

GROWTH AND REPRODUCTION OF THE INVASIVE *LIGUSTRUM SINENSE* AND NATIVE *FORESTIERA LIGUSTRINA* (OLEACEAE): IMPLICATIONS FOR THE INVASION AND PERSISTENCE OF A NONNATIVE SHRUB

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Ligustrum sinense (Oleaceae) is an invasive shrub in the southeastern United States that was introduced from China. In middle Tennessee, the species grows with *Forestiera ligustrina* (Oleaceae), a shrub native to the southeastern United States, in the redcedar and/or hardwood forests surrounding cedar (limestone) glades. Here we compare the growth and reproduction of the two species and identify attributes that might influence the invasiveness and persistence of *L. sinense*. Plants of both species were sampled along the woodland edges of cedar glades and in the (primarily) redcedar forest at Stones River National Battlefield, Rutherford County, Tennessee, between March 2000 and February 2001. MANOVAs ($P \leq 0.05$) indicated significant differences between species and habitats for several of the 23 traits measured in the study. Regardless of the habitat, *L. sinense* had a more treelike growth form—higher leaf area ratio (leafiness), leaf mass ratio (investment in leaf biomass), stem elongation rate, and number of fruits per ramet—and a lower percentage of insect-damaged leaves and leaf abscission rate than *F. ligustrina*. Height and leaf areas of *L. sinense* plants growing in the woods were greater than those of *L. sinense* plants growing along the glade and greater than those of *F. ligustrina* plants growing in both habitats. Branch architecture did not differ appreciably between the species. *Ligustrum sinense* appears to possess a competitive advantage over *F. ligustrina* because of its greater ability to spatially and temporally capture light, a phenomenon that may lead to higher photosynthetic capacity and resource-use efficiency, and because of the higher fruit production we observed.

Keywords: cedar glades, conservation biology, invasive plants, *Forestiera ligustrina*, *Ligustrum sinense*, Oleaceae.

Introduction

The threat posed by exotic species to global biodiversity is grave (Pimm et al. 1995; Wilcove et al. 1998; Higgins et al. 1999). Deliberately or accidentally introduced plant species impact biodiversity through competition, by reducing resources available to native species, and through ecosystem effects, by altering fundamental properties such as geomorphological processes, nutrient cycles, and fire regimes (Gordon 1998; Dukes and Mooney 1999; Manchester and Bullock 2000). Characteristics of the introduced species and of the ecosystem are critical to both the success and impact of the invader (Lodge 1993). Studies that compare invasive species with noninvasive species (*sensu* Richardson et al. 2000) offer a powerful test of characteristics that differentiate groups of species and directly test what makes a species successful. Moreover, identification of these traits allows recommendations to be made on how to evaluate the invasive potential of new introductions (Kolar and Lodge 2001).

Invasive plants have been shown to be unevenly distributed phylogenetically, with particular species, genera, or families having a history of invasion (Crawley et al. 1996; Kolar and

Lodge 2001). The woody plant genus *Ligustrum* represents a good example of a group of plants in which several species have become naturalized on more than one continent. *Ligustrum* taxa grow as shrubs or small trees that have been extensively cultivated for ornamental purposes (Dirr 1998). Approximately one to eight species in this genus have established to varying degrees in Argentina, Australia, New Zealand, North America, and on several Pacific Islands (Duncan and Duncan 1988; Gleason and Cronquist 1991; Dascanio et al. 1994; Swarbrick et al. 1999; Institute of Pacific Islands Forestry 2000). Where these species have been introduced, they have a history of forming dense, impenetrable thickets in both edge and woodland habitats (Lorence and Sussman 1986, 1988; Dascanio et al. 1994; Langeland and Burks 1998). Moreover, *Ligustrum* taxa often marginalize native shrubs or small trees and have been recorded to be particular threats to rare species (Burrows and Kohen 1983; Lorence and Sussman 1988; Langeland and Burks 1998; Swarbrick et al. 1999).

One way to understand the traits that enable exotic species to invade and persist outside their native range and their potential negative impacts is to compare exotic species to native species in areas where they interact. Habitat, attributes of the species themselves (e.g., growth form), and phylogeny are criteria by which species might be compared. The advantage of comparing closely related, sympatric species of similar growth form minimizes extraneous differences resulting from evolu-

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tionary history, ecogeography, or life-form (Westoby 1999). Comparisons done at the same location and during the same period of time further reduce statistical error. Because of the sparsity of comparative studies on shrubs, and in particular on *Ligustrum* species, we have a poor understanding of the attributes that determine their invasiveness. Previous comparative studies on shrubs have been done on species of similar growth form and that are sympatric but that are phylogenetically distant relatives (Harrington et al. 1989a; Witkowski 1991; Luken et al. 1997).

The structure of woody plants has two components that might influence invasiveness and persistence: growth of biomass and the architectural arrangement of this biomass. The first component results from physiological processes for carbon, water, and nutrient uptake, and the second component is a result of branching patterns and leaf display (Givnish 1988; Küppers 1989). Plant structure, therefore, remains an essential tool for interpreting plant performance and competitive ability. Among environmental factors, light probably exerts the most influence on plant survival and growth by eliciting specific growth responses (Valladares 1999). Particular architectural features, such as the growth form of the whole plant and the size, angles, distributions, and spatial relations of its leaves and branches, are advantageous in certain habitats. Photosynthetic performance under various light conditions is also greatly influenced by the morphological traits of leaves (Corré 1983). These physiological and architectural features, however, are subject to the seasonal control of their activity affecting the positions and distributions of branches and leaves in space. Moreover, reproductive output is strongly linked to the availability of resources and to the ability of plants to access those resources for carbon gain and productivity (Percy et al. 1987) and as such would be expected to influence population dynamics.

Ligustrum sinense Lour., Chinese privet, is native to China, Laos, and Vietnam (Kiew 1978; Green 1995; Mei-chen et al. 1996). The species is naturalized and is considered a severe threat to ecosystems in the United States from Massachusetts to Missouri, south to Florida and Texas (Langeland and Burks 1998), in Australia and New Zealand (Swarbrick et al. 1999), in Argentina (Montaldo 1993), and on several Pacific Islands (Institute of Pacific Islands Forestry 2000). Like other invasive members of the genus, *L. sinense* forms thickets at both the edge and interior of woods and is known to compete with other species of shrubs (Burrows and Kohen 1983; Langeland and Burks 1998; Swarbrick et al. 1999). In the southeastern United States, *L. sinense* has successfully invaded the limestone cedar (*Juniperus virginianus*) glade/woodland complex (Quarterman 1950) of the Central Basin of Tennessee (Morris 2001). This ecosystem is a hot spot of plant endemism in the southeastern United States (Estill and Cruzan 2001) but is globally imperiled as a result, in part, of the invasion of exotic species (Noss et al. 1995). *Ligustrum sinense* co-occurs with a native shrub that is in the same tribe (Oleeae) of the plant family Oleaceae (Wallander and Albert 2000), namely, *Forestiera ligustrina* (Michx.) Poir. *Forestiera ligustrina* occurs from southern Kentucky to Florida and eastern Mississippi as well as in eastern Texas and adjacent western Louisiana (Brooks 1977). Quarterman (1950) recorded that *F. ligustrina* was either the most important shrub or one of three important ones in the thickets surrounding the open area

of glades, in 50–60-, 88-, and 103-yr-old redcedar stands, and in a redcedar–oak–hickory forest.

The goal of this study was to identify differences between *L. sinense* and *F. ligustrina* that could explain the successful invasion and persistence of *L. sinense* in the cedar glade/woodland complex of middle Tennessee. Four categories of characteristics were compared between the two species: whole shrub, branch and leaf, reproduction, and phenology. These characteristics were examined on plants growing in two light environments: sunny conditions along the wooded edges of cedar glades and shady conditions in the understory of a redcedar woodland.

Material and Methods

Study Site

Field studies were conducted at Stones River National Battlefield in Rutherford County, Tennessee (35°52'35"N, 86°25'58"W). The main area of the park consists of ca. 120 ha of redcedar and/or oak/hickory forest with many cedar (limestone) glades interspersed throughout the forest (Hogan et al. 1995). *Ligustrum sinense* and *Forestiera ligustrina* are important components of the shrub layer, primarily in the redcedar woodland. Both species grow along the edges of the cedar glades in full sun and under the redcedar canopy in full shade (Hogan et al. 1995). A transparent grid was placed over an aerial photograph of the park, and three plots each were randomly selected in the glade and woodland habitats. Each plot was ground-checked to assure the accuracy of the habitat type and that plants of both species were present.

An individual shrub was defined as a group of ramets ≤ 20 cm distant from each other. On the basis of observations of underground plant structures, we believe that this group of ramets belonged to the same genet. In every plot, we picked eight shrubs >1 m tall of each species by using random points along a transect and marked the shrubs with flagging tape. The shrubs selected were the closest ones to the transect, on one side of it along the glade edge but on alternating sides in the woodland. In the glade plots, a transect was placed at the glade/woodland interface. Since the transect encompassed the glade, the shrubs faced a variety of cardinal orientations. In woodland plots, a transect was placed in an approximately straight line, avoiding canopy gaps. Lengths of transects along the glade edges and in the woods varied from 60 to 90 m.

Mean (\pm SE) photosynthetic photon flux density (PPFD; 400–700 nm) recorded in woodland habitats was $111.6 \pm 12.9 \mu\text{mol s}^{-1} \text{m}^{-2}$, along the glade edges it was $1362.0 \pm 78.8 \mu\text{mol s}^{-1} \text{m}^{-2}$, and in the middle of glades it was $1855.2 \pm 12.9 \mu\text{mol s}^{-1} \text{m}^{-2}$. We measured PPFD by using an LI-250 quantum meter with an LI-190SA quantum sensor on August 24 and 29, 2000, both cloudless days, between 1100 and 1300 hours CDT. Light measurements were recorded at the middle and ends of each of the six transects near the top of the shrub canopies and near the center of the three glades used in the study.

During the study (March 2000–February 2001), mean daily maximum and minimum temperatures were 22.1° and 9.0°C, respectively, and monthly precipitation totaled 100.8 mm in Nashville ca. 35 km from the study site. Values for

these variables did not differ appreciably from long-term data (1961–1990) recorded in Nashville. The 30-yr normal daily maximum and minimum temperatures were 21.0° and 9.1°C, respectively, and monthly precipitation was 100.1 mm (National Climatic Data Center 2000).

Whole-Shrub Characteristics

Measurements of height, canopy width, and number and diameter of ramets were obtained from all marked shrubs in each of the six plots. Height was determined from the ground to the highest point of the canopy with a 6-m-tall measuring pole. The maximum span of the canopy, projected horizontally to the ground, was recorded as the canopy width. Number of ramets per shrub was counted, and mean ramet diameter was calculated from circumferences measured at 5 cm above the ground. Data on shrub characteristics were collected in April 2000.

Branch and Leaf Characteristics

Two glade and two woodland plots were selected randomly, and all marked shrubs in these plots were used to evaluate branch and leaf characteristics. In addition, four shrubs from each of these four plots were sampled in triplicate to examine variation among branches within a shrub. Stems and leaves were sampled on two branch sizes: (1) 10-cm unbranched most-distal segments (tips) of terminal branches and (2) first-, second-, and third-order branch groups on one ramet. First-order branches are defined as terminal branches at the edge of the canopy. Working toward the base of the shrub, the order of a branch increased each time a branch intersected the junction of two similarly ordered branches. Thus, the junction of two first-order branches defined the beginning of a second-order branch, and that of two second-order branches defined a third-order branch (Whitney 1976; Pickett and Kempf 1980; Valladares 1999). The terminal-branch segments and ramets (consisting of the first-, second-, and third-order branch groups) were chosen separately and randomly, and data were collected in September 2000.

On the terminal-branch segments, the following parameters were evaluated: leaf and branch orientations, stem and leaf dry masses, leaf area, leaf damage, leaf area ratio (LAR), specific leaf area (SLA), and leaf mass ratio (LMR). In the field, inclination angles of the terminal leaf and branch segment were measured as degrees from vertical with a protractor affixed to a plumb line. For leaf measurements, the protractor was aligned along the midvein. Occasionally the 10-cm segment of the branch was not straight, and when this occurred, the inclination angle was judged from a short (5-cm) portion at the end of the segment. Each branch was cut and separated into leaves and stems; the leaves were photocopied, and both components were dried to a constant mass at 40°C in a drying oven. Photocopies of fresh (nondried) leaves were overlaid with a transparent grid, and squares of the grid overlapping leaf surface (on one side only) were counted and converted to an area basis. The percentage of leaves damaged by insect herbivory was determined.

Leaf area (A_L) and dry masses of leaves (M_L) and of stems (M_S) were used to calculate LAR, LMR, and SLA (Causton and Venus 1981; Lambers and Dijkstra 1987; Harrington et al. 1989b; Luken et al. 1997). LAR is a morphological com-

ponent of relative growth rate that measures the leafiness of a plant,

$$\text{LAR} = \frac{A_L}{M_L + M_S}. \quad (1)$$

Differences in LAR may result from LMR, i.e., investment in leaf biomass, and/or SLA, which indicates thin leaves of relatively large area (high SLA) or thick leaves of small area (low SLA):

$$\text{LMR} = \frac{M_L}{M_L + M_S}, \quad (2)$$

$$\text{SLA} = \frac{A_L}{M_L}. \quad (3)$$

Parameters recorded on each first-, second-, and third-order branch unit were as follows: number of leaves, lengths and angles of branches, lengths of secondary internodes, and bifurcation ratio. Five randomly selected angles between the first- and second-order branches were measured with a protractor (Tolvanen 1995). The secondary internode on a first-order branch was located immediately behind the most distal (primary) one. Lengths of all secondary internodes ≥ 3 mm were determined; internodes < 3 mm long were judged to be non-elongated. The proportion of first-order branches with secondary internodes ≥ 3 mm long was based on the total number of first-order branches.

The number of branches of each order was used to calculate the bifurcation ratio (R_b); R_b quantifies the architecture of a shrub by relating the degree of branching from one order to the next (higher) order (Whitney 1976; Pickett and Kempf 1980; Valladares 1999):

$$R_b = \frac{\left(\sum_1^t N_o \right) - N_t}{\left(\sum_1^t N_o \right) - N_1}, \quad (4)$$

where N_o is the number of branches of order o , N_t is the number of branches of highest-order t , and N_1 is the number of first-order branches. In this study, the highest branching order was three. Third-order branches may be accurately used to represent the bifurcation ratio for the entire shrub (Pickett and Kempf 1980). Relatively low R_b is typical of plants growing in shade with monolayered leaf distributions (i.e., leaves arranged in one or very few layers, with little self-shading, on highly forked branches). Alternatively, high R_b indicates plants with multilayered leaf distributions (i.e., leaves loosely scattered throughout the crown on many branches originating from a single parent branch) growing in full sun (Horn 1971; Whitney 1976; Veres and Pickett 1982; Valladares 1999).

Reproductive Characteristics

Numbers of flowers and of fruit per ramet were recorded on each marked shrub in two woodland plots and in two glade plots that were selected randomly. For each shrub, one ramet

of basal diameter 0.8–1.5 cm was chosen randomly and marked. The number of flowers on *L. sinense* was counted on May 25, 2000; the number of flowers on *F. ligustrina*, on August 1, 2000. *Forestiera ligustrina* branches without flowers were rechecked on August 22, 2000, and flowers, if present, were counted. Fruits were counted on the same ramets used for flower counts when most were starting to ripen, which was October 20, 2000, for *L. sinense* and September 15, 2000, for *F. ligustrina*. Since plants of *F. ligustrina* are dioecious, the sex (male vs. female) of each marked shrub in the plots was recorded.

Phenology Characteristics

Stem elongation, leaf area expansion, and leaf abscission were monitored on all marked shrubs in one glade plot and one woodland plot, both of which were chosen at random. For each shrub, one branch with expanding leaf buds was picked at random and marked on March 22, 2000. If no buds were beginning to enlarge on March 22, the branch containing the first expanding bud on a subsequent visit was marked. The length of the most distal elongating stem on a branch was measured from the bud scale scars to the tip of the stem. The largest of the third opening pair of leaves on the same stem was used for sampling of leaf area by tracing the leaf outline onto paper. Leaf tracings were covered with a transparent grid, and squares overlapping the leaf surface (one side only) were counted and converted to an area basis. Stem length and leaf area were measured at approximately 1-, 2-, or 4-wk intervals from March 22, 2000, until June 22, 2000.

A branch with at least 80 leaves, a different branch than that used to record stem elongation and leaf area expansion, was chosen randomly on each shrub and marked on October 1, 2000. The number of leaves on the branch was counted every 2 wk from October 1, 2000, to January 15, 2001, and a final count was done on February 15, 2001.

Stem lengths, leaf areas, and leaf numbers were used to calculate relative stem elongation rate (RSER), relative leaf area expansion rate (RLER), and relative leaf abscission rate (RLAR), respectively. The traditional formula for relative growth rate, which is based on total plant dry mass (Causton and Venus 1981), was modified to incorporate lengths of stems (Meyer 1998), leaf area (Potter and Jones 1977), and numbers of leaves. Therefore, RSER measures the rate of production (elongation) of new stem growth per unit of stem already present:

$$\text{RSER} = \frac{\log_e L_2 - \log_e L_1}{t_2 - t_1}, \quad (5)$$

where L_1 is the stem length at the start of the interval, L_2 is the stem length at the end of the interval, and $t_2 - t_1$ is the time interval. RLER quantifies the capacity of each unit of leaf area to produce new area:

$$\text{RLER} = \frac{\log_e A_2 - \log_e A_1}{t_2 - t_1}, \quad (6)$$

where A_1 and A_2 are the leaf areas at times t_1 and t_2 , respectively. RSER and RLER may reflect relative differences in ef-

iciencies of photosynthetic or metabolic pathways. RLAR indicates the rate of decrease in number of leaves ($N_2 - N_1$) per unit of number of leaves already present on the plant per unit of time ($t_2 - t_1$):

$$\text{RLAR} = \frac{\log_e N_2 - \log_e N_1}{t_2 - t_1}. \quad (7)$$

Statistical Analyses

Data were examined first with a MANOVA on each category of characteristics: whole-shrub, branch and leaf, reproduction, and phenology. A MANOVA analyzes all parameters of each category simultaneously (Scheiner 1993). For each category, the MANOVA consisted of a full and a reduced model. Factors and their interactions examined in the full model for the whole-shrub and reproduction categories were species, habitat, and plot; for the branch and leaf category, the factors were species, habitat, and branch; and for the phenology category, the factors were species, habitat, and time. Interactions between the third factor of each category (i.e., plot, branch, time) and species were of particular interest since they would indicate species-specific responses with respect to these (third) factors. The reduced model for each category included species, habitat, and their interaction. *P* values associated with Wilks' λ are reported for the MANOVA results (SAS Institute 1996).

Following the overall MANOVAs for each category, univariate two-way ANOVAs examined the factors species and habitat and the interaction between these two factors for each parameter. The protected least significant difference test (PLSD, $P = 0.05$) was employed for the multiple comparisons procedure (SAS Institute 1996). Transformations corrected non-normality and/or heteroscedasticity. In only a few cases were transformations unsuccessful in normalizing data, but MANOVAs and ANOVAs are robust against minor departures from normality (Neter et al. 1990; Scheiner 1993). Sex ratios of *F. ligustrina* plants in each habitat were compared to a 1 : 1 ratio using a χ^2 goodness-of-fit test (SAS Institute 1996).

Results

Whole-Shrub Characteristics

Whole-shrub characteristics differed significantly between species and habitat (full and reduced MANOVA models: $P = 0.0001$), but the characteristics of each species responded similarly to the two habitat types (interaction, $P \geq 0.1847$; table 1). Moreover, the characteristics of each species were similar among plots within each habitat type (plot factor and interactions with plot, except habitat \times plot, $P \geq 0.2018$).

Plants of *Ligustrum sinense* in the woods grew significantly taller than those along the glade, but plants of *Forestiera ligustrina* grew to about the same height in both habitats (ANOVA: $P = 0.0168$; table 2). Canopy widths, however, did not differ between species or habitat. Ramet diameter of *L. sinense* was significantly larger than that of *F. ligustrina* in both habitats, whereas *F. ligustrina* produced significantly more ramets than *L. sinense* ($P = 0.0001$).

Table 1
F-Test Values from MANOVAs for Each Category of Characteristics

	Whole shrub ^a		Branch and leaf ^b		Reproduction ^c		Phenology ^d	
	Full model	Reduced model	Full model	Reduced model	Full model	Reduced model	Full model	Reduced model
Species	27.08***	27.09***	15.13***	7.30***	5.39**	4.17*	41.21***	14.97***
Habitat	8.82***	8.71***	20.62***	9.15***	4.19*	3.38*	0.88	0.81
Species × habitat	1.57	1.59	4.32***	2.69*	1.40	1.09	1.05	0.80
Third factor	1.04	...	1.26	...	8.14***	...	18.52***	...
	(Plot)		(Branch)		(Plot)		(Time)	
Species × third factor	1.40	...	0.78	...	8.20***	...	16.39***	...
Habitat × third factor	2.30*	...	0.77	...	0.91	...	2.04**	...
Species × habitat × third factor	0.68	...	0.70	...	2.43	...	1.30	...

Note. The full model included species, habitat, and a third factor that varied among categories and is indicated in parentheses. The reduced model included only species and habitat as factors; *F*-tests associated with Wilks' lambda are reported.

^a *df* = 4, 81 and 4, 89 for species, habitat, and their interaction in the full and reduced models, respectively, and 8, 162 for plot and its interactions with all factors.

^b *df* = 14, 23 and 14, 15 for species, habitat, and their interaction in the full and reduced models, respectively, and 28, 46 for branch and its interactions with all factors.

^c *df* = 2, 55 and 2, 59 in the full and reduced models, respectively.

^d *df* = 3, 222 and 3, 250 for species, habitat, and their interaction in the full and reduced models, respectively, and 21, 638 for time and its interactions with all factors.

* $P \leq 0.05$.

** $P \leq 0.01$.

*** $P \leq 0.001$.

Branch and Leaf Characteristics

Branch and leaf characteristics differed significantly between species and habitat (full and reduced MANOVA models: $P \leq 0.0002$), and the characteristics of each species responded differently in the two habitat types (interaction, $P \leq 0.0337$; table 1). The branch and leaf characteristics for each species were similar among branches within a shrub regardless of habitat (branch factor and interactions, $P \geq 0.2377$).

Branch orientation and bifurcation ratio did not differ between species or habitat (table 2). Lengths of first-order branches for *F. ligustrina* and second-order branches for *L. sinense* were longer in the woods than along the glade (ANOVA: $P \leq 0.0467$). However, lengths of third-order branches of each species did not differ between habitats, although third-order branches of *F. ligustrina* were slightly longer than those of *L. sinense* ($P = 0.0453$). Moreover, *L. sinense* plants had a significantly higher percentage of first-order branches with elongated secondary internodes than did *F. ligustrina* along the glade ($P = 0.0013$). Angle between first- and second-order branches was significantly narrower for plants of *L. sinense* than for those of *F. ligustrina* along the glade ($P \leq 0.0192$).

Leaf area of *L. sinense* plants in the woods was significantly greater than that of plants along the glade, whereas the leaf area of *F. ligustrina* plants remained the same between habitats (ANOVA: $P = 0.0456$; table 2). Number of leaves did not differ between species or habitat. *Forestiera ligustrina* had a significantly higher percentage of damaged leaves than *L. sinense* in both habitats ($P = 0.0006$). LAR and SLA were significantly greater for plants of both species in the woods than along the glade, but only LAR differed between the species ($P \leq 0.0158$). LMR did not vary with habitat, but LMR of *L. sinense* was significantly higher than that of *F. ligustrina*

($P = 0.0001$). Leaves on *F. ligustrina* plants growing along the glade were orientated at a significantly lower angle from vertical than leaves on *F. ligustrina* plants in the woods; they were also lower than leaves on *L. sinense* plants along the glade and in the woods ($P \leq 0.0122$).

Reproductive Characteristics

Reproductive characteristics differed significantly between species and habitat (full and reduced MANOVA models: $P \leq 0.0408$), but reproduction of each species responded similarly to the two habitat types (interaction, $P \geq 0.2556$; table 1). However, reproduction of both species was dissimilar among plots (plot factor and its interaction with species, $P = 0.0008$). Regardless of the plot differences, reproduction of each species was similar within each habitat type (interactions, $P \geq 0.0971$).

Habitat significantly influenced the number of flowers produced (ANOVA: $P = 0.0208$), but the number of flowers did not differ between the species within each habitat type (table 2). However, *L. sinense* had significantly more fruits along the glade than in the woods and more fruits than *F. ligustrina* in both habitats ($P = 0.0199$). The ratios of the number of males to females did not differ from 1 : 1 in the woods ($\chi^2 = 0.143$, $P = 0.7050$) or along the glade ($\chi^2 = 0.333$, $P = 0.5640$).

Phenology Characteristics

Phenology characteristics differed significantly between species (full and reduced MANOVA models: $P = 0.0001$) but not habitat ($P \geq 0.4517$; table 1). Moreover, phenology of each species was similar between the habitats (interaction, $P \geq 0.3703$). Significant time effects were expected because of the growth (or

Table 2

F-Test Values from Two-Way ANOVAs (Species and Habitat as Factors) and Means (SE) for Parameters Measured on *Forestiera ligustrina* and *Ligustrum sinense* in Two Habitats

	Species	Habitat	Species × habitat	<i>Forestiera ligustrina</i>		<i>Ligustrum sinense</i>	
				Glade edge	Woodland	Glade edge	Woodland
Whole-shrub characteristics (per shrub): ^a							
Height (dm)	1.92	5.93*	0.89	19.21 (1.54) ^A	21.80 (1.70) ^{AB}	19.98 (1.76) ^A	25.83 (1.89) ^B
Canopy width (dm)	1.96	0.02	0.09	20.54 (1.44)	21.62 (1.95)	19.33 (1.76)	18.74 (1.60)
Ramet diameter (cm)	54.13***	3.69	0.00	1.16 (0.08) ^A	0.99 (0.08) ^A	2.29 (0.25) ^B	1.90 (0.19) ^B
Number of ramets	54.18***	0.03	4.26*	5.12 (0.77) ^A	3.96 (0.48) ^A	1.58 (0.17) ^B	2.17 (0.26) ^B
Branch and leaf characteristics: ^b							
Bifurcation ratio ^c	3.28	0.15	1.42	7.04 (0.39)	6.56 (0.62)	5.24 (0.34)	6.19 (0.88)
Length of branches (cm): ^c							
First order	2.06	4.33*	1.64	2.46 (0.31) ^A	3.93 (0.38) ^B	3.65 (0.61) ^{AB}	4.00 (0.40) ^B
Second order	0.05	8.30**	0.87	6.38 (0.76) ^{AB}	10.01 (2.22) ^A	4.22 (0.49) ^B	11.34 (2.86) ^A
Third order	4.39*	2.12	0.19	28.88 (3.38) ^{AB}	39.69 (9.59) ^A	19.44 (2.20) ^B	25.22 (4.66) ^{AB}
Internode elongation (%) ^d	12.83**	3.89	0.47	12.75 (3.55) ^A	26.75 (4.72) ^{AB}	37.50 (7.71) ^B	44.88 (7.61) ^B
Branch orientation (degrees from vertical) ^e	0.21	2.74	2.17	95.12 (8.97)	122.88 (8.31)	112.25 (7.19)	113.88 (10.64)
Branch angle (°) ^f	8.07**	6.18*	0.00	60.35 (2.61) ^A	69.20 (2.15) ^A	49.79 (5.48) ^B	59.06 (3.42) ^{AB}
Leaf area (cm ²) ^e	0.01	3.60	4.38*	38.70 (5.64) ^{AB}	37.48 (4.36) ^{AB}	26.38 (6.97) ^B	51.28 (7.51) ^A
Number of leaves ^e	0.51	0.03	0.00	135.50 (22.24)	134.25 (6.63)	144.25 (17.02)	168.38 (45.91)
Damaged leaves (%) ^e	15.14***	0.34	0.88	52.71 (10.96) ^A	52.56 (6.84) ^A	15.84 (5.33) ^B	26.51 (7.76) ^B
Leaf area ratio (cm ² /g) ^e	6.60*	64.96***	0.80	63.10 (7.11) ^A	162.65 (9.74) ^B	101.60 (13.54) ^C	181.27 (12.87) ^B
Leaf mass ratio (g/g) ^e	20.35***	2.85	0.15	0.63 (0.05) ^A	0.68 (0.03) ^{AB}	0.77 (0.03) ^{BC}	0.84 (0.02) ^C
Specific leaf area (cm ² /g) ^e	0.02	53.64***	3.38	103.22 (11.43) ^A	241.89 (13.22) ^B	133.45 (18.05) ^A	216.44 (16.87) ^B
Leaf orientation (degrees from vertical) ^e	7.18*	7.50*	1.61	132.00 (7.12) ^A	106.75 (5.42) ^B	107.12 (6.46) ^B	97.88 (6.08) ^B
Reproductive characteristics (per ramet): ^g							
Number of flowers	2.16	5.64*	1.59	116.88 (27.94) ^{AB}	54.06 (19.48) ^B	270.38 (100.84) ^A	65.88 (36.57) ^B
Number of fruits ^h	5.72*	2.84	2.19	4.81 (2.84) ^A	2.56 (1.89) ^A	46.63 (20.47) ^B	12.44 (6.00) ^A
Phenology characteristics: ⁱ							
Relative stem elongation rate (cm cm ⁻¹ wk ⁻¹)	8.04**	0.17	0.76	0.10 (0.03) ^{AB}	0.07 (0.02) ^B	0.16 (0.03) ^A	0.17 (0.03) ^A
Relative leaf area expansion rate (cm ² cm ⁻² wk ⁻¹)	1.48	1.45	1.57	0.33 (0.06)	0.33 (0.06)	0.33 (0.04)	0.50 (0.10)
Relative leaf abscission rate (number number ⁻¹ wk ⁻¹)	23.63***	0.03	0.04	-0.26 (0.06) ^A	-0.26 (0.06) ^A	-0.05 (0.01) ^B	-0.04 (0.01) ^B

Note. Means with different capital letter superscripts are significantly different from one another within rows according to protected least significant difference tests ($P \leq 0.05$).^a All df = 1, 92.^b All df = 1, 28.^c Per first-, second-, and third-order branch unit.^d Percentage of first-order branches with secondary internodes ≥ 3 mm long.^e Per 10-cm segment of most-distal portion of terminal branch.^f Angle between first- and second-order branches.^g All df = 1, 60.^h Female *F. ligustrina* plants only included in calculation since species is dioecious.ⁱ All df = 1, 252.* $P \leq 0.05$.** $P \leq 0.01$.*** $P \leq 0.001$.

abscission) of plant parts (time factor and interactions, $P \leq 0.0040$). Phenology was similar in both habitats over time for each species (three-way interaction, $P = 0.1641$).

Stems of *L. sinense* elongated significantly faster than those of *F. ligustrina* in the woods (ANOVA: $P = 0.0050$; fig. 1, table 2). Leaves of *L. sinense* expanded at the same rate as those of *F. ligustrina* in both habitats (fig. 2). However, *F. ligustrina* leaves were deciduous over winter, with most of them abscised by November 2000, whereas *L. sinense* leaves mostly remained on the plants ($P = 0.0001$; fig. 3).

Discussion

While the canopies of *Ligustrum sinense* and *Forestiera ligustrina* occupy the same horizontal space in both the woodland understory and along the glade, the larger and less numerous ramets of *L. sinense* indicate a growth form that is less shrubby and more treelike than *F. ligustrina* (table 2). The clonal growth form, exhibited more strongly by *F. ligustrina* with its multiple small-sized ramets, constrains it to exploit the light environment in a single horizontal plane (Pickett and Kempf 1980; Nicola and Pickett 1983). However, an increase in height with shaded conditions, as demonstrated by *L. sinense* but not *F. ligustrina*, has been interpreted as a response for the capture of additional light. As competition for light increases, there are greater advantages to be reaped by investments in vertical crown expansion than by investments in horizontal crown expansion to minimize shading by neighbors (Bonser and Aarssen 1994; Lee et al. 1996; Poorter and Werger 1999; Baruch et al. 2000).

The architectural arrangement of branches and leaves is closely linked with environmental conditions, particularly with regard to light (Küppers 1989; Valladares 1999). Bifurcation ratio is a relatively crude index of branching patterns (Pickett and Kempf 1980). Not only did the bifurcation ratio fail to differ between *L. sinense* and *F. ligustrina*, but no difference was detected between habitats (table 2). Other studies have

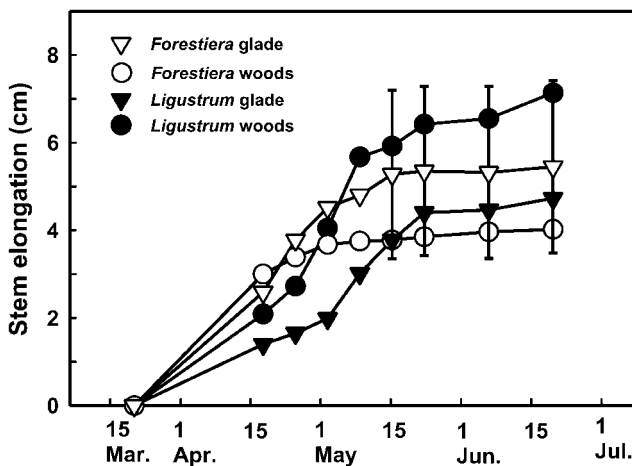


Fig. 1 Mean (\pm SE; SE shown if ≥ 1.9) stem elongation of *Forestiera ligustrina* and *Ligustrum sinense* from glade-edge and woodland habitats during spring 2000.

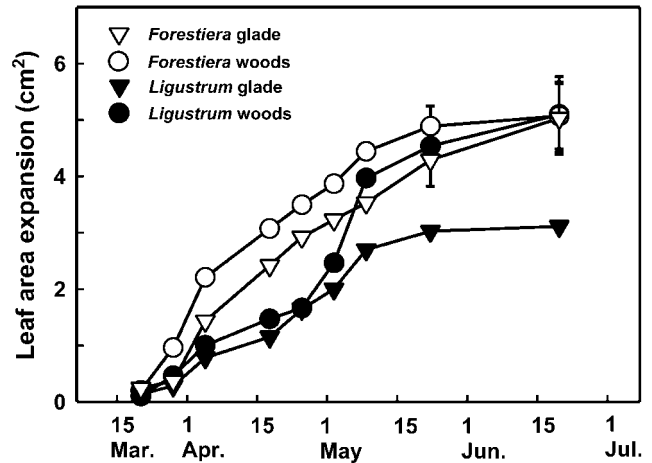


Fig. 2 Mean (\pm SE; SE shown if ≥ 0.6) leaf area expansion of *Forestiera ligustrina* and *Ligustrum sinense* from glade-edge and woodland habitats during spring 2000.

reported that bifurcation ratios may vary within a species or between species: individuals in open habitats have higher values than those in closed habitats (Whitney 1976; Steingraeber et al. 1979; Pickett and Kempf 1980; Booijh and Ramakrishnan 1982; Veres and Pickett 1982). Outstanding fine-scale structural features that differed between *L. sinense* and *F. ligustrina* were internode elongation, branch angle, and leaf orientation (table 2). Fewer internodes from first-order branches of glade-edge *F. ligustrina* elongated than did those of *L. sinense*, resulting in higher leaf overlap in the former species. However, the amount of self-shading is compensated by *F. ligustrina* having wider branch angles than *L. sinense* in the glade, reducing interference between branches. Additionally, leaves of *L. sinense* in both habitats and those of *F. ligustrina* in the woods were nearly horizontally oriented, but leaves of *F. ligustrina* along the glade were not. Horizontal display of leaves would maximize light interception, but under heat stress or excess irradiance, leaves may be at angles far from horizontal (Clearwater and Gould 1995; Smith et al. 1998). The light avoidance strategy in *F. ligustrina* may indicate heat or water stress that does not seem to affect leaf orientation in the same way for *L. sinense* along the glade.

Responses of plants to a low-light environment generally include a higher LAR and SLA and a larger leaf area (Corré 1983). These characters allow plants to increase the amount and efficiency of light capture (Walters et al. 1993; Niinemets 1998; Baruch et al. 2000). Both *L. sinense* and *F. ligustrina* had increased LAR and SLA in the woodland habitat (table 2). Although SLA was similar in magnitude for the two species, LAR was not. LAR represents the leafiness of a plant; i.e., *L. sinense* had a higher ratio of photosynthesizing to respiring material than did *F. ligustrina* (cf. Hunt 1978). Moreover, *L. sinense* had a higher allocation of biomass to leaves (LMR) than *F. ligustrina* in both habitats, and leaf area of *L. sinense* greatly increased in the woodland but that of *F. ligustrina* did not. Leaves of *L. sinense* appear to be more efficient at allocating biomass to gather light than *F. ligustrina* in both sunny and shaded conditions.

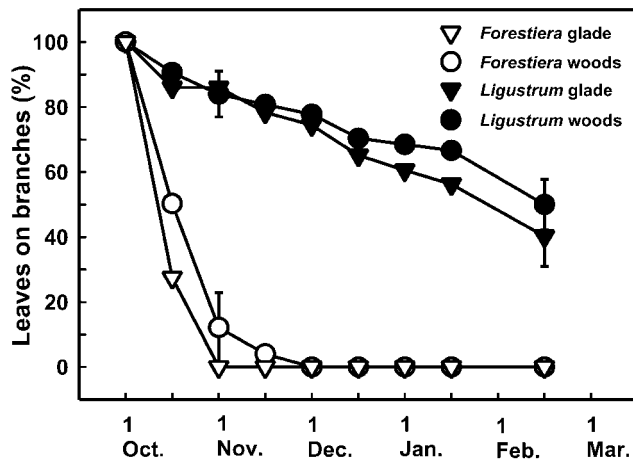


Fig. 3 Mean (\pm SE; SE shown if ≥ 7.0) percentage of leaves remaining on branches for *Forestiera ligustrina* and *Ligustrum sinense* in glade-edge and woodland habitats during autumn and winter 2000–2001.

Moreover, ca. 50% of *F. ligustrina* leaves were damaged by insect herbivory, but only 16%–27% of *L. sinense* leaves were damaged (table 2). Very few insects attack plants of the non-natives *L. sinense* and *Ligustrum lucidum* in Australia and New Zealand (and when they do, it is with negligible impact), whereas native trees and shrubs are attacked by many insect species (Fox and Adamson 1979; Swarbrick et al. 1999). Exotic plants often undergo a release from their specialist predators in the nonnative range (Shierenbeck et al. 1994; Crawley et al. 1996), giving them an advantage over other species.

Leaves expand and stems elongate at about the same time in spring for *L. sinense* and *F. ligustrina* (figs. 1, 2). However, stem elongation was most rapid for *L. sinense* in the woods (table 2). *Ligustrum sinense* has a much slower leaf abscission rate than *F. ligustrina* in autumn and winter (fig. 3). *Ligustrum sinense* is semievergreen or evergreen in its nonnative ranges (Kiew 1978; Duncan and Duncan 1988; Swarbrick et al. 1999) but is recorded to be deciduous in its native range (Mei-chen et al. 1996). The species, however, may defoliate during very dry or very cold weather in Australia, New Zealand (Swarbrick et al. 1999), and the southeastern United States (Duncan and Duncan 1988). Two other invasive shrubs, *Rhamnus cathartica* and *Lonicera \times bella*, have been shown to assimilate 38%–47% of their carbon before spring leaf emergence and after autumn leaf senescence of the overstory canopy (Harrington et al. 1989a). Moreover, *Juniperus virginiana*, a shade-intolerant conifer that occurs with the study species in all plots (Morris 2001), survives

in closed habitats by assimilating most of its carbon when the overstory canopy is leafless (Lassoie et al. 1983). Unlike *F. ligustrina*, *L. sinense* is capable of making photosynthate year-round as long as environmental conditions (air and soil temperatures, soil moisture) remain favorable for photosynthesis to take place. In contrast, Reichard and Hamilton (1997) found that evergreenness was associated with noninvasiveness among North American nonnative woody angiosperms.

In the woods, flowering and fruit production are probably limited by light for both *L. sinense* and *F. ligustrina* (table 2). However, fruit production in *L. sinense* was about 10 times higher than that in *F. ligustrina* under high light conditions and about five times higher under low light conditions. *Ligustrum sinense* would be expected to have a higher proportion of flowers resulting in fruits than *F. ligustrina*, since plants of *L. sinense* are hermaphroditic but those of *F. ligustrina* are dioecious or rarely polygamo-dioecious (Wilson and Wood 1959). The male : female ratio of *F. ligustrina* plants observed in the study plots was about 1 : 1 in both habitat types. Westoby et al. (1983) found that fruit production in *L. sinense* was positively correlated with the amount of light and with stem diameter. They counted an average of 2800 fruits per shoot on *L. sinense* in Australia, with maximum values greater than 10,000. However, fruit production differed widely between shoots, between sites in the same year, and between years at the same site (Westoby et al. 1983).

When compared to the co-occurring shrub *F. ligustrina*, *L. sinense* has advantages in spatially and temporally capturing light in both sunny and shaded conditions. The increased light capture could permit *L. sinense* to have a higher photosynthetic capacity and resource-use efficiency than *F. ligustrina*, potentially resulting in greater vigor. *Ligustrum sinense* also produces a considerable quantity of fruits, which likely translates into rapid colonization and growth of its populations, as has been observed for populations of the nonnative *L. lucidum* in Australia (Fox and Adamson 1979). Thus, *L. sinense* has distinct advantages over *F. ligustrina* in growing, persisting, and reproducing in middle Tennessee and throughout southeastern North America.

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