Research article

Lianas escape self-thinning: Experimental evidence of positive density dependence in temperate lianas *Celastrus orbiculatus* and *C. scandens*

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ABSTRACT

The neighborhood density of plants strongly affects their growth, reproduction, and survival. In most cases, high density increases competition and negatively affects a focal plant in predictable ways, leading to the self-thinning law. There are, however, situations in which high densities of plants facilitate focal plant performance, resulting in positive density dependence. Despite their importance in forest gap dynamics and distinctive growth form, there have been very few studies of the effect of density on lianas or vines. We grew an invasive (*Celastrus orbiculatus*) and a native (*Celastrus scandens*) liana species together in three different density treatments, while also manipulating the light and support availability. We found that across treatment conditions, *C. orbiculatus* always out-performed *C. scandens*, showing greater relative growth rate in height and diameter, greater biomass and higher survival. Both species responded similarly to the density treatments: with plants in high density not showing a decrease in relative height growth rate compared to medium density. Aboveground biomass for *C. scandens* was not affected by density, while for *C. orbiculatus*, the most massive plants were growing in medium density without support. More surprisingly, survival analysis indicated that the two species both had significantly lower mortality rates in the highest density treatment; this trend held true across the other treatments of light and supports. More generally, this study demonstrates that these lianas can escape the consequences of high density and thus the self-thinning law that affects self-supporting plants. This suggests a broader hypothesis about lianas in general: their greater flexibility in allocating growth resources allows them to grow taller and thinner without collapsing and thereby potentially escape shading and mortality even at high densities.

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Introduction

Despite their unique growth form and structural importance on the landscape, the ecology and biology of lianas (woody vines) remains poorly understood. They are probably best known from the tropics (Schnitzer and Bongers, 2002), but can be quite prevalent in some temperate areas (i.e., East Asia) to uncommon or rare in others (i.e., eastern North America). Exotic liana species can easily invade these liana-depauperate areas, forming dramatic tangles on the landscape (Fike and Niering, 1999; Forseth and Innis, 2004; Schierenbeck, 2004). Lianas use other plants (i.e., trees) and neighboring lianas (Putz, 1984, 1995b) as supports, which often results in large liana tangles (Schnitzer et al., 2000; Gerwing, 2001). Dense tangles can perturb succession (Schnitzer et al., 2000, 2005; Schnitzer and Carson, 2010)

and have impacts on tree growth (Dillenburg et al., 1993a,b; Schnitzer et al., 2005). Even in the absence of trees or other host species, lianas can climb on each other (Putz, 1995a) and effectively increase their height, avoiding being overtopped by other species (Letcher and Chazdon, 2009). The resulting tangles are prominent in tropical systems where tree fall gaps form (Putz, 1984; Schnitzer et al., 2000, 2004), and in temperate systems in gaps and at forest edges (Robertson et al., 1994; Kodani, 2006).

The invasive liana, *Celastrus orbiculatus* Thunb. (oriental bittersweet), is expanding its range across the eastern North American landscape and is commonly observed in large tangles overtopping the surrounding vegetation (Fike and Niering, 1999). Interestingly, its native congener, *Celastrus scandens* L. (American bittersweet), appears to have a more conservative life form (Steward et al., 2003), and while it can grow successfully into trees, is not often observed forming dense tangles or actually overtopping the host tree it is growing on (Dreyer et al., 1987; Steward et al., 2003). In many of the locations where *C. scandens* once occurred, it

is no longer found, and *C. orbiculatus* is often present (Steward et al., 2003). While other research has shown that loss of suitable habitats (Leicht-Young et al., 2007a) and hybridization with the invasive (Pooler et al., 2002; D. Zaya, unpublished data) are likely contributing to the decline of *C. scandens* on the landscape, it remains unknown whether strong competition from *C. orbiculatus* for supports where the two species co-occur has contributed to its decline. By examining the growth and mortality dynamics of these two liana species in high densities, we can assess their relative competitive abilities, while also learning in a general way how lianas respond to high density neighborhoods.

Density is one of the most important determinants of plant growth, reproduction and survival, as it often sets the level of competition for space, light, moisture and other important resources (Harper, 1977; Silvertown and Charlesworth, 2001). Often, the result of this direct interaction with neighbors is negative (e.g., lower growth rate, decreased biomass) until individual plants experience mortality via self-thinning (Harper and McNaughton, 1962; Yoda et al., 1963). Lianas growing in tangles are one of the most striking examples of plants growing in high density. Our working hypothesis in setting up this experiment was that competition for resources at high density would be so intense that it would produce a typical, negative density-dependent response: decreased biomass accumulation and self-thinning. Further, we expected that the apparently faster-growing exotic *C. orbiculatus* would perform better than and compete successfully with the native *C. scandens*.

There have been few previous studies of the responses of lianas to density (but see: Weiner, 1986; Klimeš and Klimešová, 1994; Cappuccino, 2004). The vast majority of studies researching the impacts of density on plant performance have focused on herbaceous annuals (Kira et al., 1953; Mack and Harper, 1977; Weiner, 1982; Pacala and Silander, 1985, 1987, 1990; Goldenheim et al., 2008), short-lived perennials (Gunton and Kunin, 2009; Ramula and Buckley, 2009), and trees (Mohler et al., 1978; Franklin et al., 2009; Zhang et al., 2009). The growth patterns of self-supporting plants in competition may not be comparable to lianas, mainly because lianas and other climbers are not sedentary in their growth form since they use other plants for support. Lianas and other climbing plants have the unique ability to grow both horizontally and vertically in space (Klimeš and Klimešová, 1994), affording them the opportunity to potentially escape competition by finding a support and growing away from, or over, their neighbors (Letcher and Chazdon, 2009). In addition, unlike self-supporting plants, lianas can continue to support themselves as thin stems, making them less susceptible to falling over and dying, which is a common effect of growing in high density (Harper, 1977; Schmitt and Wulff, 1993; Dudley and Schmitt, 1996). In addition, when suffering damage to the main stem, lianas can send out new leaders to continue their growth (Putz and Holbrook, 1991; González-Teuber and Gianoli, 2008). Thus, because of the unique non-self supporting growth-form attributes of lianas, they might not strictly follow the self-thinning law of plant ecology.

To investigate these questions, we conducted a study where both the invasive *C. orbiculatus* and native *C. scandens* were grown in competition across three densities in a common garden experiment. We specifically tested the following hypotheses: (1) both *C. orbiculatus* and *C. scandens* will experience negative effects from high density, including lower growth rates and higher mortality; (2) *C. orbiculatus* would be competitively superior to *C. scandens*, and would have higher growth and survival rates.

Materials and methods

Species

C. orbiculatus is native to eastern Asia, including China, Japan and the Korean peninsula (Hou, 1955). This species can climb to heights of over 30 m in tree canopies and reach stem diameters upwards of 18 cm (Leicht-Young, pers. obs.). It has been implicated in causing damage to trees by girdling (Lutz, 1943), increasing tree susceptibility to ice damage (Siccama et al., 1976), interfering with forest regeneration by shading out young seedlings and saplings (McNab and Meeker, 1987) and altering soil properties (Leicht-Young et al., 2009).

C. scandens is native to North America, ranging from the east coast of the United States and as far west as Wyoming (USDA NRCS, 2008). *C. scandens* is declining in the northeastern United States (Steward et al., 2003) and in some states (e.g., New York) is listed as a species of concern (USDA NRCS, 2008). In the Midwestern United States, this species is still present, especially in dune landscapes along Lake Michigan (Leicht-Young et al., 2007b). In these landscapes the two species co-exist and often grow intertwined with each other (Leicht-Young et al., 2007b).

Experimental design

Seeds of *C. orbiculatus* were collected on the University of Connecticut campus in fall 2001. Because of the scarcity of *C. scandens* in Connecticut, and not wanting to further deplete the remaining seed sources for this species, we purchased commercially grown seeds from Sheffield's Seed Company in Locke, NY. We germinated seeds of *C. orbiculatus* and *C. scandens* in a greenhouse in March 2002 following standard protocols (USDA, 1974). Seedlings were transplanted into peat pots and allowed to grow in the greenhouse until early June 2002. Seedlings were then transplanted out into two adjacent tilled fields at the University of Connecticut Plant Science Research Farm. Within each of these fields there were two light treatments. Seedlings received either full sunlight or experienced a shade treatment with approximately 10% of ambient light. The shade treatment was obtained by the construction of a wood-and-wire frame that measured 11.5 m × 20.4 m. We attached 80% woven black shade cloth (DeWitt Company, Sikeston, MO, USA) to the frame. Shade treatments were located at the north end of each field to avoid shading of the adjacent light treatments.

To determine the actual amount of light that the shade treatments were receiving, we used a LI-COR 190SA quantum sensor (LI-COR Inc., Lincoln, NE, USA) with a Campbell Scientific 23X micrologger (Campbell Scientific Inc., Logan, UT, USA). We collected data for four days at the end of July and beginning of August 2002 on nearly cloud-free days. Using these data, we confirmed that the shade cloth actually was shading approximately 90% of full sun. Although the shade cloth produces nearly uniform shade, unlike the highly spatially heterogeneous light regime in the region's forests, the shade treatment reduced the light available to the plants to a level comparable to conditions for establishment and competition under a Northeastern second-growth deciduous forest canopy (Leicht-Young et al., 2007a), making the treatment a meaningful proxy for the light limitation in that ecological context.

In each sun or shade treatment, there were three density treatments: low, medium, and high. In low density treatments, the plants were planted 1.5 m apart for a total of four plants per treatment. In medium density treatments, they were planted 0.5 m apart, for a total of 36 plants per treatment. In high density treatments, they were planted 0.2 m apart for a total of 144 plants. The plants were planted in a checkerboard formation; alternating *C. orbiculatus* with *C. scandens*.

Each sun or shade treatment had one density treatment with tomato stakes for climbing and one without. We used this experimental design to determine whether the species grew differently when they had supports versus without supports, whether light level affected this response, and whether the supports affected competitive interactions. The tomato stakes were approximately 1.5 m in height. The width of the stakes was well within the range of diameters of supports, such as saplings and young trees, which these species encounter and successfully climb in nature. In the low density treatment, each of the four plants had its own stake placed on the north side of the plant. For the medium and high density treatments, every cluster of four plants had a stake placed at its center. Plots were mulched with newspaper and straw in order to prevent the confounding effect of competing weedy, herbaceous vegetation between plants.

We measured height and basal diameter at the beginning (late May/early June) and end (October) of the growing season in 2002 and 2003. Basal diameter was measured to the nearest 0.1 mm at ground level using calipers. The stem was marked with a paint pen such that subsequent measures were taken in the same location from year to year. In the third and final year of the study (2004), in early September, we obtained final diameter, and we stretched the plants out to get a final length when harvesting the aboveground biomass. To measure aboveground biomass, we carefully untangled the plants, cut them at ground level, then dried them and weighed them to the nearest gram. We were unable to harvest the belowground biomass since the plants had grown extensively in three growing seasons, and extracting their roots from the ground intact was not possible due to the rocky clay soils and extensive root mass. During one attempted excavation, it took 3 h to partially excavate one two-year-old plant (J. Silander, pers. obs.). Thus, given the number of plants in the study, harvesting belowground biomass was simply not feasible. At the end of each growing season (2002–2004), we noted if plant mortality had occurred.

Data analysis

We calculated relative growth rates for height (RGRheight) and diameter (RGRdiameter) for each of the three growing seasons using the following equation:

$$RGR = \frac{In(measurement_{final}) - In(mesurement_{initial})}{(time_{final} - time_{initial})}$$

We used the number of months between the initial and final height and diameter measurements for each growing season; all observed growth occurred in this spring-to-fall interval. For 2002 it was 3.5 months, for 2003 it was 4.5 months, and for 2004 it was 4 months.

We examined the growth responses of the *Celastrus* species using linear mixed effects models (LME). We analyzed the responses of the two species separately because the species explanatory variable overwhelmed the other variables due to the large differences in the magnitude of species-specific responses. In addition, we were better able to compare the direction and magnitude of the species' responses by analyzing them separately. We conducted the LME models using the *lme4* package (Gelman and Hill, 2007; Bates and Maechler, 2009) in R (R Development Core Team, 2009). Mixed models allow for both random and fixed effects (Beckage and Clark, 2003; Gelman and Hill, 2007). In this way, variation not captured by the predetermined or fixed explanatory variables can be taken into account. Also, we can use random effects for individual plants to quantify plant-level variance and model repeated measurements of each plant through time (Pinheiro and Bates, 2000). For each response variable that we mea-

sured throughout the study (RGRheight, RGRdiameter) we tested several models that included all combinations (with and without three-way interactions of the fixed effects) of the following complete model:

Celastrus growth response~Density × Light × Stakes

+ (1|Year) + (1|Plant ID) + (1|Field/Light/Density)

The fixed effects were density, light and stakes. Density was an ordinal variable with two levels (medium and high). The low density was removed from the analysis because after high mortality (for details on density-dependent mortality, see results of survival analysis below), the sample size was extremely low, and including this level would have made the analysis of growth rates extremely unbalanced. Light and stakes (i.e., availability of supports) were also ordinal variables with two levels each: (1) shade vs. full sun, and (2) stakes vs. no stakes, respectively. The coefficients for the medium density level, the 90% shade level, and the no stakes level were set to zero for identifiability and so that the coefficients for the other level of these treatments could be interpreted as contrasts with the lower level. The random effects, denoted above as "(1|grouping variable)", were year (growing seasons 1, 2 or 3), plant ID (identity of each individual plant), and field (1 or 2). The final term (1|Field/Light/Density) was included because our experiment was a split plot design and we needed to include a random term to express the nesting in the design (Crawley, 2005). To analyze final biomass (taken once at the end of the study), we ran similar models to the ones analyzing growth rate, but we excluded the year and plant random effects because there were no repeated measurements of these responses. We used backward elimination based on improved AIC (Akaike, 1974) of non-significant interactions from the full model following the example of Crawley (2005) to select the final model (see Table 1). We examined the 95% highest posterior density intervals (HPD) using the function pvals.fnc in the *languageR* package in R (Baayen, 2010), for all of the final models to see which fixed and random effects did not overlap zero and had a significant *p*-value.

Finally, to examine mortality of the plants through the three years of the study, we analyzed time to mortality using the *survival* package in R (Therneau and Lumley, 2009). We ran parametric survival models to test for significant differences among treatments in plant mortality, while accounting for the interval- and right-censored nature of the data (Beckage and Clark, 2003). These models, implemented in the function survreg(), are accelerated failure models in which the rate at which the cumulative hazard or probability of mortality for each individual changes with time is a function of the explanatory variables and random effects (Congdon, 2006; Therneau and Lumley, 2009). The regression coefficients can thus be interpreted as factors that accelerate (negative coefficients) or decelerate (positive coefficients) the time to mortality (Venables and Ripley, 2002). We ran models with a similar structure parallel to that of the linear mixed effects models for growth rate: fixed effects for light, density level, and stakes, with both main and two way interactions and with random effects for field. The random effects in this model were implemented as gamma frailty models that allow the hazard to vary among different groups (i.e., some groups can be more susceptible to death than others) (Therneau et al., 2003; Congdon, 2006). Because there were no repeated measures in these data, we did not use plant random effects. After comparing models with different parametric distributions for the survival times using AIC, we selected the Weibull distribution for survival times (Beckage and Clark, 2003).

Table 1
Results of linear mixed effects models for *Celastrus* growth responses. RGR = relative growth rate. In the random effects column, variables separated by a "/" indicate nesting. Plant ID = identity of individual plant, year = growing seasons 1–3, field = which field plants were located in, light = full sun or 90% shade with shade as the base level, density = medium or high with medium as the base level, stakes = supports present or not with no stakes as the base level.

Response	Random effects	Variance	Fixed effects	Coefficient	Standard error	*t*-Value
Celastrus orbiculatus						
Height RGR	Plant ID	0.00	Intercept	1.78	1.69	1.05
	Year	**8.41**	Density (high)	0.60	0.29	**2.06**
	Field/light/density	0.05	Stakes (present)	0.05	0.24	0.19
	Field/light	0.02	Light (sun)	0.94	0.35	**2.73**
	Field	0.00	Stakes × density	−0.55	0.27	**−2.08**
	Residual	**2.25**	Density × light	−0.93	0.40	**−2.29**
			Stakes × light	−0.73	0.33	**−2.22**
			Density × stakes × light	1.44	0.36	**3.99**
Diameter RGR	Plant ID	0.00	Intercept	0.66	0.50	1.30
	Year	**0.57**	Density (high)	−0.18	0.12	−1.44
	Field/light/density	0.02	Stakes (present)	−0.25	0.07	**−3.51**
	Field/light	0.01	Light (sun)	0.66	0.16	**4.13**
	Field	0.09	Stakes × light	0.49	0.10	**4.87**
	Residual	**1.20**				
Biomass	Field/light/density	**0.08**	Intercept	2.50	0.40	6.19
	Field/light	0.00	Density (high)	−0.15	0.40	−0.38
	Field	0.11	Stakes (present)	−0.32	0.37	−0.88
	Residual	**0.60**	Light (sun)	1.87	0.42	**4.45**
			Stakes × density	0.38	0.38	0.99
			Density × light	−0.82	0.52	−1.58
			Stakes × light	−1.37	0.43	**−3.19**
			Density × stakes × light	1.62	0.46	**3.56**
Celastrus scandens						
Height RGR	Plant ID	0.00	Intercept	0.17	0.63	0.27
	Year	**1.07**	Density (high)	0.39	0.16	**2.40**
	Field/light/density	0.00	Stakes (present)	0.05	0.08	0.62
	Field/light	0.04	Light (sun)	0.05	0.29	0.18
	Field	0.00	Density × light	0.47	0.23	**2.07**
	Residual	**2.38**				
Diameter RGR	Plant ID	0.00	Intercept	0.21	0.50	0.43
	Year	**0.12**	Density (high)	−0.70	0.46	−1.53
	Field/light/density	**0.18**	Stakes (present)	−0.48	0.18	**−2.67**
	Field/light	0.00	Light (sun)	0.36	0.46	0.78
	Field	0.20	Stakes × density	0.61	0.18	**3.34**
	Residual	**1.67**	Density × light	0.34	0.63	0.54
			Stakes × light	0.44	0.14	**3.20**
Biomass	Field/light/density	0.00	Intercept	0.28	0.21	1.29
	Field/light	0.00	Density (high)	0.38	0.17	**2.24**
	Field	0.01	Stakes (present)	−0.13	0.10	−1.28
	Residual	**0.64**	Light (sun)	0.30	0.11	**2.75**

Values in bold indicate 95% highest posterior density intervals that did not overlap zero (i.e., significance).

Results

By the end of the third year of the study, across all treatments, the invasive *C. orbiculatus* had significantly greater RGRheight, RGRdiameter and aboveground biomass than the native *C. scandens* (Fig. 1) as well as greater survival (Fig. 2).

Linear mixed effects models indicated that RGRheight was positively influenced by the high density treatment under conditions of high resource availability—full sun (for both species) and presence of supports (for *C. orbiculatus*; Table 1 and Fig. 1). For *C. orbiculatus*, the main effect of light on RGRheight was positive. There was also a significantly positive three-way interaction of density, stakes, and light on RGRheight. This indicated that all of these factors together are responsible for the response in height growth for *C. orbiculatus*. The two-way interactions of stakes × density, density × light, and stakes × light were all significantly negative (Table 1). For *C. scandens*, there was a significant positive interaction between high density and full sun, indicating that RGRheight was greater when there was high density of neighbors and full

sun. RGRdiameter showed a different response. For both species, RGRdiameter was significantly lower with the presence of stakes (Table 1), indicating that the plants are not growing as quickly in diameter when supported—leading to thinner plants. Full sun had a positive effect on RGRdiameter in *C. orbiculatus* and there was a positive light by stakes interaction: in full sun, with stakes, the RGR-diameter was increased, while in the shade, the presence of stakes decreased RGRdiameter. For *C. scandens*, there were positive interactions between stakes and light, indicating that in high light with stakes RGRdiameter was greater and density × stakes, indicating that in high density, stakes increased RGRdiameter, while in the medium density it was decreased (Table 1).

Final aboveground biomass of *C. orbiculatus* was significantly higher in the full sun treatment. There was also a negative interaction of stakes and light and a significantly positive three-way interaction of density, stakes, and light (Fig. 1). In the high density treatment, the presence of stakes led to higher aboveground biomass, while in the medium density treatment plants without stakes had greater biomass (i.e., they became more shrub-like in
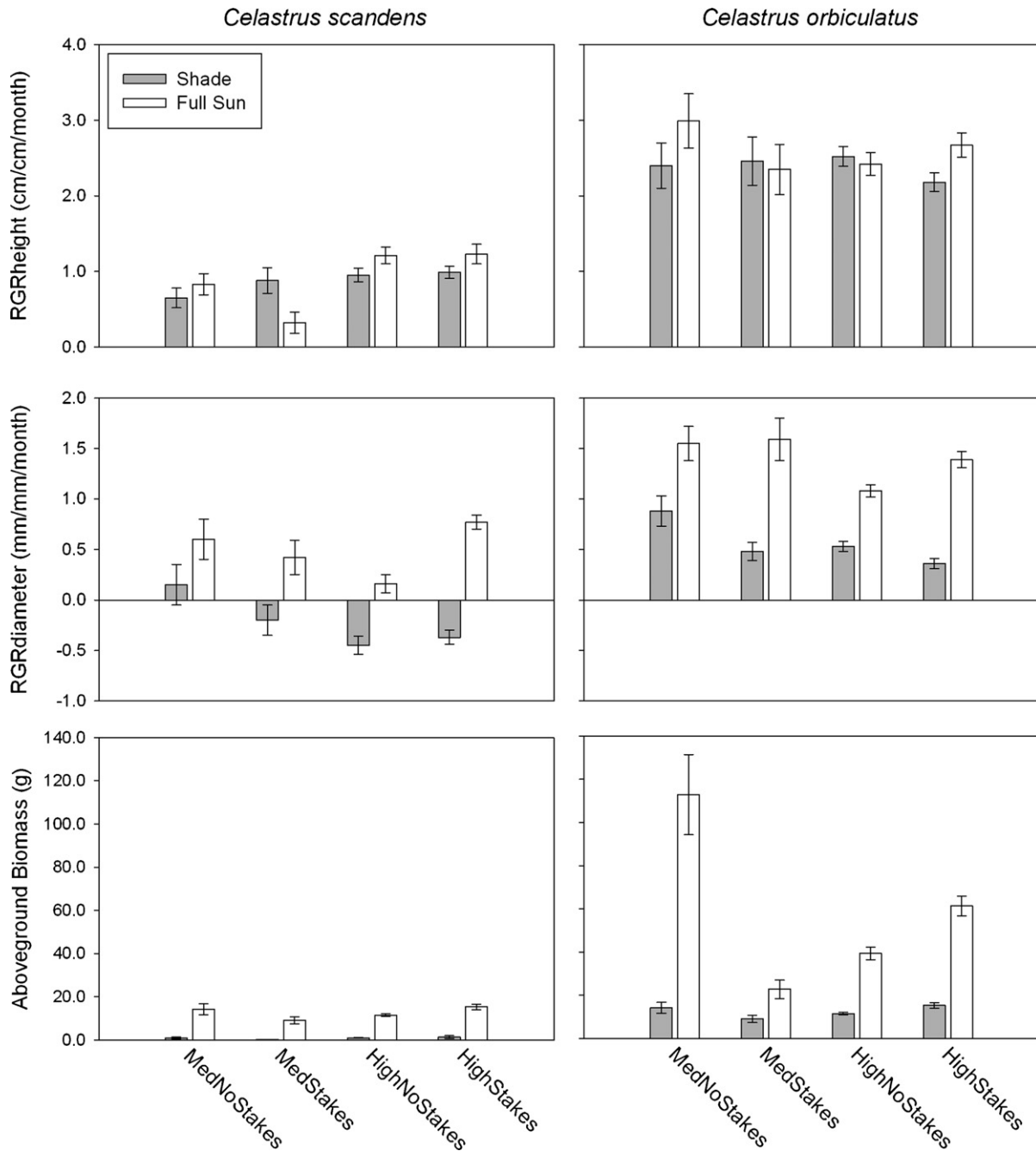
Fig. 1. Means ± SE for growth measurements of the invasive *Celastrus orbiculatus* and native *C. scandens*. RGRheight = relative growth rate of height, RGRdiameter = relative growth rate of diameter, Med = medium density, high = high density, NoStakes = no supports and Stakes = supports. Gray bars = 90% shade treatment, white bars = full sun treatment.

their habit). For *C. scandens*, full sun and high density both resulted in significantly higher aboveground biomass.

Empirically, *C. orbiculatus* had 81% survival after three growing seasons (i.e., the end of the experiment) in the high-density treatment, compared with 46% in the medium-density treatment and 44% in the low-density treatment (Fig. 2). *C. scandens* showed a similar contrast though at a lower overall level: 43% survival after three growing seasons at high density, 17% at medium density, and 19% at low density (Fig. 2). The survival analysis results were consistent with this pattern: with high density as the base level of this categorical variable for contrasts, the coefficients for medium and low density were significantly negative for both species, indicating accelerated time to mortality at the lower densities relative to high

density (Table 2). In addition, high light was significantly associated with longer survival in both species, while stakes were significantly associated with longer survival for *C. scandens* but not *C. orbiculatus* (Table 2).

Discussion

Results of linear mixed models—density, light and supports

Although one of the main objectives of this study was to determine what effect density had on liana growth and survival, interpreting the main effect of density on *Celastrus* growth is complex due to the many significant interactions revealed by the linear

Table 2
Coefficients of survival model. Positive coefficients indicate longer survival times (decelerated time to mortality) compared to the base level of the explanatory variable. For light the base level is shade, for stakes the base level is no stakes, and for density the base level is high density. Field 1 and field 2 are random effects for the field variable.

Species	Coefficient	Std. error	z-Value	p-Value
C. orbiculatus				
(Intercept)	7.43	0.50	14.74	<0.001
Light	0.51	0.15	3.30	<0.001
Stakes	−0.27	0.11	−2.41	0.02
Low density	−0.65	0.32	−2.00	0.05
Medium density	−0.72	0.14	−5.08	<0.001
Light × stakes	0.19	0.17	1.10	0.27
Light × low density	−0.72	0.39	−1.86	0.06
Light × medium density	−0.13	0.18	−0.76	0.45
Stakes × low density	0.63	0.40	1.57	0.12
Stakes × medium density	0.22	0.16	1.37	0.17
Field 1	0.13	0.49	0.25	0.80
Field 2	−0.14	0.49	−0.29	0.77
C. scandens				
(Intercept)	6.53	0.06	113.18	<0.001
Light	0.41	0.09	4.46	<0.001
Stakes	0.16	0.08	1.94	0.05
Low density	−0.42	0.29	−1.44	0.15
Medium density	−0.27	0.11	−2.44	0.01
Light × stakes	0.02	0.12	0.16	0.88
Light × low density	−0.25	0.36	−0.69	0.49
Light × medium density	−0.20	0.14	−1.46	0.14
Stakes × low density	0.35	0.37	0.94	0.35
Stakes × medium density	−0.06	0.14	−0.45	0.66
Field 1	0.00	0.01	−0.25	0.80
Field 2	0.00	0.01	0.25	0.80

mixed model analysis (see Table 1). For instance, there were three-way interactions with density, stakes, and light for *C. orbiculatus* for both RGRheight and final aboveground biomass. These interactions, however, are not surprising given that the growth form of lianas depends very strongly on available light and supports in natural settings independent of density (i.e., the plants will take on a more shrubby vs. vine habit). The analysis indicated that there was a significant main effect of high density for both species for RGRheight. However, when examining the results in Fig. 1, it can be seen that there is not that much of a difference between the medium and high densities in terms of mean values for RGRheight for either species, although *C. scandens* does appear to have greater height growth in high densities. Nonetheless it is striking that neither of these species was negatively affected by growing in such high density that they were extensively tangled by the second and third growing seasons. For the medium density plants overall, *C. orbiculatus* had higher biomass and greater RGRdiameter, indicating that these plants were more shrub-like in their morphology than those in higher densities. If the plants were not in competition, and simply growing out in the open, this shrubby morphology would not be a disadvantage. However, with the addition of competing neighboring plants, the ability to move from a self-supporting, shrubby habit to being able to exploit neighbors for height growth by climbing is a critical strategy to the survival of lianas in high densities. Our results are in contrast to previous studies on herbaceous vines, where these species showed decreased height growth in competition (Klimeš and Klimešová, 1994). Thus, the first part of our first hypothesis of decreased growth under high density conditions was not supported because growth in medium and high densities was similar.

Our primary objective in this experiment was to determine the effect of density on these two species, however, it is also important to understand how these lianas responded to the other experimental treatments (light and availability of supports) and how these responses can interact with each other and with density. It was not surprising that high light availability increased final biomass and survival for both species—clearly this is a critical limiting resource.

What was unexpected was that the light treatment did not have a definitive effect on RGRheight for either species. In another study which examined *C. orbiculatus'* performance under three light conditions (100%, 28%, and 2% transmittance), Ellsworth et al. (2004) determined that the final length and aboveground biomass of *C. orbiculatus* was significantly reduced only under the heavy shade of the 2% treatment. This study illustrates the ability of *C. orbiculatus* to respond to moderate shade with compensatory (Anten et al., 2003) growth, in that it is able to grow as tall in shaded conditions similar to a forest understory as in full sun (Olivé et al., 2007). *C. orbiculatus* apparently loses its ability to mount this response only under the most shaded conditions (2% of full sun) which is likely a prime reason this species is a successful invader of forest understories. In contrast, the native *C. scandens* has been shown in previous work to grow slowly in low light (Leicht and Silander, 2006; Leicht-Young et al., 2007a).

For lianas located in a forest understory, being able to continue to grow rapidly in height despite shading allows the liana to forage for supports and grow into the canopy (Carter and Teramura, 1988; Robertson et al., 1994; Baars and Kelly, 1996). While previous studies have demonstrated that there is a threshold light level below which height and aboveground biomass of both *Celastrus* species decline sharply compared to plants grown in the full sun (Leicht, 2005; Leicht-Young et al., 2007a), this study shows that *C. orbiculatus* can maintain its height growth at light levels typical of the broadleaf temperate forest understory, enabling it to forage for and use external supports in order to access additional light.

Lianas and above-/belowground growth

In interpreting these results, it is important to point out that after three growing seasons many of the plants had reached the top of their supports. In a natural canopy, these plants would likely have kept growing upwards and eventually across the canopy, permanently escaping the initial effects of high density (Letcher and Chazdon, 2009). However, because these plants also experience belowground competition, they may not entirely escape negative
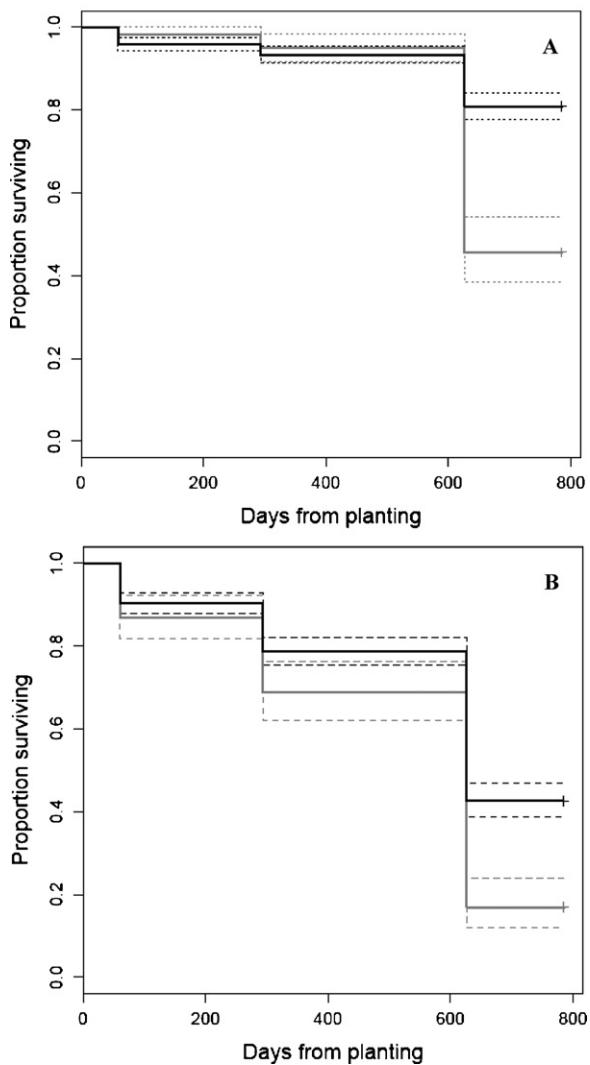
Fig. 2. Nonparametric survival curves for *Celastrus orbiculatus* (A) and *C. scandens* (B) at contrasting density levels (low and medium densities combined for clarity of presentation because survival curves very similar). Gray lines show survival curves for combined medium and low densities; black lines show curves for high density. Dotted lines represent the 95% confidence intervals.

density dependent effects. Studies by Dillenburg et al. (1993a), Schnitzer et al. (2005), and Toledo-Aceves and Swaine (2008) indicate that belowground competition from lianas had a stronger negative impact on the growth of tree saplings than aboveground competition. Similarly, it could be that the belowground competition from *C. orbiculatus* was so intense that *C. scandens* was at a competitive disadvantage; especially when the plants were supported. Supported twining vines have been observed to show an increased in allocation to roots (den Dubbelden and Oosterbeek, 1995; Schweitzer and Larson, 1999). A better understanding of the roles of above-ground and below-ground interactions in lianas remains an important open question for future research.

An additional question that arises from these results is whether there is a disadvantage for lianas in maintaining high rates of height growth when in proximity to many neighbors. In the case of herbaceous annuals, plants that grow very tall have decreased numbers of leaves and are more susceptible to etiolation and breakage than plants that are grown further apart (Harper, 1977; Schmitt and Wulff, 1993). As can be seen by the lower RGRdiameter in the shade treatment, coupled with the same RGRheight as in the full

sun, lianas will also grow tall and relatively thin under these conditions (Gianoli, 2002). For lianas, however, this increased height likely benefits the plant. Lianas can allocate less to support material in their stems that other plants (Putz and Holbrook, 1991), and as long as they find support, they have the potential to grow rapidly into the canopy and obtain further light resources. Lianas can also twine with the stems of neighboring lianas, allowing them to grow upwards using this spiral of stems as a support until they reach a stationary support and grow into the canopy: a form of structural facilitation (Campanello et al., 2007).

Density and survival

The higher survival we observed in high densities seems counterintuitive since greatly increased density typically leads to smaller stature and lower survival. Most often, plants with lower biomass suffer higher mortality and reduced fitness (Weiner, 1990; Stoll et al., 2002; Weiner and Damgaard, 2006). However, the lianas in this experiment, especially *C. orbiculatus*, did not appear to be undergoing self-thinning at higher densities, thus forming an exception – at least in its early life stages – to the self-thinning law (Weiner, 1990; Weiner and Damgaard, 2006). This result refutes the second part of our first hypothesis that lianas in high density would show increased mortality in high densities.

This is one of the first studies to our knowledge of any plant showing density-dependent facilitation via avoidance of self-thinning. Indeed, the liana growth form and its density response may provide useful insight into the assumptions of the self-thinning law itself. All of the studies done on self-thinning previously have only examined self-supporting plant growth forms. It may be an important prerequisite to self-thinning that the plants cannot escape their competition by climbing. There are situations, however, where living in high densities can have a facilitative effect for plants as a result of protection against harsh conditions such as desiccation and high temperatures (Holzapfel and Mahall, 1999; Pedersen et al., 2001; Goldenheim et al., 2008). In the case of these temperate lianas it is possible that living in high densities lowers the amount of freezing damage that they are subjected to in the winter (Schnitzer, 2005), or lowers the chance of frost heave of roots (Venn et al., 2009). For lianas, however, it may be that having increased numbers of supports in high densities increases the probability of reaching the canopy which is important for long-term liana survival (Ladwig and Meiners, 2010). What remains unknown is whether self-thinning would eventually take place under extreme high density, or if lianas could benefit indefinitely from group living. When light and supports become sufficiently limited, or are co-opted by the plants with greater fitness, density-dependent mortality may begin to occur.

Comparisons of C. orbiculatus and C. scandens

The second objective of our study was to examine the responses of *C. orbiculatus* and *C. scandens* when in direct competition. As we expected, overall, we found that the invasive *C. orbiculatus* had greater growth (growth rate and aboveground biomass, Fig. 1) and survival than the native *C. scandens* (Fig. 2). It is important to note that while both *C. orbiculatus* and *C. scandens* showed no difference in RGRheight in sun vs. shade, the growth rates of *C. scandens* were dramatically below that of *C. orbiculatus* (Fig. 1) in both light treatments. *C. orbiculatus* was 15 times taller in the sun and 11 times taller in the shade (Leicht, 2005), which complements other work indicating the lack of shade tolerance of *C. scandens* reflected in lower growth rates (Leicht and Silander, 2006; Leicht-Young et al., 2007a), and higher morality (Leicht-Young et al., 2007a; Fig. 2). A similar response at a smaller magnitude was observed in native and

invasive *Lonicera* (honeysuckle) congeners (Schweitzer and Larson, 1999). Thus, the growth of neighboring *C. scandens* likely did not have much of an impact on *C. orbiculatus*. These results supported our second hypothesis that *C. orbiculatus* would be competitively superior to *C. scandens*.

Greater relative growth rates allow for faster time to reproduction and a greater ability to obtain resources. Indeed, we observed many more flowers and fruits on the invasive *C. orbiculatus* compared to *C. scandens* after just three growing seasons, in fact, by the third year of this study, 46% of *C. orbiculatus* plants were flowering vs. only 5% of the *C. scandens* plants. Some of the *C. orbiculatus* plants had fruits after just one growing season (Leicht, 2005). Thus, the abundance of *C. orbiculatus* on the landscape may be due to faster and greater reproductive output than *C. scandens* (Dreyer et al., 1987; Steward et al., 2003; Leicht, 2005). Also, since *C. orbiculatus* grew so rapidly and exploited the stakes quickly, competition for the stakes may have prevented *C. scandens* from successfully climbing the stakes in subsequent years. In this way, *C. orbiculatus* was able to preempt the stakes and thus access light resources in the full sun treatment.

In previous studies, we have found that *C. orbiculatus* has lower mortality and greater growth and biomass than *C. scandens* when transplanted across natural landscapes in the absence of competition (Leicht-Young et al., 2007a) as well as in greenhouse conditions with differing light quality and quantity (Leicht and Silander, 2006). We can surmise that when these two species compete for the same resources in the natural environment, *C. scandens* will likely perform worse than *C. orbiculatus* in areas where the two species co-occur due to its inherently slower growth rate (Steward et al., 2003), lower plasticity (Leicht and Silander, 2006; Leicht-Young et al., 2007a), and higher mortality (Fig. 2). It is important to point out, however, that although the competitive advantage of *C. orbiculatus* in areas where the two species co-occur may partially explain the decline of *C. scandens* in the eastern United States, other important factors such as loss of suitable habitat (Leicht-Young et al., 2007a), lower fruit and seed production, and hybridization (Pooler et al., 2002; D. Zaya, unpublished data) may also contribute.

Summary

In one of the first studies of competition among lianas at differing densities, we found that lianas appear to respond in a distinctive way to increasing density. High density, surprisingly, increased survivorship while not restricting height growth or consequently the ability of the plants to forage for supports and light. This study also provides very strong evidence that where *C. orbiculatus* and *C. scandens* compete directly for space and support, *C. orbiculatus* may often suppress the native liana, resulting in more pressure on a species already on the decline in parts of its distribution where it overlaps with *C. orbiculatus*. This research, however, has potentially wider implications for understanding the dynamics of liana tangles in both the temperate and tropical landscape. The lack of a decrease in RGRheight in high densities indicates that lianas interact in such a way that increased density does not decrease their height growth. Since lianas also have higher survival in high densities than they do in lower densities, they do not appear to follow the self-thinning law at least in their early stages of growth. This finding adds further insight as to why forest succession tends be slower in sites with a high density of lianas (Schnitzer et al., 2000, 2005). In addition, with the prediction that lianas will increase on the landscape with climate change (Phillips et al., 2002; Wright et al., 2004; Allen et al., 2007) and the colonization by invasive lianas of apparently open niches in North American and European areas that are relatively depauperate in lianas (Gentry, 1991; Schnitzer, 2005; Gianoli et al., 2010), an understanding of how this unique plant growth form responds to different densities and environmental factors is critical to predicting how lianas will impact the landscapes they invade. There has been very little research on liana population and community ecology in the temperate zone in comparison to the tropics. Even less is known about the lianas of temperate East Asia, where liana diversity (Qian and Ricklefs, 1999; Cai et al., 2009) and densities (Kodani, 2006) are much higher than in other temperate areas and where the majority of invaders (both lianas and other woody species) of other temperate areas originate. Thus, further studies on the ecology of these climbing species are critical in order to gain further insight into their current and future role in temperate forest dynamics.

Acknowledgements

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