



Photograph: Chi Le (USA)

## Vine Ecology

*Note: This online review is updated and revised continuously, as soon as results of new scientific research become available. It therefore presents state-of-the-art information on the topic it covers.*

Herbaceous and woody vines, the latter also known as lianas and bush ropes, climb by using other plants for support. This characteristic of not being self-supporting allows vine stems to be narrow, flexible and capable of phenomenal rates of growth in height or length.

Vines have long attracted naturalists and story-tellers, yet despite the contributions of Darwin (1867) and other 19th Century biologists to the study of vines, it wasn't until fairly recently that ecologists turned their attention to this important group of plants. While there is still much to learn about this long-neglected group of plants, the diversity and ecological importance of vines is now widely recognized, thanks to the efforts of researchers around the world. Nevertheless, there are still many aspects of vine ecology that await investigation. See [Figure 1](#)(Dilleniaceae lianas).

### Vine Evolution and Distribution

The climbing habit has apparently evolved numerous times in the plant kingdom.

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There are vines among such diverse taxa as ferns (e.g., *Lygodium*), gymnosperms (e.g., *Gnetum*), various palm lineages (e.g., *Calamus* and *Desmoncus*), and other monocotyledons such as the pandans (e.g., *Freycinetia*). Flowering plant families that are particularly rich in climbing species include the Bigoniaceae, Vitaceae, Leguminosae, Menispermaceae, and Hippocrateaceae.

All of the species of some genera are vines (e.g., *Serjania*) whereas others include species of vines, shrubs, and trees (e.g., *Bauhinia*). There are also numerous species that grow as vines when crowded, but are free-standing shrubs or trees if they fail to encounter mechanical supports (e.g., species of *Croton*; Gallenmüller et al. 2001).

Vines are found in forests from the tropics to the boreal zones of both the northern and southern hemispheres, and in deserts as well as rainforests. However, they are most diverse near the equator (Gentry 1991). Vine abundance generally increases with forest disturbance, but also varies with other, less understood factors.

In the Amazon Basin, for example, woody vines seem most abundant in seasonally dry forests, but this may be because these areas were subject to more human interventions during pre-Columbian times when Amerindian populations were much higher than they are today. In North America, native vines (e.g., *Vitis* spp.) and exotic species (e.g., *Celastrus scandens*, *Dioscorea bulbifera*, and *Pueraria lobata*) can be exceedingly abundant, but the factors promoting this abundance are not clear.

During forest succession after disturbance, lianas typically increase at first and then decrease in abundance, but due to growth of the individuals that persist, liana biomass tends to remain a constant fraction of the total forest biomass (Dewalt et al. 2000). Of course, there also are instances of vines blanketing an area so thoroughly that succession is impeded for several decades ([Figure 2](#)).

### How Vines Function

Although the lianas dangling from the forest canopy understandably draw our attention, the regeneration phase in their life history also deserves our close consideration. Most lianas regenerate either from seed or as vegetative offshoots from the roots or fallen stems of established individuals.

Liana seedlings often escape notice, even from experienced ecologists, because they are self-supporting and otherwise resemble tree seedlings. People with the ability to recognize all the tree species in a forest, a daunting task in diverse tropical forests, often assume that the unidentified seedlings are lianas. Given the radical differences in leaf and stem morphology between liana seedlings and adults, as well as the fact that up to 30% of the woody plant species in a forest can be lianas, learning to identify all of them is a big challenge.

Only after liana seedlings reach free-standing heights of 0.5 meters to 3 or 4 meters, do they start to climb. Most liana root sprouts are also initially free-standing and therefore difficult to recognize as climbing plants, but it is a bit easier to recognize lianas that emerge from fallen liana stems. Vegetative propagation is extremely important in many species of lianas, which makes counting “individuals” challenging.

Herbaceous vines and lianas display a large diversity of climbing mechanisms. Some species climb with the aid of adventitious roots that emerge from stems, while the stems of other species twine around their supports. Many species have specialized structures for grabbing supports, sometimes referred to as “prehensile apparati.”

The most familiar prehensile apparatus is the tendril, but tendrils come in various sizes and evolutionarily are derived from a variety of structures. Tendrils can be modified leaves, leaflets, stipules, inflorescences, branches (e.g., Hippocrateaceae), or stems (e.g., *Omphalea* in the neotropics and many Leguminosae in the paleotropics). Species with stem-derived tendrils tend to be able to successfully grasp larger diameter trellises than those with other sorts of tendrils, but all vines except the root climbers are limited to climbing fairly narrow supports.

The scarcity of suitable supports that reach from near the ground up to the canopy is a major limitation for most climbing plants. Failure to locate and attach to trellises is the fate of most vine stems, other than root climbers, which are rare among tropical lianas. In the dense vegetation of forest edges, potential supports are plentiful, which helps explain why vines are so abundant there.

The likelihood of encountering supports is increased somewhat by the growth-induced circular movements of stems and tendrils called circumnutation spirals (e.g., Baillaud 1962). Using time-lapse photography in still air, researchers have revealed that circumnutation spirals of vine stems can be 50 cm in diameter and that tendrils can circumnutate over distances nearly twice as large. Even more surprising is the fact that these spirals apparently become elongated towards potential supports (e.g., Tronchet 1945), which further increases the probability of finding a support.

A similar phenomenon of directed foraging for supports has been described for root climbing herbaceous vines (Strong & Ray 1975). To increase their likelihood of encountering a large tree trunk to ascend, these vines grow along the forest floor in the direction of the darkest part of the horizon, which is often the trunk of a large tree. One possible mechanism behind these directed “foraging” behaviors involves growth responses to minor differences in concentrations of ethylene near and away from stems of other plants, but this hypothesis awaits testing.

When a climbing plant reaches the top of its host, further height growth requires the location of a taller support of the appropriate diameter. Searcher shoots of

vines emerging from the crowns of understory trees are often quite obvious. If they encounter a suitable support and successfully attach to it, their progress towards the canopy continues.

Although searcher shoots of some lianas can extend upwards for as much as 2 meters above their last support, if they fail to find a support, they fall over and are replaced by another shoot (Putz 1984). Knowing the inter-support spanning capacities of different species is important for predicting which vines are likely to be stalled on their way to the canopy.

Most vines that make it to the canopy do so with the help of a succession of taller supports. An exception are vines that climb up the stems of narrow-stemmed vines already attached in the canopy (Pinard & Putz 1998). Vines hanging from the canopy may show no evidence of their stepwise ascent, leading some observers to the mistaken conclusion that they “rode” to the canopy on their current host trees (Figure 3). Although this might happen on occasion, the deleterious effects of lianas on host trees, as well as the disadvantage to fast-growing lianas of relying on slow-growing trees, diminishes the likely importance of this canopy ascent strategy.

**Once in the canopy, vines often grow between tree crowns (Caballé 1977, 1998).**

These intercrown connections are of great importance to animals that can't fly or glide long distances (see below) and also increase the likelihood of trees pulling down their neighbors when they fall. Although vines growing between tree crowns are restricted by their abilities to span intercrown distances, many grow on several canopy trees and one individual in Panama, an *Entada monostachya* with a 51 centimeter diameter stem, connected to the crowns of 49 canopy trees (Putz 1984). Only the non-branching climbing palms (rattans) are completely restricted to the crown of a single host tree. For them, the challenge is staying in their host's crown as their stem elongates (Figure 4; Putz 1990).

### **Vine Stem Anatomy and Physiology**

Although in cross section the stems of some liana species are very tree-like, they differ by possessing large diameter vessels and abundant soft tissues (parenchyma) in the xylem (Figure 5; Carlquist 1991). Having large vessels is important to plants with narrow stems because the flow rate through xylem vessels increases with the fourth power of the radius; the xylem conducting capacities of even narrow-stemmed lianas are therefore very large (Figure 6; Schenck 1892, Zimmermann 1983, Ewers et al. 1991).

Consequently, per unit cross-section area, vine stems can hydraulically support much larger total leaf areas than trees. In fact, a liana 10 cm in diameter may have as much leaf area (or leaf mass) as a tree five times as large (Putz 1983, Gerwing & Farias 2000). This difference in allometry helps explain how in tropical forests, where lianas contribute only 5% to total above-ground biomass, liana leaves may

constitute 40% of the total forest leaf area (Hladik 1974, Schnitzer and Bongers 2002).

The abundance of soft tissues in vine stems adds to their flexibility, helps them avoid mechanical damage, and speeds the rate of recovery when damage does occur (Holbrook and Putz 1991, Fisher and Ewers 1989). Bent and twisted stems of some vines react more like multi-stranded cables than solid cylinders (Figure 7). This flexibility increases the likelihood of survival when they fall with their host trees. Consequently, many of the lianas that proliferate in treefall gaps are sprouts from lianas that survived the fall. Parenchyma tissues as well as bands and strands of phloem embedded in the xylem of some species of lianas must have other physiological consequences, but these have apparently not been studied.

### **Effects of Vines on Trees and Forests**

By displaying their leaves above those of the trees that provide them mechanical support, vines are effective competitors for light. Furthermore, because they invest little in thickening their stems and branches, vines can use a large proportion of their resources to produce additional leaves as well as for reproduction. Conversely, trees that are heavily vine-laden grow more slowly and produce fewer seeds and fruits than vine-free trees (Stevens 1987). Due to their generally deleterious effects on trees, forest managers usually advocate the removal of vines, at least those growing on future crop trees (e.g., Putz 1991).

The growth habit of vines also allows them to be effective below-ground competitors for water and nutrients. In experimental studies where vines and trees were allowed to compete in four situations (above-ground, below-ground, both above- and below-ground, and not at all), Dillenberg et al. (1993) found strong vine effects on trees in both domains. One mechanism for this impact was demonstrated in a seasonal forest in Amazonian Bolivia by Diego Perez-Salicrup and Martin Barker (2000). They found that after vines growing on canopy trees were cut, water stress decreased in the trees formerly infested with vines. A decrease could even be detected one day after the cutting.

The discovery that vines are among the deepest-rooted plants in tropical forests (Jackson et al. 1995, Tyree & Ewers 1996) suggests that some vines may avoid competing with trees while avoiding drought stress by tapping deeper stores of water. Other experiments (Putz in prep) have revealed that vines generally colonize nutrient-rich patches of soil much more quickly and with much less investment in root biomass than trees. This versatility in root foraging can be explained as another benefit of vine dependence on other plants for mechanical support; vines have no need for the large diameter structural roots trees use to hold themselves upright.

In addition to competing both above and below-ground, lianas can cause mechanical

damage to their host trees. Small twigs and large stems of trees can be mechanically girdled by tendrils and twining stems, respectively. Lianas can also proliferate so much that the branches of their host trees break under their weight. Several light-demanding and dense wooded liana species typically break their host trees, creating canopy gaps in which they proliferate (e.g. *Acacia* spp. in Central America and *Celtis* spp. in South America).

On the positive side, it has been suggested that by growing between tree crowns, lianas help stabilize trees (Smith 1973), but the evidence is that liana infested trees actually create larger gaps when they fall. Slash-and-burn farmers are well aware of this phenomenon and generally use heavily liana-laden trees as “king pins” when clearing forests.

Tree species vary in their susceptibility to liana infestations, and in their ability to shed lianas that colonize their crowns (Putz 1984b). Because of limits in the diameter of supports that lianas can use in their ascent to the canopy, fast growing trees tend to avoid liana infestations, especially if they rapidly shed their lower branches. Thick-stemmed palms are particularly immune to lianas, and lianas that do make it into their coronas are shed along with the leaves to which they are attached. By creating large “crown shyness” gaps when they bash into their neighbors in the wind, flexible stemmed trees can escape lianas attempting to grow from crown to crown or shed those that do cross the gap, at least until they become firmly attached.

Smooth bark and bark that is shed in large flakes may also deter lianas to some extent, but given the way that most lianas attach to their supports, this mechanism would not seem to be particularly effective. Some tree species also suffer reduced threats of vine colonization because the symbiotic ants that they harbor and feed keep their host tree free of parasites, including structural parasites such as lianas (Janzen 1969). Due to their vine avoiding and vine shedding characteristics, sometimes including these ant symbionts, pioneer trees are particularly common in severely vine infested areas where slower growing trees are affectively suppressed (Schnitzer et al. 2000).

Herbaceous vines and lianas often play important roles during forest succession after natural and anthropogenic (i.e. human-induced) disturbances ([Figure 8](#); Schnitzer & Carson 2001). **Most vines are light demanding (Hegarty & Caballé 1991) and thus benefit from disturbances, which they colonize with dispersed and buried dormant seeds, formerly suppressed seedlings, and rampant vegetative proliferation of vines that fell with the gap-making trees. Some lianas have also been described as growing through the forest understory, essentially “foraging” for canopy gaps and other areas of high light intensities (Peñalosa 1984).** Liana proliferation on and near the edges of forests is also one of the major causes of structural deterioration in fragmented forests (Laurance et al. 2001).

## Vine Management

Where lianas are abundant, they represent a severe nuisance for forest managers. Not only are crop trees suppressed and damaged by the lianas they support, but forest operations are also rendered more difficult and dangerous. Tree fellers are in particular danger when liana-laden trees pull down their neighbors, often on top of the worker. For these reasons, pre-felling liana cutting is a commonly prescribed silvicultural treatment for reducing logging damage to the residual forest and for enhancing worker safety (Putz 1991, Vidal et al. 1997, Gerwing 2001, Schnitzer et al. 2004).

Pre-felling liana cutting also diminishes problems with post-logging liana infestations (Gerwing & Uhl 2002). This silviculturally beneficial effect is mostly due to the removal of the fallen stems that, where lianas have not been cut, contribute the majority of stems that suppress regeneration in logging gaps (Alvira et al. 2004). Although the effect of liana cutting on understory light environments has not been well studied, it seems likely that the canopy opening resulting from the fall of liana leaves increases the vigor of trees in the understory that are intended to form the **next timber crop** (Pérez-Salicrup 2001).

### The Role of Vines: Summary

Although vines can be a major problem in forests managed for timber, their beneficial roles in forest ecosystems should not be overlooked. For example, lianas provide important intercrown pathways for many canopy-dwelling animals and so are important ecosystem engineers ([Figure 9](#)). Without these vine connections, moving from tree to tree would entail descending to the ground where these animals are very susceptible to predation (Emmons & Gentry 1983, Putz et al. 2001).

The abundant leaves, flowers, and fruits of lianas also represent important food resources for animals, and contribute substantially to biogeochemical cycles. Although many lianas have small and wind dispersed seeds, some produce delicious fruits that are important to many forest animals. Many canopy lianas also produce abundant flowers, making them an important component of pollinator communities. A larger proportion of liana species than tree species are pollinated by large bees and beetles.

Because vines are favored by forest disturbances and are more common as well as more diverse in warmer environments, human-induced disturbances and global warming are likely to promote vine abundance. Perhaps these environmental modifications are already responsible for the reported increase in the growth rates and abundance of large diameter lianas in tropical forests (Phillips et al. 2002), but more data are needed to evaluate this trend and its proposed cause.

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### Editor's Note

The author of this review, [Francis E. Putz](#), is a Professor of Botany at the University of Florida. He earned his doctorate in Ecology at Cornell University and was a Post-doctoral Fellow at Oxford University.

If you are aware of any important scientific publications about the ecology of vines that were omitted from this review, or have other suggestions for improving it, please contact the author at his e-mail address:

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The photo at the top of the page shows grapes on a vine at Temecula, California, and was taken by Chi Le (USA).

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