PART I
INTRODUCTION

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The distribution and evolution of climbing plants

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Introduction

The classic work on climbers by Schenck (1892, 1893), is focused especially on anatomical features of lianas, but also includes a taxonomic and geographic survey of the occurrence of climbing plants. Such 19th century luminaries as Charles Darwin (1867) were fascinated by the peculiarities of climbing plants. However, despite their obvious importance in the world's flora, especially in tropical forests, climbers have subsequently been generally neglected. As summarized by Jacobs (1976), 'The ecology of lianas is virtually a blank'. Indeed the significant ecological role played by lianas in tropical forests has only very recently begun to be investigated (e.g. Putz, 1984, 1985; Putz & Chai, 1987). Lianas have been no less neglected by plant collectors: quite probably lianas are the most undercollected of any major habit group of plants.

This overview of climbing plants is based largely on 0.1 ha data sets for plants > 2.5 cm in diameter at breast height (dbh). The sampling protocol under which these data were gathered was originally set up specifically to facilitate ecological sampling of lianas, which are notorious for clumped distributions related to rampant vegetative reproduction (Peñalosa, 1984; Putz, 1984; Gentry, 1985). Each sample consists of ten 2×50 m narrowly rectangular plots set up end to end or separated by c. (10–)20 m, thus covering a relatively large area of forest that exceeds in scale the frequent 'patches' of single liana species that presumably derive from vegetative reproduction. Altogether 1103 species and 3341 individual climbers and hemiepiphytes are included in the 56 available neotropical samples; for lowland neotropical sites these values are 860 species and 2636 individuals. An additional 600 species are represented in the 32 paleotropical samples, 4 island samples, and 13 temperate forest samples which have been analyzed. Altogether 82 climbing

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families are represented in these samples. Ecological data for most of the study sites are given in Gentry (1988a: Tables 1, 2); sites from which liana data were included in this analysis are indicated in Appendix 1.1.

This data set is supplemented by data from complete florulas (as summarized by Gentry & Dodson, 1987), tree plots (Gentry, 1988a, b), and from a literature survey. There is a strong neotropical bias inasmuch as my field experience is mostly in South and Central America. The lists of scandent genera from *Flora Malesiana* compiled by Jacobs (1976) and for Australia prepared by Hegarty & Clifford (1990) have been very helpful in compiling a very preliminary listing of Australasian climbing taxa. I have used traditional broad family concepts throughout, generally following the familial placements used in the Missouri Botanical Garden herbarium.

Kinds of climbers

There are several distinctly different kinds of climbers. Gentry (1985) recognized four fundamental climbing strategies differentiated by ecology as well as morphology: (i) Lianas are woody, relatively thick-stemmed climbers that begin life as terrestrial seedlings and are capable of growth in mature forests. (ii) Vines are thin-stemmed climbers or clamberers that begin life as terrestrial seedlings and generally grow in disturbed habitats or at the forest edge. Following the convention of this volume these are here referred to as 'herbaceous vines' even though many of them are subwoody. (iii) Woody hemiepiphytes, including stranglers, typically begin life as epiphytic seedlings with roots later reaching the ground. Other woody hemiepiphytes start out as terrestrial climbers, later sending out a system of adventitious roots and/or losing contact with the ground. (iv) Herbaceous epiphytes and hemiepiphytes include all herbaceous species that climb appressed to tree trunks and limbs, usually via adventitious roots, whether or not they ever establish contact with the ground. A fifth category of 'climber' might also be recognized, especially in the temperate zone, where numerous species have a sprawling or prostrate habit; I have excluded such species from this analysis unless they are clearly creeping (but not as hemiaquatics) or twining, in which case they are tabulated as herbaceous vines.

The hemiepiphyte categories, especially, are not altogether satisfactory. For example, it is not clear whether some climbing species begin life as epiphytes and even different individuals of the same species may be epiphytic or not. Although stranglers are here included with hemiepiphytes, their vine-like stems are actually descending roots. Some non-strangling *Clusia* behave in a similar fashion. Yet other species of *Clusia* and strangling figs are clearly climbing. I have tabulated stranglers and hemiepiphytes separately in Appendix 1.1. Non-climbing hemiepiphytes may be excluded from the

floristic results reported here by excluding all Bombacaceae, Araliaceae, nearly all Moraceae and (except in cloud forests and pluvial forests) most Guttiferae from the various figures.

The four habit groups are treated differently in this review. The part of this analysis based on floristic lists includes all four of the climbing categories, except as otherwise noted. The part of the analysis that is based on samples of plants > 2.5 cm dbh excludes vines on ecological (outside the forest) as well as morphological (stems < 2.5 cm diameter) grounds. Small herbaceous epiphytic climbers (e.g. *Peperomia*) are also excluded from these analyses as are those canopy hemiepiphytes which attain 2.5 cm diameter only more than 1.37 m above the ground. In these analyses liana diameters are measured at the thickest part of the accessible stem (typically a node) but hemiepiphytes are included only when they attain 2.5 cm diameter at or below breast height. A few stranglers and non-climbing hemiepiphytes like some *Clusia* species are included in these analyses if their hanging roots reach 2.5 cm diameter.

Importance of lianas

Climbing plants are an important, though often neglected, part of tropical forests. The presence of woody lianas has been called the single most important physiognomic feature differentiating tropical from temperate forests (Croat, 1978). 43–50% of the trees over 15(–20) cm dbh on Barro Colorado Island, Panama (BCI) have lianas in their crowns (Montgomery & Sunquist, 1978; Putz, 1982, 1984) and 42% of the trees over 10 cm dbh at San Carlos de Rio Negro, Venezuela have lianas (Putz, 1982). Half the trees > 20 cm dbh in Lambir National Park, Sarawak are liana-infested (Putz & Chai, 1987). Moreover, about a fifth (18–22%) of the upright plants of neotropical forest understories are usually juvenile lianas (Rollet, 1969; Putz, 1984).

Lianas are an important structural component of tropical forests, often literally tying the forest together (Fox, 1968; Jacobs, 1976; Gentry, 1983b; Putz, 1984; Appanah & Putz, 1984). Lianas have been estimated to account for 32–36% of the leaf litter of tropical forests in Thailand (Ogawa *et al.*, 1965) and Gabon (Hladik, 1974, 1978). In an extensive series of 0.1 ha plots of neotropical forest, lianas represent an average of 24% of the stems > 2.5 cm dbh in dry forest and 18% of the stems in lowland moist and wet forests (Gentry, 1982a, 1986). In general there are about as many lianas > 2.5 cm diameter as there are trees > 10 cm diameter in lowland neotropical forests.

Lianas compete with trees for light, water, and nutrients. Ogawa *et al.* (1965) suggest that competition with lianas is an important cause of tree death. Putz (1980, 1984; Putz, *et al.*, 1984) has emphasized that competition with lianas has exerted strong selective pressure on tropical trees, with liana-infested trees suffering higher mortality rates than liana-free trees.

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Lianas are also very important to forest animals, both as food and as a structural component of the habitat. The single most important factor affecting tree selection by two-toed sloths on BCI is the presence and density of lianas in their crowns (Montgomery & Sunquist, 1978). Mammals ranging from the African prosimian *Euoticus elegantulus* (Charles-Dominique, 1977) and the Amazonian pygmy marmoset to the African elephant (Short, 1981) are heavily dependent on lianas for food. An average of 21% of the plant species utilized for food by a wide variety of tropical primates are lianas (Emmons & Gentry, 1983). It has even been suggested that different liana densities on different continents may have been the key selective factor in determining distinctive vertebrate locomotor adaptations in the tropical forests of Africa, Asia, and the Neotropics (Emmons & Gentry, 1983).

Climbers are also very important floristically, making a major contribution to the taxonomic diversity of tropical forests. Even excluding epiphytic climbers and stranglers, the seven tropical field station florulas analyzed by Gentry & Dodson (1987) averaged 176 climbing species per site or 19% of each florula. Similarly, the dry forest in Chamela, Mexico has 181 climbing species or 24% of the total florula (Lott, 1985); interestingly, the two driest sites for which data are available (Chamela and Capeira, Ecuador) have the highest percentages of climber species of any site: 24% each.

Geographic perspective

Climbers are very unevenly distributed geographically. The great majority of woody lianas are restricted to tropical forests. Herbaceous vines are somewhat less restricted in occurrence, but are still overwhelmingly better represented in the tropics. I have quantitative data only for lianas and hemiepiphytic climbers > 2.5 cm diameter and will restrict this discussion of geographic distribution mostly to these groups.

It is well known that temperate zone forests have very few lianas and virtually no hemiepiphytes (e.g. Gentry, 1982a, 1985). Eastern North American forests average only five lianas > 2.5 cm diameter per 0.1 ha and European forests have even fewer (Table 1.1; Figure 1.1). North temperate forests thus differ in liana density from most tropical forests by about an order of magnitude. Curiously, south temperate forests have more lianas than north temperate ones at equivalent latitudes (Table 1.1; Dawson, 1980). For example, the Valdivian forests of Chile average about 30 lianas per 0.1 ha, 6–7 times as many as do their northern equivalents. One sampled Chilean forest, in Puyehue National Park (40°43′ S), had 52 lianas in 0.1 ha, more than in many tropical forests. Indeed, one Puyehue species, *Hydrangea integrifolia*, a giant hemiepiphytic climber, had the highest population density of any climbing species at any sample site.

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Table 1.1. *Density of climbers (and hemiepiphytes) ⩾ 2.5 cm diameter in 0.1 ha*

Region	Number of sites	Number of climbers (or regional average)
Neotropics		
Lowland Amazonian moist	20	69
Trans-Andean moist + wet	9	69
Southern subtropics	5	77
Choco pluvial forest	2	67
Upland Andes (w/o Pasochoa)	7	64
Dry forest (w/o Chamela)	10	70
Chamela dry forest	3	78
Neotropical average	56	70
Africa		
Continental Africa	8	106
Madagascar	3	122
Australasia		
Continental Asia	5	94
Borneo	2	40.5
New Guinea	2	72.5
Taiwan	2	65.5
Davies River S.P., Queensland	1	35
Riviere de Pirogues, New Caledonia	1	43
Australasian average	13	70
Islands		
Round Hill, Jamaica	1	8
Brise Fer, Mauritius	1	19(+2)
Puerto Rico[a]	2	28
Island average	4	18
North Temperate		
North America	8	5
Europe	2	2
North temperate average	10	4
Valdivian forest		
Puyehue	1	52
Bosque de San Martin	1	28
Alto de Mirador	1	11
Average	3	30

[a]Sampled in 1989, subsequent to preparation of the graphs.

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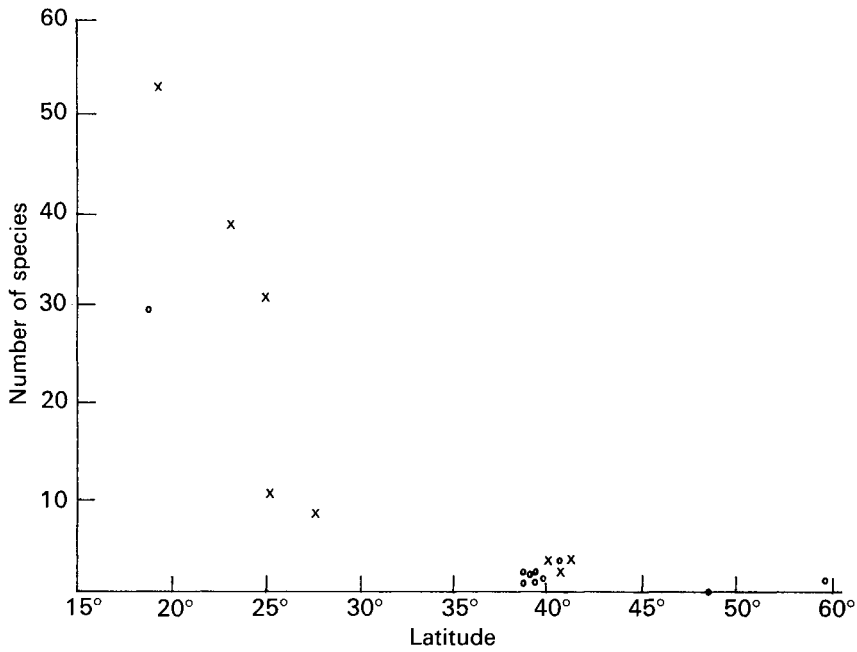
Figure 1.1. Decrease in liana diversity with increasing latitude for subtropical and temperate continental sites < 1000 m elevation. ×, southern hemisphere; ○, northern hemisphere.

In a series ($N = 18$) of tropical and temperate zone florulas (Table 1.2), tropical values averaging 176 climbing species per site (19% of each florula) contrast markedly with data from a set of eight comparable eastern North American florulas which averaged 37 climbing species per site (6% of each florula). If two larger-scale 'florulas' from the Smokey Mountains and Florida panhandle (White, 1982; Wilhelm, 1984) are excluded, they average 29 species, or 7% of each florula. Climber species richness on the tropical island, Jamaica, is intermediate. In three local florulas climbers average only 28 species, similar to temperate zone values; however, in percentage terms climbers constitute a near tropical average of 14% of these depauperate insular floras (Kelly *et al.*, 1988).

In the temperate forest florulas an average of 76% of the plant species are herbs (86% at a prairie site) (Table 1.2), and 19% woody (including lianas). In tropical forests only about half the species are herbaceous, even including herbaceous epiphytes. This tropical/temperate dichotomy between woody plants and herbs is also reflected in the climbers. In the temperate zone

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Table 1.2. *Tropical vs. temperate habitats (% of species in local florulas). Data from Gentry & Dodson (1987) except as indicated*

Region	Average number of native species in florula	Average number of climbers in florula	Climbers (lianas, vines, & woody hemiepiphytes) (%)	Vines (%)	Lianas (%)	Trees (%)	Shrubs (%)	Woody (trees shrubs, lianas) (%)	Epiphytes (incl. Loranth.) (%)	Herbs (%)
Temperate forest[a] (7 sites)	634	41	7	5	2	12	6	19	0	76
Prairie[b]	368	17	5	4	1	6	3	10	0	86
Continental tropics[c] (7 sites)	963	176	19	10	10	21	9	40	13	41
Jamaica[d] (3 sites)	218	28	14	5	9	55	3	67	18	11

[a]Data from Mitchell, 1963; Stevens & Beach, 1980; White, 1982; Wilhelm, 1984; Fitch, 1966; Yatskievych & Yatskievych, 1987; R. Coles, personal communication.
[b]Konza Prairie, Kansas. Data from Freeman, 1980.
[c]Data from Gentry & Dodson, 1987 (includes hemiepiphytes with epiphytes rather than with climbers.).
[d]Data retabulated from Kelly *et al.*, 1988.

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florulas an average of 2% of the species are lianas and 5% herbaceous or subwoody climbers, whereas in continental tropical florulas about 10% are lianas and 10% herbaceous vines.

This difference is also apparent on a larger scale. For example, Webb (1978) reports that the Flora Europaea includes 11 548 species (including 501 problematic taxa in the five large apomictic genera), of which the 24 species of woody and subwoody climbers (Baas & Schweingruber, 1987) constitute a mere 0.2%. In eastern North America there are more than twice as many species of woody climber as in Europe; Duncan (1975) lists 48 native species for the southeastern USA alone, despite excluding marginally lianescent species like *Rosa* which are included in the European data. Eight of Duncan's (1975) woody climbers do not reach north to the Carolinas, from where 40 species of woody vine constitute 1.3% of the native flora (based on data from Radford, Ahles & Bell (1968), in part compiled by D. Boufford). There are also at least 105 herbaceous climbers or scramblers in the Carolinas, constituting 3.5% of the flora. All climbing species together constitute almost 5% of the Carolina flora. The southwestern USA is even poorer in climbers, with only two lianas included among the 512 woody and subwoody species of southern California analyzed by Carlquist & Hoekman (1985); altogether there are four native liana species and 24 herbaceous vines (plus 12 species of *Cuscuta*) in the southern California flora (S. Carlquist, personal communication). In contrast, Jacobs (1976) suggests that, worldwide, 8% of all tropical plant species are lianas. My data (Tables 1.3, 1.4) indicate that scandent species constitute about 10% of the neotropical flora (assuming a neotropical flora of 90 000 species (Raven, 1976; Gentry, 1982b). Only about 200 of the 9140 scandent species listed in Table 1.4 are temperate North American.

Tropical islands, at least those that have received their floras via over-water dispersal, also tend to have very low liana densities (Table 1.1; Figures 1.1, 1.2). I have suggested that this may result from the prevalence of wind-dispersed pterochore seeds in lianas, whereas most long-distance island colonizers are bird-dispersed (Gentry, 1983a). Continental-fragment tropical islands that have never been submerged, like New Caledonia and Madagascar, have a full complement of lianas.

Different continental tropical forests also have different liana densities. On a regional scale, Australasian forests often have fewer lianas, and African and Madagascar forests more than do neotropical ones (Table 1.1; Figures 1.2, 1.3; Emmons & Gentry, 1983). The four Australasian sites reported by Gentry (1988a) average only 40 lianas > 2.5 cm diameter per 0.1 ha plot, while eight continental African sites averaged 106 lianas and three on Madagascar averaged 122. Comparable neotropical samples average 69 lianas. Apparently continental Asian forests have as many lianas as neotropical forests, however, with 10 sites averaging 80 lianas > 2.5 cm diameter, but

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