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# LIANA DISTRIBUTION AND HOST RELATIONSHIPS IN SOME TEMPERATE VERSUS TROPICAL FOREST SITES

By

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# ABSTRACT

# LIANA DISTRIBUTION AND HOST RELATIONSHIPS IN SOME TEMPERATE VERSUS TROPICAL FOREST SITES

By

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Lianas (woody vines) are an important but often neglected component of many types of forest. This study was designed to document the species of lianas in Carolina mixed mesophytic forest (Rich Gap and Conley Creek), Carolina xeric white-oak dominated forest (Cliffside), and Costa Rican seasonally dry tropical forest (Palo Verde). Another aim of this study was to investigate the liana-host relationship in each of these forests. I identified and measured the diameter at breast height (dbh) of every tree within 20 x 20 m plots. I identified and measured the diameter of lianas at 10 cm above the ground, and I recorded the primary host tree that each liana was utilizing. No lianas were observed within plots at Clifftop Vista. Palo Verde had the highest species richness in terms of lianas (15 species) and trees (33 species), and the highest percentage of trees hosting lianas (55%), compared to 0% at Clifftop Vista, 37% at Rich Gap and 29% at Conley Creek. The number of lianas per tree was greatest at Palo Verde (mean of 1.68 lianas per tree) and lower at the two temperate mesic forest sites (0.49 lianas per tree at Rich Gap and 0.48 lianas per tree at Conley Creek). Host tree species was important in explaining liana distribution at Rich Gap and Conley Creek. Host-tree size was influential at Rich Gap, Conley Creek and Palo Verde. At Rich Gap, lianas were found in proportion to the host surface area available to climb (e.g., *Vitis*), whereas at Conley Creek and Palo Verde, lianas were restricted to particular sizes of hosts (e.g., *Aristolochia* at Conley Creek). This study suggests that lianas are restricted by host tree species and host size. Thus, it seems that each species of liana may utilize a particular suite of tree species and sizes as hosts.

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# Chapter 1

## Literature review of liana (woody vine) distribution and host relationships

*The climbing habit*

Plants exhibit various growth forms, one of which is the climbing habit. Vines, climbing plants that are rooted in the soil, are "structural parasites" that occupy almost every habitat where there are trees available to climb (Stevens 1987, Dillenburg et al. 1993). The climbing habit is widespread phylogenetically, and about 133 of the approximately 400 vascular plant families include at least a few climbing species (Gentry 1991). The climbing habit has evolved independently in many plant lineages including groups as diverse as gymnosperms (Gnetaceae), dicotyledons (e.g., Vitaceae), and monocotyledons (e.g., Araceae).

Plants use many tactics to climb, and thus climbing plants as a whole form a diverse group. While discussing this diversity, Gentry (1991) states, "there must be strong selective pressure favoring evolution of a scandent habit." Darwin (1867) discusses the origin of the climbing habit by asserting, "plants become climbers, in order, as it may be presumed, to reach the light..." The climbing habit allows a plant to reach the canopy with little expenditure in structural tissue (Darwin 1867 and others). This characteristic is very important for plants that live in habitats with thick canopies.

The definition of the term "vine" is not always clear. Some species will grow as shrubs until a trellis becomes available (e.g., *Toxicodendron radicans* as shown in Gartner 1991). However, many vine seedlings will die if they are unable to access a structural support before they deplete their seed reserves (examples in Janzen 1983). The definition of the term "liana," or "woody vine," is also sometimes problematic. Some non-dicotyledonous plants climb into the canopy but do not produce secondary xylem (e.g., climbing ferns, climbing monocots, etc.). It is debatable whether to include these species in the category of liana because they do not produce anatomically true wood. This thesis will reserve the word "liana" for woody vines that add layers of secondary xylem or wood in a somewhat predictable fashion.

Lianas are important components of both temperate and tropical forest ecosystems (Darwin 1867, Putz 1984b, Gentry 1991, Teramura et al. 1991) and can cause silvicultural problems (e.g., Featherly 1941, Lutz 1943, Trimble and Tryon 1974, Siccama et al. 1976, Putz 1991). Host-dependent species are crucial for many indigenous Central and South American peoples (Bennett 1995). Recent interest in tropical biology and development of rope-assisted tree ascension has promoted the study of lianas by some canopy biologists, but fundamental questions about vine ecology remain unanswered. The objective of this literature survey will be to address some of these unanswered questions. I will first examine the geographic distribution of lianas and address host preferences of structural parasites. An overview of the effects of lianas on their hosts will be followed by a discussion of mechanisms that host trees utilize to avoid and then shed lianas. Finally, I will give suggestions for future liana research.

### *Liana geographic distribution*

Liana species diversity increases as latitude decreases. The proportion of plant species that climb relative to total number of plant species is higher in tropical compared to temperate forests. For example, climbing plants contribute only 1.3% to the flora of the Carolinas and the Southern Appalachian Mountains relative to about 10% of the Neotropical flora (Gentry 1991).

Tropical forests provide habitat for several types of structural parasites in addition to lianas, such as epiphytes and hemiepiphytes. This may be explained by the structural complexity of the tropical canopy. There is more complexity and space for climbing in the canopy of a tropical forest relative to that of a temperate forest. This has most likely encouraged the growth and diversification of structural parasites in tropical habitats.

There are other advantages to climbing in addition to reaching the well-lit forest canopy. The elevated position in the canopy improves the possibility of effective wind pollination and seed dispersal. A sought-after space in the canopy also allows a plant to escape terrestrial herbivores. Arboreal pollinators and seed dispersers will also be more readily available in the forest canopy.

It has been suggested that the hydraulic architecture of lianas restricts their distribution mainly to the tropics (Ewers et al. 1997). The wide vessels that characterize secondary xylem of lianas allow extremely efficient water conduction with limited stem width, but these vessels are also very susceptible to freeze-induced embolism (Hargrave et al. 1994), and thus lianas are less speciose and less densely distributed in frost-prone areas than in non-frost areas. It seems that lianas can only survive in the temperate zone if they produce a fresh layer of secondary xylem every spring or produce positive root pressure in the spring to refill the embolized vessels.

### *Structural parasites and host preferences*

Lianas are structural parasites, plants that rely on other plants for structural support. These plants do not seem to be distributed randomly amongst available host trees within a forest. Epiphytes (plants that grow on other plants without attachment to the ground), hemiepiphytes (plants that have an epiphytic and terrestrial phase), and lianas all show some host preferences. Epiphytes are not distributed in proportion to host species abundance (Schlesinger and Marks 1977, Bennett 1986, Benzing 1995). Instead, microhabitat availability and seed dispersal mechanisms seem to predict where epiphytes will be successful (Bennett 1986).

The most convincing evidence that structural parasites show some host preferences comes from studies on hemiepiphytes. Hemiepiphytes are plants that germinate in the canopy and later establish a connection with the ground (primary hemiepiphytes), or plants that germinate on the forest floor, climb into the canopy, lose their connection with the ground, but may later reestablish this connection by way of adventitious roots (secondary hemiepiphytes). Characteristics of hemiepiphytes have been discussed by Putz and Holbrook (1986), who mention that hemiepiphytes are among the least understood types of plants. Guy (1977) surveyed the host usage of plants within the fig genus *Ficus* (Moraceae) at the Mana Pools Game Reserve in Rhodesia. He observed that *Ficus* was distributed independent of host species abundance, and was found more often on some tree species than expected based on the relative abundance of these trees in the forest. Individuals within the host tree species *Diospyros mespiliformis* (Ebenaceae), were more likely to serve as hosts to *Ficus* than expected by their abundance in the forest. Guy (1977) notes that this tree has rough bark and suggests that rain cannot dislodge seeds as easily from trees with rough bark compared to trees with smooth bark. He also mentions that *D. mespiliformis* produces fruit around the same time as *Ficus*, so that animals are likely to deposit the fig seeds on *D. mespiliformis* after feeding on figs.

Additional evidence that hemiepiphytes are distributed independent of host tree species abundance came from a study of several species on Barro Colorado Island (BCI) in Lake Gatun, Panama (Todzia 1986). Only 1% of the individuals within the smooth-barked tree species, *Quararibea asterolepis* (Bombacaceae), serve as hosts to hemiepiphytes. However, 58% of the surveyed trees of the spiny-barked species, *Hura crepitans* (Euphorbiaceae), contain hemiepiphytes. Todzia (1986) suggested that spines may facilitate hemiepiphyte seedling establishment on the host tree. She also showed that different species of hemiepiphytes on BCI occupy distinct canopy positions.

Additional evidence that hemiepiphytes are not distributed randomly amongst potential host trees came from a study of *Ficus crassiuscula* in the Monteverde Cloud Forest in the Cordillera de Tileran in Costa Rica (Daniels and Lawton 1991). The authors show that the hemiepiphytes are distributed randomly on potential host species during the viny juvenile stage of development. In contrast, adult *F. crassiuscula* are more likely to be found on certain tree species. This evidence supports the idea that trees are not avoiding initial establishment of structural parasites, but rather have some mechanism to shed these plants after they have colonized the host's canopy. Daniels and Lawton (1991) also showed that the size of the host tree does not seem to influence its acceptability to hemiepiphytes.

A study in the Bornean rain forest found some species of *Ficus* more often on dipterocarp tree species, but others more often on non-dipterocarp host species (Laman 1996). Additionally, canopy microhabitats seem important in determining acceptability of hosts, as different species of figs occupied distinct canopy positions. Based on the above evidence, it seems that one class of structural parasites, hemiepiphytes, utilize distinct tree species and perhaps even prefer particular positions within the tree's canopy. Finally, Williams-Lindera and Lawton (1995) reassert the existence of hemiepiphytic host preferences in a review paper.

Like the epiphytes and hemiepiphytes discussed above, lianas tend to grow more successfully on some host tree species than others. Jack Putz has examined some of these issues on BCI. He examined trellis requirements for lianas with various climbing mechanisms (Putz 1984b). His work shows that trellises must be strong enough to support the weight of a climber but he observed no minimum trellis diameter requirement for any of the lianas he studied. However, although no species of liana shows a minimum trellis size requirement, some species of lianas do not seem able to climb trellises that exceed a particular size. Most tendril-climbing lianas utilize hosts less than 10 cm diameter because they must wrap around their support structure. Twiners can climb larger supports than tendril climbers. Species that climb by way of adventitious roots or adhesive discs can climb structures of any size. Putz (1984b) concluded from these observations that support availability is a major factor limiting lianas. He also mentions that canopy gaps provide ideal habitat for lianas with host size restrictions. Additionally, lianas can climb other lianas to access the canopy (Putz 1984a, 1984b, 1995), and lianas are spatially aggregated at BCI.

Putz (1984b) focused mainly on adult lianas, whereas Collins and Wein (1993) examined the spatial distribution of juvenile understory vines in a South Carolina hardwood forest. Collins and Wein (1993) found that spatial distribution differs among juvenile vine species but that the identity of the nearest support species does not influence juvenile vine location. This supports the idea that vines are initially equally likely to climb any tree, so tree mechanisms for shedding lianas become more important than mechanisms to avoid initial liana growth. The spatial location of juvenile vines are influenced by microhabitat, especially soil moisture and elevation (Collins and Wein 1993).

A study by Talley, Lawton and Setzer (1996) in an Alabama hardwood forest deals most directly with the subject of liana host specificity. They showed that poison ivy, *Rhus radicans* (Anacardiaceae), was not distributed randomly among potential host species. Instead, *Carya ovata* (Juglandaceae) and the hard-barked oaks (*Quercus* spp.: Fagaceae) hosted more lianas than expected, whereas *Acer rubrum* (Aceraceae) hosted fewer than expected based on relative tree species stem densities. They also showed that host size influences poison ivy distribution. They observed more lianas than expected on hosts larger than 60 cm in diameter, but fewer than expected on hosts less than 60 cm diameter. Additionally, small, erect poison ivy stems are not distributed randomly on the forest floor, as was also seen by Collins and Wein for juvenile vines (1993, see above). Talley, Lawton and Setzer suggest that host bark allelopathic secretions may influence host preferences of poison ivy. They also acknowledge that some tree bark types may offer better liana adhesive-root attachment success rates. Finally, trees of different species have different morphological architecture, and thus may provide differing light levels once the liana has reached the canopy. Theoretically, it would be more advantageous for lianas to climb species with thinner crowns that allow more light penetration to the liana leaves.

Based on these studies of epiphytes, hemiepiphytes and lianas, it becomes clear that structural parasites display host preferences. The remainder of this chapter will look more closely into the relationship between one class of structural parasites, lianas, and their host trees. In order to understand why lianas are found on some tree species more often than others, we must now consider why lianas would be selected to exhibit host preferences. We must also consider the selection pressure on trees to avoid and shed lianas.

### *Effect of lianas on their hosts*

Lianas are intimately associated with their hosts because they are physically in contact with each other, unlike two mutually competing trees in a given forest. Similar to two competing trees, lianas and their hosts compete for water and nutrients at the forest floor. Lianas and other structural parasites can be very detrimental to their host trees. First, liana infestation can eventually kill host trees. After only two years of study after wild grape (*Vitis* spp.: Vitaceae) was released in a West Virginia temperate hardwood forest, Trimble and Tryon (1974) reported 2% death of trees caused by lianas.

Lianas can have many negative effects on their hosts that are less severe than death. The shear weight of supporting another plant can cause mechanical damage. Lianas can structurally weaken their host trees by physically suppressing branches causing them to break. This additional weight also increases host tree susceptibility to ice damage (Siccama et al. 1976). Lianas can also cause mechanical abrasion to their hosts, sometimes resulting in passive strangulation which injures host-tree stems. Through girdling, lianas can interfere with their hosts' internal transport (Lutz 1943), restricting internal translocation of nutrients and water. Lianas can also decrease the stem incremental diameter growth rate of the host tree (Putz 1984b). The cumulative effects of lianas may result in an overall deformed tree crown and a weakened host tree.

In addition to structurally weakening or even killing their host trees, lianas also influence their hosts by competing with them for light, as liana leaves may shade out the leaves of the host trees, resulting in less photosynthetically active radiation to reach the leaves of the host tree, reducing its potential for growth and reproduction. Below-ground competition with lianas for limited nutrients and water can also reduce the host's growth (Dillenburg et al. 1993). Lianas may decrease the reproductive output of certain tree species, as in *Bursera simaruba* (Bursuraceae; Stevens 1987). Sometimes lianas connect nearby trees, constructing a canopy trellis providing access to mammalian herbivores.

In addition to the effects that lianas can have on individual trees, they can affect overall community structure. Lianas or scramblers may compete with tree or shrub saplings for limited resources. This may result in a "vine-dominated disclimax" (Whigham 1984), where succession is said to be "arrested," and will temporarily progress no further.

In spite of all of the possible negative effects of lianas on their hosts listed above, usually only a subset of these factors will actually influence a particular host tree. The rank of importance of the above negative factors of hosting lianas will probably differ from species to species and often from tree to tree.

Serving as hosts to lianas may benefit host trees in a few ways. By intertwining through several trees and connecting trees together, lianas may mechanically stabilize the canopy within a forest (Putz 1995). This effect of liana presence seems important in thin tropical soils where trees are often shallowly rooted. However, this may be detrimental if connected trees fall for any reason. Another important result of lianas in tropical forests is that they transform a disjunct, multilayered two-dimensional canopy to an intertwined, three-dimensional connected system which provides coherent routes for seed dispersers to access hosts. One mammologist who studies arboreal mammals commented that lianas seem absolutely essential to the mammals that inhabit tropical forest canopies (D. McClearn, personal communication).

### *Host mechanisms to avoid initial liana infestation*

In light of all the negative effects of lianas on their hosts listed above, it seems that host trees would be under selection pressure to avoid lianas altogether. Some tree characteristics have been purported to assist in avoiding or preventing liana infestation. The first idea proposed in the literature was that buttresses "protect" trees from lianas because twining vines would have to spend more energy maneuvering around large buttresses to reach the climbable host stem and would not be likely to succeed in accessing the host tree (Black and Harper 1979). This idea suggests that perhaps buttresses prevent initial ascent of twining lianas. This is essentially an extension of the idea that twiners will not be able to climb trees whose diameters exceed an acceptable maximum size (Putz 1984b). Buttresses would not protect a potential host tree from lianas that climb by way of adventitious roots or adhesive discs, which can utilize most tree sizes (Putz 1984b). Additionally, buttresses would not protect trees from lianas that enter the canopy of one tree from that of other nearby trees. However, Boom and Mori (1982) found that buttresses do not reduce liana load in tropical wet forest of Brazil.

Another suggestion is that trees with smooth bark will be less likely to host lianas than trees with rough bark (Putz 1980, 1984a). The idea is that rough bark provides more surface area and crevices for a liana to securely attach to the tree stem. Boom and Mori (1982) rejected this hypothesis since smooth-barked tree species were just as likely to host lianas as rough-barked trees in Brazil. However, this idea needs further testing.

Another possible mechanism to prevent liana infestation is by utilizing rapid diameter growth (Putz 1980). Fast-growing trees will theoretically more quickly escape the window of time when their diameter is climbable by twining lianas, but survey data does not support this claim (Putz 1984a).

Another recently suggested mechanism possibly utilized by trees to prevent liana infestation is the secretion of allelopathic toxins from tree bark (Talley et al. 1996). This idea needs more testing before acceptance.

### *Host mechanisms to remove lianas*

None of the mechanisms mentioned above seem satisfactory in preventing lianas from climbing an available host tree. Perhaps trees have not been selected to avoid the initial ascent of lianas (maybe with the exception of trees that produce allelopathic secretions), but rather to shed lianas (and possibly other types of structural parasites as well) after they have infested the host tree. What then becomes important is how long the liana can remain attached to its host, and whether a host tree has mechanisms to shed climbers or other structural parasites.

One suggestion in the liana-avoidance literature is that trees with peeling bark will be less likely to host lianas than trees with rough bark (Putz 1980, 1984a). Trees that shed their peeling bark periodically could dislodge their lianas when they shed their bark. The bark of the gumbo-limbo tree (*Bursera simaruba*: Burseraceae) and sycamore (*Platanus* spp.: Platanaceae) represent possible examples of this "strategy." Stevens (1987) mentions peeling *Bursera* bark as a mechanism to reduce host liana load. This "exfoliating bark" hypothesis only holds for lianas that climb by utilizing adhesive discs or adventitious roots, both of which depend on the suitability of their climbing surface to maintain their grip on their host. Utilizing exfoliating bark to shed lianas is effective both against lianas climbing the tree from the ground and against those entering from adjacent canopy.

Another mechanism proposed to help trees rid themselves of lianas is by producing self-pruning compound leaves (Putz 1980, 1984a). The advantage of large, self-pruning compound leaves, with short retention times, is that large leaves will initially support liana attachment, but when the tree drops the leaves, the tree also sheds its lianas. Leaf length seems weakly negatively correlated with liana presence (Putz 1984a). Stevens (1987) mentions the importance of *Bursera* compound-leaf shedding as a mechanism to reduce host liana load.

Spiny bark has been suggested as a mechanism to saw off lianas, but no evidence supports this claim. Putz (1984a) mechanically agitated saplings of two spiny-barked trees to see whether they would saw off their connecting lianas, but the results were inconclusive.

A final related suggested mechanism that would dislodge lianas from two connected trees would be for the trees to have high mechanical flexibility, as measured by Young's modulus (Putz 1980). Theoretically, higher flexibility would allow two interconnected trees to sway in opposite directions and dislodge or break their connectors. However, this idea seems improbable because seldom would trees be swaying in opposite directions.

One of the most effective mechanisms that some trees utilize to dislodge lianas from their crowns is by employing protective symbionts. Some tree species house ants in hollow bark (e.g., *Cecropia* spp.: Moraceae) or swollen thorns (e.g., *Acacia* spp.: Fabaceae). *Azteca* ants that colonize *Cecropia* trees rush out and attack all intruders that contact the tree, including lianas that begin to climb the trunk or enter the canopy (Janzen 1969). However, this mutualistic relationship gives several advantages to the tree and the protective symbiont in addition to protecting the tree from lianas, and may be costly for the host tree involved. It does not seem likely that this relationship arose only in response to the pressure of avoiding liana colonization or shedding lianas.

None of the above mechanisms for avoiding lianas prior to their colonization, or shedding lianas after infestation, seems entirely satisfactory to explain what we observe today. Perhaps different species of host trees utilize some unique combination of the above mechanisms to avoid or shed lianas. Because trees that can escape lianas will have higher annual basal growth (Putz 1984b) and greater reproductive output (Stevens 1987), it seems likely that lianas are a selective force influencing trees.

### *Suggested future research*

In order to understand liana distribution and the liana-host relationship, there are many issues that should be addressed. Perhaps the most effective tree "adaptations" to reduce liana load differ in different habitats and forest types. Maybe different tree species utilize different strategies to avoid or shed lianas, and perhaps the arsenal of mechanisms to avoid or shed lianas is still evolving. It would be interesting to more accurately assess which of the negative effects of lianas are more detrimental in different habitats or forest types. For example, vulnerability to seasonal weight of snow and ice, heightened by hosting lianas, is obviously more influential in temperate areas, whereas light competition with lianas may be more important in the tropics.

It should also be assessed whether trees preferentially shed liana-laden limbs or shaded limbs to reduce their liana load. Putz (1995) suggested the construction of model trees to investigate the influence of surfaces and sizes of available hosts in order to further our understanding of the relationship between host tree bark and liana host preference. Artificial support structures with smooth, rough or exfoliating surfaces could be compared for their acceptability as liana substrate. Similarly, structures with or without wide bases could be compared for their acceptability to lianas to model the effect of buttresses on host acceptance. Support structures of different diameters could be offered to juvenile lianas to experimentally test the influence of host size on initial host colonization.

Finally, more habitats and geographic locations should be examined for liana host species preferences. Perhaps with additional comparable data sets we will be better able to assess the relationship between structural parasites, particularly lianas, and their hosts.

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# Chapter 2

# Liana distribution and host relationships in Carolina temperate and Costa Rican seasonally dry forest

## Introduction

Vines are structural parasites that occupy almost every habitat where trees are available to climb (Stevens 1987, Dillenburg et al. 1993). Climbing allows a plant to reach the forest canopy with little expenditure in structural tissue (Darwin 1867 and others). The climbing habit has evolved independently in several plant lineages including groups as diverse as gymnosperms (Gnetaceae), dicotyledons (e.g., Vitaceae), and monocotyledons (e.g., Araceae).

Liana (woody vine) species diversity increases as latitude decreases. The 48 woody climbers native to the southeastern United States belong to 25 genera in 19 families (Gentry 1991). Climbing plants contribute 1.3% of the flora of the Carolinas and the Southern Appalachian Mountains (Radford et al. 1968, in part compiled by D. Boufford as noted in Gentry 1991). In contrast, lianas contribute about 10% of the Neotropical flora (Gentry 1991).

Lianas are important components of both temperate and tropical forest ecosystems (Darwin 1867, Putz 1984b, Gentry 1991, Teramura et al. 1991) and can cause silvicultural problems (e.g., Featherly 1941, Lutz 1943, Trimble and Tryon 1974, Siccama et al. 1976, Putz 1991). Recent interest in tropical biology and development of rope-assisted tree ascension have promoted the study of lianas, but fundamental questions about vine ecology remain unanswered. Although lianas are common in some habitats, they are often absent in others, and factors determining local success are unclear. In addition to a vague understanding of what habitats best support lianas and what factors favor liana growth, it is difficult to predict how lianas will be distributed in a particular forest. Previous work suggests that lianas grow more successfully on certain host tree species (Talley et al. 1996, Putz 1984a). The size of the host trees available may also influence the success of particular liana species. Although largely untested, host bark characteristics may influence liana host preference (Putz 1980, 1984a, Stevens 1987). Some work indicates that rough-barked trees provide a better substrate for hemiepiphytes than do smooth-barked trees (Guy 1977, Todzia 1986), but little data exists to evaluate whether the same is true for lianas. There is little data to allow predictions of the percentage of trees that will host lianas in a particular forest. Finally, most data on lianas have come from wet tropical forests, and very few studies have examined lianas in warm temperate forests or in seasonally dry tropical forests.

The present study was designed to document the species and densities of lianas growing in three differing habitats: 1) mixed mesic cove hardwood forest, 2) xeric white-oak dominated forest, and 3) seasonally dry tropical forest. Another goal was to investigate the liana-host relationship, including the influence of 1) host species and 2) host size on lianas, 3) the spatial distribution of lianas, and 4) the relationship between host bark morphology and liana climbing mechanism.

## Methods

Three sites were sampled in North Carolina in the United States, and one site in the Guanacaste Province of Costa Rica (Figure 1). The methods used in North Carolina differed slightly from those used in Costa Rica, and are described below along with descriptions of each of the four sites.

### *North Carolina sampling technique*

At each site I arbitrarily designated a starting point along a road or trail (usually an intersection of one trail or road with another). At least 10 m into the forest from the road or trail, I established 20 x 20 m plots (each plot = 0.04 ha). I allowed at least 20 m between each plot, and I established plots in a transect-fashion along the road or trail. I was careful not to include edges or recently-disturbed areas (e.g., gaps) in the study sites. This sampling method gave me the freedom to skip areas that contained no or few trees.

In each plot I identified and measured the diameter at breast height (dbh) of each tree larger than 10 cm dbh for comparability with earlier work (Talley et al. 1996). I identified each liana stem that was climbing a tree (the tree was considered the "primary" host for each liana), recorded which tree each liana stem was climbing, measured each liana stem 10 cm above ground level (as in Talley et al. 1996), and identified the lianas. Rarely, tree trunks were fused together in the field, so I summed the basal circumferences of each trunk to calculate one size value for the fused trunks because this was the most reliable technique for determining how much tree trunk surface area was available for the lianas to climb. Occasionally it was difficult to tell if each liana was a distinct individual, a problem other workers have noted in the past (Putz 1984b, Talley et al. 1996). I considered each independent stem one individual, unless it could be determined otherwise.

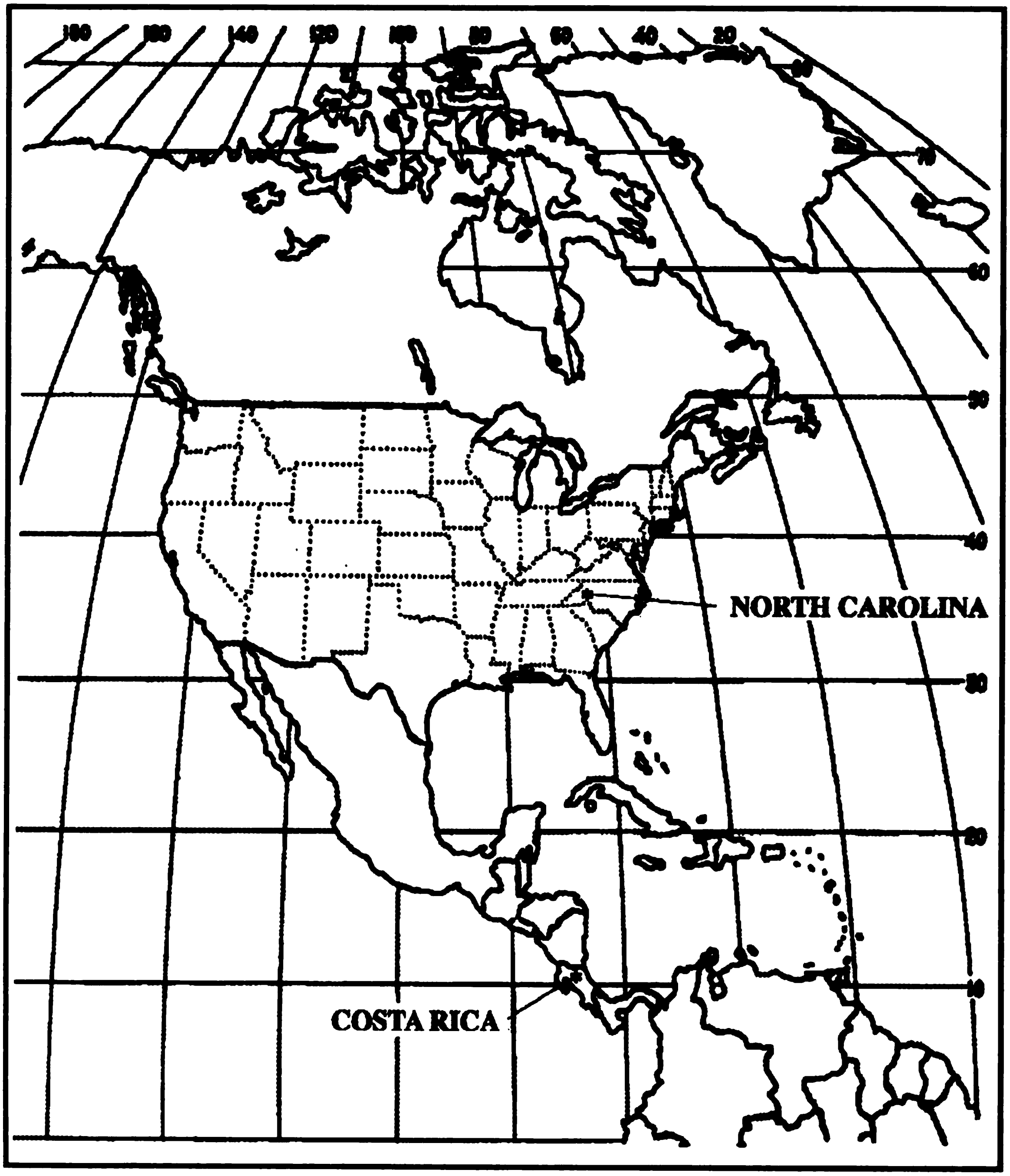


Figure 1. General location of field sites in North Carolina and Costa Rica.

### *North Carolina site descriptions*

All three temperate sites were in North Carolina within the Blue Ridge Mountains, which extend from northern Virginia through eastern Tennessee and western North Carolina to the extreme west of South Carolina and northeastern Georgia (Martin et al. 1993). These mountains contain the highest peaks in eastern North America (> 1500 m), and once rivaled the Rocky Mountains in relief and size prior to erosion (Martin et al. 1993). The Blue Ridge Mountains form part of the Southern Appalachians which is composed of the Appalachian (Cumberland) Plateau (extending from West Virginia to Alabama), the Ridge and Valley Unit (West Virginia to Alabama), and the Blue Ridge region (northern Virginia through northern Georgia; Martin et al. 1993). Soils of slopes and ridgetops are generally shallow, with deep alluvial soils in the valleys (Pitillo 1976). The soils are primarily ultisols; entisols, histosols, and inceptisols are also present (Pitillo 1976).

Nestled within this mountainous terrain is the Highlands quadrangle, in Macon County, NC, near the Georgia and South Carolina boundaries. The town of Highlands (elevation 1255 m), is located on the southern rim of the southernmost high plateau of the Blue Ridge Mountains (Ogburn 1975). The Great Smoky Mountains and the Blue Ridge Parkway lie to the northwest, the Nantahala Mountains to the west, and the Cowee Mountains to the north. The Highlands region is known for its unusually high rainfall even for the Southern Appalachians, and is considered a "frontier" between northern and southern forms of life (Ogburn 1975). This high rainfall and the many habitats sheltered by the ridges have provided a refuge to many forms of life and have resulted in a rich and diverse flora and fauna. The Blue Ridge Province, and thus, the Highlands region, is considered one of the most floristically diverse regions of the eastern United States (Wofford 1989). I chose the Highlands region for this study because of its floristic diversity, and because its moderate climate seemed favorable to liana growth. Two of the sites were in the Highlands quadrangle (Rich Gap and Clifftop Vista), and one was in the Greens Creek quadrangle (Conley Creek; Figure 2).

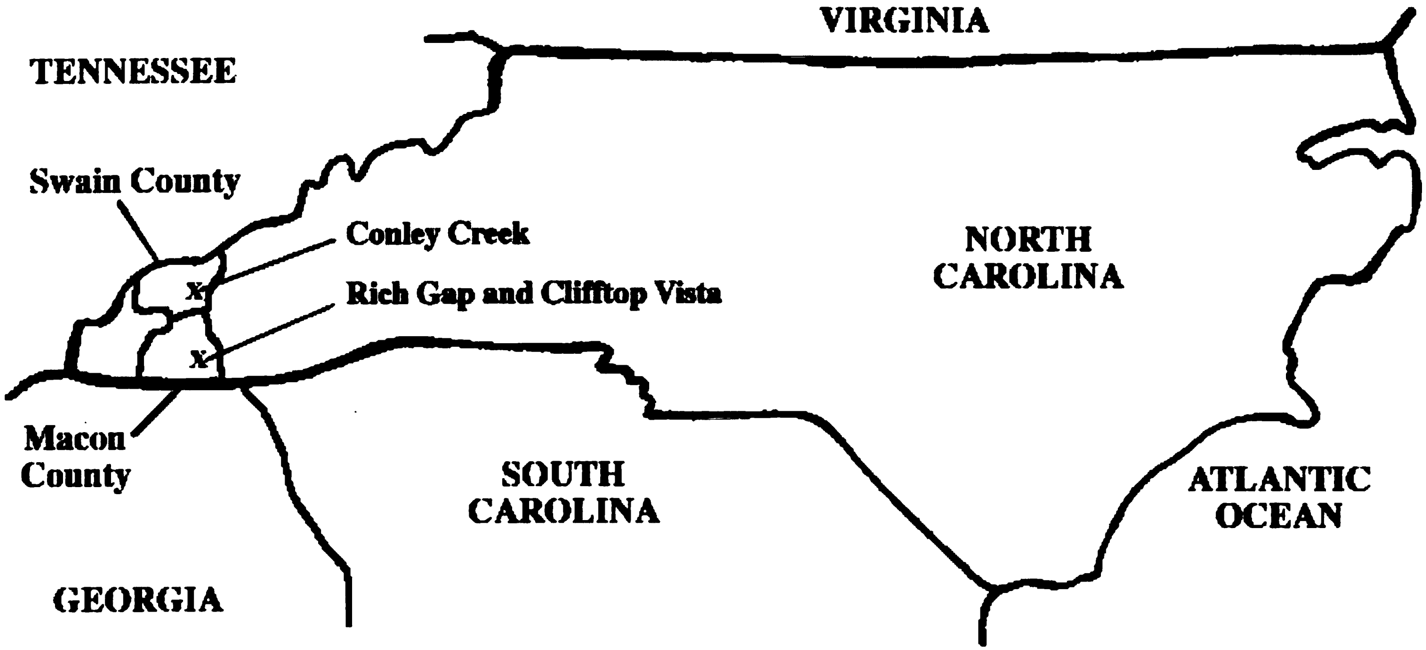


Figure 2. Map of North Carolina showing relative locations of the three temperate field sites (Rich Gap, Conley Creek, and Clifftop Vista).

*Rich Gap.* The first site was a mesic cove forest. Cove forests, in general, are the most species-rich forests in eastern North America with no consistently dominant tree species. Cove hardwood forests are found in sheltered mountain valleys, generally on north- and east-facing slopes (Clay et al. 1975). The cove forests of the Smoky Mountains contain more tree species than are found in all of temperate Europe (Clay et al. 1975). Usually the most dominant trees are: Eastern hemlock (*Tsuga canadensis* L. Carriere: Pinaceae), basswood (*Tilia heterophylla* Ventenat: Tiliaceae), sugar maple (*Acer saccharum* Marshall: Aceraceae), silverbell (*Halesia carolina* L.: Styracaceae), buckeye (*Aesculus octandra* Marshall: Hippocastanaceae) and yellow birch (*Betula lutea* Michaux: Betulaceae)(Clebsch 1989). Beech (*Fagus grandifolia* Ehrhart: Fagaceae) and tulip tree (*Liriodendron tulipifera* L.: Magnoliaceae) are also abundant.

Rich Gap is a mesic cove in the Highlands Quadrangle in Macon County, North Carolina (approximately 35°2'30" North and 83°10'11" West; southwest of benchmark SN 391 3003), southeast of the town of Highlands. This site is adjacent to Rich Gap Road (State Road 1710), a gravel road off of Horse Cove Road (Figure 3). One *Liriodendron tulipifera* tree at this site is the second largest tree in North Carolina and the third largest tree in the eastern United States (Highlands Chamber of Commerce 1994). Rich Gap Road runs north-south along the east-facing slope of Little Fodderstack and Fodderstack Mountains, part of the Cowee Mountain Range. The elevation ranges from 910 to 1040 m at this site, and several hillside seepages dissect the area. Macon County receives between 1270 and 2030 mm of precipitation per year (Clay et al. 1975). I selected Rich Gap because it represented cove hardwood forest which I wanted to sample and also because I had seen wild grape (*Vitis* spp.) in the area.

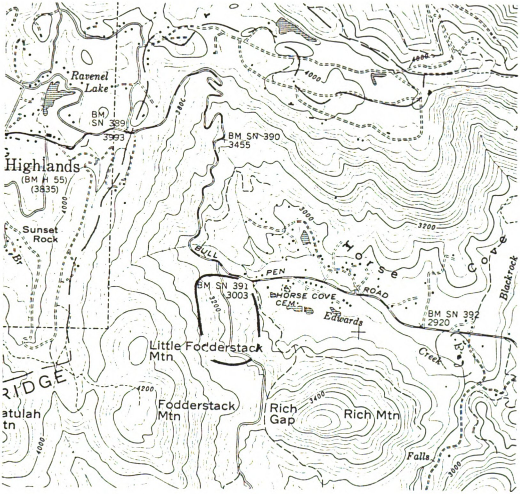


Figure 3. Rich Gap field site in the Highlands Quadrangle, Macon County, NC. (Source: United States Geological Service.)

At Rich Gap, the canopy includes abundant *Liriodendron tulipifera,* umbrella tree (*Magnolia fraseri* Walter: Magnoliaceae), *Halesia carolina*, and numerous less-abundant species. The diverse spring understory in this rich mesic cove hardwood forest includes several *Trillium* L. (Liliaceae) species, downy rattlesnake plantain (*Goodyera pubescens* [Willdenow] R. Brown: Orchidaceae), New York Fern (*Thelypteris noveboracensis* [L.] Nieuwland: Aspidiaceae), bloodroot (*Sanguinaria canadensis* L.: Papaveraceae), and many others. I established and surveyed 15 plots at this site (= 0.6 ha) because this sampling area seemed to include an adequate number of trees and lianas. The first three plots were west of the road and the remaining 12 were east of the road. I was unable to identify lianas in the genus *Vitis* L. (Vitaceae) to species because there were no leaves, flowers or fruits when the data were collected (7 through 14 May 1997).

*Conley Creek.* The second sampling site was another mesic cove forest (see general description above), but was in Swain County, North Carolina (Figure 4). This site is adjacent to Conley Creek Road (State Road 1177) near Pigpen Flats by a series of three switchbacks in the unpaved road, in the Green Creek Quadrangle (35°21'North and 83°22'West). In this area the elevation ranges from about 1160 to 1280 m. This site is located on the east-facing slope of the Alarka Mountains. The canopy includes *Liriodendron tulipifera*, *Acer rubrum*, *Magnolia fraseri*, and oak species (*Quercus*: L. Fagaceae). Swain County receives between 1100 and 1320 mm of precipiation per year (Clay et al. 1975). I selected Conley Creek because the dutchman's pipe, *Aristolochia macrophylla* is present in the area. Due to time constraints, I established and surveyed only seven plots at this site (0.28 ha; 21 May through 2 June 1997).

*Clifftop Vista.* The third site was in a white oak-dominated forest community. White oak forests usually occur at high elevations and have white oak as the dominant species (Roe and Mansberg 1984).

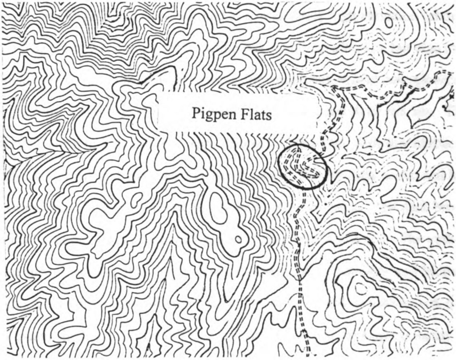


Figure 4. Conley Creek field site in the Greens Creek Quadrangle, Swain County, NC. (Modified from United States Geological Service.)

This particular site was located in Cliffside Recreation Area in the Cowee Mountain Range (Figure 5), and was in the Highlands quadrangle of Macon County, North Carolina (about 35°5' North and 83°14' West). This xeric site is part of the Van Hook White Oak Stand located at the summit along the east-facing slope of Clifftop Vista Trail that faces the scenic Cullasaja River Gorge. This site is located at a moderately high elevation (about 1150 to 1180 m). The canopy is dominated by white oak (*Quercus alba* L.), but also includes pignut hickory (*Carya glabra* (Miller) Sweet: Juglandaceae), scarlet oak (*Quercus coccinea* Muenchhausen), white pine (*Pinus strobus* L.: Pinaceae), and *Acer rubrum*. The understory is dense in *Vaccinium* L. spp. (Ericaceae) thickets, with few herbaceous plants.

Biotite schists and gneisses underlie the area. The strongly acidic soil has a clay-loam texture, and is in the dry-mesic to dry-xeric moisture class. The dark brown humus loam topsoil is about 15 cm deep with a pH ranging from 4.3 to 5.3. The yellowish-brown clay loam subsoil is more than 33 cm deep and has a pH of 5.4 (Roe and Mansburg 1984). I chose this site to investigate whether lianas would be present in a white-oak dominated forest. I established and surveyed only five plots at this site because no lianas were found within the plots (0.2 ha; 9,15 May and 3 June 1997).

### *Costa Rica site description and sampling technique*

A similar sampling technique was repeated in the seasonally dry tropical forest of Palo Verde in Costa Rica (Figure 6). Palo Verde National Wildlife Refuge is located in the south-central Guanacaste Province of lowland Costa Rica, and was leased by the Organization for Tropical Studies in 1968 (Hartshorn 1983). The park is considered a tropical dry forest in the Holdridge life zone system, receiving between 1000 and 1500 mm of rainfall per year with an average biotemperature above 24°C (Hartshorn 1983). The southward shift in the intertropical convergence zone results in a dry season from December to March when northeast tradewinds dry the land (Coen 1983).

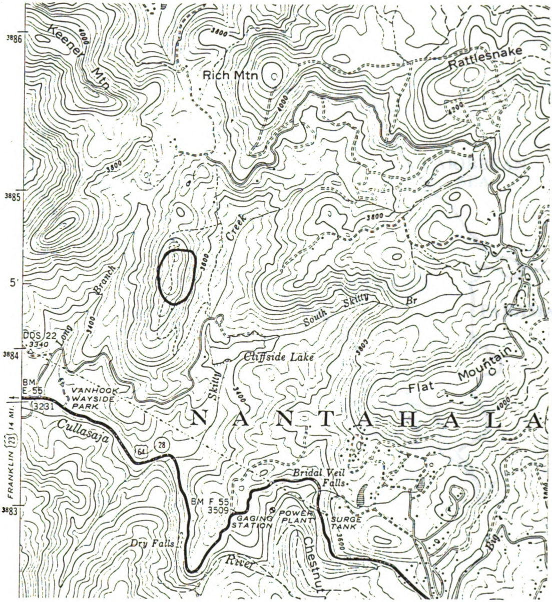


Figure 5. Clifftop Vista field site in the Highlands Quadrangle, Macon County, NC (Source: United States Geological Service.)

Figure 6. Map of Costa Rica showing location of Palo Verde National Wildlife Refuge, Costa Rica.

Over time, the limestone cliffs have eroded and produced soil for the lower slopes, whose colluvial deposits consist of limestone, clay and silt. South of the limestone cliffs, well-drained colluvial soils support a mature forest (Hartshorn 1983). This area is one of the most mature and least-disturbed patches of tropical dry forest in the Guanacaste Province. The elevation is approximately sea level.

In January 1970, Gary Hartshorn and a group of scientists from the University of Washington at Seattle established a 4 ha plot in this forest along the apiary road, 5 km west of the main station. This forest represented primary tropical dry forest. They divided this plot into 100 subplots of 20 x 20 m each (about 10°21' North and 85°23' West; E. Gonzales, personal communication). I used the ten northernmost original 20 x 20 m plots (Plots 000.000 to 000.200) as the study site (Table 1). This sampling technique did not allow the freedom to skip areas with canopy gaps, which differed from that of the North Carolina sampling technique.

On 30 June 1997, I identified all trees whose diameter exceeded 10 cm at breast height and recorded their dbh. For all trees $\geq$ 10 cm dbh I classified the bark type according to the following categories: smooth, peeling, chipping (distinct plates of bark clearly sloughing from tree), rough (sinewy but not ridged, not smooth, bark fragments seldom chip off), or spiny (=ornamented). On 1 and 2 July 1997, I identified all lianas that were climbing the trees $\geq$ 10 cm dbh, and I categorized the climbing mechanism of each liana as tendril climber, twiner, or adhesive disc climber (similar to classification in Putz 1984b). I saw no lianas utilizing adventitious roots for climbing. I included all lianas that were rooted within 2 m of the base of the tree, and each liana stem was considered a different individual unless it could be otherwise determined. I measured all lianas at 10 cm above the ground.

## Results

### *Liana species diversity and density*

At Rich Gap, I measured 154 lianas of three species in two taxonomic families (Tables 1 and 2); 148 (=96%) of these were grapevines in the genus *Vitis,* which could not be identified to species because the vines were just beginning to leaf out during sampling.

At Conley Creek, NC, I measured 63 lianas of three species in two taxonomic families (Tables 1 and 3). Of these lianas, 45 (=71%) were *Aristolochia macrophylla,* but 68% of the total liana basal area was contributed by eight *Vitis* spp. stems (Table 3).

At Clifftop Vista, NC, there were no lianas within the established sampling area. However, there were a few lianas outside of the plots that I noticed on the hike up to the field site, including one wild grape (*Vitis* spp.) stem and several juvenile poison ivy (*Rhus radicans*) stems.

At Palo Verde 157 lianas were measured belonging to at least 14 species in nine taxonomic families (Tables 1 and 4); two species remained unidentified. Bignoniaceae, represented by 66 lianas within five genera, was the most species-rich family. The other nine families present were each represented by only one genus. *Forsteronia spicata* was the most abundant species in the area.

Overall, at all sites, I measured 374 lianas in 37 plots (=0.04 ha each; total of 1.48 ha) at four sites (Table 1). Palo Verde was the most species-rich site (Table 1).

### *Tree species diversity and density*

At Rich Gap, I measured 311 trees in 21 species within 13 taxonomic families (Tables 1 and 5). One-hundred-fifteen of these trees served as host to one or more lianas (=37%; Table 5). The estimated tree basal area per hectare was 36.3 $m^2$ (Table 1). Species-area curves revealed that this sampling area was sufficient to include most of the species present in this forest for both trees (Figure 7a) and lianas (Figure 7b).

Table 1. Summary statistics for three sites in North Carolina and one site in Costa Rica.

| | | North Carolina | | | Costa Rica |
|---|---|---|---|---|---|
| | | Rich Gap | Conley Creek | Clifftop Vista | Palo Verde |
| Trees | number of tree species | 21 | 19 | 11 | 33 |
| >10 cm dbh | number of families | 13 | 10 | 5 | 20 |
| | number of trees | 311 | 133 | 98 | 94 |
| | number of trees with one or more lianas | 115 | 39 | 0 | 52 |
| | summed tree basal circumference (cm) | 25169 | 11106 | 8465 | 8530 |
| | summed tree basal area ($cm^2$) | 217529 | 95059 | 73331 | 94238 |
| | mean number of trees per plot | 20.7 | 19.0 | 19.6 | 9.4 |
| | percent of trees with one or more lianas | 37% | 29% | 0% | 55% |
| | mean tree basal circumference per plot (cm) | 1678 | 1587 | 1693 | 853 |
| | mean tree basal area per plot ($cm^2$) | 14502 | 13580 | 14666 | 9424 |
| | estimated tree basal area per ha ($m^2/ha$) | 36.3 | 33.9 | 36.7 | 23.6 |
| Lianas | number of liana species | at least 3 | at least 3 | 0 | at least 15 |
| | number of families | 2 | 2 | 0 | at least 9 |
| | number of lianas | 154 | 63 | 0 | 157 |
| | summed liana basal area ($cm^2$) | 2394 | 276 | 0 | 1827 |
| | mean liana basal area per plot ($cm^2$) | 160 | 39 | 0 | 183 |
| | mean number of lianas per tree | 0.49 | 0.48 | 0 | 1.68 |
| | mean number of lianas per plot ± SE | 10.27 ± 1.59 | 9.14 ± 2.27 | 0 | 15.70 ± 2.89 |
| | mean number of lianas per 0.1 ha | 25.7 | 22.9 | 0 | 37.8 |
| Lianas | number of lianas | 125 | 10 | 0 | 42 |
| ≥ 2.5 cm | mean number of lianas per 0.1 ha | 20.8 | 3.6 | 0 | 10.5 |

Table 2. Species of lianas present in 0.6 ha at Rich Gap, NC.

| family | species | number of lianas | summed liana basal area (cm$^2$) | mean liana basal area ± SE (cm$^2$) |
|---|---|---|---|---|
| Anacardiaceae | *Rhus radicans* L. | 1 | 1.5 | 1.5 |
| Vitaceae | *Parthenocissus quinquefolia* (L.) Planchon | 5 | 4.5 | 0.9 ± 0.3 |
| | *Vitis* L. spp. | 148 | 2387.9 | 16.2 ± 1.2 |
| total | | 154 | 2394 | |

Table 3. Species of lianas present in 0.28 ha at Conley Creek, NC.

| family | species | number of lianas | summed liana basal area (cm$^2$) | mean liana basal area ± SE (cm$^2$) |
|---|---|---|---|---|
| Aristolochiaceae | *Aristolochia macrophylla* Lam. | 45 | 76.6 | 1.7 ± 0.2 |
| Vitaceae | *Parthenocissus quinquefolia* (L.) Planchon | 10 | 12.5 | 1.3 ± 0.9 |
| | *Vitis* L. spp. | 8 | 186.8 | 23.4 ± 8.2 |
| total | | 63 | 275.9 | |

Table 4. Species of lianas present in 0.4 ha at Palo Verde, Costa Rica.

| family | lianas | number of lianas | summed liana basal area (cm$^2$) | mean liana basal area ± SE (cm$^2$) | climbing mechanism |
|---|---|---|---|---|---|
| Apocynaceae | *Forsteronia spicata* (Jacq.) G. Mey | 34 | 16.0 | 0.5 ± 0.1 | twiner |
| Bignoniaceae | *Cydista diversifolia* (Kunth) Miers | 32 | 179.8 | 5.6 ± 1.9 | tendril |
| Bignoniaceae | *Mansoa hymenaea* (DC.) A.H. Gentry | 20 | 176.7 | 8.8 ± 5.2 | tendril |
| Fabaceae | *Bauhinia* L. spp. | 17 | 866.4 | 51.0 ± 18.5 | tendril |
| Vitaceae | *Cissus rhombifolia* Vahl | 12 | 10.6 | 0.9 ± 0.1 | tendril |
| Combretaceae | *Combretum fruticosum* Kunth | 10 | 52.1 | 5.2 ± 2.3 | adhesive discs |
| Dilleniaceae | *Tetracera volubilis* L. | 9 | 307.4 | 34.2 ± 13.8 | twiner |
| Bignoniaceae | *Arrabidaea conjugata* (Vell.) Mart. | 8 | 207.6 | 26.0 ± 15.5 | tendril |
| Bignoniaceae | *Pithecoctenium crucigerum* (L.) A. H. Gentry | 4 | 1.0 | 0.3 ± 0.2 | tendril |
| Bignoniaceae | *Macfadyena unguis-cati* (L.) A. H. Gentry | 2 | 0.2 | 0.1 ± 0.0 | tendril |
| Passifloraceae | *Passiflora* L. spp. | 2 | 0.9 | 0.5 ± 0.1 | tendril |
| Polygonaceae | *Coccoloba venosa* L. | 1 | 4.5 | 4.5 | twiner |
| Hippocrataceae | *Hemiangium excelsum* (Kunth) A.C. Sm. | 1 | 2.1 | 2.1 | tendril |
| Polygalaceae | *Securidaca diversifolia* Pol. | 1 | 0.5 | 0.5 | tendril |
| unknown 1 | | 1 | 0.6 | 0.6 | tendril |
| unknown 2 | | 3 | 0.8 | 0.3 ± 0.1 | tendril |
| total | | 157 | 1827.1 | | |

Table 5. Tree composition in 0.6 ha at Rich Gap, NC.

| family | tree species | number of trees | number of trees with lianas | percent of trees with lianas |
|---|---|---|---|---|
| Magnoliaceae | *Liriodendron tulipifera* L. | 126 | 62 | 49% |
| Aceraceae | *Acer rubrum* L. | 31 | 13 | 42% |
| Styracaceae | *Halesia carolina* L. | 26 | 7 | 27% |
| Magnoliaceae | *Magnolia fraseri* Walter | 23 | 5 | 22% |
| Juglandaceae | *Carya glabra* (Miller) Sweet | 15 | 3 | 20% |
| Fagaceae | *Quercus prinus* L.* | 14 | 1 | 7% |
| Fagaceae | *Quercus rubra* L.* | 14 | 2 | 14% |
| Cornaceae | *Cornus florida* L. | 13 | 5 | 38% |
| Betulaceae | *Betula lenta* L. | 12 | 3 | 25% |
| Pinaceae | *Tsuga canadensis* (L.) Carriere | 8 | 1 | 13% |
| Rosaceae | *Prunus pensylvanica* L. | 6 | 3 | 50% |
| Tiliaceae | *Tilia heterophylla* Vent. | 6 | 2 | 33% |
| Oleaceae | *Fraxinus pennsylvanica* Marshall ψ | 4 | 0 | 0% |
| Fabaceae | *Robinia pseudo-acacia* L. ψ | 4 | 2 | 50% |
| Pinaceae | *Pinus strobus* L. ψ | 2 | 0 | 0% |
| Lauraceae | *Sassafras albidum* (Nuttall) Nees ψ | 2 | 2 | 100% |
| Betulaceae | *Betula lutea* Michaux ψ | 1 | 0 | 0% |
| Juglandaceae | *Carya ovata* (Miller) K. Koch ψ | 1 | 1 | 100% |
| Fagaceae | *Castanea pumila* (L.) Miller ψ | 1 | 1 | 100% |
| Rosaceae | *Prunus serotina* Ehrart ψ | 1 | 1 | 100% |
| Fagaceae | *Quercus coccinea* Muenchhausen * | 1 | 1 | 100% |
| total | | 311 | 115 | |

*= grouped in analysis as "hardbarked oaks."

ψ= grouped in analysis as "other trees."

Table 5. (Ctn'd)

| family | tree species | summed tree basal area (cm$^2$) | number of lianas | summed liana basal area (cm$^2$) |
|---|---|---|---|---|
| Magnoliaceae | *Liriodendron tulipifera* | 95747 | 81 | 1399.5 |
| Aceraceae | *Acer rubrum* | 33458 | 19 | 204.3 |
| Styracaceae | *Halesia carolina* | 5730 | 8 | 120.4 |
| Magnoliaceae | *Magnolia fraseri* | 26142 | 9 | 207.8 |
| Juglandaceae | *Carya glabra* | 14393 | 4 | 38.8 |
| Fagaceae | *Quercus prinus** | 9303 | 1 | 11.9 |
| Fagaceae | *Quercus rubra** | 15130 | 2 | 31.1 |
| Cornaceae | *Cornus florida* | 1203 | 6 | 56.8 |
| Betulaceae | *Betula lenta* | 3528 | 3 | 11.5 |
| Pinaceae | *Tsuga canadensis* | 1587 | 1 | 4.9 |
| Rosaceae | *Prunus pensylvanica* | 2942 | 5 | 50.2 |
| Tiliaceae | *Tilia heterophylla* | 1034 | 2 | 21.9 |
| Oleaceae | *Fraxinus pennsylvanica*ψ | 958 | 0 | 0.0 |
| Fabaceae | *Robinia pseudoacacia*ψ | 1929 | 2 | 13 |
| Pinaceae | *Pinus strobus*ψ | 738 | 0 | 0.0 |
| Lauraceae | *Sassafras albidum*ψ | 455 | 3 | 8.0 |
| Betulaceae | *Betula lutea*ψ | 107 | 0 | 0.0 |
| Juglandaceae | *Carya ovata*ψ | 754 | 3 | 151.8 |
| Fagaceae | *Castanea pumila*ψ | 375 | 2 | 23.5 |
| Rosaceae | *Prunus serotina*ψ | 979 | 1 | 9.1 |
| Fagaceae | *Quercus coccinea** | 1036 | 2 | 30.7 |
| total | | 217529 | 154 | 2394 |

*= grouped in analysis as "hardbarked oaks."
ψ= grouped in analysis as "other trees."

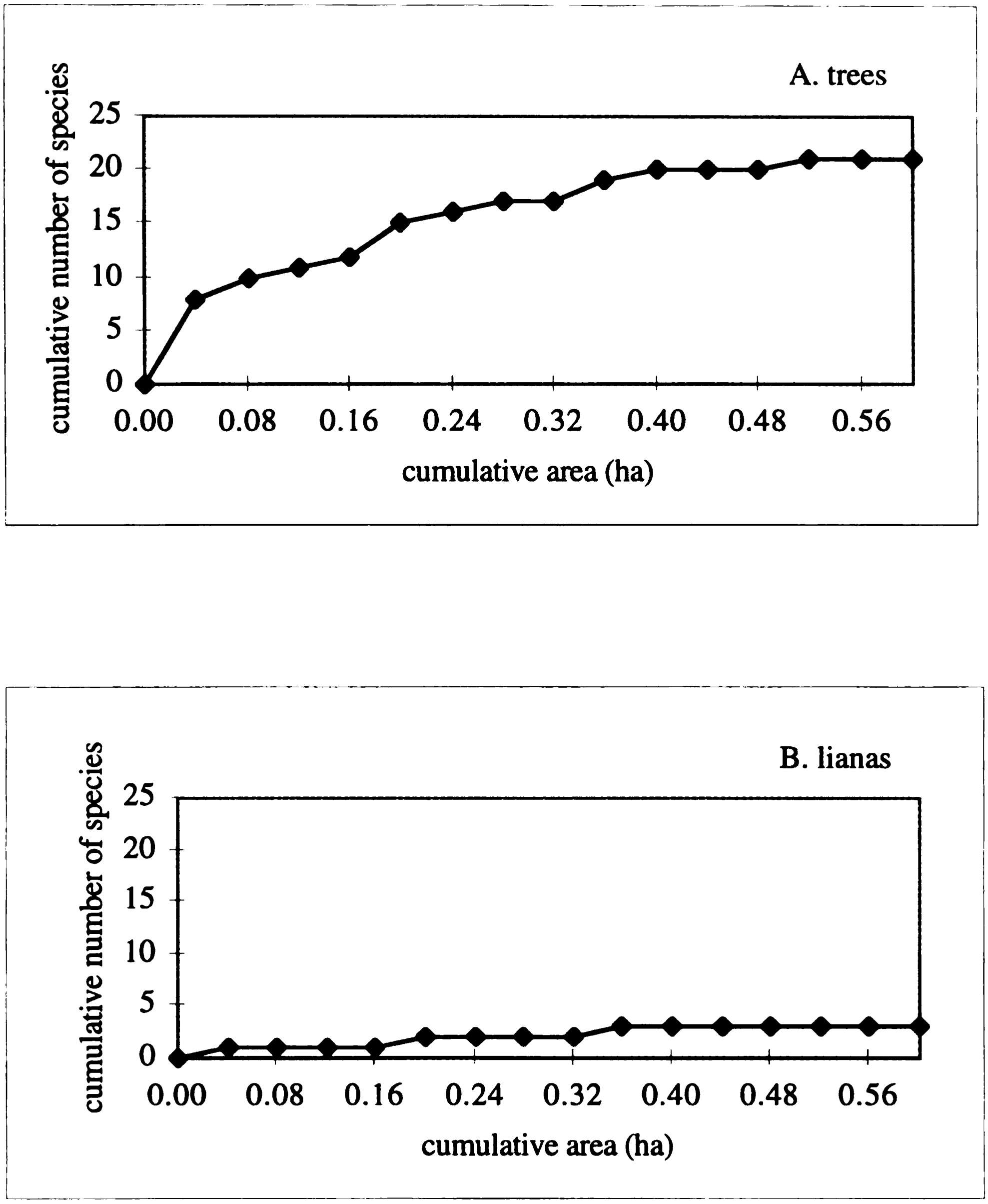


Figure 7. Cumulative number of species for cumulative area sampled at Rich Gap for (a) trees and (b) lianas.

At Conley Creek, I measured 133 trees in 19 species within 10 taxonomic families (Tables 1 and 6). Thirty-nine of these trees served as host to one or more lianas (=29%; Tables 1 and 6). The estimated tree basal area per hectare was 33.9 $m^2$ (Table 1). Species-area curves revealed that this sampling area was sufficient to include most of the species present in this forest for both trees (Figure 8a) and lianas (Figure 8b).

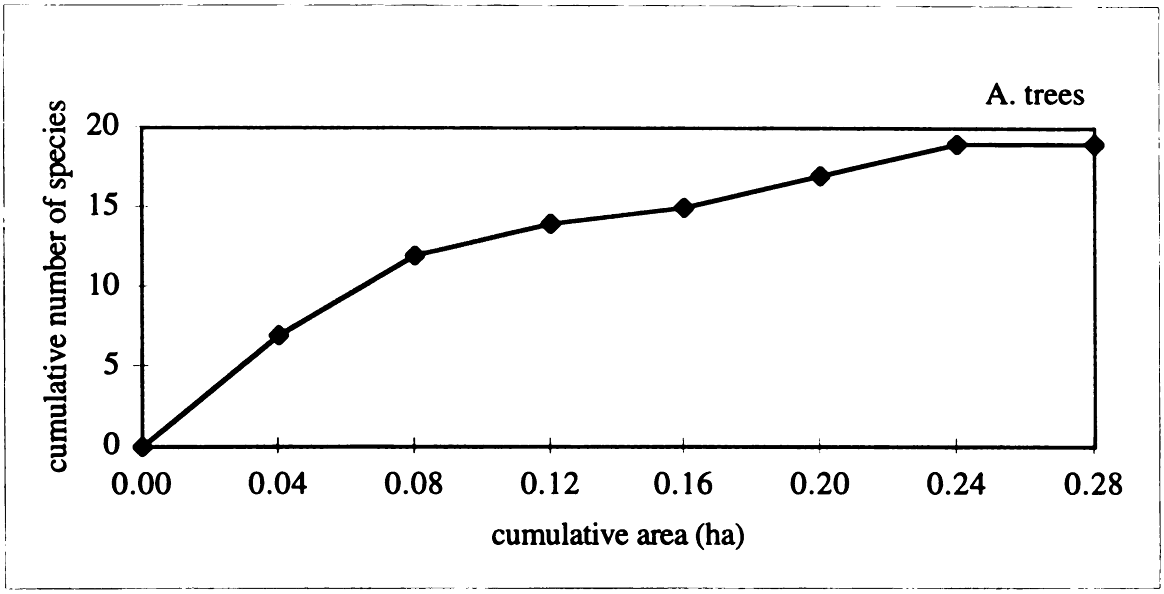
At Clifftop Vista, I measured 98 trees in 11 species within five taxonomic families (Tables 1 and 7); zero of the 98 trees served as host to a woody vine. The estimated tree basal area per hectare was 36.7 $m^2$ (Table 1). Species-area curves revealed that this sampling area was sufficient to include most of the tree species present in this forest (Figure 9).

At Palo Verde, I measured 94 trees in 33 species within 20 taxonomic families (Tables 1 and 8); 52 of the trees served as host to one or more lianas (=55%; Tables 1 and 8). The estimated tree basal area per hectare was 23.6 $m^2$ (Table 1). Species-area curves revealed that this sampling area was insufficient for trees (Figure 10a) and lianas (Figure 10b).

Overall, at all sites, I measured 636 trees, 206 of which hosted one or more lianas (32%). Palo Verde was the most species-rich site in terms of tree species (Table 1). The highest percentage of trees hosting one or more lianas was also at Palo Verde (Table 1). However, the largest estimated tree basal area per hectare was at Rich Gap Road and Clifftop Vista, and the lowest was at Palo Verde (Table 1).

Table 6. Tree composition in 0.28 ha at Conley Creek, NC. *=grouped in analysis as hard-barked oaks. $\psi$=grouped in analysis as "other trees."

| family | tree species | number of trees | number of trees with lianas | percent of trees with lianas | summed tree basal area ($cm^2$) | number of lianas | summed liana basal area ($cm^2$) |
|---|---|---|---|---|---|---|---|
| Aceraceae | *Acer rubrum* L. | 30 | 13 | 43% | 81 | 27 | 138.3 |
| Magnoliaceae | *Liriodendron tulipifera* L. | 22 | 7 | 32% | 792 | 10 | 34.4 |
| Juglandaceae | *Carya glabra* (Miller) Sweet | 16 | 1 | 6% | 79 | 1 | 0.0 |
| Fagaceae | *Quercus prinus* L.* | 14 | 3 | 21% | 89 | 5 | 10.6 |
| Fagaceae | *Quercus rubra* L.* | 12 | 2 | 17% | 89 | 3 | 68.7 |
| Cornaceae | *Cornus florida* L. | 7 | 2 | 29% | 20142 | 3 | 11.9 |
| Juglandaceae | *Carya tomentosa* (Poiret) Nuttall | 6 | 2 | 33% | 2189 | 2 | 0.1 |
| Aceraceae | *Acer pensylvanicum* L. | 6 | 3 | 50% | 999 | 3 | 3.0 |
| Fagaceae | *Quercus alba* L. ψ | 4 | 0 | 0% | 206 | 0 | 0.0 |
| Magnoliaceae | *Magnolia acuminata* L. ψ | 4 | 0 | 0% | 2950 | 0 | 0.0 |
| Tiliaceae | *Tilia heterophylla* Ventenat ψ | 2 | 1 | 50% | 1607 | 1 | 1.0 |
| Styracaceae | *Halesia carolina* L. | 2 | 2 | 100% | 297 | 3 | 3.8 |
| Juglandaceae | *Carya cordiformis* (Wang) K. Koch ψ | 2 | 0 | 0% | 5137 | 0 | 0.0 |
| Fabaceae | *Robinia pseudo-acacia* L. ψ | 1 | 1 | 100% | 18133 | 3 | 0.3 |
| Rosaceae | *Prunus serotina* Ehrhart ψ | 1 | 1 | 100% | 9988 | 1 | 1.1 |
| Magnoliaceae | *Magnolia fraseri* Walter ψ | 1 | 0 | 0% | 103 | 1 | 0.0 |
| Juglandaceae | *Carya ovata* (Miller) K. Koch ψ | 1 | 0 | 0% | 517 | 0 | 0.0 |
| Betulaceae | *Betula lenta* L. ψ | 1 | 1 | 100% | 10969 | 0 | 2.8 |
| Betulaceae | *Betula lutea* Michaux ψ | 1 | 0 | 0% | 20692 | 0 | 0.0 |
| total | | 133 | 39 | | 95059 | 63 | 275.9 |



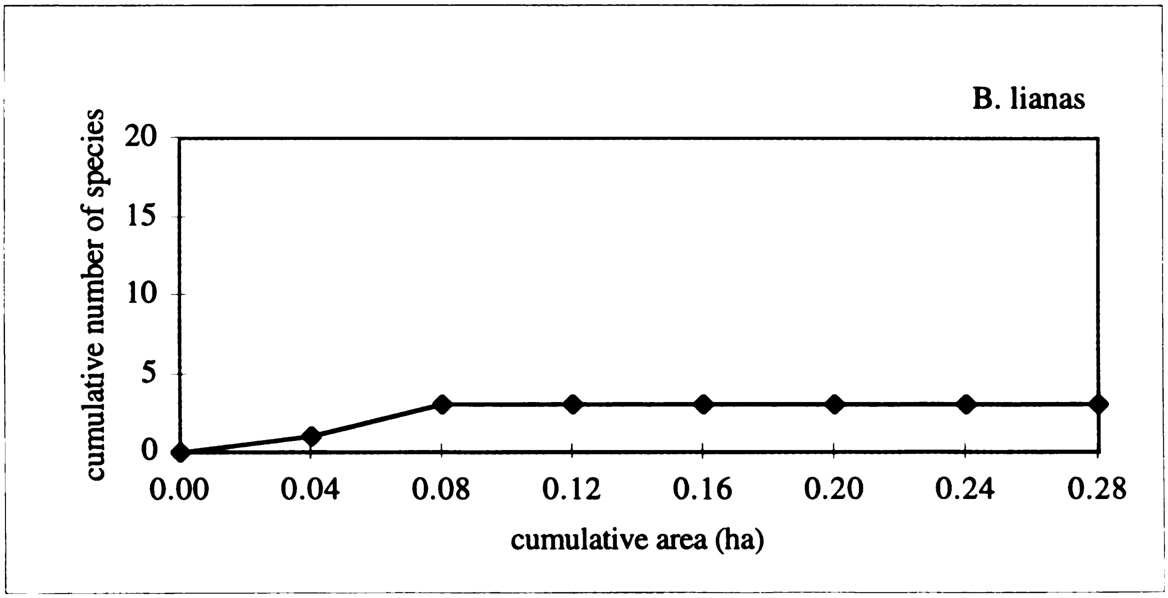


Figure 8. Cumulative number of species for cumulative area sampled at Conley Creek for (a) trees and (b) lianas.

Table 7. Tree composition in 0.2 ha at Clifftop Vista, NC. No lianas were present inside the plots.

| family | tree species | number of trees | summed tree basal area ($cm^2$) |
|---|---|---|---|
| Fagaceae | *Quercus alba* L. | 37 | 27902 |
| Fagaceae | *Quercus coccinea* Muenchh. | 22 | 5118 |
| Juglandaceae | *Carya glabra* (Miller) Sweet | 8 | 1834 |
| Pinaceae | *Pinus strobus* L. | 7 | 13681 |
| Fagaceae | *Quercus velutina* Lam. | 6 | 7023 |
| Aceraceae | *Acer rubrum* L. | 6 | 5157 |
| Fagaceae | *Quercus prinus* L. | 5 | 270 |
| Fagaceae | *Quercus muehlenbergii* Engelmann | 3 | 107 |
| Fagaceae | *Quercus rubra* L. | 2 | 5402 |
| Ericaceae | *Kalmia latifolia* L. | 1 | 2105 |
| Juglandaceae | *Carya tomentosa* (Poiret) Nuttall | 1 | 4732 |
| total | | 98 | 73331 |

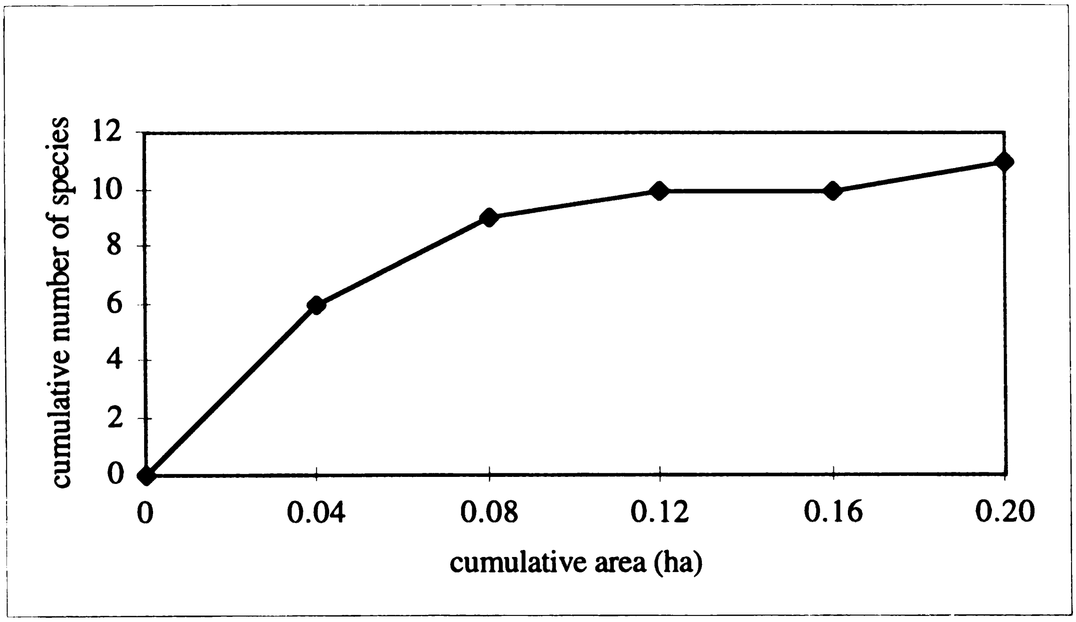


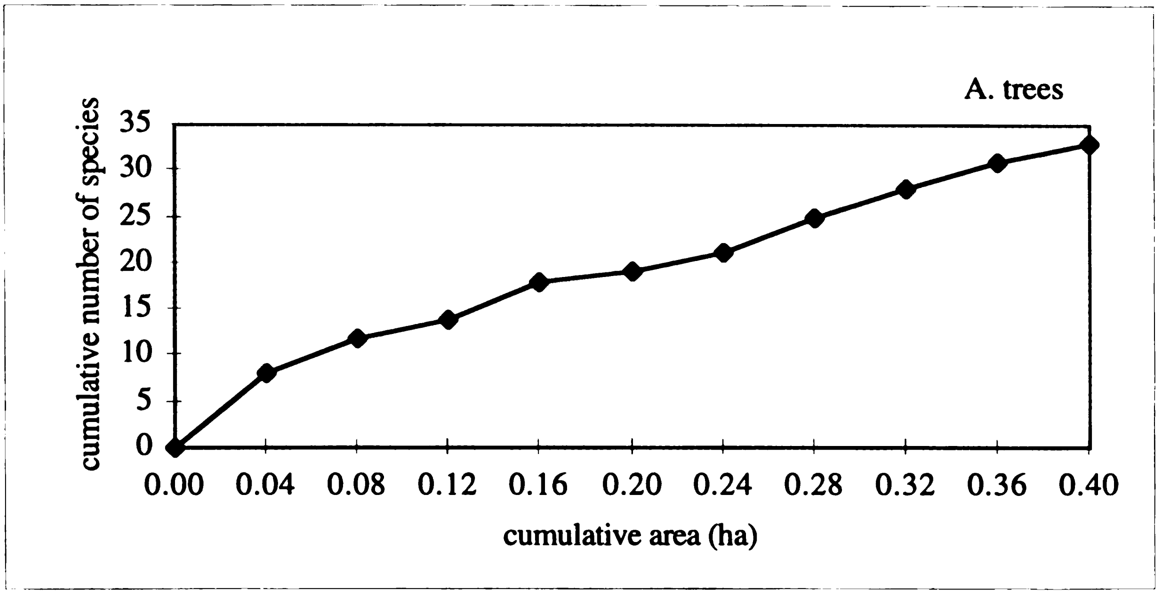
Figure 9. Cumulative number of tree species for cumulative area sampled at Clifftop Vista.

Table 8. Tree composition in 0.4 ha at Palo Verde, Costa Rica. (ba=basal area)

| family | tree species |
|---|---|
| Tiliaceae | *Luehea candida* (DC.) Mart. |
| Bignoniaceae | *Tabebuia ochracea* (Cham.) Standl. |
| Rubiaceae | *Calycophyllum candidissimum* (Vahl.) DC |
| Fabaceae | *Caesalpinia eriostachys* Benth. |
| Rubiaceae | *Chomelia spinosa* Jacq. |
| Theophrastaceae | *Jacquinia* spp. |
| Fabaceae | *Pithecellobium lanceolatum* (Humb. & Bonpl. ex. Willd.) Ben |
| Fabaceae | *Lysiloma divaricatum* (Jacq.) J. F. Macbr. |
| Meliaceae | *Trichilia hirta* L. |
| Rubiaceae | *Guettarda macrospermum* Donn. Sm. |
| Olacaceae | *Ximenia americana* L. |
| Anacardiaceae | *Astronium graveolens* Jacq. |
| Bombacaceae | *Bombacopsis quinata* (Jacq.) Dugand |
| Flaticourtiaceae | *Casearia tremula* (Griseb.) Griseb. ex. W. Wright |
| Fabaceae | *Lonchocarpus costaricensis* (Donn. Sm.) Pittier |
| Anacardiaceae | *Spondias mombin* L. |
| Salviniaceae | *Thouinidium decandrum* (Humb. & Bonpl.) Radlk. |
| Fabaceae | *Acacia cornigera* L. |
| Fabaceae | *Albizia adinocephala* (Donn. Sm.) Britton & Rose |
| Fabaceae | *Albizia caribbea* (Urban) Britt. |
| Burseraceae | *Bursera simaruba* (L.) Sarg. |
| Polygonaceae | *Coccoloba* Browne spp. |
| Cochlospermaceae | *Cochlospermum vitifolium* (Wilde.) Spreng. |
| Boraginaceae | *Cordia alliodora* (Ruiz & Pav.) Oken |
| Sterculiaceae | *Guazuma ulmifolia* Lam. |
| Menispermaceae | *Hyperbaena tonduzii* Diels |
| Theophrastaceae | *Jacquinia nervosa* C. Presl |
| Fabaceae | *Machaerium biovulatum* Micheli |
| Sapotaceae | *Manilkara zapota* (L.) Royen |
| Theophrastaceae | *Muntingia calabura* L. |
| Rubiaceae | *Randia thurberi* S. Watson |
| Simaroubaceae | *Simaruba glauca* DC. |
| Apocynaceae | *Stemmadenia obovata* (Hook. & Arn.) K. Schum. |

Table 8. (Con't)

| tree species | number of trees | number of trees with lianas | percent of trees with lianas | tree ba ($cm^2$) | number of lianas | liana ba ($cm^2$) |
|---|---|---|---|---|---|---|
| *Luehea candida* | 14 | 5 | 36% | 9907 | 15 | 209.5 |
| *Tabebuia ochracea* | 8 | 4 | 50% | 1925 | 8 | 194.6 |
| *Calycophyllum candidissimum* | 7 | 6 | 86% | 27897 | 17 | 320.7 |
| *Caesalpinia eriostachys* | 6 | 2 | 33% | 7664 | 5 | 233.3 |
| *Chomelia spinosa* | 6 | 6 | 100% | 2323 | 23 | 178.2 |
| *Jacquinia pungens* | 6 | 4 | 67% | 843 | 12 | 27.8 |
| *Pithecellobium lanceolatum* | 5 | 2 | 40% | 2923 | 3 | 0.9 |
| *Lysiloma divaricatum* | 4 | 3 | 75% | 5757 | 11 | 53.7 |
| *Trichilia hirta* | 4 | 2 | 50% | 976 | 6 | 3.5 |
| *Guettarda macrospermum* | 3 | 1 | 33% | 1621 | 3 | 16.1 |
| *Ximenia americana* | 3 | 1 | 33% | 1476 | 1 | 10.2 |
| *Astronium graveolens* | 2 | 2 | 100% | 2268 | 6 | 105.4 |
| *Bombacopsis quinata* | 2 | 1 | 50% | 8586 | 2 | 1.2 |
| *Casearia tremula* | 2 | 0 | 0% | 381 | 0 | 0.0 |
| *Lonchocarpus costaricensis* | 2 | 2 | 100% | 637 | 2 | 0.6 |
| *Spondias mombin* | 2 | 1 | 50% | 1608 | 13 | 19.0 |
| *Thouinidium decandrum* | 2 | 2 | 100% | 298 | 4 | 6.6 |
| *Acacia cornigera* | 1 | 0 | 0% | 156 | 0 | 0.0 |
| *Albizia adinocephala* | 1 | 1 | 100% | 1412 | 1 | 9.5 |
| *Albizia caribbea* | 1 | 0 | 0% | 594 | 0 | 0.0 |
| *Bursera simaruba* | 1 | 0 | 0% | 113 | 0 | 0.0 |
| *Coccoloba* spp. | 1 | 0 | 0% | 99 | 0 | 0.0 |
| *Cochlospermum vitifolium* | 1 | 0 | 0% | 1750 | 0 | 0.0 |
| *Cordia alliodora* | 1 | 1 | 100% | 275 | 3 | 4.1 |
| *Guazuma ulmifolia* | 1 | 1 | 100% | 384 | 2 | 41.9 |
| *Hyperbaena tonduzii* | 1 | 1 | 100% | 145 | 2 | 119.9 |
| *Jacquinia nervosa* | 1 | 1 | 100% | 625 | 5 | 30.8 |
| *Macairea biovulatum* | 1 | 1 | 100% | 281 | 3 | 50.3 |
| *Manilkara zapota* | 1 | 0 | 0% | 10696 | 0 | 0.0 |
| *Muntingia calabura* | 1 | 1 | 100% | 123 | 9 | 189.1 |
| *Randia thurberi* | 1 | 0 | 0% | 111 | 0 | 0.0 |
| *Simaruba glauca* | 1 | 0 | 0% | 194 | 0 | 0.0 |
| *Stemmadenia obovata* | 1 | 1 | 100% | 194 | 1 | 0.2 |
| total | 94 | 52 |  | 94238 | 157 | 1827 |



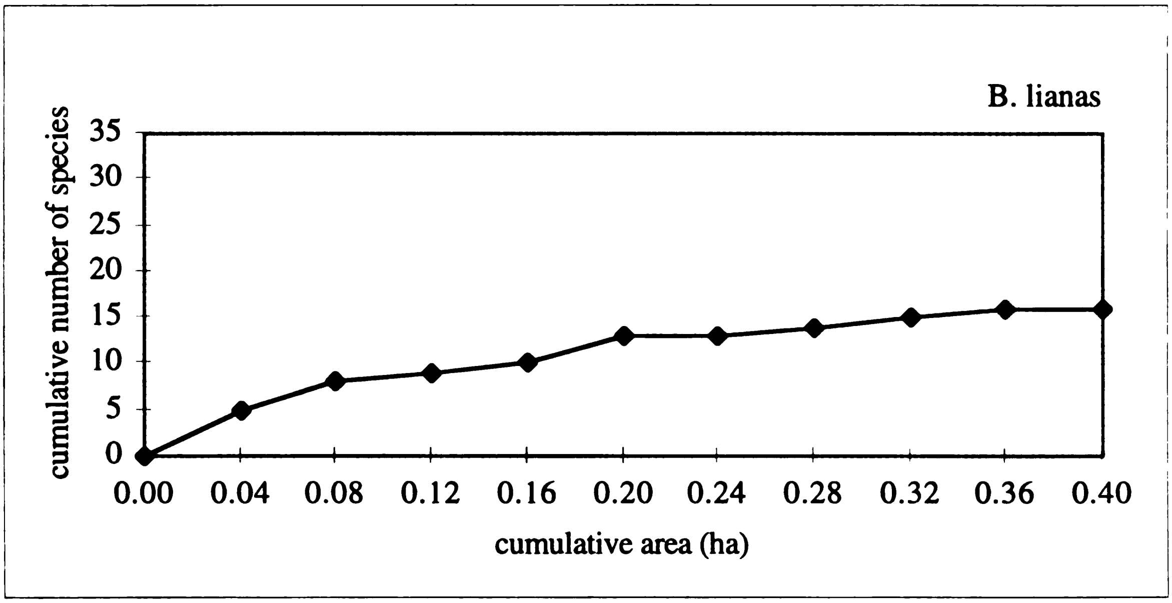


Figure 10. Cumulative number of species for cumulative area sampled at Palo Verde for (a) trees and (b) lianas.

*Liana host-species preference*

There were two ways to calculate expected frequencies of lianas on potential host tree species present in a forest. I utilized both the number of tree stems available per species and the surface area available to climb per species, which is best approximated by tree basal circumference (Daniels and Lawton 1991, Talley et al. 1996). For statistical validity, the less abundant tree species were grouped in the analysis. Additionally, the hard-barked oaks were grouped at Rich Gap and Conley Creek because they have similar non-chipping, rigid bark morphology, and for comparability with earlier work (Table 5; Talley et al. 1996). At Rich Gap, based on the number of stems available to climb, for all lianas present, the number of lianas observed climbing each tree species was independent of relative abundance of the tree species ($X^2_{11}$=26.76, $P$<.005; Table 9). This same trend was seen for the most abundant vine at Rich Gap, *Vitis* spp., when examined alone ($X^2_{11}$=26.61, $P$<.006; Table 9).

Table 9. Influence of tree species on liana distribution at Rich Gap (df=11) and Conley Creek (df=7) when test is based on number of trees available or tree basal circumference available to climb. Chi-square and $P$-values are shown.

| | Number of trees available | Tree basal circumference |
|---|---|---|
| Rich Gap | | |
| All lianas | (26.76) <0.005 | (28.96) <0.002 |
| *Vitis* spp. only | (26.61) <0.006 | (27.35) <0.005 |
| Conley Creek | | |
| All lianas | (24.68) <0.0009 | (27.89) <0.0003 |
| *Aristolochia* only | (35.01) <0.00001 | (23.39) <0.002 |

*Liriodendron tulipifera* served as host to 30% more lianas than expected, contributing 21% of the Chi-square value. The hard-barked oaks hosted only 23% of that expected based on the number of stems available, contributing 32% of the Chi-square value. Most other tree species hosted slightly fewer lianas than expected based on their relative abundances.

A similar trend was seen at Rich Gap utilizing summed tree basal circumference, which represents surface area available to climb. Again, for all lianas, climbers were not distributed among tree species based on their relative available circumferences ($X^2_{11}$=28.96, $P<.002$; Table 9). The same was true for the most dominant liana at Rich Gap, *Vitis* ($X^2_{11}$=27.35, $P<.005$; Table 9). *Cornus florida* hosted twice that expected based on basal circumference, contributing 14% of the Chi-square value. The hard-barked oaks hosted fivefold fewer lianas than expected based on their summed basal circumference available to climb, contributing 38% of the Chi-square value. *Carya glabra* hosted about half that expected, contributing 10% to the Chi-square value. Other species hosted a few more or less than expected based on species contribution to surface area available to climb.

At Conley Creek, based on the number of trees available to climb, for all lianas, Chi-square analysis showed that lianas were distributed on host trees independent of the relative abundance of potential hosts ($X^2_7$=24.68, $P<.0009$; Tables 6 and 9). Similarly, the most abundant species, *Aristolochia macrophylla*, when considered alone, was distributed independent of host relative abundance ($X^2_7$=35.01, $P<.00001$; Table 9). *Carya glabra* hosted only 8% of the lianas expected from its relative stem density, contributing 40% of the Chi-square value. The hard-barked oaks hosted only 42% of the lianas expected, contributing 39% of the Chi-square value.

A similar pattern occurred at Conley Creek when the analysis was based on relative summed tree basal circumference. Lianas were distributed independent of the surface area available to climb per tree species. This trend held true for all lianas ($X^2_7$=27.89, $P<.0003$; Table 9), and also when the most dominant species, *Aristolochia macrophylla,* was considered alone ($X^2_7$=23.39, $P<.002$; Table 9). *Acer rubrum* hosted twice that expected based on its relative surface area available to climb, contributing 50% of the Chi-square value. *Carya glabra* hosted 14% the lianas expected from its contribution to surface area available to climb, contributing 19% of the Chi-square value. The hard-barked oaks hosted one-half that expected, contributing 17% of the Chi-square value.

At Palo Verde there were too few individuals representing each tree species to enable examination of the relationship between tree species and liana presence. Overall, host-tree species was important in explaining liana distribution at the two sites where statistical analysis was possible (Rich Gap and Conley Creek in NC). This was true regardless of whether the number of tree stems available to climb or the summed-tree-basal-circumference available per species was utilized to calculate the number of lianas expected per species.

### *Liana host-size preference*

In addition to species of host, size of the host tree influenced liana distribution among potential hosts at Rich Gap. All species of trees were pooled and grouped into 10 cm-diameter size classes (Table 10 and Appendix A) and Chi-square analysis was performed based on the number of trees available to climb per size class and tree basal circumference per size class. First, expected frequencies of lianas per size class were calculated based on the number of trees available to climb, and when all lianas were included in the calculation, lianas were not distributed in proportion to the number of trees in each size class ($X^2_5$=24.23, $P<.0002$; Table 11). This same trend was seen when *Vitis* was considered alone ($X^2_5$=26.68, $P<.0001$; Table 11). Trees in the smallest size class ($10\leq x<20$ cm dbh) hosted 68% fewer lianas than expected, contributing 27% of the Chi-square value. However, trees in the largest size class ($\geq 60$ cm dbh) hosted three times as many lianas as expected by the proportion of trees in this size category, contributing 51% of the Chi-square value. Thus, based on host relative abundance there seemed to be fewer lianas than expected on smaller hosts, but more lianas than expected on the larger hosts.

Table 10. Size classes of trees of all species pooled in 0.6 ha at Rich Gap, NC. Parentheses indicate exclusion of the end point within the size class, whereas brackets indicate inclusion.

| size class (cm dbh) | number of trees | summed tree basal area ($cm^2$) | number of lianas | summed liana basal area ($cm^2$) | mean number of lianas per tree ± SE |
|---|---|---|---|---|---|
| [10-20) | 128 | 20546 | 43 | 452 | 0.34 ± 0.05 |
| [20-30) | 91 | 43097 | 49 | 649 | 0.54 ± 0.08 |
| [30-40) | 48 | 44331 | 25 | 507 | 0.52 ± 0.11 |
| [40-50) | 21 | 34635 | 15 | 316 | 0.71 ± 0.18 |
| [50-60) | 18 | 42193 | 14 | 265 | 0.78 ± 0.21 |
| ≥60 | 5 | 32727 | 8 | 205 | 1.60 ± 0.81 |
| total | 311 | 217529 | 154 | 2394 | |

Table 11. Influence of host tree size on liana distribution at Rich Gap, Conley Creek and Palo Verde when test is based on number of trees available or tree basal circumference available to climb. Chi-square and *P*-values are shown. Each case had 5 degrees of freedom. NS=Not significant.

| | Number of trees available | Tree basal circumference |
|---|---|---|
| Rich Gap | | |
| All lianas | (24.23) <0.0002 | (6.34) NS |
| *Vitis* spp. only | (26.68) <0.0001 | (5.07) NS |
| Conley Creek | | |
| All lianas | (8.52) NS | (45.62) <0.0001 |
| *Aristolochia* only | (14.20) <0.02 | (45.33) <0.0001 |
| Palo Verde | (35.29) <0.0001 | (72.74) <0.0001 |

This picture was clarified when I evaluated the effect of tree size on lianas based on summed tree basal circumference available to climb per size class. For all lianas, lianas were distributed according to host size ($X^2_5$=6.34, $P$>.38; Table 11). Similarly, there was no effect of size class when only *Vitis* was considered ($X^2_5$=5.07, $P$>.41; Table 11). Thus, the size of host does not seem to influence liana distribution.

In light of the above findings, it appears that liana density per surface area available to climb was constant at Rich Gap. Larger trees have more surface area available to climb, whereas smaller trees have less surface area available to climb. The smallest size classes had fewer lianas per tree but the number of lianas per size class was proportional to the relative surface area contribution per size class. One tree species that defied this overall trend was flowering dogwood, *Cornus florida*, which hosted more lianas than predicted by its contribution to forest available tree-surface-area, but all of the individuals were in the smallest size class.

Similar to Rich Gap, host size influenced liana distribution at Conley Creek. Trees were grouped into 10 cm diameter size classes (Table 12 and Appendix B) and Chi-square analysis was done based on number of trees available to climb per size class and tree basal circumference per size class. Based on number of trees available to climb, lianas were distributed in proportion to relative abundance of size classes ($X^2_5$=8.52, $P$>.12; Table 11). However, the most common vine, *Aristolochia macrophylla,* dutchman's pipe, when considered alone, was distributed independent of relative abundance of size classes available to climb ($X^2_5$=14.20, $P$<.02; Table 11). For *A. macrophylla*, the smallest size class hosted more lianas than expected based on relative stem densities, whereas all larger size classes hosted fewer than expected. This suggests that *A. macrophylla* was utilizing smaller hosts, and the addition of *Vitis* spp. and *Parthenocissus quinquefolia* to the analysis removed the effect of host size because these two genera were distributed independent of host size.

Table 12. Size classes of trees of all species pooled in 0.28 ha at Conley Creek, NC. Brackets indicate inclusion of the end point within the size class, whereas parentheses indicate exclusion.

| size class (cm dbh) | number of trees | summed tree basal area ($cm^2$) | number of lianas | summed liana basal area ($cm^2$) | mean number of lianas per tree ± SE |
|---|---|---|---|---|---|
| [10-20) | 58 | 9052 | 34 | 48 | 0.59 ± 0.14 |
| [20-30) | 26 | 13282 | 16 | 145 | 0.62 ± 0.19 |
| [30-40) | 25 | 24088 | 7 | 9 | 0.28 ± 0.13 |
| [40-50) | 14 | 22222 | 4 | 6 | 0.29 ± 0.22 |
| [50-60) | 6 | 13803 | 0 | 0 | 0 |
| ≥60 | 4 | 12612 | 2 | 69 | 0.5 ± 0.5 |
| total | 133 | 95059 | 63 | 276 | |

At Conley Creek, lianas were distributed independent of the surface area available to climb per species (for all lianas, $X^2_5$=45.62, *P*<.0001, Table 11; *Aristolochia macrophylla* only, $X^2_5$=45.33, *P*<.0001, Table 11). For all lianas, the two smallest tree size classes hosted more lianas than expected, whereas the four larger size classes all hosted fewer lianas than expected. This suggests that liana density is not constant over surface area available to climb. Instead, lianas at Conley Creek, the most abundant being *A. macrophylla*, are preferentially utilizing smaller hosts.

Lianas were not seen at Clifftop Vista. Trees size classes (Table 13) and species representation amongst tree size classes (Appendix C) are provided.

As with the two above sites in NC where lianas were present, host size influenced lianas at Palo Verde. Tree size classes were constructed as above (Table 14 and Appendix D).

Table 13. Size classes of trees of all species pooled in 0.2 ha at Clifftop Vista, NC.

| size class (cm dbh) | number of trees | summed tree basal area (cm²) |
|---|---|---|
| [10-20) | 37 | 6401 |
| [20-30) | 20 | 9734 |
| [30-40) | 28 | 25074 |
| [40-50) | 5 | 8084 |
| [50-60) | 4 | 9273 |
| ≥60 | 4 | 14765 |
| total | 98 | 73331 |

Table 14. Size classes of trees of all species pooled in 0.4 ha at Palo Verde. Parentheses indicate exclusion of the end point within the size class, whereas brackets indicate inclusion.

| size class (cm dbh) | number of trees | summed tree basal area (cm²) | number of lianas | summed liana basal area (cm²) | mean number of lianas per tree ± SE |
|---|---|---|---|---|---|
| [10-20) | 48 | 8308 | 74 | 831 | 1.54 ± 0.36 |
| [20-30) | 14 | 6505 | 37 | 273 | 2.64 ± 0.84 |
| [30-40) | 10 | 9848 | 15 | 336 | 1.50 ± 0.58 |
| [40-50) | 9 | 13249 | 11 | 33 | 1.22 ± 0.88 |
| [50-60) | 5 | 11433 | 9 | 236 | 1.80 ± 0.92 |
| ≥60 | 8 | 44895 | 11 | 119 | 1.38 ± 0.71 |
| total | 94 | 94238 | 157 | 1827 | |

Based on number of trees available to climb, lianas were not distributed in proportion to their relative abundances (for all lianas, $X^2_5=35.29$, $P<.0001$; Table 11). The largest contribution to the Chi-square value was from the smallest size class ($10\leq x<20$ cm dbh; 72%), which hosted fewer lianas than expected based on the relative host stem densities.

When the test was based on tree basal surface area available to climb the two smallest size classes hosted more lianas than predicted, whereas all larger size classes hosted fewer lianas than expected (for all lianas, $X^2_5=72.74$, $P<.0001$; Table 11). The smallest size class ($10\leq x<20$ cm dbh) hosted twice that expected by chance, contributing 38% of the Chi-square value; the largest size class ($\geq 60$ cm dbh) hosting one-fourth that expected by chance, contributing 27% of the Chi-square value.

To summarize, tree size class was important in explaining liana distribution at all sites where lianas were present, but with different trends at different sites. At Rich Gap, lianas were found in proportion to the host surface area available to climb, resulting in more lianas utilizing trees in larger size classes, where more climbing surface area was available. At Conley Creek, size class did not influence all lianas. However, when the dominant liana, *Aristolochia macrophylla,* was considered alone, it showed a preference for smaller hosts, independent of surface area available to climb per size class. Lianas at Palo Verde also showed a preference for smaller hosts, and were not found in proportion to host tree surface area available to climb amongst various size classes.

### *Spatial distribution of lianas*

At Rich Gap, Conley Creek and Palo Verde, there was no clear relationship between the tree basal circumference and the number of lianas per tree. There was also no linear relationship between the tree basal circumference and the liana basal area per tree.

There was a trend toward larger trees hosting more lianas per tree at Rich Gap, but this was not statistically significant (Figure 11). There was an overall mean of 0.49 lianas per tree at Rich Gap (Table 1). The observed number of lianas per tree did not differ from that expected from a Poisson random distribution ($X^2_3$=4.80, $P$>.18) nor from that expected from a negative binomial clumped distribution ($X^2_2$=4.91, $P$>.08, k=4.0; Figure 12a). This indicates that at Rich Gap, the number of trees hosting a certain number of lianas was as expected by chance.

At Conley Creek, there was no trend in the number of lianas per tree with increased size class (Figure 11), but this is difficult to interpret because *Vitis* spp. and *Aristolochia macrophylla* are both included. There was an overall mean of 0.48 lianas per tree at Conley Creek (Table 1). The observed number of lianas per tree differed from that expected from a random Poisson distribution ($X^2_5$=13.09, $P$<.02), but did not differ from that expected from a negative binomial clumped distribution ($X^2_4$=1.67, $P$>.80, $k$=0.4; Figure 12b). This indicates that there were more trees hosting more than one lianas than expected.

There is no trend in the number of lianas per tree with increased size class at Palo Verde Wildlife Refuge (Figure 11). There was an overall mean of 1.68 lianas per tree. The observed number of lianas per tree differed from that expected from a Poisson distribution ($X^2_{12}$=419500, $P$<.00001), but did not differ from that expected from a negative binomial distribution ($X^2_{11}$=14.1, $P$>.23, k=0.65; Figure 12c).

Palo Verde had the highest mean number of lianas per plot, but this was not statistically higher than the other two sites with lianas (Table 1). Palo Verde also had the highest mean number of lianas per tree (Table 1). The number of lianas per tree did not vary systematically with tree size class except for at Rich Gap Road where larger trees tended to host more lianas per tree (Figure 11).

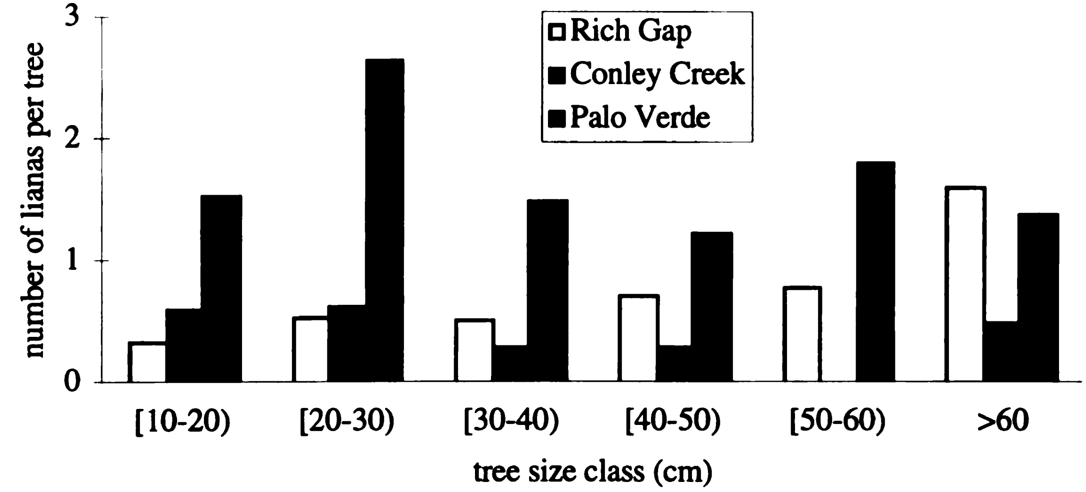


Figure 11. Average number of lianas per tree for tree size classes for three sites. Brackets indicate inclusion of end points in the size class, whereas parentheses indicate exclusion.

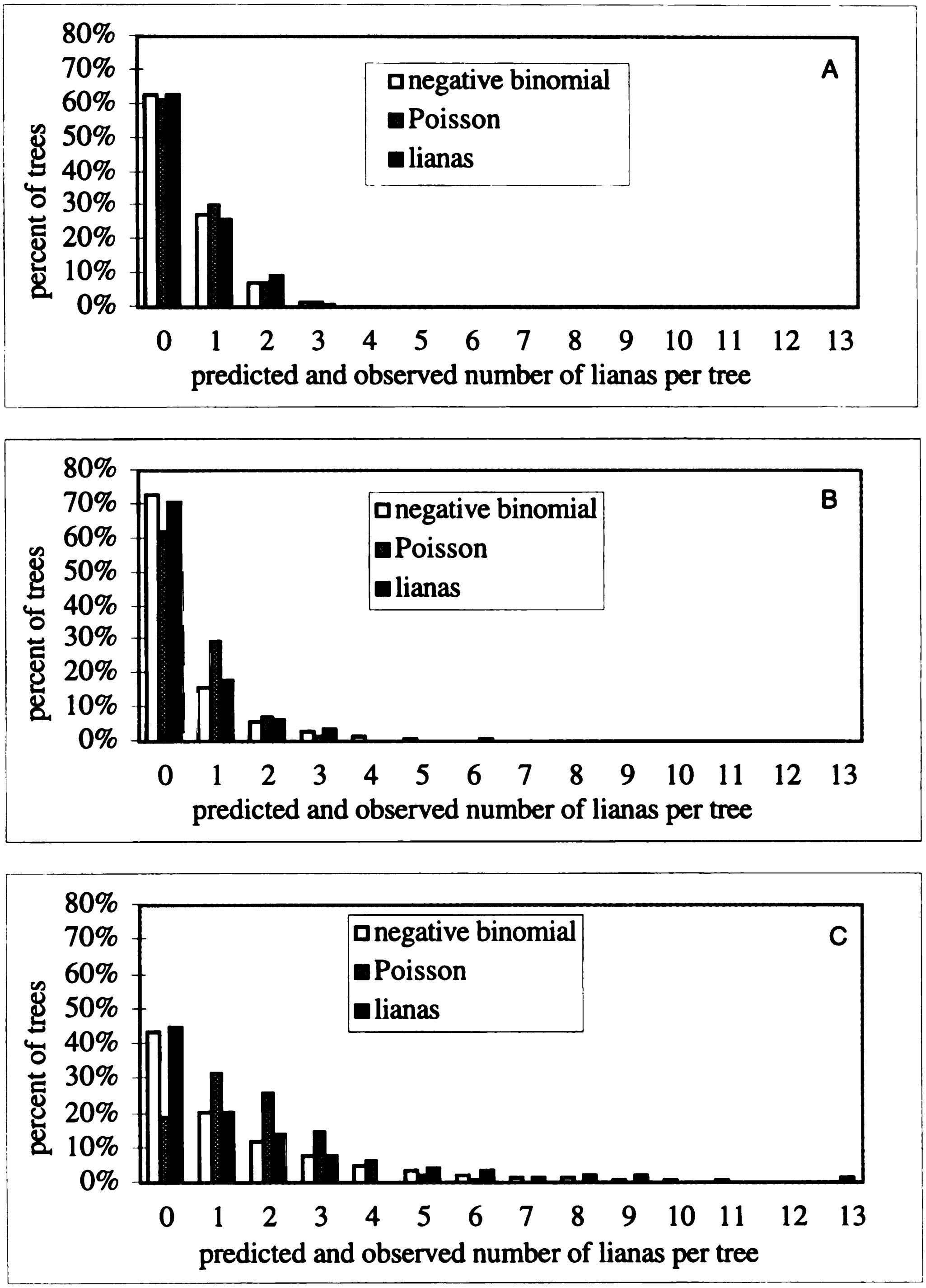
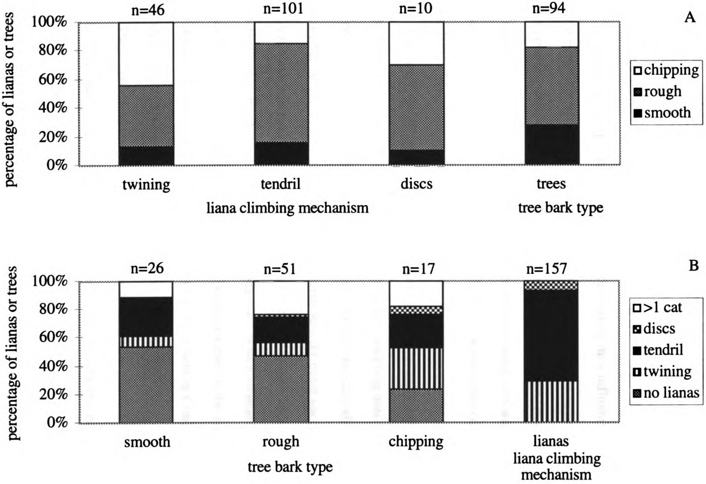


Figure 12. Percentage of trees with a specified number of lianas per tree predicted by the negative binomial (clumped) and Poisson distributions (random) given parameters observed in actual liana distribution (black) for (a) Rich Gap, (b) Conley Creek, and (c) Palo Verde.

### *Relationship between host bark type and liana climbing mechanism*

At Palo Verde, I examined the relationship between tree bark type vs. liana climbing mechanism because the liana flora was diverse with three distinct climbing mechanisms (Table 4). The data were analyzed in two ways. Each liana could be considered one individual observation, or each tree, serving as host to zero to many lianas, could be considered one observation. When each liana was treated as one individual observation (N=157; Figure 13a), there was a non-zero correlation between liana climbing mechanism and host bark type (contingency table: $X^2_4=14.6$, $P<.006$; non-zero correlation value = 4.020, df=1, $P<.05$). The greatest contribution to the Chi-square value was from the association between twining lianas climbing trees with chipping bark (48% of Chi-square value). However, when each tree is considered as one observation (N=94; Figure 13b), there was no relationship between tree bark and liana climbing mechanism (contingency table: $X^2_8=10.57$, $P>.22$).

Figure 13. Palo Verde, Costa Rica. (a) Proportion of twining, tendril-climbing or adhesive-disc climbers that were observed climbing trees with chipping, rough or smooth (includes peeling and spiny) bark. Also shown is proportion of trees with rough, smooth, and chipping bark (b) Proportion of trees that hosted lianas that are tendril climbers, twiners or adhesive disc climbers. Some trees hosted no lianas, others hosted lianas in more than one category (>1cat). Also shown is proportion of lianas that had various climbing mechanisms.

n=46
n=101
n=10
n=94
A
100%
80%
60%
40%
20%
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percentage of lianas or trees
twining
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discs
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liana climbing mechanism
tree bark type
□ chipping
▨ rough
■ smooth
n=26
n=51
n=17
n=157
B
100%
80%
60%
40%
20%
0%
percentage of lianas or trees
smooth
rough
chipping
lianas
tree bark type
liana climbing mechanism
□ >1 cat
▨ discs
■ tendril
▥ twining
▨ no lianas

## Discussion

### *Species diversity and density*

The seasonally dry tropical site, Palo Verde, had the highest species richness in both lianas and trees. The number of lianas per plot and the mean liana basal area per plot was also greatest at Palo Verde (Table 1). This follows expectations that the forested tropics are generally more species rich than even the richest temperate areas. However, it is important to note that total sampling area differed at the sites, which may influence the number of species observed at each site. Species-area curves for the three temperate sites suggested that the sampling area was large enough to include most of the species of lianas present within these forests (Figures 7b and 8b), whereas the sampling size was not large enough in Costa Rica for the number of liana species to level off with increased sampling area (Figure 10b).

The two North Carolina mesic cove forests (Rich Gap and Conley Creek) supported about the same absolute number of lianas per sampling area (Table 1), which was expected because they are similar forest types. These two sites also supported the same number of liana species, but they were nonetheless different species (Tables 2 vs. 3). *Aristolochia macrophylla* was present at Conley Creek but absent from Rich Gap. This species is listed in Radford et al. (1968) as “infrequent,” which indicates that although Rich Gap may be acceptable habitat, it may not have been dispersed to the area. Similarly, poison ivy (*Rhus radicans*) was present at Rich Gap but absent at Conley Creek. This was not an ideal habitat for this species, which prefers disturbed places.

Palo Verde had the highest mean number of lianas per plot (15.7 lianas per plot; Table 1). This number is higher than all sites in North Carolina, but is one fourth the 64 lianas per 20 x 20 m that Putz (1984b) reported for Barro Colorado Island (BCI), Panama. Palo Verde is dryer than BCI, which may explain its lower liana densities (Palo Verde receives 1500 mm of rain per year (Hartshorn 1983) whereas BCI receives 2600 mm

(Todzia 1986)). Additionally, Putz included every liana present, rather than excluding lianas that were not clearly climbing a host as in this study.

It is interesting to examine at each site the number of lianas greater than or equal to 2.5 cm diameter per 0.1 hectare because this figure is comparable with previous studies (Table 15). This number was highest at Rich Gap (20.8 lianas/ 0.1 ha), but I chose this site because it had many lianas, which I suspected would yield interesting data for liana distribution. However, this site could bias comparison with previous studies. Palo Verde contained the second highest number of lianas larger than 2.5 cm diameter per 0.1 hectare (10.5 lianas/0.1 ha, Tables 1 and 15). This is one-eighth that observed at Chamela dry forest where 78 climbers ≥ 2.5 cm diameter per 0.01 ha were seen (Gentry 1991, Table 15). However, it is unclear whether Gentry measured all lianas or just those clearly ascending a host, as in the present study, nor is it clear at what height Gentry measured the plants. The two mesic NC cove forests in the present study, Rich Gap and Conley Creek, both contained more lianas ≥ 2.5 cm diameter than the reported North American average of five lianas per 0.1 ha (Table 15, Gentry 1991). However, one of the sites in the present study contained no lianas (Tables 1 and 15), suggesting that there is high variance in the densities of lianas in temperate forests.

It is also useful to compare the percentage of trees ≥ 10 cm diameter that hosted one or more lianas to that observed in previous studies. Putz reported that 42% of trees in San Carlos de Rio Negro, Venezuela (1983), and 30 to 50% at BCI served as host to one or more lianas (1984b). In the present study, at Palo Verde, 55% of trees served as hosts to one or more lianas (Table 1). A smaller proportion of trees at Rich Gap hosted lianas (37%, Table 1), and even fewer at Conley Creek (29%, Table 1).

Table 15. Comparison of present results to previous studies: density of climbers ≥ 2.5 cm diameter in 0.1 ha, number of climbing species, and number of and families in the Neotropics and North America. Data from Gentry (1991) indicated by asterisks are regional averages, including at least two sites from the region.

| Region | Number of climbers (or regional average) | Number of species | Number of families |
|---|---|---|---|
| Neotropics | | | |
| New World lowland rainforests*ϕ | 62.1 | 38.7 | 18.6 |
| Chamela dry forest* | 78 | 14.6 | 11 |
| Palo Verde dry forest | 10.5 | 15 | 9 |
| North temperate | | | |
| North America* | 5 | 1.9 | 1.4 |
| Rich Gap-mesic cove forest | 20.8 | 3 | 3 |
| Conley Creek-mesic cove forest | 10 | 3 | 2 |
| Clifftop Vista- xeric white-oak dominated forest | 0 | 0 | 0 |

*=data from Gentry (1991) and includes hemiepiphytes
ϕ=includes sites with ≥ 4000 mm of annual precipitation

Tree species richness varied at the four sites, but these data are difficult to interpret because the sampling size was different for each site. Species-area curves suggested that the number of tree species seen in the temperate sites reflected the total number of species present in the forest (Figures 7a, 8a, and 9), but at Palo Verde the number of tree species observed was less than had a larger area been sampled (Figure 10a). Palo Verde had the most tree species, Rich Gap and Conley Creek had an intermediate number of species, and Cliffside had the fewest species. This trend was as expected. Tropical forests are, in general, more species-rich than those in the temperate zone, and, mesic coves are more species rich than white oak-dominated forests (Roe and Mansberg 1984; Clebsch 1989).

Extrapolated tree basal area per hectare in this study was lowest at Palo Verde, but similar at all three sites in North Carolina (Table 1). It is generally accepted that dry forest tree basal area will be less than that of temperate forests. Murphy and Lugo (1986) provide a range of basal areas for tropical dry forests between 17 to 40 $m^2$/ ha. The range of basal area per hectare in temperate forests is about 25 to 63 $m^2$/ ha (DeAngelis et al. 1981). The mean number of trees per plot shows the same trend as that of tree basal area per hectare (Table 1). Again, the mean number of trees per plot was lowest at Palo Verde, but higher and uniform at all three sites in North Carolina.

Although the reasons that we see increased species diversity with decreasing latitude are often debated among ecologists (e.g., Rosenzweig 1995), perhaps a more general rule exists for lianas. Lianas are poorly represented as a portion of the flora in temperate areas, perhaps because the wide vessels that characterize lianas are prone to freeze-induced embolism (Ewers et al. 1997). Most temperate woody vines must construct new vascular tissue each spring because, in the absence of positive root pressure to refill embolized vessels, the previous year's tissues are often rendered functionless by the winter's embolisms. Similarly, it has been shown that larger conduits are more susceptible to drought-induced embolism (Hargrave et al. 1994). Because lianas have such large vessels, it follows that drought-induced embolism might restrict lianas to wetter areas. However, Palo Verde does undergo drought-like conditions in the dry season, and the data from the present study suggest that these lianas can do very well in a drought-stressed environment. Lianas at Palo Verde are mainly deciduous in the dry season (E. Gonzales, personal communication), so perhaps this accounts for liana species success at Palo Verde. The susceptibility of lianas to drought stress might explain why no lianas were present within the plots at Clifftop Vista (Tables 1 and 15). The high elevation, coupled with low moisture and brutal winters with severe winds, may preclude liana survival. Although I saw no woody vines at Clifftop Vista, I noted a few herbaceous scramblers in the genus *Smilax*. These scramblers probably survive by dying back in the winter and sprouting new growth in the spring. It is interesting to note that Clifftop Vista had the largest extrapolated tree basal area per hectare (Table 1). In spite of this high measure of tree basal area in terms of trees, the forest supported no lianas. This indicates that the contribution of liana basal area to the forest is not predictable by the overall tree basal area. In fact, Palo Verde had the smallest total tree basal area per hectare compared to all other sites, yet it supported the highest liana basal area per plot (Table 1).

*Liana host-species preference*

Host tree species was important in explaining liana distribution at all sites where it was possible to investigate. This was true regardless of whether the number of tree stems available to climb, or the summed tree basal circumference available for climbing, was utilized to calculate the number of lianas expected per species (Rich Gap and Conley Creek). Thus, it seems very clear that host species influences liana distribution, as was seen in a Tropical Moist Forest at BCI (Putz 1984a). Additionally, host preferences have been shown in hemiepiphites (Guy 1979, Daniels and Lawton 1991, Todzia 1986, Laman 1996). Why are climbers more likely to be found on certain tree species than others? At both Rich Gap and Conley Creek, there were fewer lianas than expected based on relative contribution to surface area available to climb on *Carya glabra* and on the hard-barked oaks. However, in a previous study on poison ivy (Talley et al. 1996) in old-growth Alabama mesophytic forest, these tree species supported more vines than expected based on tree stem densities. Perhaps liana species and climbing mechanisms contribute to this discrepancy. Each liana species may have its own suite of suitable characteristics required to colonize a particular host species. The suggestion that host bark type may influence lianas differently based on their individual climbing mechanisms is a little-tested hypothesis. Putz (1980, 1984a) suggested that trees with smooth bark are less likely to host lianas, but Boom and Mori (1982) showed that smooth-barked tree species were no less likely to host lianas in Brazil. Putz (1984a) shows that spiny-barked trees were not likely to "saw off" lianas when the trees were mechanically agitated. The data from the present study suggest that there was a non-linear correlation between tree bark type and liana climbing mechanism at Palo Verde. However, this was not a powerful enough test to definitively answer this question.

### *Liana host-size preference*

Tree size was less consistent than tree species in its influence on lianas across sites and with different species of climbers. At Rich Gap, where *Vitis* spp. was the most common liana, I saw more lianas than expected on large trees, but there were fewer lianas than expected on small trees based on relative stem abundances. It appears that *Vitis* spp. will be found at Rich Gap according to tree trunk surface area available to climb. For approximately every 160 cm of tree basal surface circumference available to climb, one *Vitis* spp. stem was encountered. Perhaps competition for some limiting resource results in a uniform distribution of *Vitis* spp. on the tree surface area available to climb.

A different pattern in the influence of tree size on lianas arose at Conley Creek where *Aristolochia macrophylla* was the most common liana. There were more lianas on smaller trees and fewer on larger trees than expected based on relative stem abundances. Also, at Conley Creek, surface area available for climbing did not determine where lianas were found, strengthening the claim that *A. macrophylla* is preferentially utilizing smaller hosts. Thus, *A. macrophylla* seems better able to utilize smaller trees as support because it must twine around its substrate. I also noticed that it often twined around other vines, a condition that has been noted in other liana species by other workers (e.g., Putz 1984a, 1984b, 1995).

At Palo Verde where many liana species were present, there were more lianas than expected on the two smallest tree size classes based on tree surface area available for climbing. At this site, 94% of the lianas were tendril climbers and twiners that must coil around their hosts. Thus, the size of the host seems relevant when considering the type of climbing mechanism of the vines that are utilizing these host trees. Putz (1984b) showed that tendril climbers utilize small hosts (0 to 7 cm diameter), twiners utilize a larger set of supports (3 to 16 cm), whereas root- and adhesive-tendril climbers have no size restrictions. These trends in the influence of host size on lianas may be confounded with the successional age of each of these forests. Although gaps were avoided while sampling in North Carolina, they could not be avoided in Costa Rica. Perhaps sites earlier in succession will contain more smaller trees which are then utilized as hosts because they dominate the area. Additionally, lianas grow as the trees grow, so as their hosts grow larger, lianas are already committed to inhabitance and will thus be found on smaller trees earlier in time but larger trees later in time. Thus, the effects of host size will always be confounded with the influence of host age in a study that is performed at one point in time. Long-term monitoring of locations of lianas within a forest may help determine whether lianas show preferences for host size or age.

### *Spatial distribution of lianas*

The number of lianas per tree at each site presents an interesting pattern. At both Conley Creek and Palo Verde, the number of lianas per tree differed from that expected from a Poisson or random distribution, suggesting that lianas were not randomly distributed in these forests but were instead more likely to climb a tree that was already hosting at least one liana. Putz (1984b) saw that there were more trees hosting two or more lianas than expected by chance, which is similar to that observed in this study at Palo Verde (Figure 8). However, at Rich Gap, the liana distribution did not differ from that expected from a Poisson nor from that expected from a negative binomial distribution. I believe this is a statistical artifact of the test, because as the mean number of lianas per tree approaches zero, the distribution of the negative binomial approaches that of the Poisson. Or it may be that wild grape, *Vitis* spp., is no more likely to climb a tree that is already serving as host to one or more lianas than it is to climb an unutilized tree. As the present study suggests, the number of *Vitis* spp. individuals will increase at a constant rate as climbing surface area availability increases.

The present study suggests that lianas are spatially clumped amongst the trees within a forest. Plots at Rich Gap contained anywhere from two to 21 lianas, at Conley Creek, plots contained between one and 15 lianas, and at Palo Verde the range was from one to 36 lianas per plot. It is quite clear from a walk through the woods that lianas are usually spatially clumped, which has been seen in other studies (Putz 1984b, Talley et al. 1996). Collins and Wein (1993) showed that understory vines are spatially distributed based on soil moisture, ground cover or plant size. Also, an established liana can act as a trellis for new colonizers.

### *What influences liana distribution?*

It is fairly certain that habitat characteristics and environmental factors will influence liana presence in a given area. The presence of available substrate is necessary for the success of climbers. However, once an inhabitable area exists and is colonized by a liana species, what then determines its success and ultimate distribution within this particular area? This study suggests that host species and size will influence liana distribution, although these factors may influence different species of lianas differently. Additionally, preliminary data suggest that host bark type may influence various species of lianas with different climbing mechanisms differently. Lianas can also be clumped due to dispersal features.

I think that perhaps with the exception of hosts that are unacceptable due to toxic effects of allelopathic secretions (as suggested by Talley et al. 1996), most trees serve as acceptable initial hosts for lianas. What becomes important is how long the liana can hold onto the hosts, and whether the tree has mechanisms to shed climbers. Fast growth and large, self-pruning compound leaves seem influential in tree liana avoidance (Putz 1984a). Spiny bark was also suggested as a mechanism to saw off lianas, but no evidence supports this claim (Putz 1984a). Lianas are most likely a selective force in maintaining tree diversity by influencing host life histories. Trees that can escape lianas will have higher annual basal growth (Putz 1984b) and greater reproductive output (Stevens 1987).

In each of the temperate forests that contained lianas in the present study, one species was clearly the dominant climber in the area. Other species are clearly being dispersed to the area, because they were seen in these sites but in far lower abundance. What factors determine the success of a particular species over others that are also present? I don't believe that direct competition for hosts would prevent another species from successfully inhabiting a particular forest because there were always many uninhabited trees available to climb. Do those trees have properties that make them unacceptable hosts? Epiphytes and hemiepiphytes are often fairly specific as to what hosts provide suitable germination sites. Lianas may also perform better on hosts with an acceptable suite of characteristics. From the present study it seems that each species of liana may utilize a particular suite of tree species and sizes as hosts.

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# APPENDICES

# APPENDIX A

# APPENDIX A

Species representation in tree size classes (cm) for 0.6 ha at Rich Gap, NC.

| species | size class (cm dbh) | | | | | | |
|---|---|---|---|---|---|---|---|
| | [10-20) | [20-30) | [30-40) | [40-50) | [50-60) | ≥60 | total |
| *Acer rubrum* | 8 | 9 | 5 | 2 | 4 | 3 | 31 |
| *Betula lenta* | 6 | 6 | 0 | 0 | 0 | 0 | 12 |
| *Betula lutea* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Carya glabra* | 4 | 4 | 3 | 1 | 3 | 0 | 15 |
| *Carya ovata* | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| *Castanea pumila* | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Cornus florida* | 13 | 0 | 0 | 0 | 0 | 0 | 13 |
| *Fraxinus pennsylvanica* | 3 | 1 | 0 | 0 | 0 | 0 | 4 |
| *Halesia carolina* | 19 | 7 | 0 | 0 | 0 | 0 | 26 |
| *Liriodendron tulipifera* | 33 | 44 | 27 | 13 | 8 | 1 | 126 |
| *Magnolia fraseri* | 14 | 7 | 1 | 0 | 0 | 1 | 23 |
| *Pinus strobus* | 1 | 1 | 0 | 0 | 0 | 0 | 2 |
| *Prunus pensylvanica* | 4 | 1 | 0 | 1 | 0 | 0 | 6 |
| *Prunus serotina* | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| *Quercus coccinea* | 0 | 0 | 1 | 0 | 0 | 0 | 1 |
| *Quercus prinus* | 4 | 4 | 4 | 2 | 0 | 0 | 14 |
| *Quercus rubra* | 3 | 3 | 3 | 2 | 3 | | 14 |
| *Robinia pseudoacacia* | 1 | 2 | 1 | 0 | 0 | 0 | 4 |
| *Sassafras albidum* | 2 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Tilia heterophylla* | 5 | 1 | 0 | 0 | 0 | 0 | 6 |
| *Tsuga canadensis* | 7 | 0 | 1 | 0 | 0 | 0 | 8 |
| total | 128 | 91 | 48 | 21 | 18 | 5 | 311 |

# APPENDIX B

## APPENDIX B

Species representation in tree size classes (cm) for 0.28 ha at Conley Creek, NC.

| species | size class (cm dbh) | | | | | | |
|---|---|---|---|---|---|---|---|
| | [10-20) | [20-30) | [30-40) | [40-50) | [50-60) | ≥60 | total |
| *Acer pensylvanica* | 5 | 0 | 1 | 0 | 0 | 0 | 6 |
| *Acer rubrum* | 14 | 9 | 3 | 3 | 0 | 1 | 30 |
| *Betula allegheniensis* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Betula lenta* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Carya cordiformis* | 2 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Carya glabra* | 8 | 4 | 2 | 0 | 2 | 0 | 16 |
| *Carya ovata* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Carya tomentosa* | 3 | 2 | 0 | 1 | 0 | 0 | 6 |
| *Cornus florida* | 7 | 0 | 0 | 0 | 0 | 0 | 7 |
| *Halesia carolina* | 2 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Liriodendron tulipifera* | 2 | 5 | 9 | 6 | 0 | 0 | 22 |
| *Magnolia acuminata* | 3 | 0 | 0 | 1 | 0 | 0 | 4 |
| *Magnolia fraseri* | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Prunus serotina* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Quercus alba* | 2 | 0 | 0 | 1 | 0 | 1 | 4 |
| *Quercus prinus* | 3 | 3 | 7 | 1 | 0 | 0 | 14 |
| *Quercus rubra* | 1 | 2 | 2 | 1 | 4 | 2 | 12 |
| *Robinia pseudoacacia* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Tilia heterophylla* | 1 | 0 | 1 | 0 | 0 | 0 | 2 |
| total | 58 | 26 | 25 | 14 | 6 | 4 | 133 |

# APPENDIX C

# APPENDIX C

Species representation among tree size classes (cm) for 0.2 ha at Clifftop Vista, NC.

| species | size class (cm dbh) | | | | | | |
|---|---|---|---|---|---|---|---|
| | [10-20) | [20-30) | [30-40) | [40-50) | [50-60) | ≥60 | total |
| *Acer rubrum* | 3 | 1 | 1 | 0 | 0 | 1 | 6 |
| *Carya glabra* | 1 | 4 | 2 | 1 | 0 | 0 | 8 |
| *Carya tomentosa* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Kalmia latifolia* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Pinus strobus* | 2 | 2 | 2 | 1 | 0 | 0 | 7 |
| *Quercus alba* | 20 | 5 | 4 | 2 | 4 | 2 | 37 |
| *Quercus coccinea* | 6 | 5 | 11 | 0 | 0 | 0 | 22 |
| *Quercus muehlenbergii* | 1 | 0 | 2 | 0 | 0 | 0 | 3 |
| *Quercus prinus* | 0 | 1 | 3 | 1 | 0 | 0 | 5 |
| *Quercus rubra* | 0 | 0 | 2 | 0 | 0 | 0 | 2 |
| *Quercus velutina* | 2 | 2 | 1 | 0 | 0 | 1 | 6 |
| total | 37 | 20 | 28 | 5 | 4 | 4 | 98 |

# APPENDIX D

# APPENDIX D

Species representation among tree size classes (cm) for 0.4 ha at Palo Verde, Costa Rica.

| species | size class (cm dbh) | | | | | | |
|---|---|---|---|---|---|---|---|
| | [10-20) | [20-30) | [30-40) | [40-50) | [50-60) | ≥60 | total |
| *Acacia cornigera* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Albizia adinocephala* | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Albizia caribbea* | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Astronium graveolens* | 1 | 0 | 0 | 0 | 1 | 0 | 2 |
| *Bombacopsis quinata* | 0 | 0 | 0 | 0 | 0 | 2 | 2 |
| *Bursera simaruba* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Caesalpinia eleostachys* | 1 | 0 | 2 | 2 | 1 | 0 | 6 |
| *Calycophyllum candidissimum* | 0 | 0 | 1 | 1 | 0 | 5 | 7 |
| *Casearia tremula* | 2 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Chomelia spinosa* | 4 | 1 | 1 | 0 | 0 | 0 | 6 |
| *Coccoloba* sp. | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Cochlospermum vitifolium* | 0 | 0 | 0 | 1 | 0 | 0 | 1 |
| *Cordia alliodora* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Guazuma ulmifolia* | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Guettarda macrospermum* | 2 | 0 | 1 | 0 | 0 | 0 | 3 |
| *Hyperbaena tonduzii* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Jacquinia nervosa* | 0 | 1 | 0 | 0 | 0 | 0 | 1 |
| *Jacquinia pungens* | 5 | 1 | 0 | 0 | 0 | 0 | 6 |
| *Lonchocarpus costaricensis* | 1 | 1 | 0 | 0 | 0 | 0 | 2 |
| *Luehea candida* | 5 | 4 | 3 | 0 | 2 | 0 | 14 |
| *Lysiloma divaricatum* | 0 | 1 | 0 | 2 | 1 | 0 | 4 |
| *Macairea biovulatum* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Manilkara zapota* | 0 | 0 | 0 | 0 | 0 | 1 | 1 |
| *Muntingia calabura* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Pithecellobium lanceolatum* | 3 | 0 | 1 | 1 | 0 | 0 | 5 |
| *Randia thurberi* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Simaruba glauca* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Spondias mombin* | 1 | 0 | 0 | 1 | 0 | 0 | 2 |
| *Stemmadenia obovata* | 1 | 0 | 0 | 0 | 0 | 0 | 1 |
| *Tabebuia ochracea* | 6 | 2 | 0 | 0 | 0 | 0 | 8 |
| *Thouinidium decandrum* | 2 | 0 | 0 | 0 | 0 | 0 | 2 |
| *Trichilia hirta* | 3 | 1 | 0 | 0 | 0 | 0 | 4 |
| *Ximenia americana* | 2 | 0 | 1 | 0 | 0 | 0 | 3 |
| total | 48 | 14 | 10 | 9 | 5 | 8 | 94 |