Liana host preference and implications for deciduous forest regeneration 1

Authors: Ladwig, Laura M., and Meiners, Scott J.

Source: The Journal of the Torrey Botanical Society, 137(1) : 103-112

Published By: Torrey Botanical Society

URL: https://doi.org/10.3159/09-RA-041.1

Journal of the Torrey Botanical Society 137(1), 2010, pp. 103–112

Liana host preference and implications for deciduous forest regeneration[1]

Laura M. Ladwig[2,3] **and Scott J. Meiners**

Department of Biological Sciences, Eastern Illinois University, Charleston, IL 61920

LADWIG, L. M. AND S. J. MEINERS (Department of Biological Sciences, Eastern Illinois University, Charleston, IL 61920). Liana host preference and implications for deciduous forest regeneration. J. Torrey Bot. Soc. 137: 103–112. 2010.—Lianas have the potential to shape forest communities and alter forest regeneration. However, impacts of lianas on forest regeneration, particularly in temperate forests, are largely unstudied. To understand potential liana impacts on the community we need to first know the location and intensity of liana burdens on host trees. We examined liana-tree host preferences within a series of young regenerating deciduous forests in the Piedmont region of New Jersey, USA. Established trees ($\geq$ 5 cm dbh) and the lianas associated with each tree were surveyed in 2008. The five most abundant liana species were *Celastrus orbiculatus*, *Lonicera japonica*, *Parthenocissus quinquefolia*, *Toxicodendron radicans*, and *Vitis* species. Host preference for each liana species was measured in two ways, as colonization on tree trunks and coverage in the canopy. Host preferences based on tree species and tree size were compared among liana species. A total of 798 trees were measured and lianas occurred on 64% of them. Host preferences were generally consistent between colonization and canopy expansion, suggesting the same factors that regulate establishment also regulate liana growth. Most liana species had higher colonization and greater canopy cover on early successional trees, particularly *Juniperus virginiana*. In contrast, *Vitis* spp. were more abundant on canopy hardwood trees. Slight preferences based on tree size were seen for some species. The preference of lianas for early successional trees may make lianas a contributing factor to the acceleration of succession within this eastern deciduous forest. However, the continued expansion of some lianas at the site, particularly *Vitis* spp. and *C. orbiculatus*, may alter future liana-tree associations and forest trajectories.

Key words: *Celastrus orbiculatus*, deciduous forests, forest regeneration, host preference, lianas, *Lonicera japonica*, *Parthenocissus quinquefolia*, *Toxicodendron radicans*, *Vitis*.

Lianas (woody vines), well-known for their weedy growth habit and secondary growth, are strong competitors with trees for above and belowground resources (Putz 1984, Whigham 1984, Putz and Holbrook 1991, Dillenburg et al. 1993, Lewis and Tanner 2000, Schnitzer et al. 2005, Selaya and Anten 2007, Toledo-Aceves and Swaine 2008). Climbing lianas can cause trunk constriction and remove bark, shoots, and buds on host trees (Lutz 1943, Stevens 1987), form thick blankets of leaves that shade canopies (Avalos et al. 1999, Pérez-Salicrup 2001, Avalos et al. 2007), and allocate resources to rapid branch and root expansion (Barker and Pérez-Salicrup 2000). In general, lianas are fairly shade tolerant (Carter and Teramura 1988, Baars and Kelly 1996) and can wait for favorable light conditions and respond with high growth rates (Greenberg et al. 2001, Leicht and Silander 2006). Lianas colonize disturbed areas faster than trees and often have higher abundance following disturbance, especially along forest edges and within forest gaps (Putz 1984, Putz and Chai 1987, Buron et al. 1998, Schnitzer et al. 2000, Pérez-Salicrup et al. 2001, Allen et al. 2005, Londrè and Schnitzer 2006, Allen et al. 2007). Impacts of lianas on growth and regeneration of many economically important tree species also make lianas an important silvicultural concern (Gerwing 2001, Pérez-Salicrup 2001, Grauel and Putz 2004).

Most liana research has focused on the tropics where liana species richness and abundance are greatest (Gentry 1991, Schnitzer 2005, Jiménez-Castillo et al. 2007). However, the lower species richness of lianas in temperate forests does not necessarily make them less influential in forest dynamics. The ecology and impacts of temperate lianas on community processes, such as forest regenera-

---

[1] This work was supported by NSF grant DEB-0424605, funding from Eastern Illinois University Graduate School, and The Lewis Hanford Tiffany Botany Graduate Research Fund.

[2] We would like to thank N. Morris for assistance in the field and H. Buell, M. Buell, and J. Small for initiating the BSS. Appreciation extends to B. Carlsward, K. Lang, A. Methven, and N. Pisula for their helpful suggestions on previous drafts.

[3] Author for correspondence. E-mail: lladwig@unm.edu. Current address: Department of Biology, MSC03 2020, University of New Mexico, Albuquerque, NM 87131.

Received for publication July 17, 2009, and in revised form January 22, 2010.

tion, are not fully understood. The lack of sufficient research on temperate liana ecology has not gone unnoticed and research has increased in recent years (Allen et al. 2007, Ashton and Lerdau 2008, Leicht-Young et al. 2009, Morrissey et al. 2009).

To understand potential liana impacts on the regenerating forest community we need to first know the location and intensity of liana burdens on host trees. Several factors have been suggested to influence liana host selection. Climbing mechanism often dictates which host trees lianas can climb (Peñalosa 1982). Twining lianas require supports that are close together and small enough to curl around while lianas with specialized adhesive structures (aerial roots, adhesive discs) can climb nearly any host large enough to support the weight of the liana (Putz 1984, Carter and Teramura 1988). Larger hosts and those which already have a liana present are often more likely to be colonized (Putz 1984, Nabe-Nielsen 2001, Pérez-Salicrup and de Meijere 2005). Bark texture relates to liana climbing success with fewer lianas on trees with smooth bark and more lianas on rough bark that provides attachment points for climbing (Putz 1980, Campanello et al. 2007). Allelopathy of host trees has also been suggested to deter liana establishment and growth (Talley et al. 1996). Varying host preference among liana species, based on these criteria, could lead to differential impacts of lianas on trees within forests and may offer insight into impacts of lianas on forest regeneration.

We examined the liana-tree associations within young forests to determine whether liana host preference could alter deciduous forest regeneration. The objectives of this study were to determine whether liana species show host preference with regard to tree genera or tree size and how host colonization relates to liana expansion within the canopy.

Materials and Methods. STUDY SITE. The study site was located in the Piedmont region of New Jersey, USA, at the Hutcheson Memorial Forest Center (HMFC; 40.30′ N, 74.33′ W). The Buell-Small Succession Study (BSS), located within the HMFC, consists of 10 agricultural fields that were experimentally abandoned for the continual monitoring of vegetation dynamics during old-field succession. Fields were abandoned in pairs from 1958 to 1966 and at the time of abandonment, 48 permanent 1 m^2 plots were established in a regular pattern for vegetation surveys. Percent cover of vegetation in plots was visually estimated annually in late July when vegetation is at peak cover. Fields were adjacent to an old-growth oak-hickory forest which has served as a seed source for forest regeneration. In 2008 the time since abandonment of the fields ranged between 42 and 50 years and all the fields were young, closed canopy forests consisting of relatively dense stands of small trees. For more information regarding the BSS, see Pickett (1982).

STUDY ORGANISMS. The most abundant liana species at the BSS and the focus of this research were: *Celastrus orbiculatus* Thunb. (oriental bittersweet; Celastraceae), *Lonicera japonica* Thunb. (Japanese honeysuckle; Caprifoliaceae), *Parthenocissus quinquefolia* (L.) Planchon. (Virginia creeper; Vitaceae), *Toxicodendron radicans* (L.) Kuntze. (poison ivy; Anacardiaceae), and *Vitis* species (grape, including *V. aestivalis* Michx., *V. labrusca* L., *V. riparia* Michx., *V. palmata* M. Vahl., and *V. vulpina* L.; Vitaceae) (Gleason and Cronquist 1991). Within the BSS, species identification of *Vitis* in the canopy became difficult therefore plants were identified to genus only.

Although the five most abundant lianas share fundamental characteristics common to all lianas, the species vary in successional stage, climbing mechanism, origin, and invasiveness. *Celastrus orbiculatus*, which climbs via twining stems, is native to southeast Asia and has become problematic in the United States following introduction as an ornamental plant (Greenberg et al. 2001). Bird dispersal of its fruits has aided in the spread of *C. orbiculatus* which may be displacing the native *Celastrus scandens* L. in shaded forest understories of eastern North America (Leicht and Silander 2006). *Lonicera japonica* is also native to Asia and climbs via twining stems. Once established, plants become highly invasive in eastern and southern North America where it is common in early to mid successional communities (Schweitzer and Larson 1999, Schierenbeck 2004). *Lonicera japonica* fruits are bird dispersed, but seed production in North America is limited due to lack of suitable pollinators (Larson et al. 2002).

Parthenocissus quinquefolia is native and abundant in mid to late successional communities throughout eastern and midwestern

North America. Its fruits are also bird dispersed and rapid growth follows establishment of seedlings. Specialized tendrils ending with adhesive discs allow *P. quinquefolia* to climb nearly any structure large enough to support its weight (Gleason and Cronquist 1991). Similarly, *Toxicodendron radicans* has bird dispersed fruits and is native to eastern North America. Characteristic aerial rootlets produced along the stem attach *T. radicans* to woody stems as it climbs into the canopy (Mitch 1995). Like *P. quinquefolia*, *T. radicans* also often occurs in mid to late successional communities. Species of *Vitis* are also native to North America but climb by means of tendrils and commonly occur later in succession (Fike and Niering 1999, Londré and Schnitzer 2006). Fruits of *Vitis* spp. are dispersed by both birds and mammals.

FIELD SAMPLING. In the summer of 2008, dbh and canopy cover of trees and lianas within the young forests of the BSS were surveyed. All trees with a dbh ≥ 5 cm that originated in or had a crown overhanging a BSS plot were measured. 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. Successional stage of trees was determined by the presence of genera in the canopy of the adjacent old-growth forest. Lianas associated with each tree were also surveyed. For each liana species, percent cover within host tree canopy and understory was visually estimated. The number of liana stems climbing each tree trunk was counted and dbh of all stems was measured following the liana surveying protocol of Gerwing et al. (2006).

DATA ANALYSIS. Host preference was examined in two ways: 1) colonization, determined by liana stem presence on tree trunks and 2) growth, determined by amount of liana canopy cover. Presence of lianas on early and late successional trees was compared using a Chi-squared test. Probabilities of liana colonization on tree genera were calculated using a log linear analysis (Proc Catmod SAS 9.1; SAS Institute Inc., Cary, NC) based on presence or absence of lianas on the host tree trunk for each liana species. Contrasts were run between each tree genus to locate differences in the probability of liana colonization among tree genera. Probabilities of liana colonization based on tree basal area were calculated using a logistic regression for each liana species. To determine differences in growth of lianas among tree genera, liana canopy cover was first log transformed to help normalize the data and then compared to tree genera with a separate ANOVA for each liana species. Least squared means, with Bonferroni corrections for multiple comparisons to reduce the chance of Type I error, indicated differences in liana canopy cover among tree genera. Regressions were used to determine whether tree basal area was related to liana canopy cover.

Results. FOREST COMPOSITION. A total of 798 trees were sampled in 2008. Trees within the young forests included: *Acer* (including *A. negundo* L., *A. platanoides* L., and *A. rubrum* L.), *Ailanthus altissima* (Miller) Swingle., *Carya* spp. Nutt., *Cornus florida* L., *Fagus grandifolia* Ehrh., *Fraxinus* spp. L., *Juglans nigra* L., *Juniperus virginiana* L., *Morus rubra* L., *Prunus* spp. L., *Pyrus malus* L., *Quercus* (including *Q. alba* L., *Q. coccinea* Muenchh., *Q. palustris* Muenchh., *Q. rubra* L., and *Q. velutina* Lam.), *Rhamnus carthartica* L., *Sassafras albidum* (Nutt.) Nees., and *Ulmus rubra* Muhl. The five most abundant tree genera, *Acer*, *Cornus*, *Juglans*, *Juniperus*, and *Quercus*, made up 681 of these stems and were the focus of all further analysis. These most abundant trees were all native species, except for *Acer platanoides* which only made up 2% of the *Acer* trees at the site. Each tree genus had a varying degree of dominance within the canopy (Fig. 1). *Juglans nigra* and *Quercus* spp. were most abundant as canopy dominant hardwoods within the forests. *Juniperus virginiana* and *Acer* spp. were also dominant in the canopy but also had many intermediate and overtopped individuals. *Cornus florida* was mostly overtopped and abundant in the subcanopy.

The forests of the BSS were still relatively young and 73% of the trees were early

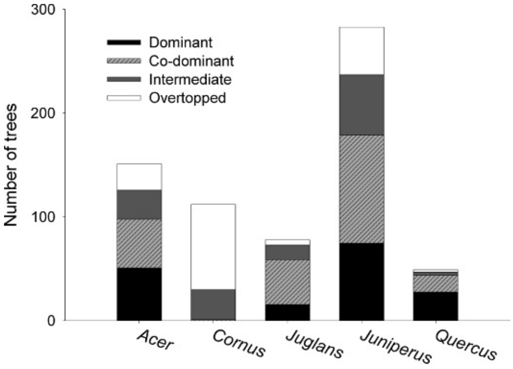

FIG. 1. Total number of trees and canopy dominance of the most abundant tree genera.

successional. Of the most abundant trees, *Juglans nigra*, *Juniperus virginiana*, and *Cornus florida* were early successional species while *Acer* spp. and *Quercus* spp. were late successional. While *C. florida* had been important as a subcanopy species in the old-growth forest, its short stature and bird dispersed fruits constrained its dominance to young forests at the BSS. *Juniperus virginiana* was the most abundant tree species overall (284 individuals) and the most abundant tree in 5 of the 10 forests. *Acer* spp., mostly *A. rubrum*, were the second most abundant tree genus (155 individuals) and was the most abundant tree in 3 of the 10 forests.

Although tree canopy composition varied between forests, liana expansion was fairly uniform across the forests. A total of 3,219 liana stems were measured and lianas were found on 64% of trees. On average, each tree supported 4.0 liana stems which covered 21.4% of the canopy. Lianas were more abundant on early successional than late successional trees ($\chi^2 = 17.44$, $P < 0.0001$). The most frequent liana to colonize tree trunks was *Lonicera japonica*, which occurred on 278 trees. *Vitis* spp. had the greatest canopy cover, occupying an average of 6.6% of each tree canopy. The size distribution of lianas based on basal area and stem count varied among species. *Lonicera japonica* and *Celastrus orbiculatus* had smaller, more numerous stems while *Toxicodendron radicans* and *Vitis* spp. had fewer, larger stems (Fig. 2). The overall greater number of *L. japonica* and *C. orbiculatus* stems resulted in more stems per colonized tree. When only trees with the liana species present were examined, *L. japonica* and *C. orbiculatus* had more liana stems per tree than *Parthenocissus quinquefolia*, *T. radicans*, and *Vitis* spp.

LIANA COLONIZATION PROBABILITY. Colonization probabilities indicated which trees lianas could successfully establish under and climb. Comparing the colonization probabilities of the lianas, *Lonicera japonica* showed the strongest host preference. *L. japonica* was most likely to colonize *Juniperus virginiana* and had equally low probabilities of colonization of the canopy hardwoods *Quercus* spp., *Acer* spp., and *Juglans nigra* (Fig. 3). Colonization of *L. japonica* was also related to tree size and was more likely to colonize smaller trees ($\beta = -0.00045$, $P = 0.0115$). In contrast to *L. japonica*, *Vitis* spp. had the greatest probability of colonizing all dominant tree canopy hardwoods (*Quercus* spp., *J. nigra*, and *Acer* spp.) and low probability of colonizing the early successional trees *J. virginiana* and *Cornus florida*. *Vitis* spp. had a higher probability of colonization on larger trees ($\beta = 0.000386$, $P = 0.0061$). *Parthenocissus quinquefolia* had the highest probability of colonizing *J. virginiana* and lower colonization probabilities on other genera with no relation to tree size ($P = 0.1292$). *Toxicodendron radicans* also had a high probability of colonizing *J. virginiana* in addition to *Quercus* spp. and was more likely to colonize larger trees ($\beta = 0.000648$, $P < 0.001$). *Celastrus orbiculatus* colonization did not significantly differ among tree genera (Fig. 3) or with tree size ($P = 0.2923$).

LIANA CANOPY COVER. Canopy cover of lianas was used to indicate locations of successful liana growth and expansion. Overall, *Vitis* spp. had the greatest mean canopy cover, followed by *Lonicera japonica*, *Toxicodendron radicans*, *Parthenocissus quinquefolia*, and *Celastrus orbiculatus*. When considering only colonized trees, *C. orbiculatus* had the greatest mean cover followed by *T. radicans*, *Vitis* spp., *L. japonica*, and *P. quinquefolia*. Therefore, *Vitis* spp. was the liana with the most canopy cover at the site but *C. orbiculatus* had the greatest canopy cover on colonized trees. *Lonicera japonica* had the greatest cover on smaller trees ($F_{1,796} = 12.38$, $\beta = -0.00029$, $P = 0.0005$, $r^2 = 0.015$) while *Vitis* spp. had greatest cover on large trees ($F_{1,796} = 9.87$, $\beta = 0.00027$, $P =$

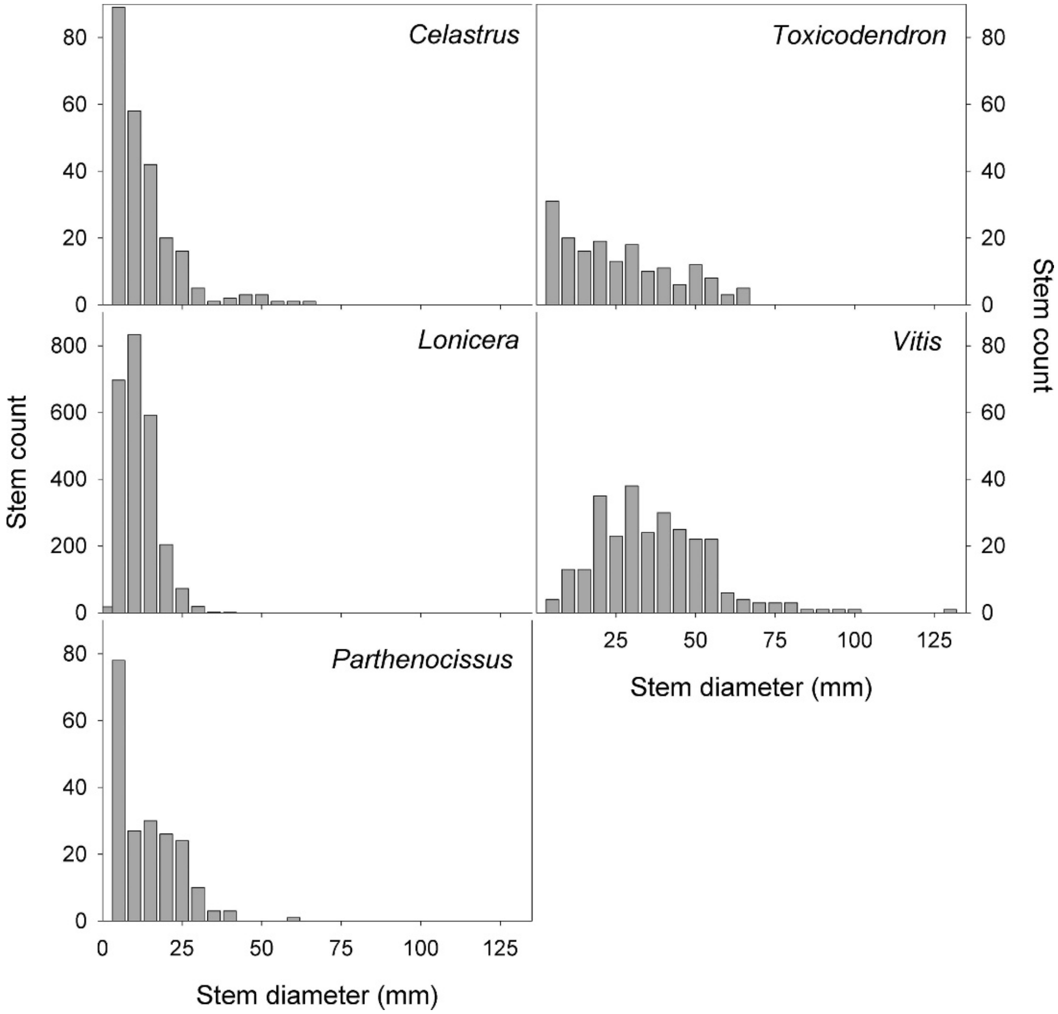

FIG. 2. Liana stem basal area (horizontal axis) relative to liana stem counts (vertical axis). The liana stem count axis for *Lonicera japonica* is an order of magnitude larger than the other liana species.

0.0017, $r^2 = 0.012$). Tree basal area was not related to canopy cover of *C. orbiculatus* ($P = 0.3641$), *P. quinquefolia* ($P = 0.6903$), or *T. radicans* ($P = 0.5407$).

Liana canopy cover varied among tree genera and the same tree genera that lianas successfully colonized also had highest liana canopy cover (Table 1). *Lonicera japonica* was most abundant in the canopies of *Juniperus virginiana* and *Cornus florida* and had equally low cover on the *Acer spp.*, *Juglans nigra*, and *Quercus* spp. (Fig. 4). *Vitis* spp. canopy cover was highest on the hardwoods *Quercus spp.*, *J. nigra*, and *Acer* spp. and lowest on *J. virginiana* and *C. florida*. *Parthenocissus quinquefolia* and *Toxicodendron radicans* had highest canopy cover on *J. virginiana* and lower cover on the other trees. *Celastrus orbiculatus* canopy cover was not significantly different among tree genera (Fig. 4).

Discussion. Liana host preference varied throughout the young forests of the BSS. Every liana species, except *Celastrus orbiculatus*, preferred some tree genera for colonization and canopy expansion (Table 1). Liana species typically had the greatest canopy cover in trees where they also had the greatest colonizing success. Therefore hosts that were favorable for liana colonization and establishment were also favorable for growth and dominance in the canopy. Previous studies have indicated strong liana host preferences resulting in highly variable liana burdens among tree species and

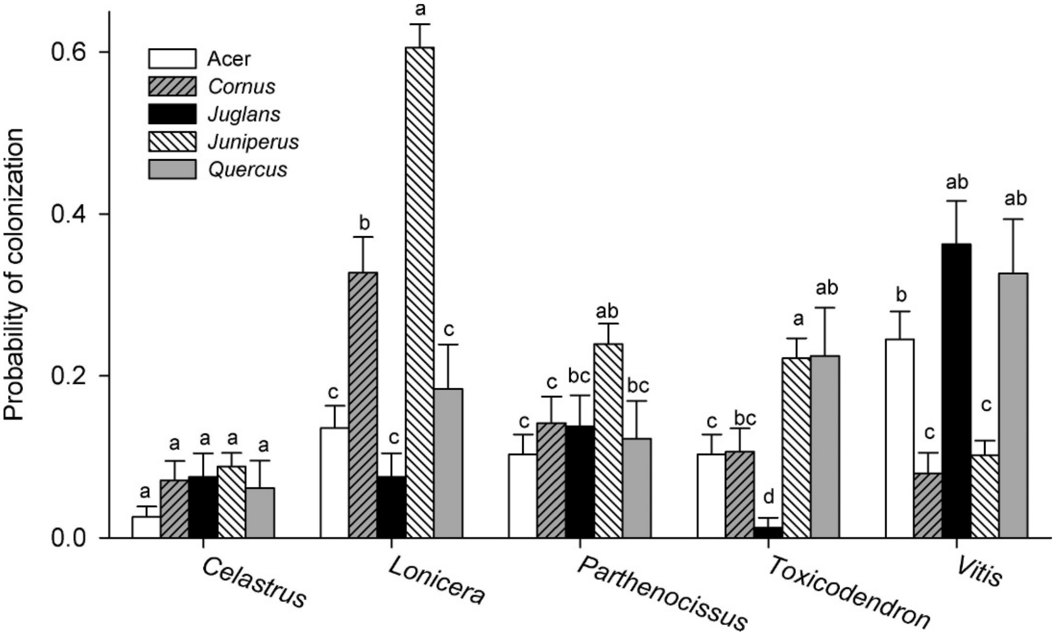

FIG. 3. Probability of liana colonization on tree trunks based on most abundant tree genera. Letters above bars indicate significant differences in probabilities of colonization based on pair-wise contrasts.

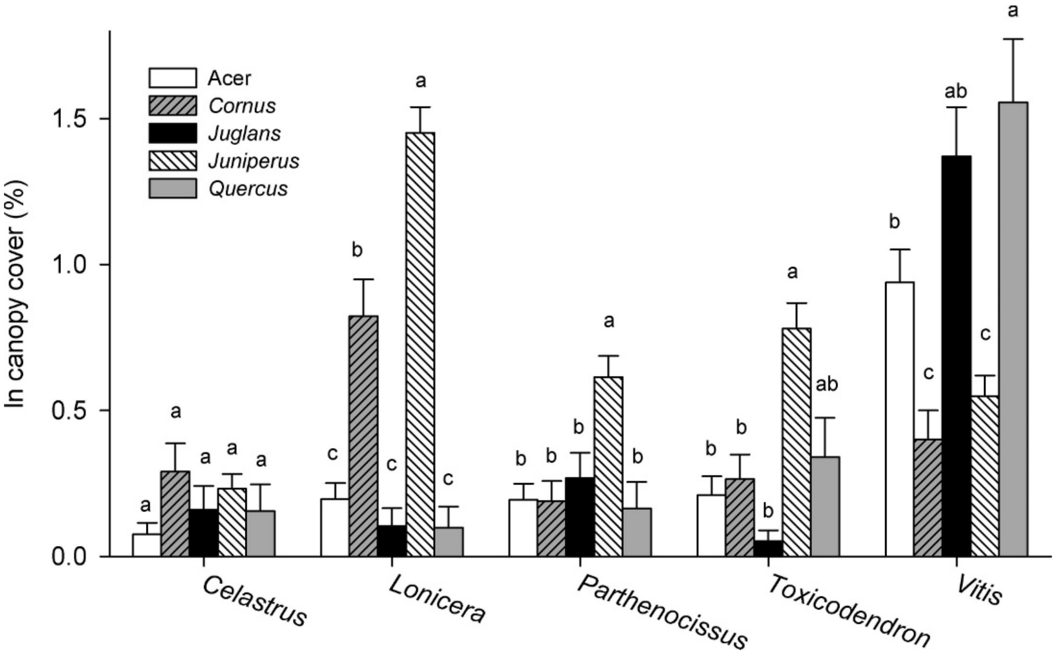

FIG. 4. Mean natural log of liana canopy cover on most abundant tree genera. Letters above bars indicate significant differences in cover among tree genera based on least squared means.

Table 1. Results from ANOVAs comparing the natural log of liana canopy cover among the five most abundant trees (*Acer* spp., *Cornus florida*, *Juglans nigra*, *Juniperus virginiana*, and *Quercus* spp.).

Species	df	MS	*F*	*P*	r^2
Celastrus	4, 676	0.94	1.52	0.1959	-
Lonicera	4, 676	60.00	43.28	< 0.0001	0.201
Parthenocissus	4, 676	7.09	7.81	< 0.0001	0.044
Toxicodendron	4, 676	14.27	11.29	< 0.0001	0.063
Vitis	4, 676	23.19	13.94	< 0.0001	0.076

some trees remaining free of lianas (Putz and Chai 1987, Muoghalu and Okeesan 2005). At the BSS, intensities of host preference varied among lianas and lead to differences in total liana loads among tree genera, but no tree genera were completely free of lianas.

HOST PREFERENCES OF LIANA SPECIES. *Parthenocissus quinquefolia* was most likely to colonize, and had the greatest cover in, *Juniperus virginiana*. Tree size was not important for colonization or canopy expansion of *P. quinquefolia* as the adhesive discs of *P. quinquefolia* allowed it to climb any host with a dbh ≥ 5 cm. *P. quinquefolia* was one of the least abundant lianas found climbing at the site. Low canopy abundance of *P. quinquefolia* relative to other liana species has been reported in other deciduous forests (Buron et al. 1998). Although it had lower abundance on trees, *P. quinquefolia* was often present as a dense groundcover within forests. The amount of *P. quinquefolia* in the understory was not measured since only climbing lianas were evaluated for this study. Previous research on lianas at the site indicated that *P. quinquefolia* has the same frequency as other lianas in the system when both canopy and understory cover were considered (Ladwig and Meiners in press).

Toxicodendron radicans had a slightly greater tendency for colonizing larger trees but canopy cover was not related to host tree size. In other words, it preferentially colonized larger hosts, but occupied a similar amount of the canopy, regardless of tree size. Based on long-term data, *T. radicans* was abundant throughout the site well before canopy closure and may have climbed some of the earliest trees to establish. Older trees were presumably some of the largest trees in 2008, therefore it is unknown whether *T. radicans* colonization was more closely associated with tree age or size. Previous studies have also noted a greater abundance of *T. radicans* on larger trees (Talley et al. 1996, Buron et al. 1998). In contrast, *Parthenocissus quinquefolia* and *Lonicera japonica* were also abundant prior to canopy closure, but they did not show a preference for larger trees. Both canopy cover and host preference of *T. radicans* varied among tree genera. The probability of *T. radicans* colonization was similarly high on *J. virginiana* and *Quercus* spp., and canopy cover was greatest on *J. virginiana*. Even though *T. radicans* equally colonized both trees, it may have a greater impact on *J. virginiana* because of the greater canopy cover. In one deciduous forest, it was suggested that *T. radicans* selected the least allelopathic hardwood species as hosts (Talley et al. 1996). *Juglans nigra* was an abundant canopy tree at the BSS and is well-known for being allelopathic. Whether allelopathy played a role in *T. radicans* host selection at the BSS is unknown but can not be ruled out since the lowest host preference of all the lianas, for both colonization and canopy cover, was between *T. radicans* and *J. nigra* (Figs. 3 and 4).

Vitis spp. were most likely to colonize *Juglans nigra*, *Quercus* spp., and *Acer* spp., the three most abundant hardwood trees. *Vitis* spp. also had the greatest canopy cover within these same trees. Larger trees were more colonized by *Vitis* spp. and also supported the greatest cover of *Vitis* spp. In south-central Indiana, Morrissey et al. (2009) found most *Vitis* stems climbing canopy hardwoods (*Prunus serotina*, *Juglans* spp., and *Ulmus* spp.) and associated *Vitis* spp. host selection with the crown architecture of the host tree. Trunk diameters were presumably too large for direct climbing of *Vitis* via tendrils, therefore vines either climbed trees when they were young or climbed other liana stems (Putz 1995). Once in the canopy, tendrils allowed the liana to extend into the upper canopy on smaller branches that are potentially too weak to support other lianas. *Vitis* may also have a greater longevity than other liana species, allowing it to persist in more trees (Allen et al. 2005).

Lonicera japonica was the most abundant liana at the site, occurring on over a third of all trees. It was most likely to colonize

Juniperus virginiana and also developed the greatest cover within *J. virginiana* canopies. In contrast to *Toxicodendron radicans* and *Vitis* spp., *L. japonica* was more likely to colonize smaller trees, potentially due to its mode of climbing. *Lonicera japonica* climbs via twining which requires small supports in close proximity (Carter and Teramura 1988, Putz 1995). Additionally, *L. japonica* stems were small relative to other liana stems (Fig. 2). The smaller size of liana stems may cause a physiological constraint which does not allow *L. japonica* to frequently occur in the upper canopy. Due to its climbing habit, *L. japonica* generally spreads best in the subcanopy of smaller stature trees, such as *Cornus florida* or saplings, and can decrease sapling growth through belowground competition (Dillenburg et al. 1993, Gao 2008). In addition to having a greater probability of colonizing smaller trees, *L. japonica* had greater cover on smaller trees such as *J. virginiana* and *C. florida*.

Celastrus orbiculatus colonized the least amount of trees and did not show host preference in the forests. *Lonicera japonica* and *C. orbiculatus* are regionally problematic non-native invasive species (Greenberg et al. 2001, Schierenbeck 2004). While *L. japonica* has been abundant for the past 35 years, *C. orbiculatus* only recently began increasing in abundance at the site (Ladwig and Meiners in press). *Celastrus orbiculatus* is a twining liana that requires small supports for climbing and other liana stems present on trees make ideal climbing supports for *C. orbiculatus*. As 64% of the trees at the site currently host lianas, site conditions could potentially aide in rapid colonization of *C. orbiculatus*.

IMPLICATIONS FOR FOREST REGENERATION. Several studies have found more lianas associated with larger trees, yet, with the exception of *Toxicodendron radicans*, we did not find this relation (Jiménez-Castillo and Lusk 2009). This is surprising since tree size is closely linked to tree age and the longer a tree is present the more time lianas have for colonization (Nabe-Nielson 2001, Pérez-Salicrup and de Meijere 2005). Inherent differences among tree genera were more important than overall size of tree when determining liana host preference.

The greatest liana abundance, and potential influence, was on early successional trees, in particular *Juniperus virginiana*. The timing of the measurements during forest regeneration may have played a role in the host preferences observed. At the time of sampling, the forests of the BSS were relatively young, with canopy closure occurring about 20 years prior. The forests were in the stem exclusion stage of forest development and late successional trees were starting to replace early successional trees in the canopy (Oliver and Larson 1996). Other work at this site indicated that early and late successional trees established simultaneously, but early successional trees were much more abundant. During this time, early successional trees, especially *J. virginiana* and *Cornus florida*, were growing slower than late successional trees (Ladwig and Meiners, unpubl. data). In addition, significantly more liana stems were present on early successional trees than late successional trees. Suppressed early successional trees may have been less competitive with lianas. At this stage, slower tree growth combined with greater liana competition associated with early successional trees may accelerate canopy transitions within this eastern deciduous forest.

Continued expansion of some lianas at the site, particularly *Vitis* spp. and *Celastrus orbiculatus*, may alter future liana-tree associations and community trajectories. Both early and late successional lianas were present at the site (Ladwig and Meiners, in press). Abundances of *Lonicera japonica*, *Parthenocissus quinquefolia*, and *Toxicodendron radicans* peaked early in succession before forest canopy closure. Meanwhile, *C. orbiculatus* and *Vitis* spp. entered the community later and continue expanding at the site. The non-native *C. orbiculatus* has a 'sit and wait' strategy which allows it to persit in shady understories and quickly take advantage of light gaps and is also potentially more tolerant of insect herbivory than native lianas (Greenberg et al. 2001, Ashton and Lerdau 2008). Therefore seemingly small amounts of *C. orbiculatus* can have distroportionately large community impacts and high persistence following disturbance. *Vitis* spp. were most abundant on the late successional trees becoming dominant in the canopy. At the site, lianas abundance in tree canopies was related to decreased tree growth (Ladwig and Meiners 2009). *Vitis* spp. are long lived lianas, therefore their presence and influence may last late into forest development (Allen et al. 2005). Additionally, *C. orbiculatus* and *Vitis* spp. have together halted forest regeneration in the region (Fike and Niering 1999). As late successional lianas continue increasing at the site, liana abundance and impacts on forest regeneration could also increase. Whether the liana host preferences described here will persist as the forest matures is unknown, but will determine future impacts on the forest.

Literature Cited

Allen, B. P., R. R. Sharitz, and P. C. Goebel. 2005. Twelve years post-hurricane liana dynamics in an old-growth southern floodplain forest. Forest Ecol. Manage. 218: 259–269.

Allen, B. P., R. R. Sharitz, and P. C. Goebel. 2007. Are lianas increasing in importance in temperate floodplain forests in the southeastern United States? Forest Ecol. Manage. 242: 17–23.

Ashton, I. W. and M. T. Lerdau. 2008. Tolerance to herbivory, and not resistance, may explain differential success of invasive, naturalized, and native North American temperate vines. Divers. Distrib. 14: 169–178.

Avalos, G., S. S. Mulkey, and K. Kitajima. 1999. Leaf optical properties of trees and lianas in the outer canopy of a tropical dry forest. Biotropica 31: 517–520.

Avalos, G., S. S. Mulkey, K. Kitajima, and S. J. Wright. 2007. Colonization strategies of two liana species in a tropical dry forest canopy. Biotropica 39: 393–399.

Baars, R. and D. Kelly. 1996. Survival and growth responses of native and introduced vines in New Zealand to light availability. New Zeal. J. Bot. 34: 389–400.

Babweteera, F., A. Plumptre, and J. Obua. 2000. Effect of gap size and age on climber abundance and diversity in Budongo Forest Reserve, Uganda. Afr. J. Ecol. 38: 230–237.

Baret, S., E. Nicolini, T. Le Bourgeois, and D. Strasberg. 2003. Developmental patterns of the invasive bramble (*Rubus alceifolius* Poiret, Rosaceae) in Reunion Island: an architectural and morphometric analysis. Annu. Bot. Co. 91: 39–48.

Bargeron, C. T., D. J. Moorhead, G. K. Douce, R. C. Reardon, and A. E. Miller. 2003. Invasive plants of the eastern United States: Identification and control. The University of Georgia, USDA APHIS PPQ and USDA Forest Service Forest Health Technology Enterprise Team. <www.invasive.org> accessed January 2009.

Barker, M. G. and D. Pérez-Salicrup. 2000. Comparative water relations of mature mahogany (*Swietenia macrophylla*) trees with and without lianas in a subhumid, seasonally dry forest in Bolivia. Tree Physiol. 20: 1167–1174.

Buron, J., D. Lavigne, K. Grote, R. Takis, and O. Sholes. 1998. Association of vines and trees in second-growth forest. Northeast. Nat. 5: 359–362.

Campanello, P. I., J. F. Garibaldi, M. G. Gatti, and G. Goldstein. 2007. Lianas in a subtropical Atlantic forest: host preference and tree growth. Forest Ecol. Manage. 242: 250–259.

Carter, G. A. and A. H. Teramura. 1988. Vine photosynthesis and relationships to climbing mechanics in a forest understory. Am. J. Bot. 75: 1011–1018.

Dillenburg, L. R., D. F. Whigham, A. H. Teramura, and I. N. Forseth. 1993. Effects of below- and aboveground competition from vines *Lonicera japonica* and *Parthenocissus quinquefolia* on the growth of a tree host *Liqidambar styaciflua*. Oecologia 93: 48–54.

Fike, J. and W. A. Niering. 1999. Four decades of old field vegetation development and the role of *Celastrus orbiculatus* in the northeastern United States. J. Veg. Sci. 10: 483–492.

Forseth, I. N. and A. H. Teramura. 1987. Field photosynthesis, microclimate and water relations of an exotic temperate liana, *Pueraria lobata*, kudzu. Oecologia 71: 262–267.

Gao, S. 2008. Support host selection of *Lonicera japonica* and its interactions with different environmental and biotic factors in Cameron Park, Waco, Texas. M.S. thesis. Baylor University, Waco, TX.

Gentry, A. H. 1991. The distribution and evolution of climbing plants, p. 3–49. *In* F. E. Putz and H. A. Mooney [eds.], The Biology of Vines. Cambridge University Press, New York, NY.

Gerwing, J. J. 2001. Testing liana cutting and controlled burning as silvicultural treatments for a logged forest in the eastern Amazon. J. Appl. Ecol. 38: 1264–1276.

Gerwing, J. J., S. A. Schnitzer, R. J. Burnham, F. Bongers, J. Chave, S. J. Dewalt, C. E. N. Ewango, D. Kenfack, M. Martinez-Ramos, M. Parren, N. Pathasarathy, D. R. Perez-Salicrup, F. E. Putz, and D. W. Thomas. 2006. A standard protocol for liana censuses. Biotropica 38: 256–261.

Gleason, H. A. and A. Cronquist. 1991. Manual of Vascular Plants of Northeastern United States and Adjacent Canada. The New York Botanical Garden, Bronx, NY. 910 p.

Grauel, W. T. and F. E. Putz. 2004. Effects of lianas on growth and regeneration of *Prioria copaifera* in Darien, Panama. Forest Ecol. Manage. 190: 99–108.

Greenberg, C. H., L. M. Smith, and D. J. Levey. 2001. Fruit fate, seed germination and growth of an invasive vine–an experimental test of 'sit and wait' strategy. Biol. Invasions 3: 363–372.

Horvitz, C. C. and A. Koop. 2001. Removal of nonnative vines and post-hurricane recruitment in tropical hardwood forests in Florida. Biotropica 33: 268–281.

Jiménez-Castillo, M., S. K. Wiser, and C. H. Lusk. 2007. Elevational parallels of latitudinal variation in the proportion of lianas in woody floras. J. Biogeogr. 34: 163–168.

Jiménez-Castillo, M. and C. H. Lusk. 2009. Host infestation patterns of the massive liana *Hydrangea serratifolia* (Hydrangeaceae) in a Chilean temperate rainforest. Austral. Ecol. 34: 829–834.

Ladwig, L. M. and S. J. Meiners. 2009. Impacts of temperate lianas on tree growth in young deciduous forests. Forest Ecol. Manage. 259: 195–200.

LADWIG, L. M. AND S. J. MEINERS. In press. Spatiotemporal dynamics of lianas during 50 years of succession to temperate forest. Ecology.

LARSON, K. C., S. P. FOWLER, AND J. C. WALKER. 2002. Lack of pollinators limits fruit set in the exotic *Lonicera japonica*. Am. Midl. Nat. 148: 54–60.

LEICHT, S. A. AND J. A. J. SILANDER. 2006. Differential responses of invasive *Celastrus orbiculatus* (Celastracae) and native *C. scandens* to changes in light quality. Am. J. Bot. 93: 972–977.

LEICHT-YOUNG, S. A., H. O'DONNELL, A. M. LATIMER, AND J. A. SILANDER. 2009. Effects of an invasive plant species, *Celastrus orbiculatus*, on soil composition and processes. Am. Midl. Nat. 161: 219–231.

LEWIS, S. L. AND E. V. J. TANNER. 2000. Effects of above- and belowground competition on growth and survival of rain forest tree seedlings. Ecology 81: 2525–2538.

LONDRÈ, R. A. AND S. A. SCHNITZER. 2006. The distribution of lianas and their change in abundance in temperate forests over the past 45 years. Ecology 87: 2973–2978.

LUTZ, H. J. 1943. Injuries to trees caused by *Celastrus* and *Vitis*. Bull. Torrey Bot. Club 70: 436–439.

MITCH, L. W. 1995. Poison-ivy/poison-oak/poison-sumac–the virulent weeds. Weed Technol. 9: 653–656.

MORRISSEY, R. C., M. M. GAUTHIER, J. A. J. KERSHAW, D. F. JACOBS, J. R. SEIFERT, AND B. C. FISCHER. 2009. Grapevine (*Vitis* spp.) dynamics in association with manual tending, physiography, and host tree associations in temperate deciduous forests. Forest Ecol. Manage. 8: 1839–1846.

MUOGHALU, J. I. AND O. O. OKEESAN. 2005. Climber species composition, abundance and relationship with trees in a Nigerian secondary forest. Afr. J. Ecol. 43: 258–266.

NABE-NIELSEN, J. 2001. Diversity and distribution of lianas in a neotropical rain forest, Yasuní National Park, Ecuador. J. Trop. Ecol. 17: 1–19.

OLIVER, C. D. AND B. C. LARSON. 1996. Forest Stand Dynamics. John Wiley and Sons, New York, NY. 521 p.

PANDE, A., C. L. WILLIAMS, C. LANT, L. , AND D. J. GIBSON. 2007. Using map algebra to determine the mesoscale distribution of invasive plants: the case of *Celastrus orbiculatus* in Southern Illinois, USA. Biol. Invasions 9: 419–431.

PEÑALOSA, J. 1982. Morphological specialization and attachment success in two twining lianas. Am. J. Bot. 69: 1043–1045.

PÉREZ-SALICRUP, D. 2001. Effect of liana cutting on tree regeneration in a liana forest in Amazonian Bolivia. Ecology 82: 389–396.

PÉREZ-SALICRUP, D. R. AND W. DE MEIJERE. 2005. Number of lianas per tree and number of trees climbed by lianas at Los Tuxtlas, Mexico. Biotropica 37: 153–156.

PÉREZ-SALICRUP, D. R., V. L. SORK, AND F. E. PUTZ. 2001. Lianas and trees in a liana forest of Amazonian Bolivia. Biotropica 33: 34–37.

PICKETT, S. T. A. 1982. Population patterns through twenty years of old-field succession. Vegetatio 49: 45–59.

PUTZ, F. E. 1980. Lianas vs. trees. Biotropica 12: 224–225.

PUTZ, F. E. 1984. The natural history of lianas on Barro Colorado Island, Panama. Ecology 65: 1713–1724.

PUTZ, F. E. 1995. Relay ascension of big trees by vines in Rock Creek Park, District of Columbia. Castanea 60: 167–169.

PUTZ, F. E. AND P. CHAI. 1987. Ecological studies of lianas in Lambir National Park, Sarawak, Malaysia. J. Ecol. 75: 523–531.

PUTZ, F. E. AND M. HOLBROOK. 1991. Biomechanical studies of vines, p. 73–97. *In* F. E. Putz and H. A. Mooney [eds.], The Biology of Vines. Cambridge University Press, New York, NY.

RAGHU, S., K. DHILEEPAN, AND M. TREVIÑO. 2006. Response of an invasive liana to simulated herbivory: implications for its biological control. Acta Oecologica 29: 335–345.

SCHIERENBECK, K. A. 2004. Japanese honeysuckle (*Lonicera japonica*) as an invasive species; history, ecology, and context. Crit. Rev. Plant Sci. 23: 391–400.

SCHNITZER, S. A. 2005. A mechanistic explanation for global patterns of liana abundance and distribution. Am. Nat. 166: 261–276.

SCHNITZER, S. A., J. W. DALLING, AND W. P. CARSON. 2000. The impact of lianas on tree regeneration in tropical forest canopy gaps: evidence for an alternative pathway of gap-phase regeneration. J. Ecol. 88: 655–666.

SCHNITZER, S. A., M. E. KUZEE, AND F. BONGERS. 2005. Disentangling above- and below-ground competition between lianas and trees in a tropical forest. J. Ecol. 93: 1115–1125.

SCHWEITZER, J. A. AND K. C. LARSON. 1999. Greater morphological plasticity of exotic honeysuckle species may make them better invaders than native species. J. Torrey Bot. Soc. 126: 15–23.

SELAYA, N. G. AND N. P. R. ANTEN. 2007. Differences in biomass allocation, light interception and mechanical stability between lianas and trees in early secondary tropical forests. Funct. Ecol. 22: 30–39.

SMITH, D. M. 1986. The practice of silviculture. John Wiley & Sons, Inc., New York, NY. 527 p.

STEVENS, G. C. 1987. Lianas as structural parasites: the *Bursera simaruba* example. Ecology 68: 77–81.

TABANEZ, A. A. J. AND V. M. VIANA. 2000. Patch structure within Brazilian Atlantic forest fragments and implications for conservation. Biotropica 32: 925–933.

TALLEY, C. M., R. O. LAWTON, AND W. N. SETZER. 1996. Host preference of *Rhus radicans* (Anacardiaceae) in a southern deciduous hardwood forest. Ecology 77: 1271–1276.

TOLEDO-ACEVES, T. AND M. D. SWAINE. 2008. Above- and below-ground competition between the liana *Acacia kamerunensis* and tree saplings in contrasting light environments. Plant Ecol. 196: 233–244.

WHIGHAM, D. F. 1984. The influence of vines on the growth of *Liquidambar styraciflua* L. (sweetgum). Can. J. Forest Res. 14: 37–39.