

## LIANA INFESTATION OF TREES: SOME OBSERVATIONS IN A NEOTROPICAL LOWLAND FOREST

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The way lianas use trees as support to reach better light conditions in the canopy and the strategies that trees have developed to shed them is one of the most conspicuous examples of resource competition in tropical forests. Steady outshading of crown leaves in liana-infested individuals reduces diameter increment of trees (Clark & Clark 1990) and eventually leads to higher mortality rates than in liana-free trees (Putz 1984a). Putz (1984b) tested whether rapid growth, trunk spines, large leaves, or flexible stems have any positive influence on keeping lianas away on Barro Colorado Island (BCI), Panama. He found that the latter two factors are associated with predominantly liana-free species. Campbell & Newbery (1993) reported that bark types and a long branch-free bole influence the degree of liana infestation in lowland rain forest in Sabah, Malaysia. This study, by examining a broad array of pioneer to primary species sampled in logged and unlogged forests, tests the hypotheses that (1) leaf size and leaf form, (2) bark surface, (3) branch-free bole height, and (4) the successional status of species do influence the degree of liana infestation.

The study site was Unit I of the Forest Reserve of Caparo (7° 30' N, 70° 45' W, 170,000 ha, c. 100 m a.s.l.) which lies in the western Venezuelan plains. The area is managed by the Universidad de Los Andes in Mérida. The average annual rainfall is 1750 mm with a pronounced dry season from December to March (monthly precipitation < 40 mm). Mean annual temperature is 24.6 °C. Caparo forests are classified as 'moist deciduous lowland forest' (Lamprecht 1989). Of 429 plant species identified in Unit I (7,000 ha), 125 are tree and 80 are liana species. Liana is defined as 'woody climbing plant that esta-

blish on the forest floor'. Most liana species were found in the Bignoniaceae and Convolvulaceae (10 and 9 species, respectively) (Hernandez & Guevara 1994). The forest is located on alluvial soils. Further details about the study site can be found in Kammesheidt (1998).

Sampling plots of 400 m<sup>2</sup> each were established in logged (n = 75) and unlogged stands (n = 40). For all trees ≥ 10 cm diameter at breast height (DBH) the branch-free bole height was measured and liana infestation assessed, using a modified version of the classification system of Lowe & Walker (1977) (cf. Table 1). To obtain a substantial data set, only the commoner species (n ≥ 12) were considered in this study. Liana regeneration at seedling size (30–130 cm tall) was counted in eight sub-plots (2 x 2 m each; 32 m<sup>2</sup>) within every plot of 400 m<sup>2</sup> in both logged and unlogged stands. Leaf size was classified as 'mesophyll' (20–180 cm<sup>2</sup>) or 'macrophyll' (180–1500 cm<sup>2</sup>) corresponding to the definitions in the scheme for leaf size of Raunkiaer (1934). Other leaf sizes in that scheme were not encountered. Leaf form was either simple or compound. The bark texture was classified as (1) smooth, (2) rough, the surface being large scales or fissures, or (3) spiny. Study species were categorized as (1) pioneers, species occurring exclusively in logged areas where they are often gregariously distributed, (2) secondary, species which were found in both unlogged and logged areas but predominantly in the latter, and (3) primary, species occurring chiefly in unlogged areas.

Only a few species differed significantly from the average percentage of crown-infested individuals (41%; Table 1), which corresponds to the 47% found by Putz (1984a) on BCI. The crowns of *Cecropia peltata* and *Ochroma lagopus* were hardly ever invaded by lianas, while the other pioneers, *Cochlospermum*

TABLE 1. The degree of liana infestation (1: free from liana; 2: lianas on main stem only, crown free; 3: crown partly infested by lianas; 4: whole crown infested; cf. Lowe & Walker 1977, modified) in 28 tree species  $\geq 10$  cm DBH in the Forest Reserve of Caparo, Venezuela. The distribution pattern of individual species was tested against the average degree of liana infestation by applying the G-test (Fowler *et al.* 1998). \*\*\* =  $P < 0.001$ , \*\* =  $P < 0.01$ , \* =  $P < 0.05$ . Not significant if  $P > 0.05$  (n.s.).

Taxa	Leaf size/form	Bark surface	Successional Status	Degree of liana infestation				P	
				N	1	2	3		4
<i>Bixa orellana</i> L.	Meso/simple	Smooth	Secondary	33	18	8	6	1	n.s.
<i>Bombacopsis quinata</i> (Jacq.) Dugand	Meso/compound	Spiny	Secondary	16	5	5	5	1	n.s.
<i>Brosimum alicastrum</i> Sw.	Meso/simple	Smooth	Primary	48	11	11	18	8	*
<i>Cecropia peltata</i> L.	Macro/simple	Smooth	Pioneer	126	108	10	4	4	***
<i>Chrysothallum avratum</i> Miq.	Meso/simple	Smooth	Primary	19	4	2	8	5	*
<i>Coccoloba padifloris</i> Meissn.	Meso/simple	Smooth	Primary	37	16	6	10	5	n.s.
<i>Cochlospermum vitifolium</i> (Willd.) Spr.	Meso/compound	Smooth	Pioneer	12	7	-	3	2	n.s.
<i>Cordia thaisiana</i> Agostini	Meso/simple	Rough	Primary	29	11	7	7	4	n.s.
<i>Guazuma tomentosa</i> H.B.K.	Meso/simple	Smooth	Secondary	32	21	1	8	2	n.s.
<i>Fissicalyx fendleri</i> Benth.	Meso/compound	Rough	Secondary	27	8	10	4	5	n.s.
<i>Heliocarpus popayanensis</i> H.B.K.	Macro/simple	Smooth	Pioneer	42	23	3	14	2	n.s.
<i>Inga</i> sp.	Meso/compound	Smooth	Primary	31	9	9	8	5	n.s.
<i>Lonchocarpus pictus</i> Pittier	Meso/compound	Smooth	Secondary	23	10	3	9	1	n.s.
<i>Lonchocarpus sericeus</i> (Poirlet) DC.	Meso/compound	Smooth	Secondary	14	4	5	5	-	*
<i>Luehea cymulosa</i> Spr.&Benth.	Meso/simple	Rough	Secondary	28	11	6	5	5	n.s.
<i>Ochroma lagopus</i> (Cav.ex Lam.) Urban	Macro/simple	Smooth	Pioneer	111	98	9	4	-	***
<i>Pleurothryium</i> aff. <i>reflexum</i> Lasser	Meso/simple	Smooth	Primary	18	10	3	5	-	*
<i>Pouteria anibaefolia</i> (Smith) Bachui	Meso/simple	Rough	Primary	59	21	17	20	1	n.s.
<i>Protium crenatum</i> Sandw.	Meso/compound	Rough	Primary	19	8	5	3	3	n.s.
<i>Sapium sylvare</i> Muell. Arg.	Meso/simple	Rough	Secondary	38	13	9	6	10	n.s.
<i>Sloanea terniflora</i> (Moc.&Sesse) Standl.	Meso/simple	Smooth	Primary	27	11	5	8	2	n.s.
<i>Spondias mombin</i> L.	Meso/compound	Rough	Secondary	38	16	9	9	4	n.s.
<i>Terminalia guianensis</i> Aubl.	Meso/simple	Rough	Primary	38	17	9	10	2	n.s.
<i>Trichanthera gigantea</i> H.B.K.	Meso/simple	Smooth	Primary	17	9	4	4	-	n.s.
<i>Trichilia palmerorum</i> Pittier	Meso/simple	Smooth	Primary	28	11	9	6	2	n.s.
<i>Trichilia unifoliata</i> P.Br.	Meso/simple	Smooth	Primary	23	7	3	11	2	n.s.
<i>Triplaris caracasana</i> Cham.	Macro/simple	Smooth	Secondary	38	37	1	-	-	***
<i>Zanthoxylum</i> sp.	Meso/compound	Spiny	Secondary	24	11	8	4	1	n.s.

*vitifolium* and *Heliocarpus popayanensis*, showed no significant difference from the overall pattern of liana infestation. The low proportion of liana-laden individuals in *C. peltata* and *O. lagopus* may be due to the ants hosted by both tree species. *Cochlospermum vitifolium* and *H. popayanensis* lack this symbiosis (pers. obs.) which is found to be effective in removing lianas in *C. peltata* and *O. lagopus* (Janzen 1973, O'Dowd 1979). Putz & Holbrook (1988), however, found that even outside its natural habitat, and thus lacking the symbiosis with *Azteca* ants, *C. peltata* was less often liana-laden than Malaysian pioneer species growing together with it. Apart from fast vertical growth, found in all pioneers, a long branch-free bole seems to be important because it discourages the successful anchorage of lianas (cf. Putz 1980, Campbell & Newbery 1993). The proportion of liana-free individuals was significantly correlated with the branch-free bole height in trees of 10–20 cm DBH ( $r_s = 0.87$ ,  $P < 0.001$ ; all study species), but in trees of  $\geq 20$  cm DBH, no correlation was found ( $r_s = 0.22$ ,  $P > 0.05$ ; all study species). This suggests that in more advanced successional stages the probability of liana invasion increases independently of branch-free bole height, e.g., by crossing-over of lianas from neighboring trees. The fact that both *C. peltata* and *O. lagopus* branch on average later and at higher levels than the other two pioneers (Kammesheidt, unpubl. data) makes them perhaps less susceptible to liana infestation.

*Triplaris caracasana* was the only study species essentially free of lianas (Fig. 1). As in most species of the genus *Triplaris*, the hollow branches and twigs of *T. caracasana* are inhabited by ants of the genus *Pseudomyrmex* (Brandbyge 1986). These very aggressive ants (pers. obs.) are apparently more effective in keeping lianas off trees than *Azteca* ants in *C. peltata*, which are reported to have a pronounced seasonal pattern of activity (Schupp 1986). As in *C. peltata* and *O. lagopus*, *T. caracasana* branches on average later than the other species with simple leaves (Kammesheidt, unpubl. data). Moreover, the slender, conical crown of *T. caracasana* did not, in general, touch neighboring trees (pers. obs.) so reducing crossing-over by lianas. A similar effect was found by Campbell & Newbery (1993) in species of the family Dipterocarpaceae that are well-known for their 'crown shyness'.

Other species that differed significantly from the average degree of liana infestation showed no consistent pattern. Although *Brosimum alicastrum* and



FIG. 1. The crown shape of the essentially liana-free *Triplaris caracasana*.

*Chrysophyllum auratum* suffered more from liana invasion than the overall average, another primary species, *Pleurothrium* aff. *reflexum*, showed a low proportion of liana-laden individuals.

The proportion of individuals without lianas was significantly higher in smooth-barked species than in both spiny and rough-barked species ( $G = 7.2$ ,  $df = 1$ ,  $P < 0.01$ ;  $G = 40.0$ ,  $df = 1$ ,  $P < 0.001$ ), whereas between the latter species no significant difference was found ( $G = 1.1$ ,  $df = 1$ ,  $P > 0.05$ ). Campbell & Newbery (1993), by contrast, found that rough-barked species had significantly fewer liana infestations than both smooth and slightly rough-barked species. The present data support the finding of Putz (1984b) that spiny trunks do not effectively prevent trees from liana infestation. Individual bark types may not, in general, offer any effective protection against liana invasion because the evolution of different climbing modes enables particular liana species to ascend successfully on any kind of bark surface (cf. Hegarty 1991, Putz & Holbrook 1991).

Species with macrophylls had significantly fewer liana-infested individuals than species with mesophylls ( $G = 181.5$ ,  $df = 1$ ,  $P < 0.001$ ). However, the growth habit of trees in conjunction with leaf size and leaf arrangement, rather than the leaf size alone, influence the probability that a tree will carry lianas. For example, the unbranched habit of *C. peltata* and *O. lagopus* at initial stages, with single macrophylls on branch-like petioles that are continuously shed with height extension (Coley 1983), seems to be a strategy for remaining free of lianas (Putz 1984b). This is also true for species with compound (pinnate) leaves (Putz 1980). In this study, however, the proportion of liana-infested individuals between species with compound leaves and species with simple mesophylls was not significantly different ( $G = 0.1$ ,  $df = 1$ ,  $P > 0.05$ ).

Tree species benefitting from disturbance are exposed to a liana-abundant environment, indicated by the significantly higher seedling density of lianas in logged areas (unlogged:  $\bar{x} = 9.5$  seedlings/32 m<sup>2</sup>,  $SD = 6.1$ ,  $n = 40$ ; logged:  $\bar{x} = 13.0$  seedlings/32 m<sup>2</sup>,  $SD = 9.8$ ,  $n = 75$ ;  $z = 2.42$ ,  $P < 0.05$ ). Short-lived pioneers, completing their life cycle in early successional stages, have evolved the most effective strategies to escape the ravages of lianas. This is reflected by the significantly lower proportion of liana-laden individuals than in either secondary ( $G = 67.9$ ,  $df = 1$ ,  $P < 0.001$ ) and primary species ( $G = 140.6$ ,  $df = 1$ ,  $P < 0.001$ ). The difference was less pronounced between secondary and primary species ( $G = 10.6$ ,  $df = 1$ ,  $P < 0.01$ ), suggesting that major trade-offs towards effective liana protection become less important in more advanced seral stages. Potential host trees in mature forest use other 'more indirect' forms of protecting themselves from liana infestation. Hegarty (1991), for example, suggests that the deeply shaded forest floor results in poor liana regeneration.

The results suggest that the probability of liana assault is most successfully reduced by a mixture of many factors, such as ant-symbiosis, large simple or compound leaves which are shed continuously, and a long branch-free bole at early life stages, rather than by any single factor alone. This strategy was represented par excellence in *Triplaris caracasana*.

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