

## Effects of scale insect herbivory and shading on net gas exchange and growth of a subtropical tree species (*Guaiacum sanctum* L.)

B. Schaffer and L.J. Mason

University of Florida, IFAS, Tropical Research and Education Center, 18905 S.W. 280 Street, Homestead, FL 33031, USA

Received January 23, 1990/Accepted in revised form May 31, 1990

**Summary.** The scale insect, *Toumeyella* sp., feeds exclusively on the subtropical hammock tree lignum vitae (*Guaiacum sanctum* L.). The combined effects of scale herbivory and shading on leaf gas exchange characteristics and growth of lignum vitae trees were studied using a factorial design. Trees grown in full sun or in 75% shade were manually infested with scale or left noninfested. Beginning 4 weeks after infestation, net CO<sub>2</sub> assimilation, stomatal conductance, transpiration, internal partial pressure of CO<sub>2</sub>, and water-use efficiency were determined on single-leaves at 4-week intervals for trees in each treatment. At the end of the experiment, net CO<sub>2</sub> assimilation was determined for whole plants. Total leaf area, leaf, stem, and root dry weights, and leaf chlorophyll and nitrogen concentrations were also determined. Scale infested trees generally had lower net CO<sub>2</sub> assimilation, stomatal conductance, and transpiration rates as well as less leaf area, and root, stem, and leaf dry weights than noninfested trees. Twenty four weeks after the shade treatment was imposed, sun-grown trees had approximately twice the leaf area of shade-grown trees. Shade-grown trees compensated for the reduced leaf area by increasing their photosynthetic efficiency. This resulted in no difference in light saturated net CO<sub>2</sub> assimilation on a whole plant basis between sun-grown and shade-grown trees. Chlorophyll and nitrogen concentrations per unit leaf area were greater in leaves of shade-grown trees than in leaves of sun-grown trees. Shading and herbivory by *Toumeyella* sp. each resulted in decreased growth of *Guaiacum sanctum*. Scale insect herbivory did not result in greater detrimental effects on leaf gas exchange characteristics for shade-grown than for sun-grown trees. Herbivory by *Toumeyella* resulted in a greater decrease in tree growth for sun-grown than for shade-grown trees.

**Key words:** *Toumeyella* sp. – Insect-plant interaction – Photosynthesis – Chlorophyll – Nitrogen

der saturating light intensities (Bazzaz and Carlson 1982; Bjorkman and Holmgren 1963; Chabot and Chabot 1977; Jurick et al. 1979; Nobel 1976; Schaffer and Gaye 1989; Syvertsen 1984). However, light saturated net CO<sub>2</sub> assimilation of certain tropical species is greater for shade-grown than for sun-grown plants (Friend 1984; Kurihara 1979; Schaffer and O'Hair 1987).

Insect herbivory has been shown to reduce leaf gas exchange of several plant species (Andrews and LaPre 1979; Sances et al. 1979; Sances et al. 1982; Wood et al. 1985; Youngman et al. 1986). Plant damage due to herbivory by insects can vary across light intensity gradients (Collinge and Louda 1988). For example, some insect herbivores are more damaging to plants growing in the sun (Williams 1983; Louda and Rodman 1983; Lincoln and Mooney 1984; Louda et al. 1987a, b), whereas others are more damaging to shade-grown plants (Lincoln and Langenheim 1979; Rausher 1979). Most research on the interactions between insect herbivory and shading has focused on the effects of environmental conditions or plant quality on herbivore activity (Lincoln and Langenheim 1979; Lincoln and Mooney 1984; Louda and Rodman 1983; Louda et al. 1987a, b; Williams 1983) rather than the effects of the combined stresses on the host plant. The removal of carbohydrates by phloem feeding insects such as scale (Risebrow and Dixon 1987) combined with the reduced production of photoassimilates in the shade may result in synergistic or additive reductions in plant growth. However, plants may be able to compensate for these stresses by an increase in photosynthetic efficiency. Lignum vitae trees (*Guaiacum sanctum* L.), infested with *Toumeyella* sp., an undescribed species of scale insect which feeds exclusively on this tree species, provide an opportunity to study the interaction between herbivory by a phloem feeding insect and shading on photosynthesis and growth of a tropical hardwood species.

*Guaiacum sanctum* is indigenous to the Caribbean area including Lignumvitae Key State Botanical Site, which is one of the few remaining habitats and the only protected site for the tree in the United States. During the past 20 years, many remaining lignum vitae trees on Lignumvitae Key have exhibited severe defoliation and several of these have subsequently died. The possibility exists that this native population will eventually be-

Sun-grown leaves of several plant species exhibit greater net CO<sub>2</sub> assimilation rates than shade-grown leaves un-

come extinct. The loss of lignum vitae trees on Lignumvitae Key may be due to infestation by *Toumeyella* sp. and/or the lack of sufficient light for maximum photosynthesis. Large populations of *Toumeyella* sp. have been observed on declining trees (Baranowski et al., unpubl.). In addition, lignum vitae trees were once continuously exposed to full sun due to the removal of overstorey vegetation by tropical storms and hurricanes which occurred every few years. These trees are now shaded by dense overstories because of the lack of hurricanes over the past 20 years. Under shaded conditions, the rate of photosynthesis and subsequent production of photoassimilates may be too low to replenish carbohydrates removed by *Toumeyella* sp. In addition, shading may have a direct effect on the insect, resulting in changes in their feeding efficiency, growth, or reproductive rates (Collinge and Louda 1988; Louda et al. 1987a). Therefore, tree mortality may be due to insect herbivory, shading or a combination of both factors.

The objective of this study was to determine the combined effects of shading and herbivory from *Toumeyella* sp. on net gas exchange characteristics and growth of lignum vitae trees.

## Materials and methods

Two-year old lignum vitae trees in a well fertilized potting soil were grown in an air-conditioned glasshouse. Trees of uniform height (ave. height from the base of the trunk to the top of the canopy was 110 cm) and with no observable differences in canopy densities were randomly placed in either full sun [maximum photosynthetic photon flux (PPF) =  $1600 \mu\text{mol m}^{-2} \text{s}^{-1}$ , as measured with a LiCor 190SA quantum sensor] or within individual enclosures covered with 75% shade cloth (maximum PPF =  $400 \mu\text{mol m}^{-2} \text{s}^{-1}$ ). Day and night air temperatures in the glasshouse were maintained between 25–30°C. The degree of shading corresponded to the average shading above the canopy of an understory tree on Lignumvitae Key as determined between 1000 and 1200 h with a LiCor Li-1000/191SA data logger/line quantum sensor (LiCor, Inc., Lincoln, Nebraska) placed perpendicular to incident radiation. One-half of the trees growing under each light level in the glasshouse were initially infested with *Toumeyella* sp. collected from Lignumvitae Key. Scale populations were allowed to become established and 4 weeks after infestation, populations were reduced from 4 or more mature scale per 5 cm of branch to 1 mature female scale per 5 cm of branch. Populations were maintained at this level by monthly removal of all scales exceeding this number. Thus, the treatments were: 1) full sun, no scale; 2) full sun, scale; 3) shade, no scale; 4) shade, scale. Each treatment consisted of 5 single-plant replicates in a completely randomized design.

Beginning 4 weeks after scale infestation, and at 4-week intervals throughout the experiment, net CO<sub>2</sub> assimilation, stomatal conductance of CO<sub>2</sub>, transpiration, internal partial pressure of CO<sub>2</sub>, and water-use efficiency were determined on single, fully-expanded leaves in an open gas exchange system in the laboratory as described by Ploetz and Schaffer (1989). To select leaves of the same age for gas exchange determinations, newly emerging leaves were tagged at the same time for each treatment and gas exchange was determined for these leaves when they were fully expanded. Leaves were sealed in a modified Plexiglass chamber (Syvertsen and Smith 1983). Scale insects were not found on leaf laminae at any time during the study and thus did not physically block light interception or gas exchange during determinations. The flow rate of air (containing 340 ppm CO<sub>2</sub>) through the chamber was 4 liters min<sup>-1</sup>, PPF in the chamber was maintained at 800  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , temperature was  $32 \pm 3^\circ \text{C}$ , and relative humidity was 50%.

$\text{m}^{-2} \text{s}^{-1}$ , temperature was  $32 \pm 3^\circ \text{C}$ , and relative humidity was 50%.

Light response curves of net CO<sub>2</sub> assimilation were determined at 14 different PPFs by placing shade cloths of four different mesh sizes between the lights and the leaf chamber. Four single-plant replications for each treatment were used in a randomized complete block design to calculate response curves from nonlinear regression analysis, plotting the predicted values for net CO<sub>2</sub> assimilation at each PPF level. Leaves were allowed to equilibrate for 20 min at each light level prior to determinations. Treatments were replicated over days with one replication per treatment per day.

Twenty four weeks after initial leaf gas exchange determinations, net CO<sub>2</sub> assimilation was determined for whole plants by placing the entire tree in a 80 × 80 × 1312 cm Plexiglass chamber. Two additional 500-watt reflector-flood lamps were positioned on the side of the chamber and a fan was positioned between the lights and the chamber to reduce heat build-up. Flow rate through the chamber was maintained at 20 L min<sup>-1</sup>. Pots were sealed in polyethylene bags to prevent root respiration in the chamber from interfering with net gas exchange determinations of leaves.

After net CO<sub>2</sub> assimilation was determined for whole-trees, trees were harvested, and total leaf area was determined. Plant tissues were then dried at 70°C, and leaf, stem, and root dry weights as well as leaf chlorophyll and nitrogen concentrations were determined. Chlorophyll concentration was determined as described by Marini and Marini (1983). For chlorophyll determinations, eight 0.32-cm<sup>2</sup> leaf discs from each leaf were placed in 10 ml of 80% methanol and held in darkness at room temperature for 48 h. Leaf chlorophyll concentration was calculated from absorption values obtained at 642 and 664 nm with a Bausch and Lomb Spectronic-21 spectrophotometer. Leaf nitrogen content was determined by the micro Kjeldahl technique (Bremner and Mulvaney 1982).

## Results

Light response curves for net CO<sub>2</sub> assimilation of single leaves were defined by the equation  $y = a(1 - e^{-bx})$ , where  $a$  and  $b$  are the regression coefficients (Fig. 1). There were no differences in the light compensation points (intercepts) or quantum yields (linear slopes) of leaves of trees grown in the sun and trees grown in 75% shade (standard  $t$ -test,  $P > 0.05$ ). The light saturation point (asymptotic region) for leaves of both sun-grown and shade-

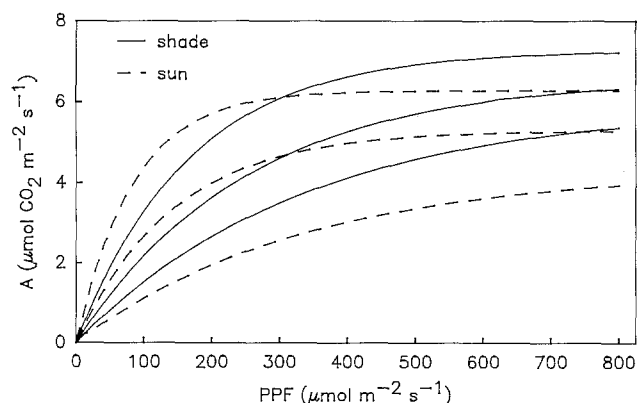


Fig. 1. Light response [photosynthetic photon flux (PPF)] curves for net CO<sub>2</sub> assimilation (A) of lignum vitae leaves developed in the sun and in 75% shade. The light response for shade-grown trees is represented by the equation:  $y = 6.6(1 - e^{-0.004x})$ ,  $r^2 = 0.93$  and the equation for sun-grown trees is  $y = 5.3(1 - e^{-0.007x})$ ,  $r^2 = 0.65$ . Center lines represent predicted mean values, upper and lower lines represent upper and lower 95% confidence limits

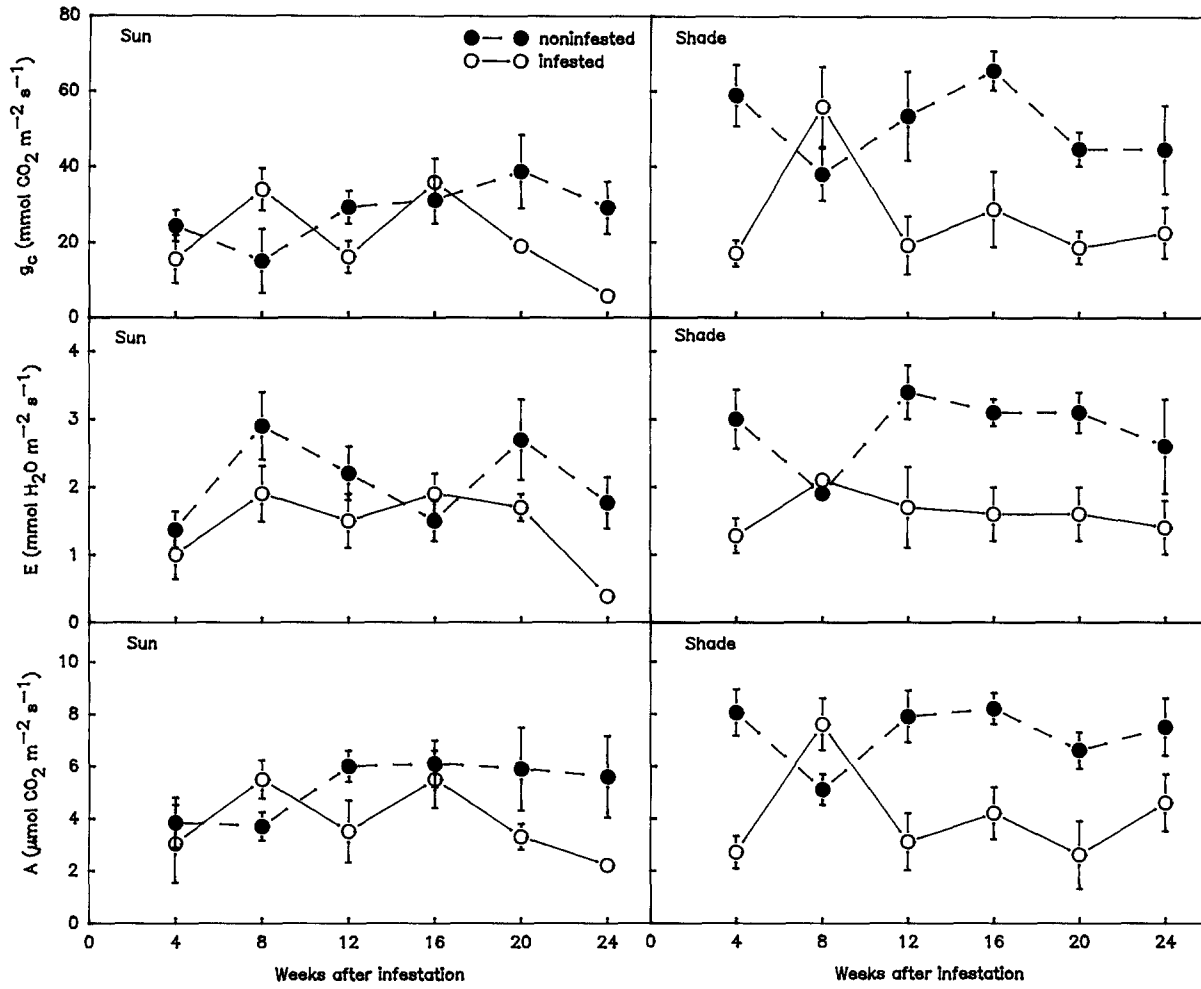


Fig. 2. Net CO<sub>2</sub> assimilation (A), transpiration (E), and stomatal conductance ( $g_c$ ) of scale-infested and noninfested lignum vitae leaves developed in sun and in 75% shade. Symbols represent means  $\pm 1$  SE,  $n = 5$

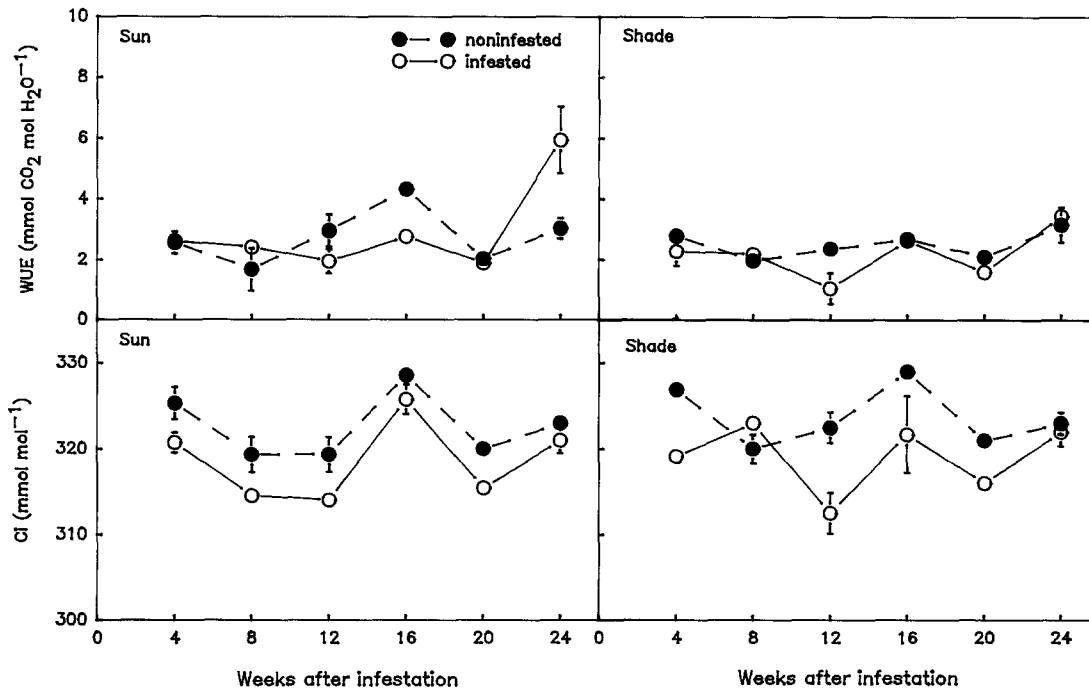


Fig. 3. Water-use efficiency (WUE) and internal partial pressure of CO<sub>2</sub> (C<sub>i</sub>) of scale-infested and noninfested lignum vitae leaves developed in sun and in 75% shade. Symbols represent means  $\pm 1$  SE,  $n = 5$

**Table 1.** Total leaf chlorophyll and nitrogen concentrations, net CO<sub>2</sub> assimilation on a whole plant basis, and total leaf area for lignum vitae trees grown in sun and 75% shade, and trees infested or noninfested with scale insects

Treatment*	Chlorophyll ( $\mu\text{g cm}^{-2}$ )	Nitrogen (% dry weight)	Net CO <sub>2</sub> Assimilation (A) ( $\mu\text{mol plant}^{-1} \text{s}^{-1}$ )	Leaf Area ( $\text{cm}^2$ )
Sun	24.1	1.2	0.19	865.5
Shade	29.9	1.6	0.21	460.4
Significance**	0.05	0.01	ns	0.10
Infested	25.7	1.4	0.07	640.4
Noninfested	28.3	1.5	0.25	2271.4
Significance**	ns	ns	0.01	0.01

\* There were no significant interactions between shade and scale according to an analysis of variance ( $P > 0.05$ ). Therefore scale treatments were pooled for testing shading effects and shading treatments were pooled for testing scale effects

\*\* Significance levels determined by a standard *t*-test

grown trees was 400–500  $\mu\text{mol m}^{-2} \text{s}^{-1}$ , though net CO<sub>2</sub> assimilation of shade grown leaves at this PPF tended to be higher (Fig. 1).

There was a significant interaction between scale infestation and shading with respect to leaf gas exchange characteristics as tested by an analysis of variance ( $P < 0.05$ ). Therefore, scale effects were analyzed independently within each shading level. Four weeks after trees were infested, there were no differences in net CO<sub>2</sub> assimilation, transpiration, and stomatal conductance between leaves of infested and noninfested sun-grown trees (Fig. 2). At that time, noninfested shade-grown trees had greater rates of net CO<sub>2</sub> assimilation, transpiration, and stomatal conductance than infested shade-grown trees (Fig. 2). After 8 weeks, light saturated net CO<sub>2</sub> assimilation, stomatal conductance, and transpiration of leaves of noninfested, shade-grown trees were always greater than that of infested, shade-grown trees.

Internal partial pressure of CO<sub>2</sub> was generally greater for noninfested than infested trees with the exception of week 24 for sun-grown trees and weeks 8 and 24 for shade-grown trees (Fig. 3). Water-use efficiency, calculated as net CO<sub>2</sub> assimilation/transpiration, generally did not differ between noninfested and infested treatments for both sun-grown and shade-grown trees. However, 24 weeks after scale infestation, infested sun-grown trees had a significantly greater water-use efficiency than noninfested sun-grown trees (Fig. 3).

At the end of the experiment, leaf chlorophyll concentration per unit leaf area and nitrogen concentration were greater for shade-grown trees than sun-grown trees (Table 1). There were no significant differences in chlorophyll and nitrogen concentrations between scale infested and noninfested plants (Table 1).

Sun-grown trees had almost twice the leaf area as shade-grown trees at the end of the experiment (Table 1). Total leaf area was significantly greater for noninfested trees than infested trees. This was primarily due to defoliation of the infested trees since few newly emerging leaves were observed for plants in any treatment during the course of this study. Net CO<sub>2</sub> assimilation, on a whole-plant basis, was greater for noninfested trees than infested trees (Table 1). There was no significant diffe-

rence in whole-plant net CO<sub>2</sub> assimilation between sun-grown and shade-grown trees.

There was a significant interaction between scale infestation and shading for leaf, stem, root, and plant dry weights according to an analysis of variance ( $P < 0.05$ ). Therefore, differences in dry weights between scale treatments were determined independently within each shade treatment and differences within each shade treatment were determined independently within each scale treatment. Scale infestation resulted in a significant biomass reduction of all tissues measured for both sun-grown and shade-grown trees. Dry weights of each tissue were greater for noninfested, sun-grown trees than noninfested, shade-grown trees (Table 2). For scale-infested trees, there was no significant difference in tissue biomasses between trees grown in the sun or in the shade.

**Table 2.** Effect of scale infestation and shading on leaf, stem, root, and plant dry weight of lignum vitae trees

Scale	Sun	Shade	Significance*
	Leaf dry weight (g)		
Noninfested	35.4	19.1	0.05
Infested	9.9	5.2	ns
Significance <sup>1</sup>	0.01	0.01	
	Stem dry weight (g)		
Noninfested	121.7	68.2	0.01
Infested	46.1	47.8	ns
Significance	0.01	0.01	
	Root dry weight (g)		
Noninfested	65.3	33.0	0.01
Infested	18.6	25.5	ns
Significance	0.01	0.01	
	Plant dry weight (g)		
Noninfested	234.8	120.4	0.01
Infested	74.6	82.8	ns
Significance	0.01	0.05	

\* Significance levels were determined by a standard *t*-test

## Discussion

Herbivory by *Toumeyella* sp. generally caused a reduction in net CO<sub>2</sub> assimilation, transpiration and stomatal conductance for leaves of lignum vitae trees, with the exception of 4 weeks after the initial scale population was reduced (8 weeks after the initial infestation). At that time, infested trees had a greater photosynthetic rate than noninfested trees, an apparent over-compensation for the large reduction of the scale population. In general, our results were similar to those of others, who observed reduced net CO<sub>2</sub> assimilation, on a leaf area basis, due to herbivory (Andrews and LaPre 1979; Sances et al. 1979; Sances et al. 1982; Wood et al. 1985; Youngman 1986). From the beginning of the experiment to 20 weeks after infestation, reductions of net CO<sub>2</sub> assimilation on a leaf area basis due to scale insect herbivory were generally greater for shade-grown trees than sun-grown trees. Insect population levels in this study were maintained at constant levels per cm length of branch. Therefore, by week 20, constant feeding pressure by *Toumeyella* sp. resulted in lower leaf gas exchange for infested sun-grown trees as well. There were concomitant reductions in stomatal conductance, internal partial pressure of CO<sub>2</sub>, and net CO<sub>2</sub> assimilation on a leaf area basis due to scale infestation. Thus, reductions in net CO<sub>2</sub> assimilation due to scale infestation were presumably the result of decreased stomatal conductance and not a direct effect on the photosynthetic apparatus.

Collinge and Louda (1988) observed that herbivory by leaf miners was greater on shaded than sun-exposed cruciferous plants. They related this to an increase in insect feeding efficiency and growth rate as a result of increased nitrogen and amino acid concentration in shade-grown plants. Although we did not monitor the feeding efficiency or growth rate of *Toumeyella* sp., shade-grown lignum vitae trees had a greater total leaf nitrogen concentration than sun-grown trees. Greater nitrogen concentration for leaves of shade-grown trees than sun-grown trees has also been observed for other plant species (Schaffer and Gaye 1989; Syvertsen and Smith 1984). Since *Toumeyella* sp. are phloem-feeders, determining N concentration in the phloem would provide a better indication of the possible influence of plant N on insect feeding efficiency. However, fecundity of some phloem-feeding insects has been positively correlated with plant N (Risebrow and Dixon 1987). Therefore, an increase in leaf N resulting from shading may result in larger scale populations on shaded plants.

The reduction in total leaf area that was observed for lignum vitae trees grown in the shade has also been observed by other workers (Baranowski et al., unpubl.). Young lignum vitae trees appear to be shade-tolerant since the reduced leaf area of trees grown in the shade was compensated for by an increased net CO<sub>2</sub> assimilation rate of the leaves. Therefore, on a whole plant basis, light saturated net CO<sub>2</sub> assimilation was the same for shaded and nonshaded trees. The lower net CO<sub>2</sub> assimilation rates of sun leaves may be attributed to photoinhibition of this shade-tolerant species at high PPF levels (Bjorkman and Holmgren 1963; Bazzaz and Carlson

1982). Increased net CO<sub>2</sub> assimilation of shade-grown plants may also be explained by an increase in chlorophyll concentration which is often found in leaves of plants grown in the shade (Holmgren 1968; Schaffer and O'Hair 1987; Syvertsen and Smith 1984). Greater chlorophyll concentration of leaves of shade-grown lignum vitae trees was observed in the present study.

Water-use efficiency was generally similar for all treatments since reductions in net CO<sub>2</sub> assimilation were concomitant with reductions in transpiration. At the end of the experiment, water-use efficiency was greater for infested sun-grown plants than for any other treatment. At that time, reductions in transpiration and stomatal conductance for infested sun-grown plants were greater than reductions in net CO<sub>2</sub> assimilation. Thus, conductance was more limiting to water-vapor exchange than CO<sub>2</sub> exchange.

Over the course of this experiment, noninfested, shaded trees assimilated less carbon than noninfested, sun-grown trees. This was reflected in the reduced biomass accumulation for the shade-grown trees. Although on a whole-plant basis shade-grown trees had the same net CO<sub>2</sub> assimilation rates under saturating light conditions as sun-grown trees, the shaded trees were below the light saturation point during much of the experimental period. Figure 4 shows a typical diurnal pattern of PPF in the sun and shade in the glasshouse during the experimental period. For several hours during the day, the shaded trees received less than 400 μmol m<sup>-2</sup> s<sup>-1</sup> of photons, which is the light saturation point for lignum vitae photosynthesis (Fig. 1). Sun-grown trees received saturating light for photosynthesis for several more hours per day than the shaded trees (Fig. 4). Therefore, over the course of a day, sun-grown trees were able to assimilate more CO<sub>2</sub>. The removal of carbohydrates by the constant scale population level maintained in this study resulted in drastic biomass reductions for both shaded and sun-grown plants. In fact, biomass reductions due to scale infestation were greater for sun-grown plants than shade-grown plants. Since lignum vitae is apparently shade-tolerant and scale populations were maintained at a constant level, there were no synergistic or additive stress

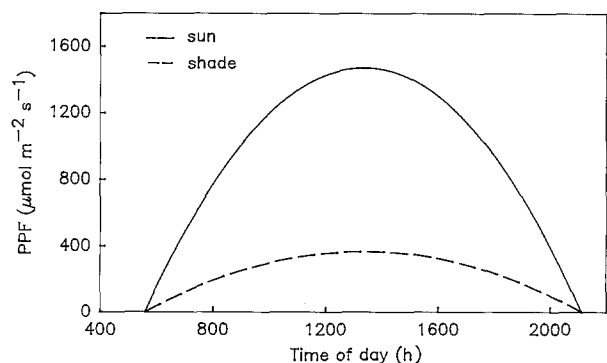


Fig. 4. Diurnal pattern of photosynthetic photon flux (PPF) in full sun and 75% shade within the greenhouse in which lignum vitae trees were grown. Curves were determined from actual data by 2nd order polynomial regression, for sun:  $y = -2890 + 6.5x - 0.0024x^2$ ,  $r^2 = 0.96$ , for shade:  $y = -722 + 1.6x + 0.0061x^2$ ,  $r^2 = 0.96$

effects on the host-plant when herbivory and shading were combined. However, in nature, herbivore activity and feeding preference can be influenced by environmentally induced physiological changes in the host (Collinge and Louda 1988). Considerable differences in natural herbivore population levels and subsequent feeding damage may result between sun and shade-grown trees. Thus, the improved tree vigor which was observed after overstory vegetation on Lignumvitae Key was mechanically removed from infested trees (Baranowski et al., unpubl.) may have been due to differential patterns of herbivory and not the combined effect of both factors on tree physiology.

*Acknowledgements.* We thank C.A. Sanchez for the nitrogen analysis, R.M. Baranowski, J.P. Syvertsen, T. Eisner, P.C. Andersen, R.F. Denno, S.F. Oberbauer, and D.P. Pashley for suggestions and critical review of the manuscript, and J. Parks for assistance with scale collections at Lignumvitae Key. Florida Agricultural Experiment Station Journal Series No. R-00230.

## References

- Andrews KL, LaPre LF (1979) Effects of pacific spider mite on physiological processes of almond foliage. *J Econ Entomol* 72:651–654
- Bazzaz FA, Carlson RW (1982) Photosynthetic acclimation to variability in the light environment of early and late successional plants. *Oecologia* 54:313–316
- Bjorkman O, Holmgren P (1963) Adaptability of the photosynthetic apparatus to light in ecotypes from exposed and shaded habitats. *Physiol Plant* 16:889–914
- Bremner JM, Mulvaney CS (1982) Nitrogen – total. In: AL Page (ed). *Methods of soil analysis. Part II. Agronomy* 9:595–624
- Chabot BF, Chabot JF (1977) Effects of light and temperature on leaf anatomy and photosynthesis in *Fragaria vesca*. *Oecologia* 26:363–377
- Collinge SK, Louda SM (1988) Herbivory by leaf miners in response to experimental shading of a native crucifer. *Oecologia* 75:599–666
- Friend DJC (1984) Shade adaptation of photosynthesis in *Coffea arabica*. *Photosynthesis Res.* 5:325–334
- Holmgren P (1968) Leaf factors affecting light-saturated photosynthesis in ecotypes of *Salidago virgavrea* from exposed and shaded habitats. *Physiol Plant* 21:676–698
- Jurick TW, Chabot JF, Chabot BF (1979) Ontogeny of Photosynthetic performance in *Fragaria virginiana* under changing light regimes. *Plant Physiol* 63:542–547
- Kurihara H (1979) Trends and problems of Konjak (*Amorphophallus konjak*) cultivation in Japan. *Japan Agr Q* 13:174–179
- Lincoln DE, Langenheim JH (1979) Variation of *Satureja douglasii* monoterpenoids in relation to light intensity and herbivory. *Biochem Syst Ecol* 7:289–298
- Lincoln DE, Mooney HA (1984) Herbivory on *Diplacus aurantiacus* shrubs in sun and shade. *Oecologia* 64:173–176
- Louda SM (1988) Insect Pest and Plant Stress as Considerations for Revegetation of Disturbed Ecosystems. CRC Press, Boca Raton, FL
- Louda SM, Rodman JE (1983) Ecological patterns in the glucosinolate content of a native mustard, *Cardamine cordifolia*, in the Rocky Mountains. *J Chem Ecol* 9:397–421
- Louda SM, Dixon PM, Huntly NJ (1987a) Herbivory in sun versus shade at a natural meadow-woodland ecotone in the Rocky Mountains. *Vegetatio* 72:141–149
- Louda SM, Huntly NJ, Dixon PM (1987b) Insect herbivory in response to experimentally-induced *in situ* plant stress: sun versus shade. *Acta Oecologia, Oecologia Generalis* 8:357–363
- Marini RP, Marini MC (1983) Seasonal changes in specific leaf weight, net photosynthesis, and chlorophyll content of peach leaves as affected by light penetration and canopy position. *J Am Soc Hort Sci* 108:600–604
- Nobel PS (1976) Photosynthetic rates of sun versus shade leaves of *Hyptis emoryii* Torr. *Plant Physiol* 58:218–223
- Ploetz RC, Schaffer B (1989) Effects of flooding and phytophthora root rot on net gas exchange and growth of avocado. *Phytopathology* 79:204–208
- Rausher MD (1979) Larval habitat suitability and oviposition preference in three related butterflies. *Ecology* 60:503–511
- Risebrow A, Dixon AFG (1987) Nutritional ecology of phloem-feeding insects in: Slansky F, Rodriguez JG (eds) *Nutritional ecology of insects, mites, spiders, and related invertebrates*. John Wiley and Sons, New York, pp 422–448
- Sances FV, Toscano NC, Hoffmann MP, LaPre LF, Johnson MW, Bailey JB (1982) Physiological responses of avocado leaves to avocado brown mite feeding injury. *Environ Entomol* 11:516–518
- Sances FV, Wyman JA, Ting IP (1979) Physiological responses to spider mite infestation on strawberries. *Environ Entomol* 8:711–714
- Schaffer B, Gaye GO (1989) Gas exchange, chlorophyll and nitrogen content of mango leaves as influenced by light environment. *HortScience* 24:507–509
- Schaffer B, O'Hair SK (1987) Net CO<sub>2</sub> assimilation of taro and cocoyam as affected by shading and leaf age. *Photosynthesis Res* 11:245–251
- Syvertsen JP (1984) Light acclimatization in citrus leaves: II. CO<sub>2</sub> assimilation and light, water, and nitrogen use efficiency. *J Am Soc Hort Sci* 109:812–817
- Syvertsen JP, Smith ML (1983) An inexpensive leaf chamber for measuring net gas exchange. *HortScience* 19:556–557
- Syvertsen JP, Smith ML (1984) Light acclimatization in citrus leaves: I. Changes in physical characteristics, chlorophyll, and nitrogen content. *J Am Soc Hort Sci* 109:807–812
- Williams KS (1983) The coevolution of *Euphydryas chalcedona* butterflies and their larval host plants. III. Oviposition behavior and host plant quality. *Oecologia* 56:336–340
- Wood BW, Tedders WL, Thompson JM (1985) Feeding influence of three pecan aphid species on carbon exchange and phloem integrity of seedling pecan foliage. *J Am Soc Hort Sci* 110:393–397
- Youngman RR, Jones VP, Welter C, Barnes MM (1986) Comparison of feeding damage caused by four tetrachynid mite species on gas-exchange rates of almond leaves. *Environ Entomol* 15:190–193