planted outside the trenches; 6) trenched plots with no vines present = (Control #2).

Soil trenching was used to minimize root competition. Trenches (1 m long, 40 cm deep, and 15 cm wide) were dug 30 cm to the east and west sides of the tree, lined with 4-mil plastic, and refilled with soil. The area was divided into 60 regularly spaced 1-m \times 1-m plots, the center of each plot being spaced 2.5 m from its nearest adjacent plot. Due to space limitations, border plants were not used in this experiment. Plots were organized according to a randomized complete block design, with six replicates per treatment. Criteria for blocking included field location and initial size of trees. In November of 1988, a single 2-year-old tree (height \pm SD = 65.3 \pm 5.39 cm) was planted at the center of each plot. Two vines of

the same species, grown from rooted vine cuttings (approximately five 30-cm-long branches per vine), 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 two trenches. When aboveground competition was excluded, vine shoots were entwined on wire trellises away from the trees. Plots were covered with shredded hardwood mulch and weeded periodically.

Stomatal conductance—Stomatal conductance (g) of one to two most recently fully expanded, sun-exposed leaves from the upper and outer tree canopy were sampled every 2 hours from 0900 to 1700 hours using a steady-state porometer (LICOR, Lincoln, NE, Model LI-1600). For each sampling period during the day, measurements were taken a block at a time. In 1989, data collected from the same 2-hour period of the day were pooled among the different sampling days of each month. Days of measurements were 11, 12, and 18 June ($N = 6$ trees), 8 and 9 August ($N = 4$), and 4 October ($N = 3$). In 1990, all replicates were measured in the same day. Sampling dates were 19 May ($N = 6$), 19 July ($N = 6$), 18 August ($N = 6$), 4 September ($N = 6$), and 2 October ($N = 3$).

Micrometeorological data—On the days g was measured, diurnal patterns of photosynthetic photon flux (PPF , radiation between 400 and 700 nm) on a horizontal surface, air temperature (T), relative humidity (RH), and vapor pressure deficit (VPD) were recorded in the area. Photosynthetic photon flux was averaged from five to six quantum sensors (Campbell Scientific, Logan, UT, Model

LI190SB), and T and RH were measured using a temperature-humidity probe (Campbell Scientific, Logan, UT, Model 207). All sensors were connected to dataloggers (Campbell Scientific, Logan, UT, Models CR21 and 21x).

Photosynthetic capacity—Light- and CO_2 -saturated rates of photosynthetic oxygen evolution (A_{max}) were measured using a leaf disc oxygen electrode (Hansatech, King's Lynn, Norfolk, UK, Model LD2), with water bath temperature at 25 C, PPF of $1,800 \mu\text{mol m}^{-2} \text{sec}^{-1}$, and saturating levels of CO_2 (5%). The leaf chamber was humidified by passing the CO_2 through a flask with water before flushing it into the chamber. Leaf discs were illuminated with a fan-cooled quartz lamp housing (Hansatech, King's Lynn, Norfolk, UK, Model LS2). Measurements were taken three times each year: 6 to 13 July ($N = 6$ trees), 14 to 21 August ($N = 4$), and 6 to 10 October ($N = 6$) in 1989, and 28 May to 1 June ($N = 4-6$), 16 to 20 July ($N = 6$), and 18 to 21 September ($N = 5$) in 1990. One sun-exposed, most recently fully expanded leaf per tree was sampled.

Effects of shading on light responses of photosynthesis—The photosynthetic oxygen evolution responses of leaf discs from sun and shade leaves to varying light levels were measured under the same temperature and CO_2 conditions described previously, on 14 to 16 August 1990. Different $PPFs$ (1,900, 960, 380, 115, and $0 \mu\text{mol m}^{-2} \text{sec}^{-1}$) were achieved by using neutral density filters. Only trees competing below and above ground with *L. japonica* (LJ A + B), for which shading of tree leaves by vines was most pronounced (Dillenburg et al., 1993b), were measured. Leaves from the upper and outer canopy that were judged to be deeply shaded by *L. japonica* leaves throughout most of the day were sampled. An unshaded leaf from a similar canopy position on the same tree was also sampled as a control. Five trees were sampled.

Photosynthetic nitrogen-use efficiency—Photosynthetic nitrogen use efficiency (PNUE, Field and Mooney, 1986) was computed by dividing A_{max} , expressed on a weight basis, by leaf N concentration. Leaf N was measured in leaves harvested on 27 September in 1989, and on 30 May, 18 July, and 24 September in 1990. Eight to ten fully expanded leaves at branch tips of the upper canopy were collected from each tree, oven-dried, ground, and analyzed for total Kjeldahl N at the Plant Analysis Laboratory, Pennsylvania State University, University Park, Pennsylvania. Although A_{max} and N were not measured in the same leaf material, they were measured on comparable leaves collected in the same week.

Allocation parameters—Leaves were harvested on 26 September 1990, and total leaf area (La , measured with an area meter, LICOR, Lincoln, NE, Model 3100) and total leaf biomass (Lb) recorded for each tree. Total stem length (Stl) was measured in November 1990, by summing the height of the main stem and the lengths of all branches at least 1 cm long. Trunk diameter (D) was measured 10 cm above the ground. The leaf area present per unit of total stem length or trunk diameter (La/Stl , La/D) and the whole-canopy leaf mass per area ($LMA = Lb/La$) were then calculated ($N = 3$ trees).

Tree growth—Measurements of trunk diameter taken at the beginning and end of the growing season were used to calculate the annual relative diameter growth rate (RDGR).

Data analysis—An analysis of variance (ANOVA) was performed for all variables, followed by the least significant difference (LSD) mean separation technique. Except where noted, the model for ANOVA included block and treatment effects. Homogeneity of variances of the residuals was tested using Hartley's F_{max} test, and data were transformed if needed. The pooled standard error of the mean (SEM) is presented. All statistical analyses were performed using SAS (SAS Institute, Inc., 1985).

Because g measurements were replicated on different days in 1989, the model for ANOVA also included the effects of day, block within day, treatment, and day-treatment interaction. The interaction term was removed from the model when not statistically significant for $\alpha \leq 0.05$. For photosynthetic light responses, each tree was treated as a block or replicate, and a two-way ANOVA (tree and sun-exposure effects) performed. Least squares regression analysis was used for correlation analysis. Absolute residuals were examined for independence from predicted Y values, and data were transformed if needed.

RESULTS

Stomatal conductance—Values of daily maximum g (g_{max}) of trees were higher in 1990 than in 1989, especially during the summer, and ranged from about 100 to 400 $\text{mmol m}^{-2} \text{sec}^{-1}$ (Fig. 2). In most cases g_{max} was attained in the early morning hours (0900 hr, EDT), with a steady decrease in g commonly observed as the day progressed (data not shown). The absence (Fig. 2A) and presence (Fig. 2B) of trenches had no significant negative effect on g_{max} of the host tree. In fact, in 1990, g_{max} of trees in the PQ A + B (May, August) and LJ B (August) treatments was significantly higher than that of controls (Fig. 2A).

Photosynthetic capacity—Although sampling periods were not the same in both years, the photosynthetic capacity (A_{max}) of trees was apparently greater in 1990 than in 1989, reaching a maximum value at the end of each growing season (Fig. 3). Vine competition had no significant negative effect on A_{max} in 1989, in both untrenched and trenched treatments. Instead, leaf A_{max} was significantly greater for trees in the PQ B (October) and LJ A (August) treatments than in controls (Fig. 3A). In early June of 1990, competition below and above ground with either vine species (LJ A + B and PQ A + B) and belowground competition with *L. japonica* (LJ B) resulted in significantly lower A_{max} than controls. Later in 1990, A_{max} values of competing trees and controls were similar to one another (Fig. 3B).

Photosynthetic nitrogen-use efficiency—The PNUE of trees in response to vine competition closely mirrored the responses of A_{max} . In 1989, PNUE of trees in the LJ A + B and PQ B treatments were significantly higher than that of controls (Table 1). In June of 1990, PNUE of trees in the LJ A + B and PQ A + B treatments were significantly

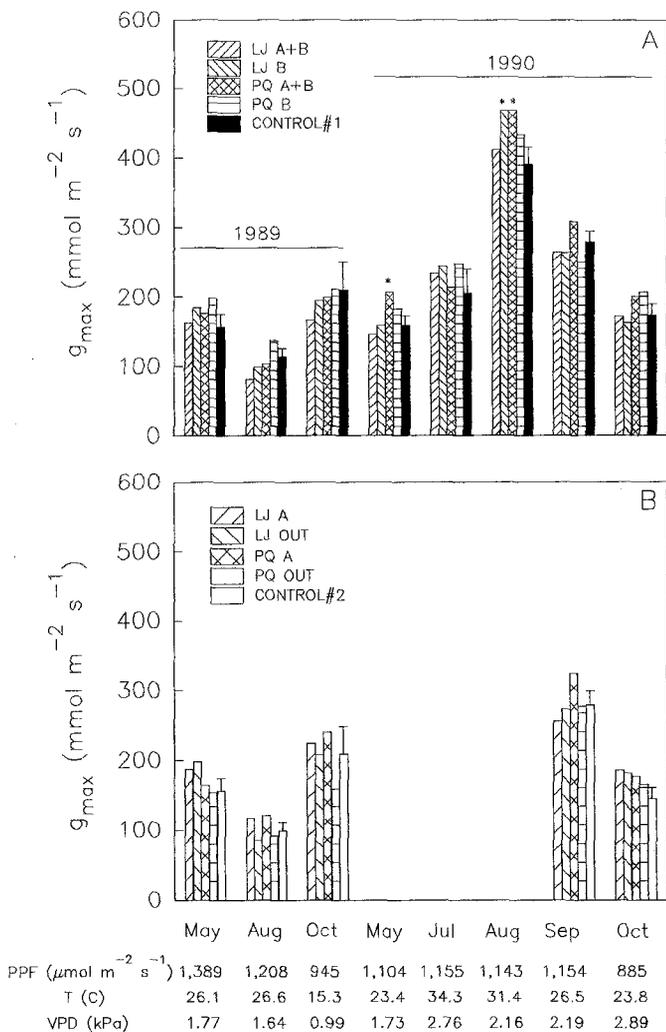


Fig. 2. Seasonal values of daily maximum stomatal conductance (g_{max}) for 1989 and 1990 in untrenched (A) and trenched (B) treatments. Within each month, every treatment was compared to the control (“**”) indicates significant difference at $P \leq 0.05$). Pooled SEM from ANOVA is shown for the controls. Mean values of photosynthetic photon flux (PPF), air temperature (T), and vapor pressure deficit (VPD) for the hour interval when g_{max} was recorded are presented for each month.

less than controls. Reduction in PNUE for trees in the LJ B treatment showed a strong tendency for statistical significance ($P \leq 0.10$). Similar to A_{max} , differences disappeared later in the season, and, in July of 1990, PNUE of trees in the PQ B treatment was even higher than controls (Table 1).

Effects of shading on photosynthetic responses to light—At $1,900 \mu\text{mol m}^{-2} \text{sec}^{-1}$, the photosynthetic rate (A) of shaded leaves was 29% lower than that of sun-exposed leaves in trees competing below and above ground with *L. japonica*, when photosynthesis was expressed on an area basis (Fig. 4). When expressed on a weight basis, however, A for shaded leaves was similar to that of sun-exposed leaves. This was due to the significantly lower leaf mass per area of shaded compared to sun leaves (63.3 vs. 87.3 g m^{-2} , SEM = 2.93, $P \leq 0.05$). Dark respiration (R_d) of shaded leaves was not significantly different from

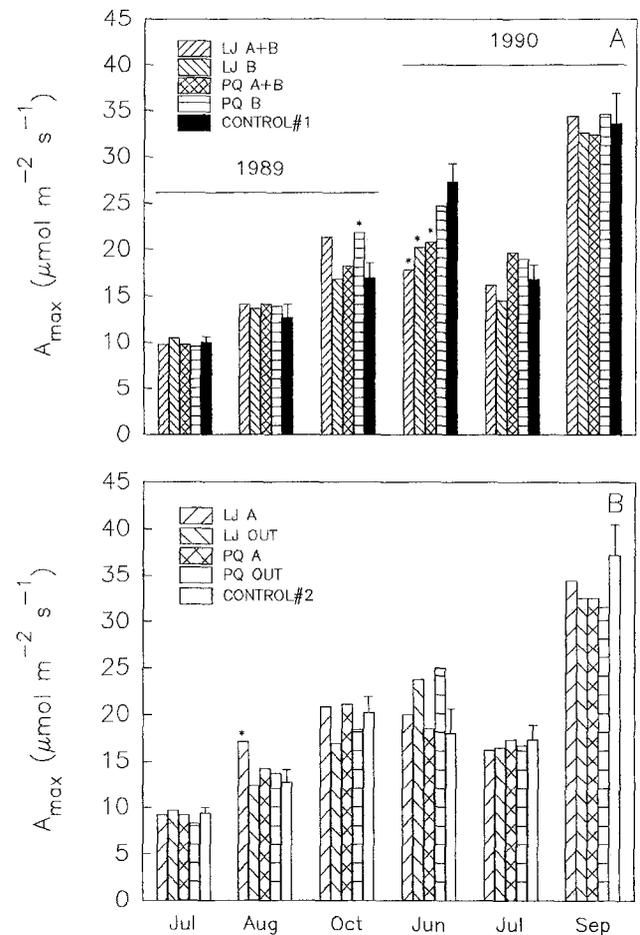


Fig. 3. Seasonal values of photosynthetic capacity (A_{max}) for 1989 and 1990 in untrenched (A) and trenched (B) treatments. Within each month, every treatment was compared to the control (“**”) indicates significant difference at $P \leq 0.05$). Pooled SEM from ANOVA is shown for the controls.

that of sun leaves, when expressed on an area (-1.65 vs. $-2.24 \mu\text{mol m}^{-2} \text{sec}^{-1}$, SEM = 0.42) or weight (-0.028 vs. $-0.026 \mu\text{mol g}^{-1} \text{sec}^{-1}$, SEM = 0.0055) basis.

Allocation parameters—Overall, competition with *L. japonica* in the absence of trenches significantly reduced La/Stl and La/D below control values (Table 2). Reductions due to competition with *P. quinquefolia* only approached significance ($P \leq 0.10$). Reductions in La/Stl and La/D were due to a greater effect of competition on La (57 and 48% reduction below the control values for LJ A + B and LJ B, respectively) than on either D or Stl. On the other hand, trees interacting above ground only with either vine species tended to have higher La/D values than controls (significant effect for PQ A). In this case, aboveground competition led to a greater increase in La (76% above the control value for the PQ A treatment) than in either D or Stl. There was no significant effect of vine competition on the canopy LMA (Table 2).

Growth relationships—No significant correlation was found between the annual mean A_{max} (averaged across the three monthly measurements) and the relative diameter

TABLE 1. Mean photosynthetic nitrogen-use efficiency (PNUE, $\mu\text{mol O}_2 \text{ g N}^{-1} \text{ s}^{-1}$) of trees.^a

Treatment	10/89	06/90	07/90	09/90
Untrenched				
LJ A + B	15.5*	14.7*	12.1	20.4
LJ B	13.1	15.6	10.8	18.6
PQ A + B	12.7	15.3*	13.7	17.0
PQ B	16.2*	17.2	15.0*	20.1
Control #1	11.6	19.6	11.5	20.2
Trenched				
LJ A	—	11.6	11.2	19.1
LJ Out	—	13.8	11.7	18.9
PQ A	—	10.6	12.6	17.8
PQ Out	—	14.1	11.8	18.3
Control #2	—	11.4	11.5	20.0
Pooled SEM	1.0	1.5 (1.9)	1.0	1.8
N	4	6 (4)	6	5

^a Significant differences from the control at $P \leq 0.05$ are indicated by “*.” Values of pooled SEM and N outside and inside parentheses are for untrenched and trenched treatments, respectively.

growth rate (RDGR) of trees in 1990 (Fig. 5A). When A_{max} measured in each month was separately tested for correlation with RDGR, no relationship was found as well ($r^2 \leq 0.04$ for all months).

In contrast, the ratio between leaf area and trunk diameter (La/D) was positively correlated to RDGR ($r^2 = 0.58$; $P \leq 0.0001$; Fig. 5B). Similar results were found for La/Stl vs. RDGR ($r^2 = 0.36$, $P \leq 0.0005$). Very similar r^2 values were found when using absolute rather than relative diameter growth (data not shown).

DISCUSSION

Stomatal conductance of *L. styraciflua* was not adversely affected by competition with vines (Fig. 2). Dillenburg et al. (1993b) had previously shown that the pre-dawn ψ_1 of trees was consistently above -0.5 MPa in both growing seasons and was not affected by belowground competition with vines. Pre-dawn ψ_1 above -0.5 MPa is indicative of mesic conditions, with little or no water stress for trees (Bahari, Pallardy, and Parker, 1985; Reich, Walters, and Tabone, 1989; Weber and Gates, 1990).

Photosynthetic capacity (A_{max}), on the other hand, was reduced by belowground competition with *L. japonica* (singly or in combination with aboveground competition) and by below- and aboveground competition with *P. quinquefolia*, particularly early in the 1990 growing season (Fig. 3A). The leaf N status of trees competing with *L. japonica* in the absence of trenches had been reduced below control values by the end of the first growing season, and was also particularly pronounced in the beginning of the second growing season (Dillenburg et al., 1993b). Vines and trees were transplanted to the experimental garden in November of 1988. The lack of any significant effect of competition on tree growth during the 1989 growing season (Dillenburg et al., 1993a) suggests that competition was not very intense during the first months of interaction. This may explain the delay on the development of competitive effects on both N status and photosynthesis.

Because measurements of CO_2 - and light-saturated O_2

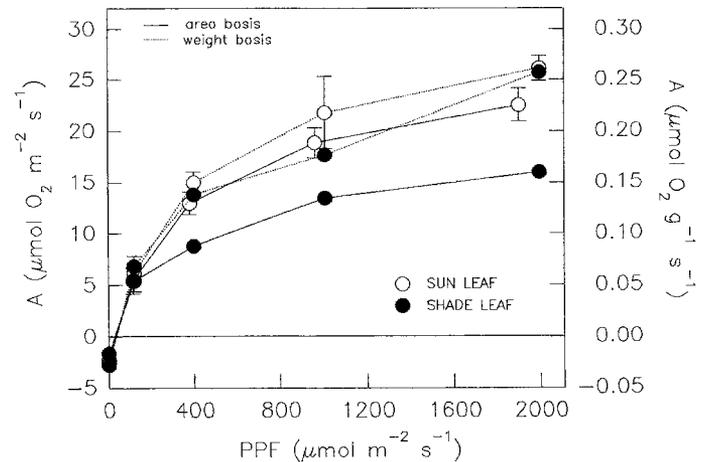


Fig. 4. Light responses of photosynthesis (A) of sun and shade leaves. Significant differences between A (area basis) of sun and shade leaves were detected for PPFs of 380 and 1,900 $\mu\text{mol m}^{-2} \text{ sec}^{-1}$ ($P \leq 0.05$). Pooled SEM from ANOVA is shown for sun leaves.

evolution eliminated the effects of stomatal conductance, the observed reductions in A_{max} were most likely due to biochemical limitations to photosynthesis. Since tree water relations were apparently unaffected by competition, reductions in photosynthetic capacity could be related to the lower leaf N status of the competing trees (Dillenburg et al., 1993b) rather than to water stress. The great similarity between PNUE and A_{max} responses to vine competition (Fig. 3; Table 1) suggests that the efficiency of the photosynthetic machinery and/or the allocation of N to photosynthetic processes varied in concert with the photosynthetic capacity of leaves (Field and Mooney, 1986).

Dillenburg et al. (1993b) reported a 65% reduction in gap fraction (probability of light penetration through the tree canopy without interception) in trees competing below and above ground with *L. japonica*, compared to uninfested controls. Comparisons between sun-exposed and shaded leaves of these competing trees revealed that

TABLE 2. Allocation responses of trees to vine competition (La = total leaf area; D = tree diameter; Stl = total stem length; LMA = leaf mass per area.^a

Treatment	La (m ²)	D (cm)	Stl (m)	La/Stl (cm ² /cm)	La/D (m ² /cm)	LMA (g/m ²)
Untrenched						
LJ A + B	0.52*	2.25*	7.09	7.47*	0.23*	78.6
LJ B	0.63*	2.37	6.98	9.07	0.27*	81.3
PQ A + B	0.89	2.68	9.30	9.51	0.33	82.7
PQ B	0.80	2.65	8.80	9.21	0.30	89.1
Control #1	1.22	2.79	10.17	11.92	0.43	86.9
Trenched						
LJ A	1.32*	2.99	12.93*	10.50	0.44	85.1
LJ Out	0.99	2.65	10.33	9.66	0.37	80.5
PQ A	1.51*	3.20*	12.90*	11.73	0.47*	85.6
PQ Out	1.28	2.86	11.25	11.60	0.45	82.0
Control #2	0.86	2.58	9.10	9.22	0.33	81.6
Pooled SEM	0.16	0.16	1.15	1.24	0.04	4.4

^a Significant differences from the control at $P \leq 0.05$ are indicated by “*.” $N = 3$.

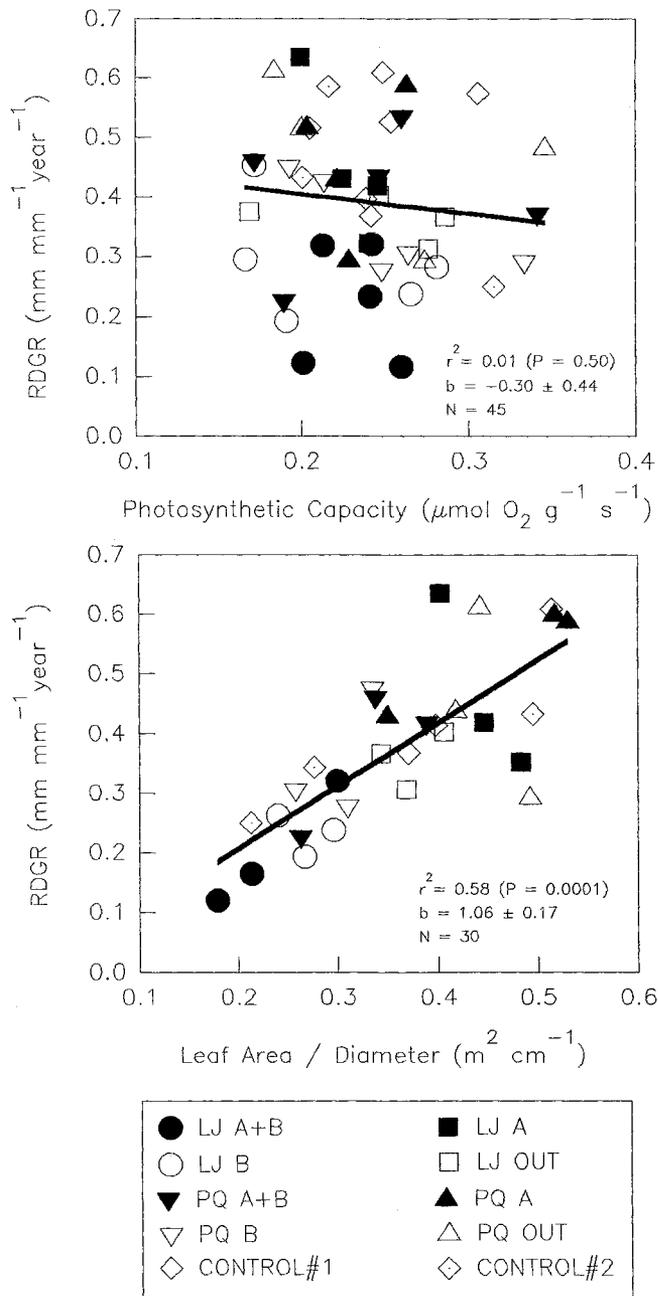


Fig. 5. Relationship between annual mean photosynthetic capacity (A_{max} , averaged across the three 1990 monthly measurements) and relative diameter growth rate (RDGR) and between leaf area per unit of trunk diameter (La/D) and RDGR. The coefficient of determination (r^2), regression coefficient (b) \pm SE, probability level associated to b , and sample size (N) are presented in each graph.

vine shading can significantly reduce A_{max} of the host tree when A_{max} is expressed on an area basis (Fig. 4). Thus, tree leaves developing under the shade of vine leaves will have a significantly lower capacity to utilize occasional periods of high light for photosynthesis. Expressing photosynthetic rates on a leaf dry weight basis can be more informative, because differences in photosynthetic rates per unit leaf area between sun and shade leaves may reflect

only a change in leaf density, and not in concentration of photosynthetic enzymes (McMillen and McClendon, 1983; Givnish, 1988). When photosynthesis was expressed on a dry weight basis, sun and shade leaves had very similar responses throughout the range of irradiance used (Fig. 4). Therefore, the shading effects were not mediated through changes in biochemical and photochemical processes of leaves, but acted mostly through reduction in leaf mass per area. The similarity in dark respiration and light-limited photosynthetic rates between sun and shade leaves, both on an area and weight basis (Fig. 4), suggests that leaves of *L. styraciflua* did not acclimate to shade imposed by aboveground competition (Björkman and Holmgren, 1966; Boardman, 1977; Loach, 1967).

Plant carbon uptake and growth depend not only on photosynthetic rates of individual leaves but also on the total leaf area or mass present in the canopy (Schulze, Küppers, and Matyssek, 1983; Küppers, Koch, and Mooney, 1988; Jones and McLeod, 1990; Poorter, Remkes, and Lambers, 1990; Körner, 1991). The increasing similarity in A_{max} , leaf N (Dillenburg et al., 1993b), and PNUE among treatments, as the season progressed, can be explained by changes in growth allocation. At the single leaf level, the reduced allocation to leaves compared with stems (Table 2) as well as the reduced growth (Dillenburg et al., 1993a) in trees competing with vines below ground may have compensated for the reduced availability of soil N. Thus, trees were able to keep the photosynthetic status of their leaves closer to optimal values by reducing total leaf area. The regulation of leaf N concentration is an important means by which plants can adjust their physiological status to the prevailing environment (Hilbert, 1990). Photosynthetic capacity is nearly a linear function of leaf N concentration up to the highest N levels observed in nature (Field, 1988), and positive rates of photosynthesis can only be attained with nitrogen levels above a substantial threshold. Therefore, reductions in leaf allocation in trees experiencing root competition probably represented an important contribution to the optimization in the use of limiting N.

For trees competing only above ground with vines, the increased allocation to leaves compared with stems (Table 2) may have compensated for any shading effect observed at the single leaf level. This compensation could help explain why those trees had less shading by vines (Dillenburg et al., 1993b) and no reduction in growth (Dillenburg et al., 1993a) compared to trees that competed with vines both below and above ground.

While the annual growth of *L. styraciflua* trees was directly related to the annual average N concentration of its leaves (Dillenburg et al., 1993b), no correlation was found between leaf A_{max} and tree growth in the present study (Fig. 5). These contrasting results suggest that N availability may have affected tree growth independently from its effects on leaf photosynthesis, probably acting directly on leaf production. This conclusion is further supported by the positive correlation between leaf area per unit of trunk diameter or stem length and tree growth. Chapin (1991) and Ingestad and Ågren (1991) suggested that the primary plant response to N stress is a cessation of leaf growth. Tschaplinski and Norby (1991) showed that, when water was not a limiting factor, leaf production in sycamore trees better reflected changes in growth in

response to nitrogen availability than did leaf photosynthesis. Other competition studies showed that increased leaf production may be the most important factor driving the increased productivity of trees when competition with herbaceous weeds is reduced, instead of increased photosynthesis per unit leaf area (Britt et al., 1990; Green et al., 1991).

Several studies have shown a stronger link between plant allocation and growth than between leaf photosynthesis and growth (Küppers, 1985; Caldwell, 1987; Walters and Reich, 1989; Beyschlag et al., 1990; Rice et al., 1992). This study has shown that allocation rather than leaf-level photosynthetic responses to vine competition were more important in determining tree growth. Of particular importance in the growth responses of the host tree was the altered allocation to leaf production. Below- and aboveground competition from vines had opposing effects on leaf allocation patterns of the host tree, but the similar reduction in leaf allocation of trees competing below ground and below and above ground with vines reflects the much greater effect of belowground competition during this 2-year study.

The results from this study are particularly relevant to high-light situations, where interactions between vines and trees are particularly intense. These include successional forests, where vines are known to arrest tree growth and alter forest structure. Our study has shown that changes in leaf allocation patterns are particularly important in understanding the mechanisms by which vines affect tree growth and forest regeneration and structure. It also suggests that a better understanding of the mechanisms of competition between plants will arise by not only focusing on leaf level physiology but also accounting for whole-plant responses such as the reallocation of biomass.

LITERATURE CITED

- AERTS, R., R. G. A. BOOT, AND P. J. M. VAN DER AART. 1991. The relation between above- and belowground biomass allocation patterns and competitive ability. *Oecologia* 87: 551–559.
- BAHARI, Z. A., S. G. PALLARDY, AND W. C. PARKER. 1985. Photosynthesis, water relations, and drought adaptation in six woody species of oak-hickory forests in Central Missouri. *Forest Science* 31: 557–569.
- BEYSCHLAG, W., P. W. BARNES, P. W. RYEL, M. M. CALDWELL, AND S. D. FLINT. 1990. Plant competition for light analyzed with a multispecies canopy model. II. Influence of photosynthetic characteristics on mixtures of wheat and wild oat. *Oecologia* 82: 374–380.
- BJÖRKMAN, O., AND P. HOLMGREN. 1966. Photosynthetic adaptation to light intensity in plants native to shaded and exposed habitats. *Physiologia Plantarum* 19: 854–859.
- BOARDMAN, N. K. 1977. Comparative photosynthesis of sun and shade plants. *Annual Review of Plant Physiology* 28: 355–377.
- BRITT, J. R., B. R. ZUTTER, R. J. MITCHELL, D. H. GJERSTAD, AND J. F. DICKSON. 1990. Influence of herbaceous interference on growth and biomass partitioning in planted loblolly pine (*Pinus taeda* L.). *Weed Science* 38: 497–503.
- CALDWELL, M. M. 1987. Plant architecture and resource competition. In E.-D. Schulze and H. Zwolfer [eds.], *Ecological studies*, vol. 61, 164–179. Springer, Berlin.
- CHAPIN, F. S. III. 1991. Integrated responses of plants to stress. *BioScience* 41: 29–36.
- CROMER, R. N., AND P. G. JARVIS. 1990. Growth and biomass partitioning in *Eucalyptus grandis* seedlings in response to nitrogen supply. *Australian Journal of Plant Physiology* 17: 503–515.
- DILLENBURG, L. R., D. F. WHIGHAM, A. H. TERAMURA, AND I. N. FORSETH. 1993a. Effects of below- and aboveground competition from the vines *Lonicera japonica* and *Parthenocissus quinquefolia* on the growth of the tree host *Liquidambar styraciflua*. *Oecologia* 93: 48–54.
- _____, _____, _____, AND _____. 1993b. Effects of vine competition on availability of light, water, and nitrogen to a tree host (*Liquidambar styraciflua*). *American Journal of Botany* 8: 244–252.
- FIELD, C. 1988. On the role of photosynthetic responses in constraining the habitat distribution of rainforest plants. *Australian Journal of Plant Physiology* 15: 342–358.
- _____, AND H. A. MOONEY. 1986. The photosynthesis-nitrogen relationship in wild plants. In T. J. Givnish [ed.], *On the economy of plant form and function*, 25–55. Cambridge University Press, Cambridge.
- FITTER, A. H. 1987. An architectural approach to the comparative ecology of plant root systems. *New Phytologist* 106: 61–77 (Supplement).
- FREDEEN, A. L., J. A. GAMON, AND C. B. FIELD. 1991. Responses of photosynthesis and carbohydrate partitioning to limitations in nitrogen and water availability in field-grown sunflower. *Plant Cell and Environment* 14: 963–970.
- FRIEDLAND, A. J., AND A. P. SMITH. 1982. Effects of vines on successional herbs. *American Midland Naturalist* 108: 402–403.
- GIVNISH, T. J. 1988. Adaptation to sun and shade: a whole-plant perspective. *Australian Journal of Plant Physiology* 15: 63–92.
- GREEN, T. H., R. J. MITCHELL, K. C. PALIWAL, U. V. PATHRE, B. R. ZUTTER, AND D. H. GJERSTAD. 1991. Effects of herbaceous weeds on fourth year water relations and gas exchange of loblolly pine. *Weed Technology* 5: 753–758.
- HILBERT, D. W. 1990. Optimization of plant root:shoot ratios and internal nitrogen concentration. *Annals of Botany* 66: 91–99.
- INGESTAD, T., AND G. I. ÅGREN. 1991. The influence of plant nutrition on biomass allocation. *Ecological Applications* 1: 168–174.
- JONES, R. H., AND K. W. MCLEOD. 1990. Growth and photosynthetic responses to a range of light environments in Chinese tallow tree and Carolina ash seedlings. *Forest Science* 36: 851–862.
- KIRBY, R. M., AND E. D. MATTHEWS. 1973. Soil survey of Anne Arundel County, Maryland. U.S. Dept. of Agriculture, Soil Conservation Service, Washington, DC.
- KOLB, T. E., K. C. STEINER, L. H. MCCORMICK, AND T. W. BOWERSOX. 1990. Growth response of northern red-oak and yellow-poplar seedlings to light, soil moisture and nutrients in relation to ecological strategy. *Forest Ecology and Management* 38: 65–78.
- KÖRNER, C. H. 1991. Some often overlooked plant characteristics as determinants of plant growth: a reconsideration. *Functional Ecology* 5: 162–173.
- KÜPPERS, M. 1985. Carbon relations and competition between woody species in a Central European hedgerow. IV. Growth form and partitioning. *Oecologia* 66: 343–352.
- _____, G. KOCH, AND H. A. MOONEY. 1988. Compensating effects to growth of changes in dry matter allocation in response to variation in photosynthetic characteristics induced by photoperiod, light and nitrogen. *Australian Journal of Plant Physiology* 15: 287–298.
- LOACH, K. 1967. Shade tolerance in tree seedlings. I. Leaf photosynthesis and respiration in plants raised under artificial shade. *New Phytologist* 66: 607–621.
- MCMILLEN, G. G., AND J. H. MCCLENDON. 1983. Dependence of photosynthetic rates on leaf density thickness in deciduous woody plants in sun and shade. *Plant Physiology* 72: 674–678.
- PENFOUND, W. T. 1974. The role of vines in plant communities. *Advanced Frontiers in Plant Sciences* 17: 187–192.
- POORTER, H., C. REMKES, AND H. LAMBERS. 1990. Carbon and nitrogen economy of 24 wild species differing in relative growth rate. *Plant Physiology* 94: 621–627.
- PUTZ, F. E. 1984. The natural history of lianas on Barro Colorado island, Panama. *Ecology* 65: 1713–1724.
- RANNEY, T. G., T. H. WHITLOW, AND N. L. BASSUK. 1990. Response of five temperate deciduous tree species to water stress. *Tree Physiology* 6: 439–448.
- REICH, P. B., M. B. WALTERS, AND T. J. TABONE. 1989. Responses of *Ulmus americana* seedlings to varying nitrogen and water status. 2. Water and nitrogen use efficiency in photosynthesis. *Tree Physiology* 5: 173–184.

- RICE, K. J., R. A. BLACK, G. RADAMAKER, AND R. D. EVANS. 1992. Photosynthesis, growth, and biomass allocation in habitat ecotypes of cheatgrass (*Bromus tectorum*). *Functional Ecology* 6: 32–40.
- SAS INSTITUTE, INC. 1985. SAS user's guide: statistics, version 5. SAS Institute, Inc., Cary, NC.
- SCHULZE, E.-D., M. KÜPPERS, AND R. MATYSSEK. 1983. The roles of carbon balance and branching pattern in the growth of woody species. In T. J. Givnish [ed.], *On the economy of plant form and function*, 585–602. Cambridge University Press, Cambridge.
- THOMAS, L. K., JR. 1980. The impact of three exotic plant species on a Potomac island. National Park Service Scientific Monograph Service, No. 13. U.S. Dept. of Interior, Washington, DC.
- TSCHAPLINSKI, T. J., AND R. J. NORBY. 1991. Physiological indicators of nitrogen response in a short rotation sycamore plantation. I. CO₂ assimilation, photosynthetic pigments and soluble carbohydrates. *Physiologia Plantarum* 82: 117–126.
- WALTERS, M. B., AND P. B. REICH. 1989. Responses of *Ulmus americana* seedlings to varying nitrogen and water status. 1. Photosynthesis and growth. *Tree Physiology* 5: 159–172.
- WEBER, J. A., AND D. M. GATES. 1990. Gas exchange in *Quercus rubra* (northern red oak) during a drought: analysis of relation among photosynthesis, transpiration, and leaf conductance. *Tree Physiology* 7: 215–225.
- WHIGHAM, D. F. 1984. The influence of vines on the growth of *Liquidambar styraciflua* L. (sweetgum). *Canadian Journal of Forest Research* 14: 37–39.