

## EFFECTS OF VINE COMPETITION ON AVAILABILITY OF LIGHT, WATER, AND NITROGEN TO A TREE HOST (*LIQUIDAMBAR STYRACIFLUA*)<sup>1</sup>

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Competitive effects of vines on their tree hosts are well documented, but the mechanisms involved in these interactions are poorly understood. The objectives of this study were to measure the effects of below- and/or aboveground competition from the vines *Lonicera japonica* and *Parthenocissus quinquefolia* on availability of light, water, and nitrogen to the host tree *Liquidambar styraciflua*, and to examine the relationship between resource availability and tree growth. Light penetration through tree canopies, pre-dawn leaf water potential, and leaf nitrogen concentration were used as predictors of light, water, and nitrogen availability to the tree, respectively. Vine presence significantly reduced light penetration through the tree canopies, but this reduction was not clearly related to the growth responses of trees. Vines did not reduce the pre-dawn leaf water potential of competing trees, which was consistently above  $-0.5$  MPa for the duration of the study. Leaf nitrogen concentration of trees, on the other hand, was significantly reduced by belowground competition with *L. japonica*. The positive correlation between the annual average leaf nitrogen concentration and tree diameter growth suggested that competition for nitrogen mediated the effects of belowground competition of vines on tree growth.

Plants compete for resources directly and/or indirectly by interfering with each other (Keddy, 1989; Connell, 1990; Tilman, 1990). Resource depletion is widely accepted as the most important competitive mechanism, and light, water, and nutrients are the three major resources for which plants compete (Grime, 1979; Tilman, 1989; Goldberg, 1990). Some evidence suggests that direct interference (i.e., mechanical damage) may be the most important component of vine-host interactions (Lutz, 1943; Siccama, Weir, and Wallace, 1976; Thomas, 1980; Putz, 1984; Stevens, 1987), but other studies have indicated that resource competition may also be important. Vine leaves can shade leaves of their hosts (Featherly, 1941; Lutz, 1943; Monsi and Murata, 1970; Putz, 1984), and vine roots can compete with host roots for water and nutrients (Patterson, 1973; Kennedy, 1981; Whigham, 1984b).

Light reduction is the most apparent aspect of competition between plants (Caldwell, 1987), and it is particularly obvious in the case of vine-host interactions. In contrast to light, water and nutrients can accumulate in the environment (Harper, 1977), making the effects of root competition less predictable than those of light competition. Nitrogen (N) is one of the mineral nutrients most limiting to plant growth (Field and Mooney, 1986). Be-

cause of its high mobility, broad zones of N depletion may develop around roots, and competition for N may be intense (Caldwell and Richards, 1986; Wilson and Newman, 1987).

Dillenburg et al. (in press) showed that belowground competition with the exotic, evergreen vine Japanese honeysuckle *Lonicera japonica* [L.] Thunb.), either alone or in combination with aboveground competition, significantly reduced the growth of sweetgum saplings (*Liquidambar styraciflua* L.). Tree growth was less affected by belowground competition with the native, deciduous vine Virginia creeper (*Parthenocissus quinquefolia* L.), and was not affected by canopy competition alone with either vine species. Only minor mechanical effects of vines on trees (incipient bending of the main stem) were observed by the end of the study. In this paper, we examine the effects of those two vines on the availability of resources to the tree host. Because competition for resources involves not only resource depletion but also a positive growth response to resource availability (Goldberg, 1990), the relationship between resource level and tree growth was also examined. Canopy light penetration, pre-dawn leaf water potential ( $\psi_{pd}$ ), and leaf nitrogen concentration of the tree were used as indicators of availability of light, water, and nitrogen, respectively. Two major questions were addressed in this study: 1) To what extent does competition with vines affect the availability of light, water, and nitrogen to the host?, and 2) What is the relationship between the effects of vine competition on availability of resources and the effects on tree growth?

### MATERIALS AND METHODS

**Study site and plant material**—The study was conducted in an experimental garden at the Smithsonian Environmental Research Center (SERC), Edgewater, Maryland, on the inner coastal plain of the Chesapeake Bay (38°53'20"N, 76°33'20"W), during 1989 and 1990. The site was located on a gently sloping Donlonton sandy loam

<sup>1</sup> Received for publication 1 June 1992; revision accepted 30 October 1992.

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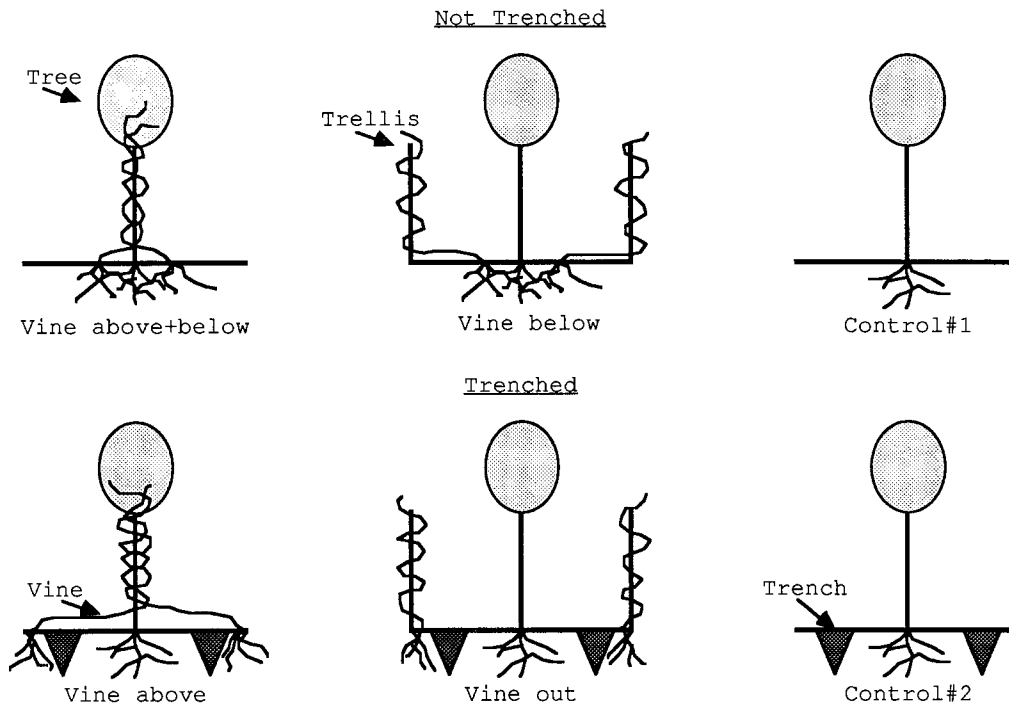


Fig. 1. Schematic representation of treatments. Diagrams represent the six different types of vine competition.

soil (Ultisol), described as being moderately well drained, with high available moisture capacity (Kirby and Matthews, 1973). Characteristics of the soil at the study site are shown in Table 1. The tree host *Liquidambar styraciflua* is widespread in forests throughout the Atlantic Coastal Plain region, and it is common in early successional habitats that often have abundant vines, particularly introduced species such as *L. japonica*. Two-year-old, commercially grown saplings of *L. styraciflua* (height = 65.3 ± 0.70 cm, and diameter 10 cm above the ground = 1.26 ± 0.013 cm) and rooted vine cuttings (approximately five 30-cm-long branches per vine) were used in this experiment.

**Experimental design**—The study used a 2 × 2 × 3 incomplete factorial design, with trees as the experimental units. The three factors and their 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 ten were used, because the two vine species were not distinguished from each other in the “vines absent” treatments. A schematic representation of the treatments is shown in Fig. 1. The following terminology will be used throughout the paper: 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; and 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, and lined with a double layer of 4 mil plastic before being refilled with soil. We periodically uprooted any vine shoots that had rooted inside the trenches. When aboveground competition was excluded, vines were grown on wire trellises, placed to the east and west sides of each tree (Fig. 2).

The study site was divided into 60 regularly spaced 1-m × 1-m plots, the center of each plot being spaced 2.5 m from its nearest adjacent plot. In November of 1988, a single tree was planted at the center of each plot, and two vines of the same species were planted, one at the east and the other at the west side of the tree, either inside the plot and 30 cm away from the tree trunk (for untrenched plots), or just outside each of the two trenches. All plots were covered with shredded hardwood mulch to reduce weed infestation and weeded periodically. Plots and treat-

TABLE 1. Soil chemical characteristics of the experimental area<sup>a</sup>

Soil property (0–20 cm)	Levels
pH <sup>b</sup>	5.25 ± 0.04
OM (%) <sup>c</sup>	1.55 ± 0.03
P <sub>2</sub> O <sub>5</sub> (ppm) <sup>d</sup>	35.8 ± 1.41
Mg (ppm) <sup>d</sup>	110.9 ± 2.55
Ca (ppm) <sup>d</sup>	508.4 ± 22.6
K <sub>2</sub> O (ppm) <sup>d</sup>	119.1 ± 5.19
NO <sub>3</sub> (ppm) <sup>e</sup>	8.6 ± 0.74

<sup>a</sup> Means (±SE) of 36 composite samples collected in the area, away from the direct influence of experimental treatments, on 04/89 (N = 18) and 07/89 (N = 18). Analyses done by the Soil Analysis Laboratory, University of Maryland.

<sup>b</sup> pH in water (1:1).

<sup>c</sup> OM = organic matter (digestion with sodium dichromate and H<sub>2</sub>SO<sub>4</sub>).

<sup>d</sup> HCl/H<sub>2</sub>SO<sub>4</sub> extractable.

<sup>e</sup> Sodium-acetate extractable.



Fig. 2. *Liquidambar styraciflua* under above- and belowground competition from *L. japonica*. Picture was taken in late September of 1990, after all tree leaves were excised. Height in cm is presented on both sides of the background screen.

ments were organized according to a randomized complete block design, with six replicates per treatment. Criteria for blocking included location within the site and initial tree size. Measurements were taken a block at a time.

**Light availability**—The effects of vines on light penetration through the tree canopy were estimated by: 1) measuring the gap fraction of tree canopies on 31 August 1990, when both vine and tree leaves were present, and 2) by measuring openness of vine canopies present on trees on 26 September 1990, just after all tree leaves were excised, and only vine leaves remained on the tree canopies. These last measurements allowed an assessment of the degree of vine infestation on trees, without the confounding presence of tree leaves.

Gap fraction (probability of light penetration through the tree canopy without interception) was measured with a sunfleck ceptometer (Decagon Devices, Pullman, WA, SF-80) between 1230 and 1400 hr. The 80-cm-long ceptometer was held in an oblique position along the shaded side of the tree, approximately normal to the sun rays, so as to maximize its interception of direct light passing through the tree canopy. Values for each tree represent the average of ten readings.

The openness of vine canopies present on hosts was

TABLE 2. Tree gap fraction and vine canopy openness. Data were square-root transformed prior to ANOVA. Untransformed means are shown inside parentheses<sup>a</sup>

Treatment	Gap fraction (%) <sup>b</sup>	Canopy openness (%) <sup>c</sup>
Untrenched		
LJ A + B	2.31e** (5.6)	1.58e** (2.7)
LJ B	4.69d* (23.1)	8.57d (73.5)
PQ A + B	3.21e** (10.4)	4.55e** (21.1)
PQ B	4.63d* (21.9)	8.46d (71.7)
Control #1	4.01 (16.1)	8.75 (77.0)
Trenched		
LJ A	3.38e** (11.7)	4.71e** (23.9)
LJ OUT	4.58d (21.4)	7.84d (61.5)
PQ A	3.54d* (12.6)	4.39e** (19.3)
PQ OUT	3.99d (16.3)	8.09d (65.7)
Control #2	4.24 (18.2)	7.89 (62.3)
Pooled SEM	0.26 (2.24)	0.37 (4.03)

<sup>a</sup> Within untrenched and trenched treatments, means followed by “\*\*” or “\*\*\*” are significantly different from the control at  $P \leq 0.10$  and  $P \leq 0.05$ , respectively. Different letters between paired treatments indicate significant difference at  $P \leq 0.05$ .

<sup>b</sup> Tree leaves present;  $N = 6$ .

<sup>c</sup> Tree leaves removed (openness of vine canopies present on the host);  $N = 3$ .

estimated from hemispherical photographs taken with a 180° view fisheye lens horizontally placed at the base of each tree. Photographs of three replicates (trees) per treatment were taken, and canopy openness calculated using the SOLARCALC program (Chazdon and Field, 1987), by dividing the number of open points in the image by the total number of points possible in an unobstructed sky. A ceptometer could not be used in this case, because, for some trees, the vine leaf canopy was not extensive enough to cover the ceptometer throughout its length.

**Water availability**—The pre-dawn water potential of tree leaves was measured on 11 June, 16 July, and 9 August in 1989, and on 7 and 29 June, 20 July, 18 August, 3 and 7 September, and 3 October in 1990. Measurements were taken only on treatments involving root competition (LJ A + B, PQ A + B, LJ B, PQ B) and untrenched controls (CONTROL #1). Except for October 1990 ( $N = 3$ ), four trees were sampled in each treatment. One leaf per tree was removed from the lower canopy, and  $\psi_{pd}$  measured using a Scholander-type pressure chamber (PMS Instruments, Corvallis, OR, Model 1000). Because of a false end-point at high values of water potential,  $\psi_{pd}$  measurements taken in 1989 and in June of 1990 may have been overestimated. However, measurements taken on the vines at the same time (data not presented) indicated that the tree values were at the correct range. For measurements taken from July through October of 1990, the true end-point was more precisely detected, and checked by periodically reading  $\psi_{pd}$  in small branches of the tree.

Monthly precipitation totals and temperature means for 1989 and 1990 were collected from a weather station located at SERC, about 100 m away from the study site. The data were plotted following Walter's scale guidelines for climate diagrams (Walter, 1979), to allow for the identification of potentially dry periods. The 30-yr normal value of precipitation was based on data collected from

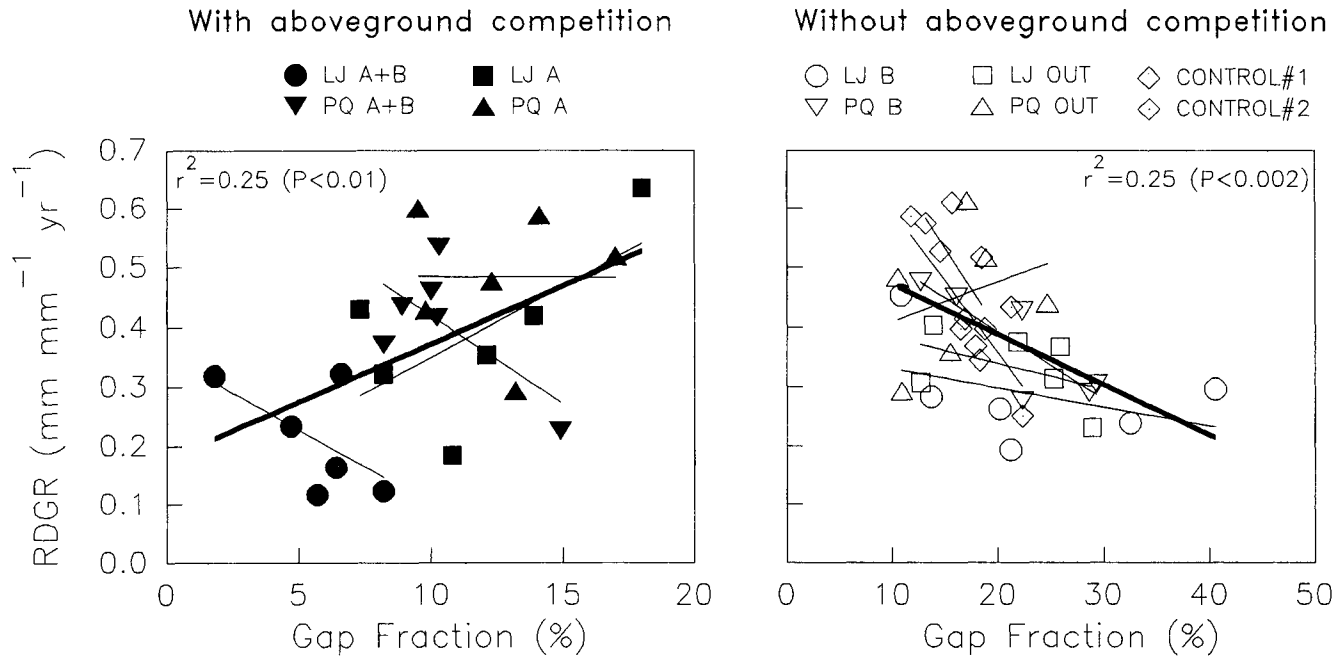


Fig. 3. Relationship between tree canopy gap fraction and the 1990 annual relative diameter growth rate (RDGR) for trees with and without aboveground competition. Values of  $r^2$  refer to the average regression (bold line) of each graph. Regression parameters are listed in Table 3.

weather stations located at the Baltimore-Washington International Airport, Maryland (1961–1967, about 30 km from the study site) and at SERC (1968–1990).

**Nitrogen availability**—Leaf harvest for N analysis was performed on 20 July and 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 half of the canopy were combined into one composite sample, oven-dried, and ground. Four and six trees from each treatment were sampled in 1989 and 1990, respectively. Additionally, all leaves from three trees in each treatment were harvested on 26 September 1990, oven-dried, ground, and a subsample removed for N analysis. Total Kjeldahl

N of all samples was determined at the Plant Analysis Laboratory, Pennsylvania State University.

**Tree growth**—The annual relative diameter growth rate (RDGR) of trees in 1990 was used as the dependent variable for regression analysis. Absolute growth and final diameter were also tested as dependent variables, producing the same overall results as RDGR (data not presented). Diameter was measured 10 cm from the ground at the beginning and end of the growing season.

**Data analysis**—Statistical analysis was based on pairwise comparisons of individual treatment means. A two-way analysis of variance (block and treatment effects) was

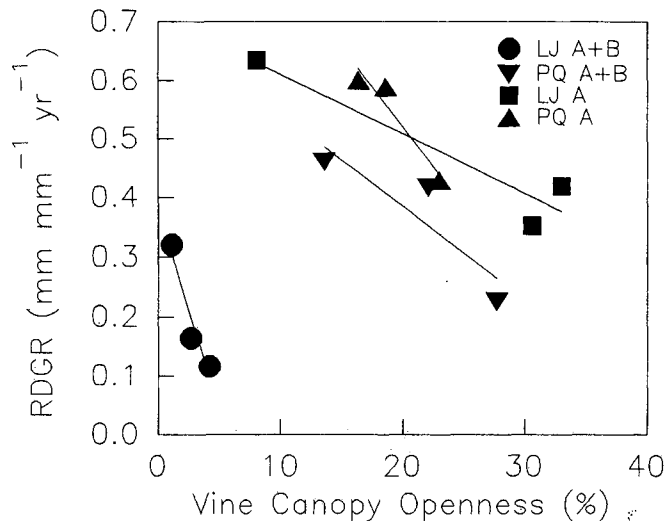


Fig. 4. Relationship between vine canopy openness and the 1990 annual relative diameter growth rate (RDGR) for trees with aboveground competition.

TABLE 3. Regression statistics for data presented in Fig. 3<sup>a</sup>

Treatment	Gap fraction × RDGR			
	b	SE	P ≤	r <sup>2</sup>
<b>With aboveground competition</b>				
LJ A + B	-0.025	0.017	0.22	0.35
PQ A + B	-0.030	0.016	0.15	0.44
LJ A	0.024	0.015	0.18	0.39
PQ A	-0.000	0.020	0.99	0.00
Overall	0.019	0.007	0.01	0.25
<b>Without aboveground competition</b>				
LJ B	-0.003	0.004	0.42	0.17
PQ B	-0.011	0.004	0.04	0.70
LJ OUT	-0.004	0.004	0.35	0.21
PQ OUT	0.006	0.010	0.55	0.10
Control #1	-0.028	0.018	0.21	0.36
Control #2	-0.024	0.008	0.05	0.62
Overall	-0.008	0.002	0.002	0.25
Overall	-0.04	0.05	0.42	0.01

<sup>a</sup> b, regression coefficient; SE, standard error of the regression coefficient; P, probability level associated with regression coefficient; r<sup>2</sup>, coefficient of determination.

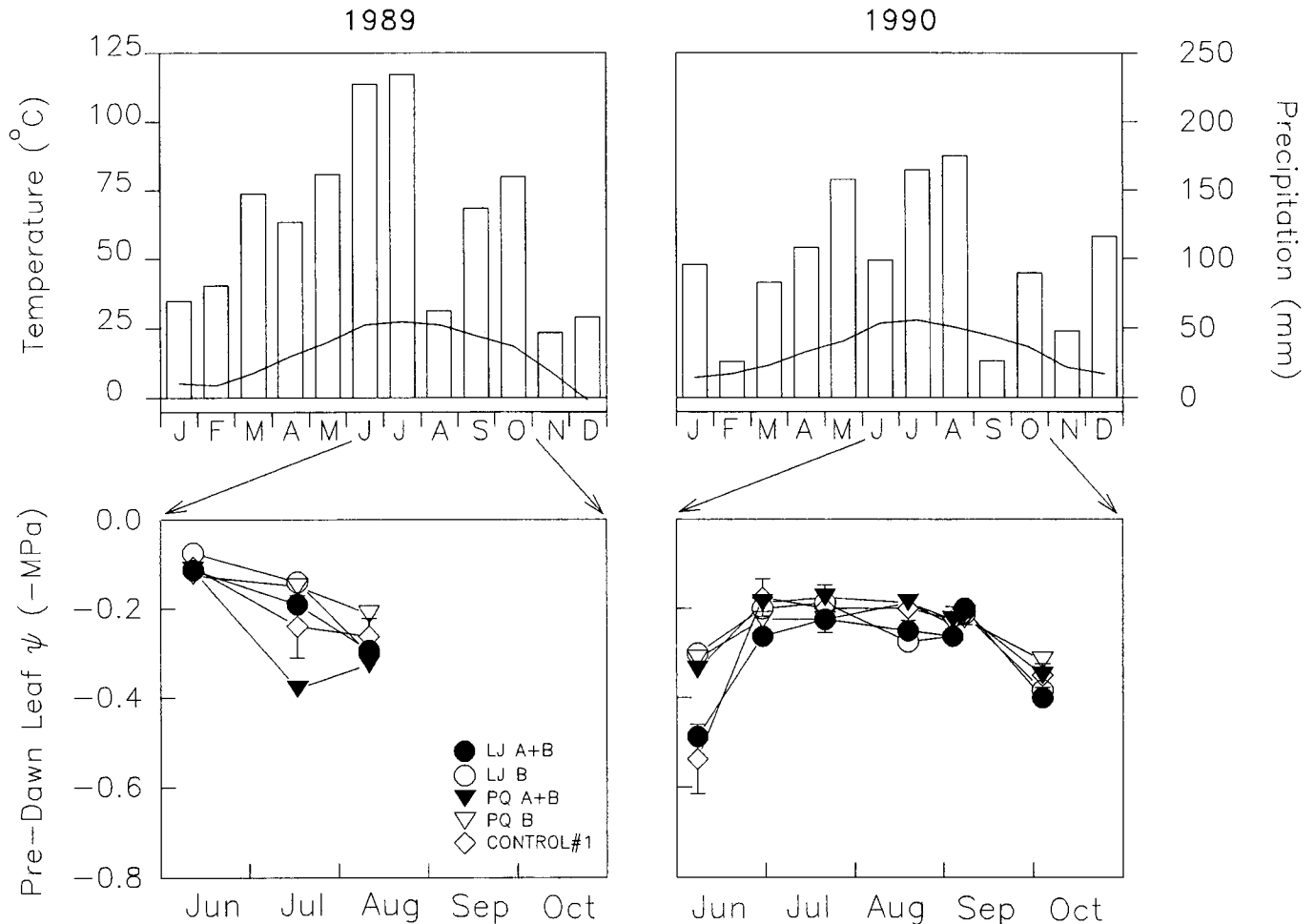


Fig. 5. Monthly precipitation (bars) and mean temperature (lines) in 1989 and 1990 (top). The scales used for precipitation and temperature follow Walter's guidelines for climate diagrams (1 mm = 2 °C; Walter, 1979). Leaf pre-dawn water potentials ( $\psi_{pd}$ ) of trees in 1989 and 1990 (bottom). Pooled standard error of the mean from ANOVA is shown for the controls. PQ A + B < PQ B (08/09/90,  $P \leq 0.10$ ), PQ A + B < PQ B (07/16/89,  $P \leq 0.05$ ), and LJ B > CONTROL #1 (06/07/90,  $P \leq 0.05$ ).

performed, followed by the least significant difference (LSD) mean separation technique. Means were compared within trenched and untrenched treatments. Every treatment was compared to the appropriate control, and treatments involving the same vine species were compared to each other. Homogeneity of variances of the residuals was tested using Hartley's  $F_{max}$  test, and data were transformed as needed.

Least squares regression analysis was used to test for correlation between estimates of light, water, and N availability and tree growth. Absolute residuals were examined for independence from predicted Y values, and data transformation performed when needed. All statistical analyses were performed using SAS (SAS Institute, 1985).

## RESULTS

**Light availability**—Vine cover on trees was limited during the first year. In the second year, most trees were overtopped and noticeably shaded by *L. japonica*, especially in untrenched plots (Fig. 2). Gap fraction was expected to decrease as the amount of vine foliage present on the tree canopy increased, provided that the amount of tree foliage was not proportionally reduced. Although

gap fraction does not actually measure the amount of light available to the tree leaves, it should be a good indicator of the potential shading between foliage elements within tree canopies. In August of 1990, the gap fraction of vine-infested tree canopies was reduced by 65%, 42%, 35%, and 31% in the LJ A + B, LJ A, PQ A + B ( $P \leq 0.05$ ), and PQ A ( $P \leq 0.10$ ) treatments, respectively, compared to controls (Table 2). On the other hand, belowground competition alone (LJ B and PQ B) acted to increase gap fraction (more open canopies) above control values ( $P \leq 0.10$ ). Not surprisingly, vine canopy openness of the aboveground competition treatments was significantly less than leafless controls ( $P \leq 0.05$ ) (Table 2).

*Lonicera japonica* clearly reduced gap fraction and openness to a greater extent than did *P. quinquefolia*, and reductions in gap fraction and openness by *L. japonica* were greater for the LJ A + B than for the LJ A treatment (Table 2).

In order to examine the relationship between gap fraction and growth, trees were separated into two groups: one including trees that competed with vines above ground, and the other including trees that did not compete with vines above ground. For vine-infested tree canopies, there was an overall positive relationship between gap fraction

and annual relative diameter growth rate (RDGR) ( $r^2 = 0.25$ ) (Fig. 3; Table 3). An examination of each treatment separately, however, revealed that, except for the LJ A treatment, a negative relationship was present. The greatest  $r^2$  values were obtained for trees competing below and above ground with *L. japonica* ( $r^2 = 0.52$ ) and *P. quinquefolia* ( $r^2 = 0.54$ ), and only in these two cases did the regression approach significance ( $P \leq 0.10$ ) (Fig. 3; Table 3). For unfested tree canopies, the overall relationship was negative ( $r^2 = 0.25$ ), and most treatments followed the same general pattern (Fig. 3; Table 3).

The degree of openness of vine canopies present on trees had a negative relationship with RDGR in all four treatments which involved aboveground competition (Fig. 4). No regression analysis was performed in this case due to the small sample size for each treatment ( $N = 3$ ).

**Water availability**—Annual precipitation was higher in 1989 (1,514 mm) than in 1990 (1,188 mm), and in both years it exceeded the 30-year normal value (1961–1990) of 1,125 mm. Monthly rainfall during the growing season (April–September) exceeded 100 mm, except in August 1989 and September 1990 (Fig. 5). September 1990, the month in which the precipitation curve fell below the temperature curve, was the only potentially dry period (Walter, 1979). Compared to the 30-yr average, there was a surplus of 357 mm and 137 mm of rainfall during the 1989 and 1990 growing seasons, respectively.

Values of  $\psi_{pd}$  of trees were consistently above  $-0.5$  MPa, and were not reduced by vine competition, in 1989 and 1990. Instead, in June of 1990,  $\psi_{pd}$  of trees competing below ground with *L. japonica* (LJ B) was significantly greater than controls ( $P \leq 0.05$ ) (Fig. 5).

**Nitrogen availability**—In July of 1989, leaf N was very similar among all untrenched treatments, although trees in the PQ A + B treatment had greater leaf N than controls ( $P \leq 0.05$ ) (Table 4). In September of 1989, trees in the LJ B treatment had lower leaf N than controls ( $P \leq 0.10$ ). Trees in the LJ B ( $P \leq 0.10$ ) and LJ A + B ( $P \leq 0.05$ ) treatments had lower leaf N concentrations than controls in May of 1990. In July of 1990, leaf N of the LJ A + B trees was still less than controls ( $P \leq 0.10$ ), and leaf N of trees in the PQ B treatment was also reduced below control values ( $P \leq 0.05$ ). In September of 1990, there were no significant reductions in leaf N for any competition treatment. However, the N concentration of bulked samples from all canopy leaves was significantly reduced by the LJ A + B, LJ B ( $P \leq 0.05$ ), and PQ A + B ( $P \leq 0.10$ ) treatments (Table 4).

No reduction in leaf N due to aboveground competition alone was detected (Table 4). Instead, in May 1990, aboveground competition with either vine species (LJ A and PQ A) resulted in significantly greater leaf N than controls, although no difference was detected when comparing them with the treatments where vines were growing outside the trenches (LJ OUT and PQ OUT). Similarly, leaf N concentration of the whole canopy increased above control values in the LJ A treatment ( $P \leq 0.05$ ; Table 4).

The three measurements of leaf N taken from each tree in 1990 were averaged, and those averages tested for correlation with tree growth in that year. A significant overall positive relationship between the annual average leaf N concentration and the annual RDGR of trees was found

TABLE 4. Nitrogen concentration of *L. styraciflua* leaves<sup>a</sup>

Treatment	Leaf nitrogen (%)					
	1989		1990			
	July	Sep- tember	May	July	September <sup>b</sup>	
Untrenched						
LJ A + B	0.90	1.38	1.23**	1.33*	1.57	1.26**
LJ B	0.92	1.29*	1.30*	1.36	1.70	1.16**
PQ A + B	1.14**	1.43	1.43	1.44	1.88	1.36*
PQ B	0.91	1.35	1.46	1.26**	1.69	1.38
Control #1	0.93	1.48	1.45	1.46	1.71	1.52
Trenched						
LJ A	0.92	—	1.70**	1.47	1.83	1.48**
LJ OUT	0.93	—	1.64	1.36	1.77	1.33
PQ A	1.01	—	1.68*	1.37	1.88	1.40
PQ OUT	0.90	—	1.72**	1.40	1.74	1.29
Control #2	0.94	—	1.51	1.51	1.85	1.26
Pooled SEM	0.05	0.07	0.06	0.06	0.07	0.07

<sup>a</sup> Within untrenched and trenched treatments, means followed by “\*\*” or “\*\*\*” are significantly different from the control at  $P \leq 0.10$  and  $P \leq 0.05$ , respectively. No significant differences between paired treatments involving the same vine species ( $P \leq 0.10$ ).

<sup>b</sup> Second column shows values of leaf N from samples representing the whole leaf canopy.

(Fig. 6; Table 5). The separate correlation analysis for treatments that included and excluded vine competition revealed that the overall linear relationship can be mostly attributed to trees that competed with vines ( $r^2 = 0.40$ ), in particular with *L. japonica*. The role of leaf N in explaining growth variation of trees free from vine competition was significant ( $r^2 = 0.03$ ) (Fig. 6; Table 5).

## DISCUSSION

**The role of light on vine-tree competition**—Two years of aboveground interactions with vines, particularly with *L. japonica*, resulted in reduced light penetration through the combined canopies of vines and *L. styraciflua* (Table 2), suggesting a reduction in light availability to trees. The lower amounts of *P. quinquefolia* cover on tree canopies,

TABLE 5. Regression statistics for data presented in Fig. 6<sup>a</sup>

Treatment	Leaf N × RDGR			
	b	SE	$P \leq$	$r^2$
With competition				
LJ A + B	0.37	0.19	0.13	0.48
PQ A + B	0.34	0.53	0.55	0.09
LJ A	0.93	0.42	0.09	0.56
PQ A	0.80	0.44	0.14	0.46
LJ B	0.79	0.27	0.04	0.68
PQ B	0.01	-0.14	0.82	0.01
Overall	0.64	0.11	0.0001	0.50
Without competition				
LJ OUT	0.18	0.25	0.52	0.11
PQ OUT	-0.10	0.57	0.98	0.01
Control #1	0.01	0.57	0.98	0.0002
Control #2	-0.33	0.54	0.57	0.09
Overall	-0.17	0.23	0.46	0.02
Overall	10.6	2.1	0.0001	0.26

<sup>a</sup> b, regression coefficient; SE, standard error of the regression coefficient;  $P$ , probability level associated with regression coefficient;  $r^2$ , coefficient of determination.

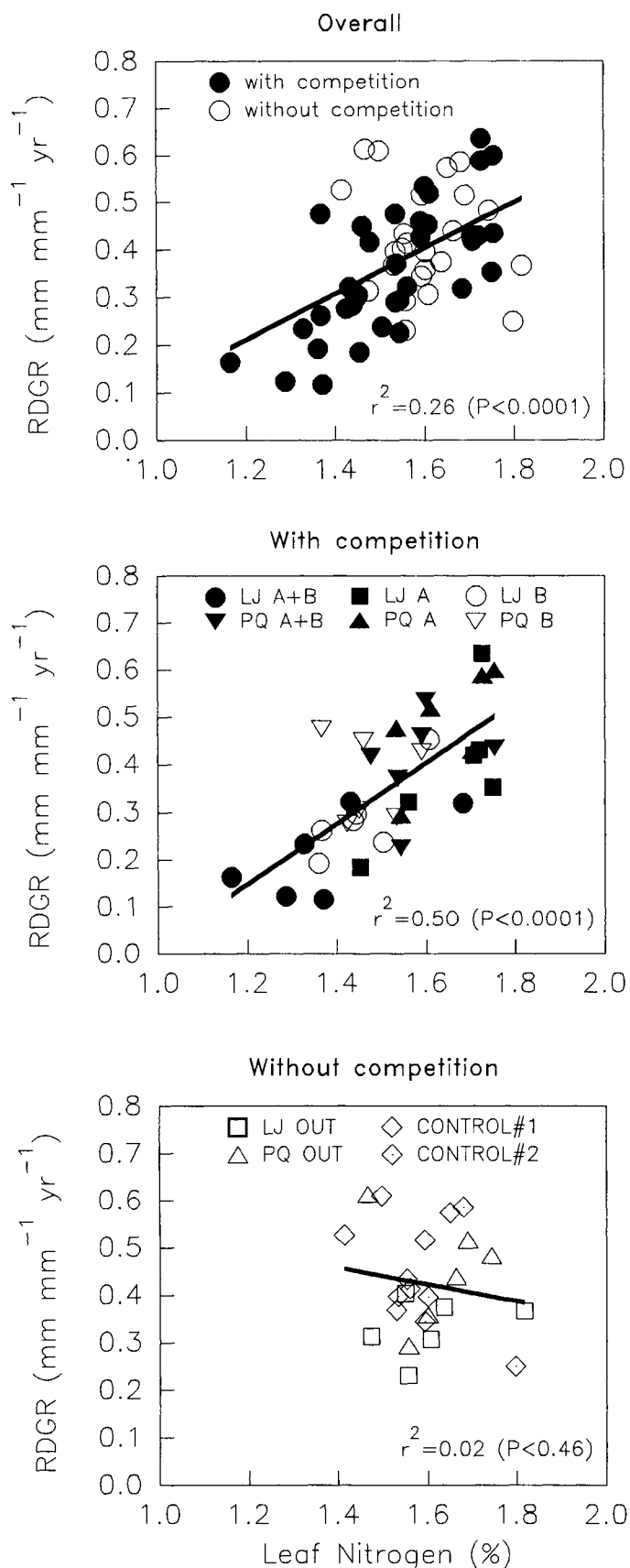


Fig. 6. Relationship between annual average leaf N concentration and relative diameter growth rate (RDGR) in 1990. Values of  $r^2$  refer

and consequently, the smaller reductions in gap fraction caused by this vine than by *L. japonica* resulted, in part, from differences in phenology and degree of leaf loss by grazing and disease between the two species. The evergreen *L. japonica* can exhibit shoot growth even during the winter months, and has an early burst of growth in the spring. The phenology of the deciduous *P. quinquefolia* is comparable to that of the tree host, initiating new leaves in April and shedding most of its leaves in October. The longer growing season of *L. japonica* gives this species an advantage over the deciduous vine in exploring the light environment in competition with the host. In contrast with *L. japonica*, leaf damage by powdery mildew and leaf grazing by Japanese beetle (*Popillia japonica*) were very common in *P. quinquefolia*, further contributing to the reduced cover of this vine on the tree host.

The overall positive relationship between gap fraction and tree growth, when aboveground competition was present (Fig. 3), would suggest that reduction in light availability was an important operative factor in competition. However, with the exception of trees competing above ground only with *L. japonica*, gap fraction had either no relationship to growth or the relationship tended to be negative, when each treatment was examined separately (Table 2). Furthermore, a negative relationship between vine canopy openness and tree growth was consistently observed (Fig. 4), although these results should be interpreted with caution, since only three trees per treatment were measured.

Dillenburg et al. (in press) have shown that aboveground competition with *L. japonica* reduced tree growth only when in association with belowground competition, and that the magnitude of this reduction was similar to that observed for trees competing below ground only with that vine. This suggests that the overall positive relationship between gap fraction and tree growth was mostly governed by belowground competition (i.e., trees with the smallest gap fraction grew less because of belowground competition effects). The greater gap fraction reduction by *L. japonica* when belowground competition was also present (Table 2) may have resulted from synergistic interactions between below- and aboveground competition. Such interactions in plant competition have been suggested (Clements, Weaver, and Hanson, 1929; Donald, 1958; Caldwell, 1987), and they would favor a greater vine cover on trees already suppressed due to root competition with vines, thus amplifying vine shading. The distance between the bases of trees and vines imposed by trenches could help explain the greater infestation with *L. japonica* on untrenched than on trenched trees. However, the much smaller difference in gap fraction and vine canopy openness between trenched and untrenched trees infested with *P. quinquefolia* (Table 2) and the fact that belowground competition with *P. quinquefolia* had only a small effect on tree growth (Dillenburg et al., in press) suggest that the degree of vine cover on trees depends on the outcome of belowground interactions. Although the loss of leaf tissue by *P. quinquefolia* could have masked

← to the average regression (bold line) of each graph. Regression parameters are listed in Table 5.

differences in vine cover between the PQ A + B and the PQ A treatment, no differences between the two treatments were observed even before most of the damage occurred (L. Dillenburg, personal observation).

Although light interference between vines and trees was apparent in this study, its role in competition was probably smaller than would be expected, a result commonly reported in competition experiments (Donald, 1958; Aspinnall, 1960; Martin and Snaydon, 1982; Caldwell, 1987; Wilson and Newman, 1987). Other studies on vine-host interactions have also downplayed the importance of light competition as a primary competitive mechanism. Stevens (1987) suggested that vine attachment to the tree canopy, rather than shading, was the key mechanism by which vines reduced the fecundity of the tropical tree *Bursera simaruba*, because of the slow response of trees to the removal of vines. Based on the growth responses of *L. styraciflua* to vine removal (*Lonicera japonica* and *Rhus radicans*) either from the crown or from both the crown and the ground, Whigham (1984b) concluded that availability of soil resources was a major component of the competitive interactions between vines and trees. Greenhouse experiments on the partitioning of root and canopy competition between *C. orbiculatus* and two herbaceous species (Patterson, 1973) revealed that belowground competition from the vine had a much greater effect on the growth of the herbs than light competition, despite the observation by the author that the major impact of the vine on its natural habitat was to reduce the amount of light reaching the ground below it.

**The role of water on vine-tree competition**—Water availability did not appear to be a major limiting resource to trees under any competitive situation (Fig. 5). This can be attributed to adequate amounts of precipitation during the duration of the experiment, and to the high water-holding capacity and insufficient drainage of the terrain. Because water availability can be excluded as an important factor in this experiment, the observed effects of belowground competition from *L. japonica* on tree growth (Dillenburg et al., in press) were probably mediated by changes in nutrient availability.

**The role of N on vine-tree competition**—The concentration of N in leaf tissues should reflect the nutritional status of the tree for this nutrient (Van den Driessche, 1974; Erdmann, Crow, and Rauscher, 1987), and it has been used as a predictor of N availability in the soil in different studies (Carter et al., 1984; Wilson, 1989; Brand, 1990; Eissenstat and Newman, 1990). Because nutrient status is not only a function of nutrient availability, but also of plant uptake rates (Chapin and Van Cleve, 1989), reduced growth under conditions of low N availability may result in increased N uptake on a plant weight basis, resulting in the nitrogen status of leaves being maintained closer to optimal conditions. The same treatments that showed reductions in leaf N late in the season in 1989 (LJ B) and early in the season in 1990 (LJ B and LJ A + B) also experienced significant reductions in tree diameter growth, leaf biomass, and leaf biomass per unit of stem length during the 1990 growing season (Dillenburg, 1991). We suggest that reductions in leaf N concentration in trees competing with *L. japonica* were associated with reduced

N availability in the soil. The increasing similarity in leaf N between those trees and the controls as the 1990 growing season progressed was probably related to the reductions in leaf biomass they experienced.

Treatment differences in leaf N concentration measured on samples representing the whole tree canopy should reflect not only differences in leaf nutritional status, but also differences in leaf microenvironment and leaf age. The lower leaf N concentration measured in trees competing below ground with *L. japonica* than in controls was most likely related to lower nutritional status and/or higher percentage of senescing leaves, since the degree of shading within canopies of the competing trees was even less than in controls (Table 2). Reductions in leaf N for trees competing below and above ground with *L. japonica* were not greater than reductions in trees competing only below ground. Also, canopy competition alone did not result in any reduction in leaf N, suggesting that vine shading had no impact on the N status of the trees.

The role of N availability on vine-tree competition is further supported by the positive relationship between the annual average concentration of N in mature leaves and tree growth, particularly evident when vine competition was present (Fig. 6; Table 5). Contrary to gap fraction, leaf N tended to be positively related to tree growth in all competition treatments, although the degree of correlation and statistical significance was much greater in some treatments than in others.

Among other factors, the relative importance of competition for below- and aboveground resources seems to depend on the species involved, on their habitat, and on the timing and duration of the interaction. Our results are particularly relevant to high-light environments such as early successional forests and forest edges, where vines are commonly abundant (Lutz, 1943; Gysel, 1951; Boring, Monk, and Swank, 1981; Putz, 1984). *Lonicera japonica* is a very aggressive and effective competitor in a wide variety of habitats in the eastern United States. It can form extensive low-growing colonies on disturbed, open sites, arresting the growth of tree saplings (Slezak, 1976). This study suggests that belowground competition for nitrogen in environments where *L. japonica* is abundant can be an important factor determining the outcome of competition between the vine and tree saplings, like *L. styraciflua*. The importance of nitrogen availability on competition and community structure has been demonstrated for different plant and vegetation types (Evans, 1960; Berendse and Aerts, 1984; Whigham, 1984a; Warren, Skroch, and Hinesley, 1987; Tilman, 1989; Wilson, 1989; Aerts et al., 1990; Gurevitch et al., 1990; Van Auken and Bush, 1990).

Grime (1979) pointed out that light competition can be strongly influenced by competition for soil resources. This study further indicates that, besides suppressing tree growth, root competition for nitrogen plays a very important role in determining whether or not trees will be outgrown and severely shaded by vines.

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