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Impacts of temperate lianas on tree growth in young deciduous forests

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ABSTRACT

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 postagricultural secondary forests in the Piedmont region of New Jersey, USA. Five lianas, Celastrus orbiculatus, Lonicera japonica, Parthenocissus auinauefolia, 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 cm² 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.

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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 9year 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 m² 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 oldgrowth 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 °C in January to 22.4 °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; Vita-

ceae), *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 \geq 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.

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