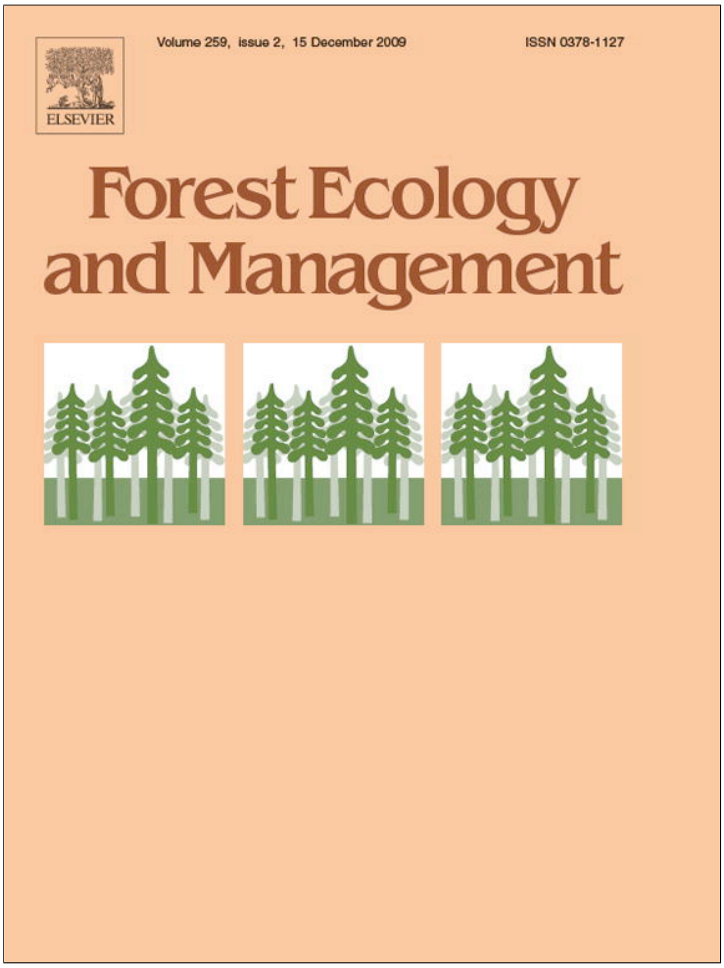

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Impacts of temperate lianas on tree growth in young deciduous forests

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Lianas are often overlooked in temperate ecological studies even though they are important components of forest communities. While lianas have been shown to damage tropical canopy trees and reduce the growth of juvenile trees, the impact of lianas on canopy tree growth in temperate systems is largely unknown. Growth of trees $\geq$8 cm dbh was examined over a 9-year period within 50-year old post-agricultural secondary forests in the Piedmont region of New Jersey, USA. Five lianas, *Celastrus orbiculatus*, *Lonicera japonica*, *Parthenocissus quinquefolia*, *Toxicodendron radicans*, and *Vitis* species, occurred throughout the forest. Total liana basal area, number of stems, and percent cover within host trees were evaluated to assess liana burdens on 606 previously censused trees. These data were related to tree growth to assess liana impacts. Forest trees were separated based on their dominance in the canopy to determine whether lianas had the potential to influence forest composition. In general, lianas in the forests were fairly abundant, with 68% of the trees having at least one liana present. On average, each tree supported 9.7 cm^2 of liana basal area and 23% of the canopy was covered by lianas. Most of the variation in tree growth was related to the dominance of trees within the canopy, with canopy dominant and co-dominant trees growing 2.5× more than suppressed trees. Liana basal area and number of lianas stems were not related to tree growth, but liana canopy cover decreased tree growth. However, not all trees were equally affected as canopy cover of lianas only reduced growth in dominant and co-dominant trees. Lianas were most influential on host tree growth in unsuppressed trees when occupying a majority of the canopy, only a minority of forest trees. This suppression was not related to differential liana colonization of canopy trees as all canopy classes supported equivalent liana burdens. Though lianas impacted only a minority of the trees in this system, some liana species, *C. orbiculatus* and *Vitis* spp., are still increasing and may pose future risks to forest growth and development.

1. Introduction

Despite the ubiquity of lianas (woody vines) in most forests, their role in tree growth and forest dynamics are poorly understood relative to other life forms, especially in temperate systems. Abundances and potential impacts of lianas may often be underestimated due to the greater leaf biomass per basal area of lianas compared to trees (Gerwing and Farias, 2000). For example, lianas can contribute 5% of forest basal area while occupying 30% of the canopy in the tropics (Putz, 1983). The ability of lianas to cover more space with less biomass than trees can increase competitive potential of lianas (Gartner, 1991; Collins and Wein, 1993). For this reason, lianas must be incorporated into forest regeneration research to develop a thorough understanding of forest dynamics and effective management strategies.

Temporally, liana composition and abundance vary with age of the forest. Following disturbance and fragmentation, liana abundance increases within young communities and the adjacent remnant forests (Putz, 1984; Putz and Chai, 1987; Balée and Campbell, 1990; Laurance et al., 2001; Pérez-Salicrup et al., 2001; Londré and Schnitzer, 2006; Allen et al., 2007). Increased liana abundance in young and disturbed forests suggests that these forests may be at a higher risk for liana impacts. Lianas persist in mature forests but remain more abundant along edges. Even in mature tropical forests with little structural disturbance, liana abundances have increased in recent years, possibly due to increased atmospheric CO_2 (Phillips et al., 2002; Wright et al., 2004).

Although lianas are important components of many forest ecosystems, most liana research has focused on tropical systems. On mature tropical trees, lianas remove tree parts (bark, branches and buds) and reshape crowns which can lead to decreased growth, fecundity, and dominance of trees (Lowe and Walker, 1977; Stevens, 1987; Clark and Clark, 1990; Pérez-Salicrup and Barker, 2000; Schnitzer et al., 2005). Once in the canopy, lianas overtop the highest layer of tree leaves, reducing light availability to the canopy and forest below (Avalos et al., 1999; Pérez-Salicrup, 2001). In several tropical communities,

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lianas have a greater association with late successional trees than early successional trees and this has been speculated to influence tropical forest succession (Putz, 1984; Clark and Clark, 1990; Schnitzer et al., 2000).

Compared to the tropics, lianas are typically less abundant and diverse in temperate forests. Temperate liana abundance is greatest in disturbed areas and along forest edges (Buron et al., 1998; Londré and Schnitzer, 2006). In areas of heavy liana cover, it has been suggested that lianas may stall deciduous forest regeneration at a shrub dominant community (Fike and Niering, 1999). Several temperate lianas persist in the understory as suppressed individuals until resources, usually light, become available and growth rates increase rapidly (Greenberg et al., 2001; Leicht and Silander, 2006). Impacts of lianas on canopy trees can be visually apparent, including trunk constriction and increased injury and mortality in winter storms (Lutz, 1943; Siccama et al., 1976). Some studies examining liana–canopy tree interactions measure short-term impacts such as fecundity or mortality (Stevens, 1987), though most research has focused on the growth of seedlings and saplings (Dillenburg et al., 1993; Lewis and Tanner, 2000; Schnitzer et al., 2005). As they occur in both the understory and forest canopy, lianas appear potentially capable of influencing tree growth at all demographic stages. Competition with lianas can reduce the growth of tree saplings, but the impact of lianas on canopy tree growth has not been directly assessed in temperate systems. As canopy tree growth is critical for the health and economic value of a forest, this represents a critical research need.

To understand the recovery of deciduous forest communities and to assess management needs, it is important to quantify liana impacts on canopy tree growth. We examined forest trees over a 9-year period to determine whether lianas had an impact on canopy tree growth in a series of young secondary temperate forests. Furthermore, we evaluate the role of canopy dominance in mediating liana effects. Finally, we compared the influence of several measures of liana burdens (canopy cover, number of stems and basal area) on tree growth to assess whether growth impacts were likely driven by above- or belowground liana–tree interactions.

2. Material and methods

2.1. Study site

The study area was located within the Piedmont region of New Jersey, USA in the Hutcheson Memorial Forest Center (HMFC; 40.30°N, 74.34°W). The Buell–Small Succession Study (BSS) is located within the HMFC and consists of 10 agricultural fields that were experimentally abandoned between 1958 and 1966. In each field, 48 permanent 1 m^2 plots were established in a regular pattern for annual vegetation surveys. Due to long term goals of the BSS, to continually examine natural vegetation dynamics during old field succession, manipulations within the study area are prohibited. The experimental BSS fields are adjacent to an old-growth oak-hickory forest which has served as a seed source for forest regeneration in the fields (Buell, 1957; Monk, 1961; Buell et al., 1971). Mean monthly temperatures range from $-1.6\,^{\circ}C$ in January to $22.4\,^{\circ}C$ in August and mean annual precipitation is 116.1 cm evenly distributed throughout the year (New Jersey State Climatologist; National Climate Data Center). For more information regarding the BSS, see Pickett (1982).

2.2. Study species

The liana species most abundant in the BSS and the focus of this research were: *Parthenocissus quinquefolia* (Virginia creeper; Vitaceae), *Toxicodendron radicans* (poison ivy; Anacardiaceae), *Vitis* spp. (grape, including *V. aestivalis*, *V. labrusca*, *V. riparia*, *V. palmata*, and *V. vulpina*; Vitaceae), *Lonicera japonica* (Japanese honeysuckle; Caprifoliaceae), and *Celastrus orbiculatus* (oriental bittersweet; Celastraceae). Within the BSS, understory *Vitis* plants were initially identified to species, but once in the canopy correct species identification became difficult and plants were identified to genus only. Therefore, all *Vitis* species were evaluated collectively.

Although all five lianas spread via bird dispersed fruits and share the fundamental characteristics of lianas, the species vary in origin, climbing mechanisms, and invasiveness. *P. quinquefolia* is native and abundant in mid to late successional communities throughout eastern and midwestern North America. Specialized tendrils ending with adhesive discs allow *P. quinquefolia* to climb nearly any structure large enough to support its weight (Gleason and Cronquist, 1991). *T. radicans* is native to eastern North America. Characteristic aerial rootlets produced along the stem attach *T. radicans* to woody stems as it climbs to the forest canopy (Mitch, 1995). *Vitis* spp. are native to North America and commonly occur later in succession (Fike and Niering, 1999; Londré and Schnitzer, 2006). Tendrils that aid *Vitis* spp. in climbing allow the liana to extend into the upper canopy on smaller branches and to easily enter neighboring canopies. *Lonicera japonica* is native to Asia and climbs via twining stems. Once established, plants become highly invasive in eastern and southern North America (Schweitzer and Larson, 1999; Schierenbeck, 2004). However, seed production of *L. japonica* in North America is limited due to lack of suitable pollinators (Larson et al., 2002). *C. orbiculatus* is native to southeast Asia and has since become a problematic twining liana in the eastern United States following introduction as an ornamental plant (Greenberg et al., 2001).

2.3. Field sampling

In the summer of 1999, all trees with a dbh ≥8 cm that originated in or overhung one of the permanent BSS plots were surveyed. Each tree was tagged with a unique identification number and dbh was recorded. For each tree, level of canopy dominance (dominant, co-dominant, intermediate, or overtopped) was recorded based on Smith's (1986) classifications. Dominant trees had crowns above the general canopy layer and received full light. Co-dominant trees formed the canopy layer and generally received full sun, except along the edge of the crown. Intermediate trees also had crowns that reached into the canopy, but received less direct light and generally had small crowns. Overtopped trees received no direct light and were found below the canopy layer. Based on data from the BSS plots, lianas were present in 1999 but climbing lianas were not surveyed at this time.

In the summer of 2008, tagged trees were re-surveyed, repeating the methods used in 1999. In addition to measuring trees, all lianas growing on tagged trees were surveyed in 2008. There was no diameter minimum for liana stems; all lianas which climbed at least 1 m up a host tree were measured. For each liana species, percent cover within the host tree canopy was visually estimated and dbh measured for all stems, following the standard liana measuring protocol of Gerwing et al. (2006). Canopy cover of lianas was used to assess aboveground competition while measurements for lianas along tree trunks, stem count and basal area, were used as a proxy for belowground competition. Although liana stems present on tree trunks were not the ideal measurement for belowground competition, limitations of the study site prohibited us from manipulations that could more clearly examine belowground interactions, such as trenching or liana cutting. When lianas entered a marked tree via an adjacent tree canopy, only percent canopy cover was recorded to allow for partial separation of above- and belowground effects.

2.4. Data analysis

Tree growth from 1999 to 2008 was evaluated using both relative growth rate and absolute radial growth. Changes in tree basal area (BA) between 1999 (t_1) and 2008 (t_2) were used to calculate relative growth rates [$(\ln \mathrm{BA}_2 - \ln \mathrm{BA}_1)/(t_2 - t_1)$] of individual trees. Absolute radial growth was calculated as the difference in radius (cm) from 2008 and 1999 ($r_{t_2} - r_{t_1}$). Both absolute and relative tree growth were related to liana load variables (liana basal area, stem count, and canopy cover) of all liana species collectively. Impacts of individual liana species on tree growth could not be examined due to an inadequate sample size of species specific liana burdens. Results from absolute growth and relative growth rates of trees were similar, so only absolute radial growth is reported here. For analysis, trees were grouped based on level of liana burden (none, low and high). These groups were defined for each liana burden measure as: basal area (0, <1, and ≥1 cm^2), stem count (0, 1–10, and >10 stems), and canopy cover (0, 1–50%, and >50% cover). Separate ANOVAs for each variable of liana burden were utilized to relate liana burdens to tree growth (SAS 9.1; SAS Institute Inc., Cary, NC). Tree canopy dominance (dominant, co-dominant, intermediate, and overtopped) was included in each ANOVA since it was expected that differences in canopy position, and thus light levels, would generate differences in tree growth. Least squared means, with Bonferroni corrections for multiple comparisons to reduce the chance of type I error, indicated differences among individual liana burden categories and among canopy dominance classes of trees.

3. Results

Within the forests of the BSS, two-thirds of the trees were dominant or co-dominant canopy trees (dominant, 179 individuals; co-dominant, 219 individuals; intermediate, 97 individuals; overtopped, 106 individuals). Tree species within the forest included: *Acer* (including *A. negundo*, *A. platanoides* and *A. rubrum*), *Ailanthus altissima*, *Carya* (including *C. glabra*, *C. ovalis*, and *C. ovata*), *Cornus florida*, *Fraxinus* (including *F. americana* and *F. pennsylvannia*), *Juglans nigra*, *Juniperus virginiana*, *Prunus* (including *P. avium*, *P. hortulana*, and *P. serotina*), and *Quercus* (including *Q. alba*, *Q. coccinea*, *Q. palustris*, *Q. rubra*, and *Q. velutina*). The most abundant tree species at the site was *J. virginiana* (241 individuals) followed by *Acer* spp. (139) and *C. florida* (66). Dominant and co-dominant trees grew 2.5× more than intermediate and overtopped trees.

A total of 2708 liana stems were measured in 2008. Of the 606 trees measured in 1999 and alive in 2008, 413 (68.2%) had one or more lianas present on the trunk or in the canopy. On average, each tree supported 4.47 ± 0.31 liana stems totaling a basal area of 9.7 ± 0.66 cm^2, which covered 22.8 ± 1.28% of the canopy. Also, an average of one liana species was present per tree. Liana densities at the site were 4893 liana stems/ha with a basal area of 10,725 cm^2 of lianas/ha. The distribution of lianas was relatively consistent across tree canopy classes. Liana basal area ($F_{3,597} = 0.95$; $p = 0.416$; $R^2 = 0.005$) and canopy cover ($F_{3,597} = 1.82$; $p = 0.1421$; $R^2 = 0.009$) did not vary with host tree canopy class. The number of liana stems was weakly associated with tree canopy class ($F_{3,597} = 11.91$; $p = 0.0001$; $R^2 = 0.056$), with dominant trees supporting more liana stems than all other canopy dominance class.

Liana burdens in the canopy and on the trunk had different associations with tree growth. Both canopy dominance of host tree and liana canopy cover were significantly related to tree growth (Table 1). Trees with >50% liana canopy cover grew significantly less than trees with less canopy cover. The interaction between canopy dominance and liana cover was not significant, however growth of only dominant and co-dominant trees decreased as liana canopy cover increased. Of the variation in tree growth explained collectively by the model, tree canopy dominance accounted for roughly two-thirds of the variation (Table 1). Models examining relationships of lianas located on tree trunks and host tree growth were significant, but tree growth varied only with host tree canopy dominance class (Table 1). The interactions between host tree canopy dominance and liana trunk variables were also not significant (Table 1, Figs. 1–3).

Table 1
Results from ANOVAs examining the impacts of the liana load variables and tree canopy dominance (canopy cover, stem count, and basal area) on tree growth.

	R^2	df	F	p
Model	0.2540	11, 589	18.23	<0.0001
Canopy cover		2, 589	8.17	0.0003
Canopy dominance		3, 589	38.20	<0.0001
Dominance × cover		6, 589	1.45	0.1945
Model	0.2266	11, 589	15.69	<0.0001
Stem count		2, 589	1.38	0.2525
Canopy dominance		3, 589	49.10	<0.0001
Dominance × stem		6, 589	0.66	0.6859
Model	0.2250	11, 589	15.55	<0.0001
Basal area		2, 589	1.03	0.3568
Canopy dominance		3, 589	53.72	<0.0001
Dominance × BA		6, 589	0.45	0.8483

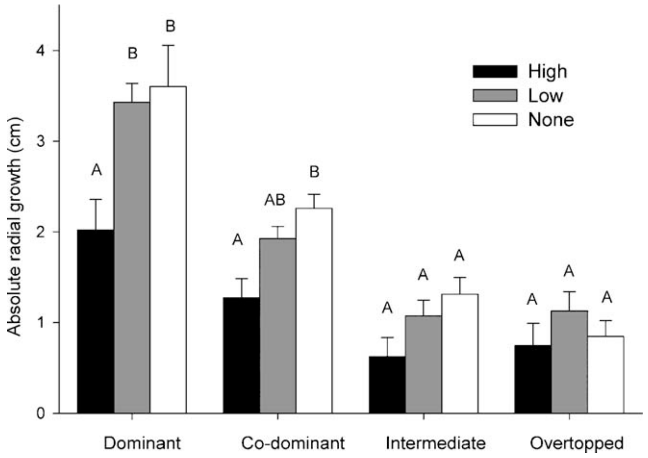

Fig. 1. Tree growth over 9 years in relation to liana canopy cover and tree canopy dominance. Liana burden class indicated by bar color: high is shown in black, low in light grey and none in white. Tree growth among dominance and liana burden classes was significantly different and letters above bars indicate differences in tree growth within each dominance class based on least squared means.

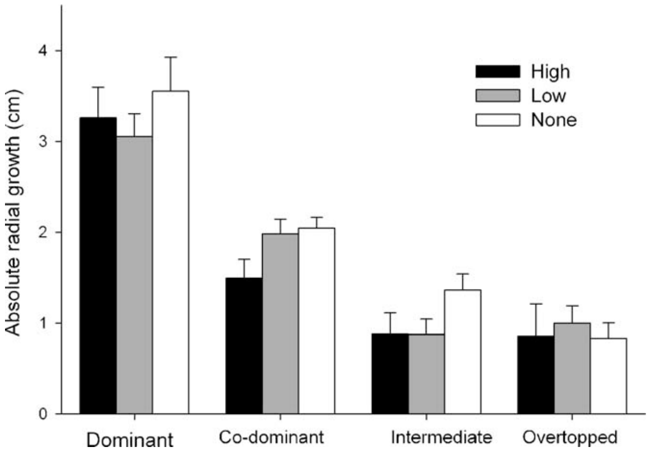

Fig. 2. Tree growth over 9 years in relation to liana stem count and tree canopy dominance. Liana burden class indicated by bar color: high is shown in black, low in light grey and none in white. Tree growth among canopy dominance classes was significantly different, but there were no differences among liana burden classes.

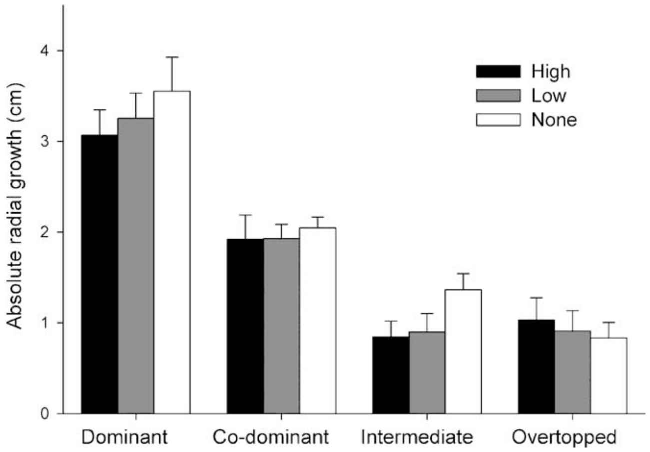

Fig. 3. Tree growth over 9 years in relation to liana basal area (cm^2) and tree canopy dominance. Liana burden class indicated by bar color: high is shown in black, low in light grey and none in white. Tree growth among canopy dominance classes was significantly different, but there were no differences among liana burden classes.

4. Discussion

In 2008, the forests of the BSS were still young, with canopy closure occurring about 20 years prior. The tree community at the time of sampling was dominated by early successional genera. Most of the variation in tree growth explained by our analysis was related to canopy dominance of the tree. Overall, dominant and co-dominant trees grew 2.5× more than intermediate and overtopped trees. The difference in growth was probably a result of light availability. Dominant and co-dominant trees received direct sunlight while light availability to intermediate and overtopped trees was limited. During this time, growth of intermediate and overtopped trees was presumably suppressed by shading from dominant and co-dominant trees.

Lianas in this system were fairly abundant, occurring on 68% of trees and on average occupying 23% of a tree's canopy. Although there is not a unified method for calculating liana densities within forests, liana densities at the BSS were similar to other temperate, deciduous forests. With a liana density of 4893 liana stems/ha, liana density at the BSS was less than densities found by Talley et al. (1996) who found 43,000 stems/ha in an old-growth mixed mesophytic hardwood of Alabama and greater than densities found by Londré and Schnitzer (2006) who found 275 ± 90 stems/ha within the edge habitat of temperate deciduous forests of southern Wisconsin. Even when only genera present at both sites were considered (*Vitis* spp., *T. radicans*, *C. orbiculatus*, *P. quinquefolia*), the BSS site still had greater liana density (1259 stems/ha) than the temperate deciduous forest of southern Wisconsin. At a more similar latitude to the BSS, Fike and Niering (1999) found lianas to be problematic to forest regeneration at basal areas of 15,000 cm^2/ha within young oak and central hardwood forests of Connecticut. Liana basal area at the BSS was 10,725 cm^2/ha and although individual trees had reduced growth, liana density was not great enough to uniformly alter forest dynamics.

Liana impacts on tree growth may be generated by both aboveground light competition in the canopy and belowground root competition. Differentiating the effects of above- and belowground competition provides a mechanistic understanding of liana–tree interactions. For example, belowground liana competition of *L. japonica* and *P. quinquefolia* has been shown to decrease growth of *Liquidambar styraciflua* tree seedlings, while aboveground competition had no effect (Dillenburg et al., 1993). On isolated trees in an abandoned field, *L. japonica* reduced growth of mature *L. styraciflua* trees through belowground competition (Whigham, 1984). As the previous studies were conducted in open habitats, it is unclear whether the above- and belowground effects of lianas on tree growth will be consistent in temperate forests.

By comparing tree growth between liana canopy cover and amount of stems climbing the trunk, above- and belowground liana–tree interactions were able to be partially separated at the site. Although lianas in the canopy also frequently competed with trees belowground and lianas climbing trees were not necessarily rooted directly beneath trees, differences between measures of liana burden were seen. Liana stems and their associated underground interactions did not appear to impair tree growth, as reduced tree growth was not seen with increased density and basal area of liana stems. In contrast, liana canopy cover was associated with decreased tree growth, particularly in unsuppressed individuals. Though we cannot definitively separate above- and belowground effects, our results suggest that canopy interactions were more directly linked to decreased tree growth in this forested system.

These results indicate that lianas were associated with decreased tree growth at the BSS. The model examining liana canopy cover explained ~25% of the total variation in tree growth, with about one-fourth of this associated with liana canopy cover, and the remaining associated with tree canopy dominance. Many factors influence tree growth within young forests and lianas were only one influence. In unsuppressed trees with over half of their canopy covered by lianas a ~50% decreased in tree growth was observed. Although this was a substantial decrease in growth, only 8.9% of the trees were dominant or co-dominant with >50% liana canopy cover. Lianas were related to decreased growth of individual trees, but did not appear to have as much of an impact on the entire system. Lianas may have a greater and more consistent influence on tree growth in forests that develop higher liana canopy cover. Forests with higher liana densities may include sites experiencing increased liana growth associated with global climate change, recently disturbed sites, and those with increasing populations of invasive lianas (Wright et al., 2004; Londré and Schnitzer, 2006).

The successional nature of the forest and liana communities poses some difficulties in interpreting these data. Many of the suppressed trees would have been early successional species, making direct comparison of dominance classes problematic. Furthermore, early successional trees were associated with early successional lianas, such as *L. japonica* and *P. quinquefolia*, and resulted in variation in the composition of lianas in the canopy (Ladwig, unpublished data). This variation makes it difficult to determine whether the lack of impacts of lianas on suppressed trees is due to the composition of suppressed trees, the composition of their liana communities, or their position within the canopy. However, comparisons within dominance classes should not be confounded and show clear suppression of tree growth at high liana canopy cover.

Liana cover and tree growth over the past 9 years are not necessarily indicative of future interactions at the BSS. While canopy cover of three of the liana species has remained constant or declined over the past 9 years, *C. orbiculatus* and *Vitis* spp. cover increased steadily during this period (Ladwig and Meiners, in press). *C. orbiculatus* is a regionally problematic invasive species present at the site, but had low frequency and cover relative to other liana species within the BSS. Likewise, canopy coverage of *Vitis* spp. was low early in succession and has steadily increased over the past 15 years (Ladwig and Meiners, in press). In another northeastern forest, *C. orbiculatus* acted as a trellis for *V. labrusca* and the pair halted forest succession as they became the dominant species in the community (Fike and Niering, 1999). Young *C. orbiculatus* were observed climbing existing liana stems which offered a quick pathway to the canopy. Due to the high number of trees with lianas already present, *C. orbiculatus* colonization of the forest canopy has the potential to be faster than that of earlier colonizing lianas. Additionally, *Vitis* spp. are able to extend to the top-most layer of even the largest trees in the canopy (Gleason and Cronquist, 1991). Continued expansion of these lianas that are likely to develop extensive cover in the canopy may generate reduction in tree growth as the forest matures.

This study suggests some methodological approaches to studying liana impacts in forests. Of the three liana burden variables, canopy cover, stem count, and basal area, only liana canopy cover was significantly related to tree growth. In addition to being the most useful measurement associated with decreased tree growth, liana canopy cover was also by far the fastest sampling technique. If our methods were to be repeated for studies of liana–tree interactions within forests, measuring basal area of lianas, the most time intensive liana load measurement, may be unnecessary.

5. Conclusions

Lianas have been an important component of these regenerating forests ever since entering the community early in succession. Though we specifically focus here on the growth of established trees, lianas were abundant throughout the site during succession (Ladwig and Meiners, in press). These forests regenerated with high liana cover, so lianas did not precluded the regeneration of forests, though they may have had some influence. Similarly, lianas reduced the growth of some trees over the 9-year period investigated, but this influence was restricted to a small portion of the community despite the abundance of lianas.

Although they did not have catastrophic effects on overall forest health and regeneration, lianas may decrease the economic value of a forest by reducing the growth of dominant trees and therefore delay harvests. As decreased tree growth under high liana loads were mostly seen for dominant and co-dominant trees, these trees may respond well to management practices that release them from liana competition. However, lightly colonized trees are unlikely to benefit from this treatment. The abundance of lianas both in the canopy and in the understory (this study; Ladwig and Meiners, in press) suggests that lianas are likely to remain in high abundance for long periods of time and may represent a continual management concern. Sites which develop greater liana densities than those documented here are likely to show even greater impacts.

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