

DIFFERENTIAL RESPONSES OF INVASIVE *CELASTRUS ORBICULATUS* (CELASTRACEAE) AND NATIVE *C. SCANDENS* TO CHANGES IN LIGHT QUALITY¹

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When plants are subjected to leaf canopy shade in forest understories or from neighboring plants, they not only experience reduced light quantity, but light quality in lowered red : far red light (R : FR). Growth and other developmental responses of plants in reduced R : FR can vary and are not consistent across species. We compared how an invasive liana, *Celastrus orbiculatus*, and its closely related native congener, *C. scandens*, responded to changes in the R : FR under controlled, simulated understory conditions. We measured a suite of morphological and growth attributes under control, neutral shading, and low R : FR light treatments. *Celastrus orbiculatus* showed an increase in height, aboveground biomass, and total leaf mass in reduced R : FR treatments as compared to the neutral shade, while *C. scandens* had increased stem diameter, single leaf area, and leaf mass to stem mass ratio. These differences provide a mechanistic understanding of the ability of *C. orbiculatus* to increase height and actively forage for light resources in forest understories, while *C. scandens* appears unable to forage for light and instead depends upon a light gap forming. The plastic growth response of *C. orbiculatus* in shaded conditions points to its success in forested habitats where *C. scandens* is largely absent.

Key words: Celastraceae; *Celastrus orbiculatus*; *Celastrus scandens*; invasive species; lianas; red : far red ratio; shade responses.

Lianas are species that are often observed in the forest understory both as shade-adapted species and as seedlings waiting for the opportunity to make their way into the canopy should a gap open in the forest (Putz, 1984; Carter and Teramura, 1988; Greenberg et al., 2001). In order to understand how plants with the liana growth form are able to survive and adapt in a shaded understory environment, one needs to examine both the effect of both the quantity and quality of light. Lianas and other plants that are under the canopy in the forest understory encounter both low irradiance as well altered quality (i.e., different wavelengths) of light compared to plants growing in open areas.

Light quantity, the amount of irradiance a plant receives in a given environment (photon flux density [PFD] integrated from 400 to 700 nm), can be affected by the canopy both intercepting and reflecting light (Lee et al., 1996). Light quantity can be experimentally manipulated using neutral shade cloth or other neutral filters. Light quality, on the other hand, refers to the spectral distribution of the light that plants are receiving under a canopy (Lee, 1988; Schmitt and Wulff, 1993; Lee et al., 1996) or when growing close to neighboring plants (Schmitt and Wulff, 1993; Ballaré et al., 1997). One aspect of the spectral properties of light that changes as it

passes through a leafy canopy is the red : far red ratio (R : FR) (Schmitt and Wulff, 1993; Smith, 2000). In full sunlight, this ratio ranges from 1.10 to 1.25 (Smith, 2000), but it can be as low as 0.10 under an intact canopy (Lee, 1987). Such changes in R : FR can have profound effects on plant development and growth processes (Schmitt and Wulff, 1993; Ballaré et al., 1997; Smith and Whitelam, 1997; Smith, 2000).

Many growth parameters can be altered by a change in light quality, including differences in the internode lengths, plant height, branching patterns, patterns of plant tissue allocation, leaf size, and biomass (Lee, 1988; Lee et al., 1996, 1997, 2000; Stuefer and Huber, 1998; Fisher et al., 2002; Croster et al., 2003; Griffith and Sultan, 2005). Plants that are commonly found in open habitats (i.e., shade-avoiding plants) have been reported to be more sensitive to changes in light quality than those that occupy more shaded environments (i.e., shade tolerant) (Schmitt and Wulff, 1993; Lee et al., 1996). However, not all species respond in the same way to the same changes in light quality (Lee, 1988; Lee et al., 1996, 1997, 2000; Stuefer and Huber, 1998; Croster et al., 2003; Griffith and Sultan, 2005). The ability of a plant to respond and adjust to natural shade is critical to survival in the forest understory.

Only two studies have examined the response of lianas to changes in spectral quality of light (Lee, 1988; Fisher et al., 2002). Both were conducted on tropical lianas; none have examined temperate lianas. In contrast, more studies have focused on the response of lianas to light quantity (Carter and Teramura, 1988; Avalos and Mulkey, 1999; Nabe-Nielsen, 2002; Ellsworth et al., 2004). The results of these studies on both light quantity and light quality indicate that growth responses by lianas are highly species-specific and despite their plastic growth form, do not always respond to decreased R : FR or reduced photosynthetically active radiation (PAR) in the same manner.

In the northern temperate regions, lianas make up only a small proportion of the native flora (Gentry, 1991). However,

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with the advent of invasive lianas into the United States, this component of the vegetation has greatly increased. The consequences of filling a vacant niche (Mack, 2003) with these new species can be devastating. Introduced lianas can blanket and girdle trees in temperate forests as well as shade out young seedlings, ultimately arresting succession (McNab and Meeker, 1987). One of the most threatening of these introduced lianas in the Northeast is *Celastrus orbiculatus* Thunb. (oriental bittersweet), which was introduced to the United States in the 1860s from East Asia (Patterson, 1974). This species commonly grows along edges of forest and open areas, but also grows in the forest understory (Gleason and Cronquist, 1991; S. Leicht, personal observation). There is also a closely related native bittersweet, *C. scandens* L. (American bittersweet), that is sympatric with the invasive in the Northeast and, in fact, can hybridize with *C. orbiculatus* (Pooler, 2002). The native species is most often found in open fields, edges, and sand dunes, but rarely in the forest understory (Gleason and Cronquist, 1991; S. Leicht, personal observation). This native species is widespread in the United States and Canada, but in the Northeast, populations appear to be rapidly declining (Steward et al., 2003; L. Mehrhoff, University of Connecticut, personal communication).

Celastrus orbiculatus can survive in the forest understory under very low light conditions, while *C. scandens* does poorly in these same conditions (Leicht, 2005; S. Leicht and J. Silander, unpublished manuscript). In addition, when both species were grown at high densities, they had a strong, positive aboveground growth response in terms of aboveground biomass, height, and stem diameter; however, the magnitude of the response of *C. orbiculatus* was much greater than that of *C. scandens* (Leicht, 2005). No such positive growth response was observed at low plant densities. Based on these two separate observations, we predicted that these two species would respond differently to a low R : FR. Specifically, we predicted that *C. orbiculatus* would have a stronger positive growth response in terms of aboveground biomass, height, and diameter to decreased R : FR than the native *C. scandens*. Our prediction was based on a separate field transplant study in which *C. scandens* was generally less responsive (i.e., less developmentally plastic) to environmental changes than *C. orbiculatus* under both sun and shade conditions. These results are reported in detail elsewhere (Leicht, 2005; S. Leicht and J. Silander, unpublished manuscript). This prediction, however, does not agree with the general hypothesis that species of open habitats would be more responsive to changes in R : FR (Morgan and Smith, 1979; Schmitt and Wulff, 1993; Lee et al., 1996; Ballaré et al., 1997). Both of these species are more suited to open habitats, and it would follow that both should respond to changes in light quality. In particular, *C. scandens*, which is more of an obligate, open-habitat species, should respond even more strongly to canopy shading. Thus, our goal was to add to the little that is known about how lianas respond to a change in light quality as well as to compare the specifics of closely related invasive and native congener responses in order to contrast their success in the forested landscapes that dominate northeastern North America.

MATERIALS AND METHODS

Fruit of *C. orbiculatus* were collected from a population of plants on the campus of the University of Connecticut in October 2003, and seeds were

extracted from the dried fruit. Seeds of *C. scandens* were purchased from Sheffield's Seed Co. (Locke, New York, USA). We did not use seeds from local sources because this species is declining and rare in the Northeast (it is a "listed" species in nearby states such as New York; New York State Department of Environmental Conservation, 2000) and to have enough seed to get ample seedling numbers, we would have had to remove the majority of the fruit from local populations. Seeds of *C. orbiculatus* and *C. scandens* were cold-stratified for 3 months in cold storage at 4°C to maximize germination (Leicht, 2005). The germinated seedlings were transplanted into 3.8-L pots in the University of Connecticut Ecology and Evolutionary Biology Research Greenhouse when the cotyledons were fully expanded. They were planted in standard potting soil with Nutricote 18–6–8 with minors, Type 180 slow release fertilizer (Agrivert, Webster, Texas, USA) to sustain plant growth. The plants were watered using drip irrigation to maintain even moisture. Shade frames were constructed for all light treatments, and bamboo stakes were provided so that the plants could climb. The shading treatments were similar to the methods of Lee et al. (1996, 1997, 2000), and we used shade films from 3M (St. Paul, Minnesota, USA), the only shade films that we could obtain commercially. The control treatment was comprised of only a wooden shade frame, with plants receiving greenhouse ambient light. The low R : FR treatment was created using the 3M film (NEARL20) attached to the wooden frame. This reduced the R : FR to 0.29 and the PAR to approximately 16% of ambient. A neutral shade treatment was created using another 3M film (REAL20) that did not alter the R : FR from ambient, but reduced the PAR to 16% of ambient. Although the plants were significantly shaded as a result of both the greenhouse glass and the shade films, the PAR on cloudy days was on average 20 $\mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. This value is similar to that in New England mixed hardwood forests, where *C. orbiculatus* is commonly found in the understory (Kobe et al., 1995; Pacala et al., 1996; Caspersen et al., 1999; S. Leicht and J. Silander, unpublished manuscript; S. Leicht, unpublished data). In a separate study, *C. scandens* was able to show positive growth even under hemlock (*Tsuga canadensis*) canopies where PAR on cloudy days can be as low as 1 $\mu\text{mol photons} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Leicht 2005; S. Leicht and J. Silander, unpublished manuscript). Thus, we felt this was an appropriate light level to simulate natural forest canopy understory conditions and to examine mechanistic responses to significantly altered R : FR environment. There were two replicates of each light treatment and six plants of each species within each light treatment. The treatment frames as well as the plants within a treatment were rotated weekly to minimize positional effects in the greenhouse.

The PAR levels in each treatment type were measured using LI-COR 1400 data loggers and LI-COR 170SA quantum sensors at soil level (LI-COR, Lincoln, Nebraska, USA). One quantum sensor was located in the greenhouse without shading and the other in the shade treatment to obtain the percentage transmittance on overcast days (Nicotra et al., 1999; de Gouvenain, 2001). To determine the R : FR, we used a Skye SKR 110 sensor (Skye Instruments, Powys, UK) that reports quantum flux at 660 and 730 nm.

We measured the initial heights of the seedlings at the beginning of the experiment in May 2004. In September 2004, we measured final height, diameter, leaf number, leaf area, and the length of the internode two leaves back from the most recently expanded leaf. Leaf area was measured on the most recently fully expanded leaf using a LI-COR LI-3000A portable leaf area meter. We harvested this same leaf and weighed it to obtain both single leaf mass and specific leaf area (SLA). We cut the plant at pot level, then dried and weighed it for aboveground biomass. Finally, the stems and leaves were separately weighed to get leaf and stem mass for each plant.

Statistical analyses—Using *t* tests, we determined that the replicates of each light treatment were not significantly different from each other and thus combined them for analysis (Lee et al., 1996). We used a one-way ANOVA followed by Bonferroni multiple comparisons to determine if there were differences in the measured responses to the different light treatments. We adjusted the α level using a sequential Bonferroni procedure to avoid Type I error potentially resulting from multiple testing (Quinn and Keough, 2002). This same procedure was used to compare differences between the two species for a given response within the same light treatment. One-way ANOVA was used as opposed to a two-way ANOVA because we were interested specifically in the response of each species to the different light treatments (i.e., the main effects). We found that all the morphological measurements that were significant before the Bonferroni procedure were still significant after the adjustment. All statistical analyses were performed using the S-Plus statistical program (Insightful Corp., 2003).

TABLE 1. Comparisons of growth responses of *Celastrus orbiculatus* (CO) and *C. scandens* (CS) within a given light treatment.

| Light treatment | Height (cm) | Diameter (mm) | Internode length (cm) | Leaf number | Biomass (g) | Single leaf area (cm ²) | Single leaf mass (g) | Specific leaf area (cm ² /g) | Total leaf mass (g) | Stem mass (g) | Leaf mass : stem mass ratio |
|-----------------|-------------|---------------|-----------------------|-------------|-------------|-------------------------------------|----------------------|---|---------------------|---------------|-----------------------------|
| Control | CO = CS | CO = CS | CO = CS | CO > CS | CO > CS | CO = CS | CO = CS | CO = CS | CO > CS | CO > CS | CO = CS |
| Neutral | CO > CS | CO > CS | CO > CS | CO > CS | CO > CS | CO > CS | CO = CS | CO > CS | CO > CS | CO > CS | CO = CS |
| Low R : FR | CO > CS | CO > CS | CO > CS | CO > CS | CO > CS | CO = CS | CO = CS | CO > CS | CO > CS | CO > CS | CO > CS |

Notes: > and < indicate significant differences at the $\alpha \leq 0.05$ level; = indicates that the two species were not significantly different. R : FR, red : far red light.

RESULTS

Celastrus orbiculatus and *C. scandens* responded differently to the different light treatments. There were significant differences in response variables between species within and across light treatments (Table 1). Across all light treatments, *C. orbiculatus* had overall greater aboveground biomass, a greater number of leaves, greater total mass of leaves, and a greater stem mass than *C. scandens*. Under neutral shade, *C. orbiculatus* had significantly greater height, diameter, internode length, single leaf area, and SLA than *C. scandens*. In the low R : FR, *C. orbiculatus* had significantly greater height, greater diameter, greater internode length, SLA, and leaf mass to stem mass ratio than *C. scandens*.

Both *C. orbiculatus* and *C. scandens* had a stronger response to reduced irradiance than to the low R : FR (Table 2). Compared to unshaded controls, plants under both shade treatments were shorter, had smaller diameter stems, shorter internodes, fewer leaves, lower aboveground biomass, smaller leaf area, lower single leaf mass, lower total leaf mass, and lower stem mass than the control. The only response variable in both species that did not differ between the control and the two shade treatments was the SLA for *C. scandens*.

Several growth responses differed notably between the two shaded treatments reflecting differential effects of the low R : FR treatment. *Celastrus orbiculatus* increased in height, aboveground biomass, and total leaf mass in the low R : FR treatment as compared to the neutral shade. In contrast, *C. scandens* had no differences in aboveground biomass or height in the neutral vs. low R : FR treatments. In fact, *C. orbiculatus* in the low R : FR treatment had a height that was 15 times that of *C. scandens* on average, approximately seven times the total leaf mass, and nearly seven times the biomass. *Celastrus scandens*, however, did have a greater stem diameter, greater single leaf area, and a greater leaf mass to stem mass ratio in the low R : FR treatment compared to its performance in neutral shade (Table 2).

DISCUSSION

As expected, both species of *Celastrus* grew less in both shade treatments (16% ambient light) compared to the unshaded control. Only one character in one species (SLA for *C. scandens*) was unaffected by reduced irradiance. In a related study on both species of *Celastrus* (Leicht, 2005; S. Leicht and J. Silander, unpublished manuscript), plants grown under 10% transmittance (neutral shade) in a common garden were shorter, had smaller stem diameter, fewer leaves, and lower biomass than those grown in 100% sun under field conditions. Similar results were found by Ellsworth et al. (2004) for *C. orbiculatus* also under field conditions; plants

grown in 28% full sun were as much as 21 times greater in height and 44 times greater in biomass than those under 2% shade. Although both species in this study had a reduction in height and biomass in neutral shade, *C. orbiculatus* showed less of a reduction than *C. scandens*: 72% reduction in height vs. 95%, 95% reduction in biomass vs. 98%, and 86% reduction in leaf numbers vs. 92%. Thus, reducing the light quantity had an overall greater impact on the native *C. scandens* than on *C. orbiculatus*.

Celastrus orbiculatus and *C. scandens* also responded differently to changes in light quality (i.e., the low R : FR and neutral shade treatment responses were different). *Celastrus orbiculatus* responded to the low R : FR treatment by increasing aboveground biomass, height, and total leaf mass relative to the neutral shade. *Celastrus scandens* responded by increasing its leaf area, leaf mass to stem mass ratio as well as stem diameter. These differences represent a response due to light quality (Croster et al., 2003). The response of *C. orbiculatus* to a simulated canopy indicates that the species, if in the forest understory, may increase its height and ultimately aboveground biomass, enabling it to more efficiently forage for light gaps. In a field transplant study (Leicht, 2005; S. Leicht and J. Silander, unpublished manuscript), *C. orbiculatus* adjusted under natural canopies by increasing its height and aboveground biomass more than *C. scandens*. By significantly increasing individual leaf area, as well as the amount of leaf mass compared to stem mass, *C. scandens*, under closed canopies (relative to neutral shade), increases its ability to capture available understory light but appears to be unable to actively forage for potential gaps. In other studies on the effect of reduced R : FR on congeners of various growth forms, the species studied also differed in the response of various measured traits. For example, when examining tropical Asian *Hopea* tree species, Lee et al. (1997) showed that one congener increased internode length when subjected to changes in light quality and quantity, while the other was not affected. Two *Potentilla* species also responded differently from one another, with one species increasing its leaf area more than the other when subjected to lowered R : FR (Stuefer and Huber, 1998). *Polygonum* congeners also differed in their response to neutral shade vs. natural shade; *P. persicaria* had greater plasticity to neutral shade compared to natural shade than *P. hydro Piper* (Griffith and Sultan, 2005).

The prevailing hypothesis is that plants of open habitats (i.e., shade avoiding) respond more strongly to a change in the R : FR (Morgan and Smith, 1979; Schmitt and Wulff, 1993; Lee et al., 1996; Ballaré et al., 1997; Smith and Whitelam, 1997; Croster et al., 2003). Additionally, these more shade-intolerant plants are thought to allocate fewer resources to leaves under shaded conditions (Morgan and Smith, 1979). These hypotheses, however, may not always hold true. Studying Asian *Hopea* species, Lee et al. (1997) found that

TABLE 2. Comparisons of growth parameters in different light treatments of *Celastrus orbiculatus* and *C. scandens*.

| Light treatment | Height (cm) | Diameter (mm) | Internode length (cm) | Leaf number | Biomass (g) | Single leaf area (cm ²) | Single leaf mass (g) | Specific leaf area (cm ² /g) | Total leaf mass (g) | Stem mass (g) | Leaf mass : stem mass |
|------------------------------|---------------------------|------------------------|------------------------|-----------------------|-------------------------|-------------------------------------|----------------------------|---|-------------------------|-------------------------|------------------------|
| <i>Celastrus orbiculatus</i> | | | | | | | | | | | |
| Control | 285.5 ± 21.4 ^A | 3.8 ± 0.4 ^A | 3.3 ± 0.6 ^A | 297 ± 51 ^A | 26.9 ± 3.9 ^A | 27.5 ± 3.5 ^A | 0.097 ± 0.018 ^A | 289.2 ± 49.2 ^A | 14.3 ± 2.1 ^A | 12.7 ± 2.7 ^A | 1.2 ± 0.3 ^A |
| Neutral | 81.3 ± 48.8 ^B | 1.0 ± 0.2 ^B | 2.4 ± 1.1 ^B | 40 ± 15 ^B | 1.4 ± 0.6 ^B | 23.5 ± 3.9 ^B | 0.038 ± 0.007 ^B | 632.9 ± 74.0 ^B | 0.9 ± 0.3 ^B | 0.5 ± 0.3 ^B | 2.1 ± 0.8 ^B |
| Low R : FR | 124.2 ± 34.5 ^C | 1.3 ± 0.3 ^B | 3.0 ± 1.1 ^A | 55 ± 12 ^B | 2.0 ± 0.6 ^C | 23.0 ± 3.8 ^B | 0.036 ± 0.008 ^B | 657.2 ± 78.3 ^B | 1.3 ± 0.3 ^C | 0.7 ± 0.3 ^B | 1.9 ± 0.4 ^B |
| <i>Celastrus scandens</i> | | | | | | | | | | | |
| Control | 211.9 ± 37.7 ^A | 3.9 ± 0.6 ^A | 3.3 ± 0.8 ^A | 113 ± 47 ^A | 13.6 ± 4.2 ^A | 31.1 ± 6.7 ^A | 0.092 ± 0.028 ^A | 351.0 ± 71.2 ^A | 7.7 ± 2.4 ^A | 5.9 ± 1.9 ^A | 1.3 ± 0.2 ^A |
| Neutral | 10.1 ± 3.5 ^B | 0.4 ± 0.2 ^B | 1.2 ± 0.5 ^B | 9 ± 5 ^B | 0.2 ± 0.1 ^B | 13.8 ± 5.0 ^B | 0.035 ± 0.011 ^B | 400.8 ± 82.6 ^A | 0.2 ± 0.1 ^B | 0.1 ± 0.03 ^B | 1.9 ± 0.5 ^B |
| Low R : FR | 8.1 ± 3.6 ^B | 0.7 ± 0.3 ^C | 1.0 ± 0.7 ^B | 8 ± 3 ^B | 0.3 ± 0.2 ^B | 21.5 ± 8.9 ^C | 0.055 ± 0.021 ^B | 386.0 ± 62.0 ^A | 0.2 ± 0.1 ^B | 0.1 ± 0.04 ^B | 2.9 ± 0.9 ^C |

Notes: Values are means ± SD. Different letters indicate significant differences between treatments at the $\alpha \leq 0.05$ level within a given species. R : FR = red : far red light.

a species characteristic of open habitats responded less to changes in R : FR than the forest understory species. But, in another study, Lee et al. (1996) showed that the apparent habitat preferences of certain species do not necessarily predict how the species will respond to changes in light quality. The response of *C. orbiculatus* to reduced R : FR under canopy cover seems to indicate a switch to a “searching” (Lee et al., 1996) or “foraging” strategy (Ballaré et al., 1997). By increasing its height (15 times that of *C. scandens* in the low R:FR), *C. orbiculatus* has considerably greater potential to forage for light gaps or sunflecks. *Celastrus scandens* did not increase in height under altered shade, but instead had a 96% reduction in height compared to the control and a 20% reduction compared to neutral shade. This reduction in growth would result in a reduced ability to forage for light gaps in the forest understory. The increased allocation to leaves of *C. scandens* might be interpreted as it being a more shade-tolerant species than *C. orbiculatus*. However, when *C. scandens* was transplanted under natural forest canopies, 32% were dead after two growing seasons as compared to only 10% of *C. orbiculatus* transplants (Leicht, 2005; S. Leicht and J. Silander, unpublished manuscript). In a common garden study using neutral shade conditions (10% transmittance), after 3 years, 78% of *C. scandens* were dead compared to 38% of *C. orbiculatus* (Leicht, 2005). Thus, *C. scandens* appears to follow a “sit and wait” strategy (Greenberg et al., 2001). Its only plastic response appears to be an increased leaf area in a strategy to capture more light. But unless a gap opens up within a short period of time, it will die.

Because *C. scandens* is a species that prefers more open habitats, it is surprising that it does not respond with increased foraging behavior like *C. orbiculatus*. However, *C. scandens* also has lower photosynthetic rates compared to *C. orbiculatus*, in both full-sun and shade conditions (Leicht, 2005). This reduced photosynthetic ability under shade could reduce this species’ ability to successfully forage for additional light resources, effectively excluding it from the forest understory. The larger leaves it produces is likely an attempt to compensate for a lowered photosynthetic rate by increasing the leaf area for photosynthesis (Griffith and Sultan, 2005). *Celastrus orbiculatus* on the other hand, although it is more successful in open habitats, has the ability to acquire enough photosynthate even under shaded conditions in order to grow into the forest canopy (Leicht 2005; S. Leicht and J. Silander, unpublished manuscript).

Lianas, because of their plastic growth form (Schnitzer and Bongers, 2002), may be expected to respond readily to a low R : FR. However, this study, as well as others, has shown that the responses of lianas to changes in light quality can be variable. When three tropical lianas (confamilial, but not congeners) were compared in their responses to different shading regimes (Lee, 1988), they all responded very differently. The one exotic liana (*Abrus precatorius*) in the study by Lee (1988) had an increased allocation to total leaf mass under low R : FR conditions similar to that observed in *C. orbiculatus*. However, it also had an increase of stem mass to length, greater specific leaf mass (measured in milligrams per square centimeter), greater leaf area, and shorter internodes (Lee, 1988). The increased allocation to leaf mass as well as greater leaf area could have given the exotic *A. precatorius* an advantage over the native species, in that the additional leaf mass could lead to an increase in potential photosynthesis in the understory.

The ability to respond to low R : FR has implications for the

ability of lianas to respond to neighboring competitors especially to those at high densities (Leicht, 2005). The greater transmitted and reflected FR light can allow a plant to sense its neighbors and in some cases respond by rapidly growing to overtop them (Schmitt and Wulff, 1993). For example, Ballaré et al. (1990) showed that if the reflectance of FR light from neighboring plants was reduced, the plants did not elongate rapidly when surrounded by neighbors. These studies, however, only examined herbaceous annuals, which are obviously very different from woody perennial climbers. For a liana, the ability to sense neighbors could be important in order to exploit nearby plants to use as climbing supports. Additionally, if lianas were able to sense their neighbors, especially neighboring lianas, through transmitted and reflected FR light, rapid elongation would allow them to overtop their neighbors. This result is reflected in the large, highly dense stands of *C. orbiculatus* that are seen in some of the worst incursions of the species where individuals send out long intertwining and self-supporting leaders vs. where they grow singly at low densities (Leicht, 2005).

Clearly, more research is needed in order to understand how light quality under a forest canopy affects plant growth. The research on the effects of a low R : FR ratio does not apparently reveal any single set of predictable patterns in plants. This study has added to the slowly growing body of literature that illustrates that the significant responses of a given plant to low R : FR may be species specific and that generalizations about the effect of a low R : FR cannot be made at this time. Studying the different ways that plants respond to a low R : FR is important because it provides a mechanistic understanding of the response process in forest understory conditions. An increased growth response to a low R : FR may give invasive species an advantage over their native counterparts in a shaded forest understory. The use of neutral shade simply cannot provide this information. Even closely related congeners can behave differently when exposed to low R : FR, which emphasizes the need for studying these responses on a species-by-species basis.

In summary, *C. orbiculatus* has the ability to increase its height to 15 times that of *C. scandens* when under low R : FR, which would allow it to successfully infiltrate a forest understory and more effectively forage for limiting light resources. The ability of *C. orbiculatus* to grow across such a wide range of light conditions presents a challenge for its control. This species must be removed, even from the forest understory, because it can forage successfully for canopy gaps. The ability to respond to low R : FR therefore, may explain why *C. orbiculatus* is observed in the forest understory while *C. scandens* is absent in this habitat type. The inferiority of *C. scandens* across a range of conditions will make its preservation in the Northeast challenging. Because the forests of the Northeast are regenerating, suitable habitat for *C. scandens* is rapidly disappearing. It is important to preserve open habitats for the growth of this unique native temperate liana species, while at the same time excluding other invasive plants (such as *C. orbiculatus*) that have come to dominate these disturbed areas in much of the Northeast.

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