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Liana -Tree species associations in a Bolivian dry forest

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Abstract: Associations between tree species and degree of woody liana colonization were identified and the mechanisms explaining these relationships were investigated in a dry forest in eastern Bolivia. For 3158 individual trees >20 cm in diameter representing 72 tree species, 77% had at least 1 liana. Of the total number of trees colonized by lianas, 35% of trees had lianas totally covering their crowns, 37% had lianas within the crowns but not covering them, and 28% had lianas only on their boles. Based on natural tree species abundances, the tree species *Anadenanthera colubrina* and *Attalea phalerata* had significantly lower colonization rates than expected, whereas *Neea hermaphrodita* was the only species having significantly more liana-colonized individuals than expected. Ranks were assigned for each tree species according to morphological and physiological features thought to facilitate or inhibit liana establishment (shedding of branches or large branch like leaves, rate of bark exfoliation, bark texture, stem flexibility, and branch-free bole height) in an attempt to explain relative differences in liana colonization among species. Only shedding of branches or large compound leaves was negatively correlated with the proportion of liana-infested trees.

Resumen: Se establecieron relaciones entre especies de árboles y grado de colonización por bejucos, y se investigaron los mecanismos que explican dichas relaciones en un bosque seco del oriente de Bolivia. Para 3158 árboles de diámetro mayor a 20 cm, representando a 72 especies, la tasa general de colonización por bejucos fue de 77%. De este porcentaje, 35% corresponde a bejucos que cubrían totalmente las copas, 37% a bejucos sobre las copas, pero sin cubrirlas, y 28% a bejucos solo en el fuste. En general, no se hallaron relaciones marcadas, negativas o positivas, entre las tasas de infestación por bejucos y las especies de árboles. Sobre la base de los datos de abundancia de árboles y las tasas de infestación por bejucos, las especies *Anadenanthera colubrina* y *Attalea phalerata* mostraron tasas de colonización significativamente memores a las previstas, mientras que *Neea hermaphrodita* fue la única especie con una tasa de colonización significativamente mayor a la esperada. Se asignaron rangos a cada especie de árbol, de acuerdo a rasgos morfológicos y fisiológicos que se considera podrían facilitar o inhibir el establecimiento de bejucos (pérdida de ramas inferiors, exfoliación y textura de la corteza, flexibilidad de los árboles, y altura del fuste exento de ramas), con el fin de explicar las diferencias relativas entre especies, con respecto a la colonización por bejucos. Se determinó que la pérdida de ramas o hojas largas y compuestas está correlacionada con el impedimento del avance de bejucos.

Resumo: Associações entre as espécies arbóreas e o grau de colonização com lianas lenhosas foram identificadas e os mecanismos explicativos destas relações foram investigados numa floresta seca na Bolívia oriental. Em 3158 árvores individuais, com diâmetros superiores a 20 cm e representando 72 espécies arbóreas, 77% tinham, pelo menos, uma liana. No total das árvores colonizadas pelas lianas 35% tinham lianas cobrindo totalmente as copas, e 28%

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tinham lianas somente nos troncos. Com base na abundância arbórea natural específica, as espécies *Anadenanthera colubrina* e *Attalea phalerata* apresentavam taxas de colonização significativamente menores do que as esperadas, enquanto que a *Neea hermaphrodita* era a única espécie com uma significativa maior colonização individual que a esperada. Numa tentativa de explicar as diferenças relativas na colonização das lianas entre espécies foi efectuado o ordenamento de cada espécie arbórea de acordo com os caracteres morfológicos e fisiológicos, pensados como susceptíveis de facilitar ou inibir o estabelecimento das lianas (sombra dos ramos ou ramos grandes com forma de folha, taxa de esfoliação da casca, textura da casca, flexibilidade do tronco e altura do tronco livre de ramos). Só o sombreamento dos ramos our folhas largas compostas se encontravam negativamente correlacionadas com a proporção das árvores infestadas por lianas.

Key words: Bolivia, lianas, tropical dry forest, tropical forest management, vines.

Introduction

Lianas (woody vines) present particular problems in natural forest management for timber where climbing plants are notorious for causing larger canopy gaps on felling and increasing damage to the residual forest stand (Putz 1992; Vidal *et al.* 1997). In addition to the problems incurred on felling, lianas can have detrimental effects on tree development through a number of mechanical and biophysical actions (Kennard 1998; Putz 1984, 1992, 1995). Tree growth increment is negatively influenced by liana colonization through abrasion, passive strangulation (Kennard 1998), increased competition for light, nutrients and water (Holbrook & Putz 1996; Putz 1992; Putz & Windsor 1987) and inhibition of regeneration (Putz 1984). In addition, lianas can increase pathogen susceptibility, act as 'fire ladders', and increase access to the tree canopy by folivores (Putz 1992).

In natural forest management, where reducing the environmental impact of logging is a high priority, pre-felling liana cutting is often practised to minimize climber proliferation in felling gaps and reduce logging damage in the residual stand. However, the management of lianas is time-consuming and expensive (Appanah & Putz 1984; Vidal *et al.* 1997). By predicting the degree of vine colonization for particular trees of commercial importance, forest managers can better estimate costs of liana cutting on a per species basis and direct silvicultural treatments towards species which may be susceptible to liana colonization.

A number of factors have been suggested to influence tree susceptibility to liana colonization. Relationships have been detected between the degree of vine colonization and such variables as tree diameter, distance between tree branches, bark characteristics, and branch shedding frequency (Pinard & Putz 1992; Putz 1984; Putz 1995). Campbell & Newbery (1993) also found that infestation was inversely correlated with mean branch-free bole height. Other characteristics such as stem flexibility, leaf size, bark texture and exfoliation rates also influence colonization success (Putz 1995). Finally, larger bole diameters were also found to decrease susceptibility to liana colonization due to biomechanical limitations of liana climbing abilities on larger trees (Putz & Chai 1987; Pinard & Putz 1992).

In this study, we used forest inventory data to identify species that have higher or lower than expected liana colonization and searched for correlations between tree morphological characteristics and the degree of liana colonization.

Methods

The study was carried out in Las Trancas, a dry subtropical forest in the Lomerio region of eastern Bolivia (16°13 S, 61°50 W) at an elevation of 400-600 m. Mean annual precipitation is 1100 mm and the average annual temperature is 24°C. There is a marked dry season of approximately 6 months which includes significant drops in temperature following the passage of Antarctic fronts. Light selective logging has occurred historically on the site. Mean forest canopy height is 12-18 m with emergent trees to 30 m. Mean total basal area for trees >10 cm dbh is 23 m^2ha^{-1}. A total of

85 species of liana were found in the study site with Bignoniaceae, Sapindaceae, and Malpighiaceae being the most diverse liana families (Killeen *et al.* 1998).

Pre-logging forest inventory data collected in October 1995 in Las Trancas were used to test associations between tree species and degree of liana colonization. The data included observations on 3158 commercial and non-commercial tree species with dbh >20 cm in hundred 20 x 50 m permanent plots distributed over 300 ha. All tree species within the 100 plots were included in this study. Species diameter at breast height (dbh) and the degree of liana colonization were noted for each tree. Degree of liana infestation was classified according to the method of Alder & Synott (1992): (1) no lianas on tree, (2) lianas on bole only, (3) lianas within tree crown, (4) lianas completely covering crown.

The relationship between tree morphological characteristics and liana colonization was analysed based on the ranking of five tree characteristics suggested to either facilitate or repel liana colonization by various workers (Campbell & Newbery 1993; Putz 1984, 1985). All species represented by at least 15 individuals in the 3158 tree sample were ranked from 1-3 according to the following characteristics :

(A) Shedding of branches or large branch-like leaves : where 1 = readily/commonly shed, 2 = shed on occasion, 3 = do not readily shed. (B) Bark texture : where 1 = smooth, 2 = bark with some furrowing or scaling, 3 = heavily furrowed or with spines. (C) Bark exfoliation : 1 = high rate of exfoliation, 2 = medium rate of exfoliation, 3 = slow rate of exfoliation. (D) Branch-free bole height in relation to total tree height : where 1 = high bole-to-crown ratio (tree species with crowns beginning above 75% of the total height of the tree), 2 = medium bole-to-crown ratio, 3 = low bole-to-crown ratio (tree species with crowns beginning below 50% the total height of the tree). (E) Tree stem flexibility : where 1 = very flexible (stem bends readily in even moderate winds), 2 = has some flexibility, 3 = inflexible (stem rarely bends visibly even in strong gusts).

A Chi-square test was used to determine if lianas colonized host tree species more or less than expected based on tree abundances. The average percent colonization of all trees was calculated to provide the expected proportion of liana colonization. Actual liana occurrence rates were calculated for each species as a percentage of colonized trees. A regression analysis was used to determine the relationship between dbh and degree of liana colonization for all tree species combined based on the liana colonization classification of Alder & Synott (1992) described above.

The percentage of trees with lianas was determined for each species and a Spearman's test was used to determine the correlation between this variable and the rank scores for each of the tree characteristics thought to influence liana. In addition, a correlation was conducted for the sum of all the ranks for the characteristics with the percentage of trees with lianas for each species. Relationships were considered significant at P 0.05.

Results

The percentage of trees with lianas varied among species, but 77.7% of trees observed hosted one or more lianas. Of the tree species observed, only the deciduous canopy tree *Anadenanthera colubrina* and the palm *Attalea phalerata* had significantly lower liana colonization than expected (Table 1). In addition, the three *Cecropia concolor* trees in our sample did not host lianas. The only species with a significantly higher number of trees hosting lianas than expected was *Neea hermaphrodita.*

Species particularly susceptible to liana infestation were arbitrarily defined as those with >60% of observations in class 3 and 4 (lianas entering or covering canopy) (Table 2). Using this classification, *Phyllostylon rhamnoides* had the highest percentage of liana infestation at 78% of observations in categories 3 or 4. *Bougainvillea modesta, Aspidosperma cylindrocarpon* and *Simira rubescens* also had high rates of liana infestation, with 71-72% of observations in these classes. Other species with percentages ranging from 60-70% colonization rates in classes 3-4, included *Acacia bonariensis, Sterculia apetala, Neea hermaphrodita, Caesalpinia pluviosa* and *Acosmium cardenasii.*

A weak positive relationship was found between tree dbh and degree of liana colonization ($P<0.001$, $r^2 = 0.174$), but no significant relationship was found between the scores for liana susceptibility based on individual tree characteristics, nor between the sums of the scores for all susceptibility characteristics (Fig. 1). However, two palm species that had low rank values also had low rates of liana colonization. Similarly there was a

Table 1. Actual and expected numbers of trees with lianas based on average liana colonization rates for all species. Table of probabilities of Chi-square test are presented for species with n >15 trees. Authorities for Latin names follow Kolleen *et al.* (1998).

Species	N	Family	Actual Values	Expected Values	Probability $P>X^2$
Acacia bonariensis	171	Mimosaceae	149	132	0.282
Acosmium cardenasii	632	Caesalpinaceae	506	487	0.525
Amburana cearensis	5	Fabaceae	3	4	N/A
Anadenanthera colubrina	478	Mimosaceae	259	368	0.001
Aspidosperma australe	2	Apocynaceae	1	2	N/A
Aspidosperma rigidum	174	Apocynaceae	125	134	0.576
Aspidospermum cylindrocarpon	116	Apocynaceae	97	89	0.557
Astronium urundeuva	46	Anacardiaceae	25	35	0.197
Attalea phalerata	40	Arecaceae	13	31	0.010
Bougainvillea modesta	27	Nyctaginaceae	21	20	0.876
Brosmium gaudichaudii	7	Moraceae	6	5	N/A
Caesalpinia paraguarensis	1	Caesalpinaceae	1	1	N/A
Caesalpinia pluviosa	148	Caesalpinaceae	120	114	0.695
Campomanesia aromatica	5	Myrtaceae	4	4	N/A
Capparis prisca	42	Capparaceae	29	32	0.701
Cariana estrellensis	8	Lecythidaceae	3	2	N/A
Cariniana ianeirensis	20	Lecythidaceae	12	9	0.513
Casearia gossypiosperma	76	Flacourtiaceae	52	59	0.567
Cecropia concolor	3	Moraceae	0	2	N/A
Cedrela fissilis	7	Meliaceae	4	5	N/A
Ceiba samauma	12	Bombaceae	12	9	0.513
Celtis pubescens	2	Ulmaceae	1	2	N/A
Centrolobium microchaete	97	Fabaceae	79	75	0.792
Cereus tacuaralensis	6	Cactaceae	5	5	N/A
Chorisia speciosa	98	Bombaceae	57	76	0.502
Chrysophyllum gonocarpum	3	Sapotaceae	2	2	N/A
Combretum leprosum	40	Combretaceae	40	31	0.232
Copaifera chodatina	52	Caesalpinaceae	41	40	0.912
Cordia glabrata	7	Boraginaceae	7	5	N/A
Cyclolobium blanchetianum	2	Fabaceae	1	1	N/A
Dalbergia riparia	4	Fabaceae	5	5	N/A
Ficus gomeillera	8	Moraceae	4	7	N/A
Galipea trifoliata	18	Rutaceae	11	13	0.683
Gallesia integrifolia	60	Phytolaccaceae	60	46	0.174
Rheedia brasiliensis	8	Guttiferae	5	7	N/A
Hymenaea courbaril	1	Caesalpinaceae	1	1	N/A
Inga nobilis	4	Mimosaceae	3	3	N/A
Luehea paniculata	7	Tilaceae	6	5	N/A
Machaerium acutifolium	100	Fabaceae	87	73	0.423
Machaerium scleroxylon	68	Fabaceae	51	53	0.922
Machaerium hirtum	1	Fabaceae	0	1	N/A
Maclura tinctoria	1	Moraceae	1	1	N/A
Myrciara cauliflora	2	Myrtaceae	1	2	N/A
Neea hermaphrodita	97	Nyctaginaceae	77	75	0.001
Phyllostylon rhamnoides	55	Ulmaceae	48	43	0.527

Table 1. *contd.*

Species	N	Family	Actual Values	Expected Values	Probability P>X²
Physocalymma scaberrium	1	Lythraceae	1	1	N/A
Platymiscium ulei	6	Fabaceae	3	5	N/A
Pogonopus tubulosus	4	Rubiaceae	4	3	N/A
Pseudobombax longifolium	27	Bombaceae	22	21	0.758
Pseudobombax marginatum	12	Bombaceae	6	9	0.439
Qualea grandiflora	3	Vochysiaceae	3	2	N/A
Rollinia herzogii	17	Annonaceae	12	13	0.841
Salacia elliptica	1	Hippocrataceae	0	1	N/A
Samanea tubulosa	2	Mimosaceae	2	6	N/A
Sapium haematospermum	1	Euphorbiaceae	1	1	N/A
Schinopsis brasiliensis	12	Anacardiaceae	8	9	0.808
Simira rubescens	56	Rubiaceae	49	43	0.532
Spondias mombin	17	Anacardiaceae	9	13	0.394
Sterculia apelata	27	Fabaceae	20	20	1.000
Swartzia jorori	3	Fabaceae	1	2	N/A
Syagrus sancona	15	Arecaceae	4	11	0.071
Tabebuia impetiginosa	86	Bignoniaceae	63	66	0.792
Tabebuia serratifolia	2	Bignoniaceae	2	2	0.564
Talisia esculenta	13	Sapindaceae	11	5	0.532
Urera baccifera	6	Urticaceae	6	30	N/A
Vitex cymosa	4	Verbenaceae	3	3	N/A
Ximenia americana	3	Olaceae	3	2	N/A
Zanthoxylum hasslerianum	31	Rutaceae	31	24	0.276
Zeyheria tuberculosa	2	Bignoniaceae	2	2	N/A
Unidentified	8		6	1	N/A
Unidentified	8		7	6	N/A

clustering of species with high rank values for expected liana colonization and high actual liana colonization rates. A group of three species (*Astronium urundeuva, Spondias mombin* and *Anadenanthera colubrina*) had high rank values but low liana colonization rates. Conversely, another group of species including *Phyllostylon rhamnoides* and *Bougainvillea modesta*; had high colonization rates, yet low rank values.

Discussion

Over three quarters of trees >20 cm dbh were colonized by lianas. This quantity is on the high end of the range when compared to that of other tropical forests. In a tropical wet forest in Costa Rica, Clark & Clark (1990) found percentages of liana infestation between 50-97%. Campbell & Newbery (1993) noted 57% infestation in a tropical humid forest in Sabah, Malaysia. In a sub-humid Bolivian tropical forest, Perez-Salicrup (1998) found that 86% of trees hosted lianas.

Only two species had significantly lower infestation rates than expected. *Anadenanthera colubrina* had only 51% of trees with lianas. This species is the most abundant of all commercial tree species representing 22% of the commercial basal area in this forest. *Attalea phalerata*, a palm species, had only 33% of species with lianas. The only species found to have significantly higher liana infestations was *Neea hermaphrodita* at 79% of the population infected with lianas.

Degree of vine infestation is important for predicting effects on tree growth and potential damage during logging due to liana connections among adjacent trees (Kennard 1998; Putz 1984). Once colonized, some species appear to be susceptible to liana infestation, where lianas nearly envelope the entire crown. Trees with high infestation rates included *Sterculia apetala, Caesalpinia pluviosa* and *Acosmium cardenasii*. Other species have high

Table 2. Percentage of liana infestation observed for each class: (1) no lianas on tree, (2) lianas on stem only, (3) lianas within tree crown, (4) lianas completely covering crown with number of observations for each tree. Tree species with commercial value are noted with asterisks: *species of low commercial value, **valuable species, ***very valuable species.

Species	Family	Scale of Liana Infestation (%)				
		N	1	2	3	4
Acacia bonariensis	Mimosaceae	171	13	23	24	40
*Acosmium cardenasii**	Caesalpinaceae	632	20	19	33	28
*Amburana cearensis****	Fabaceae	5	40	20	40	0
*Anadenanthera colubrine***	Mimosaceae	478	49	22	20	12
Aspidosperma australe	Apocynaceae	2	50	0	50	0
*Aspidospermum cylindrocarpon***	Apocynaceae	116	15	13	35	37
*Asidosperma rigidum***	Apocynaceae	174	24	28	22	27
*Astronium urundeuva**	Anacardiaceae	46	46	28	13	13
Attalea phalerata	Arecaceae	40	68	15	15	3
Bougainvillea modesta	Nyctaginaceae	27	22	7	41	30
Brosimum gaudichaudii	Moraceae	7	14	14	43	29
Caesalpinia paraguariensis	Caesalpinaceae	1	0	0	0	100
*Caesalpinia pluviosa**	Caesalpinaceae	148	19	18	27	36
Campomanesia aromatica	Myrtaceae	5	20	60	0	20
Capparis prisca	Capparaceae	42	31	24	29	17
*Cariniana estrellensis**	Lecythidaceae	8	38	13	38	13
*Cariniana ianeirensis**	Lecythidaceae	20	40	25	25	10
Casearia gossypiosperma	Flacourtiaceae	76	32	16	28	25
Cecropia concolor	Moraceae	3	100	0	0	0
*Cedrela fissilis****	Meliaceae	7	43	4	29	14
Ceiba samauma	Bombaceae	12	0	41	25	33
Celtis pubescens	Ulmaceae	2	50	0	0	50
*Centrolobium microchaete**	Fabaceae	97	19	24	40	18
Cereus tacuaralensis	Cactaceae	6	17	0	0	83
Chorisia speciosa	Bombaceae	98	32	15	20	33
Chrysophyllum gonocarpum	Sapotaceae	3	33	0	33	33
Combretum leprosum	Combretaceae	40	23	20	30	28
*Copaifera chodatiana***	Caesalpinaceae	52	21	31	25	23
*Cordia glabrata****	Boraginaceae	7	43	29	0	29
*Cyclolobium blanchetiamum**	Fabaceae	2	0	100	0	0
Dalbergia riparia	Fabaceae	4	20	20	0	60
Ficus gomeillera	Moraceae	8	50	13	25	13
Galipea trifoliata	Rutaceae	18	33	28	22	17
*Gallesia integrifolia**	Phytolaccaceae	60	30	20	22	28
Rheedia brasiliensis	Guttiferae	8	38	13	38	13
*Hymenaea courbaril***	Caesalpinaceae	1	0	0	0	100
Inga nobilis	Mimosaceae	4	25	50	0	25
Luehea paniculata	Tilaceae	7	14	14	14	57
*Machaerium acutifolium**	Fabaceae	100	16	27	31	26
Machaerium scleroxylon ***	Fabaceae	68	25	22	24	29
Machaerium hirtum	Fabaceae	1	100	0	0	0
Maclura tinctoria	Moraceae	1	0	0	100	0
Myrciara cauliflora	Myrtaceae	2	50	50	0	0
Neea hermaphrodita	Nyctaginaceae	97	21	14	32	33
*Phyllostylon rhamnoides**	Ulmaceae	55	13	9	38	40

Table 2. *contd.*

Species	Family	Scale of Liana Infestation (%)				
		N	1	2	3	4
Physocalymma scaberrium	Lythraceae	1	0	0	100	0
*Platymiscium ulei**	Fabaceae	6	50	17	33	0
Pogonopus tubulosus	Rubiaceae	4	0	25	25	50
Pseudobombax longilorum	Bombaceae	27	19	22	30	30
Pseudobombax marginatum	Bombaceae	12	50	8	25	17
*Qualea grandiflora**	Vochysiaceae	3	0	33	33	33
Rollinia herzogii	Annonaceae	17	29	12	29	29
Salacia elliptica	Hippocrataceae	1	100	0	0	0
Samanea tubulosa	Mimosaceae	2	0	0	0	100
Sapium haematospermum	Euphorbiaceae	1	0	0	0	100
*Schinopsis brasiliensis**	Anacardiaceae	12	33	33	33	0
Simira rubescens	Rubiaceae	56	13	16	36	36
*Spondias mombin**	Anacardiaceae	17	47	35	12	6
*Stericulia apetala**	Fabaceae	27	26	11	33	30
*Swartzia jorori**	Fabaceae	3	67	0	0	33
Syagrus sancona	Aracaceae	15	73	20	7	0
*Tabebuia impetiginosa**	Bignoniaceae	86	27	15	40	19
*Tabebuia serratifolia**	Bignoniaceae	2	0	50	50	0
Talisia esculenta	Sapindaceae	13	23	15	23	39
Urera baccifera	Urticaceae	6	0	17	33	50
Vitex cymosa	Verbenaceae	4	25	25	50	0
Ximenia americana	Olacaceae	3	0	0	33	67
Zanthoxylum hasslerianum	Rutaceae	31	7	13	4	45
*Zeyheria tuberculosa**	Bignoniaceae	2	0	50	0	50
Unidentified		8	25	38	13	25
Unidentified		8	13	0	13	75

colonization rates, but do not often become infested, such as *Simira rubescens, Bougainvillea modesta, Acacia bonariensis* and *Luehea paniculata*. Only *Neea hermaphrodita* had a significantly higher than expected incidence of both liana colonization and intensive infestations than expected.

The degree of infestation for tree species has been related to a number of their physical characteristics (Clark & Clark 1990; Campbell & Newbery 1993; Pinard & Putz 1992; Putz 1984, 1995; Putz & Chai 1987). Despite the lack of a significant relationship between tree morphological traits and liana infestation, there was evidence of some clusterings of species with high rank values that were also susceptible to high liana infestation, such as *Aspidosperma cylindrocarpon, Copaifera chodatiana* and *Centrolobium microchaete*. These species have a rough and mostly non-exfoliating bark, have inflexible stems, and do not shed branches. Similarly, the palm species *Attalea phalerata* and *Syagrus sancona* have high rates of shedding of their large branch-like compound leaves and a high bole-to-crown ratio. *Syagrus sancona* also has a flexible stem, rarely colonized by lianas. Two species, *Phyllostylon rhamnoides* and *Acosmium cardenasii*, had relatively low rank values but high infestation rates. The boles of both these species frequently have hollows and fluting which may favor liana establishment. Three species had high rank values and low liana infestation, including *Anadenanthera colubrina, Spondias mombin* and *Astronium urundeuva*, with only 12%, 6% and 13% having liana infestations, respectively. The bark of *Astronium urundeuva* has a powdery texture that may hinder liana establishment. *Anadenanthera colubrina* reportedly has the same feature on branches (Jose Ledezma, *pers. comm.*). Despite these bark characteristics that should inhibit liana establishment on these tree species, it should be noted that we observed

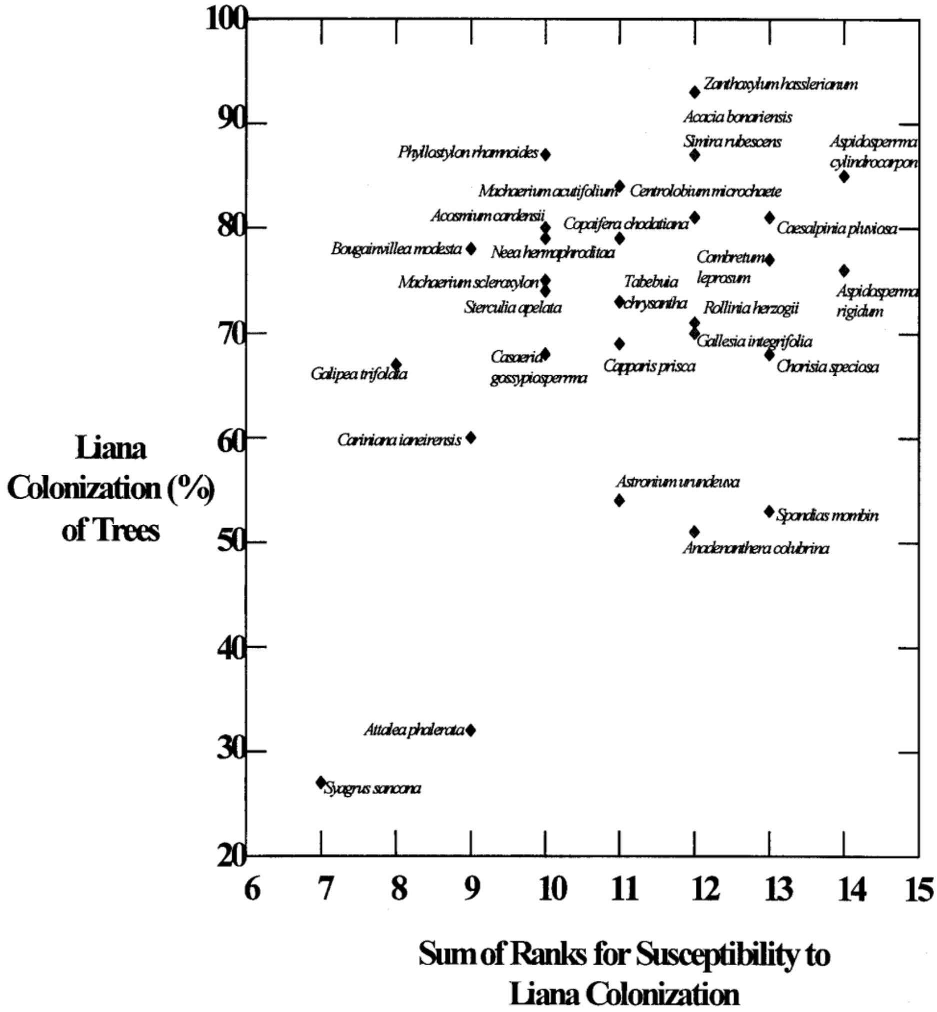

Fig. 1. Correlation of rank sums of tree characteristics against percentage of liana colonization for tree species in a Bolivian dry forest. Tree characteristics considered include shedding of branches or large compound leaves, bark texture, rate of bark exfoliation, bole to crown ratio, and stem flexibility.

many lianas colonizing trees via the crowns of neighbouring trees. Therefore, bark characteristics and some other tree features that may help deter vine colonization (e.g., bole-to-crown ratio) may be circumvented by vines. Only a weak relationship was found between tree dbh and liana infestation. This differs with the findings of Pinard & Putz (1992) in Malaysia, who found a sequence of liana infestation with increasing tree diameters and also Clark & Clark (1990), who showed a negative relationship between tree dbh and liana infestation.

Lianas appear to present a problem for natural forest management in Lomerio and other forests. In commercial forestry, high liana colonizations are economically undesirable due to an increase in tree stem deformations, thus increased problems in handling boles and a decrease in commercial value. Particular problems with lianas exist in natural forest management where climbing plants are notorious for causing larger canopy gaps on felling and increasing damage to the residual forest stand (Putz 1992; Vidal *et al.* 1997). Because of the costs of liana cutting and the ecological risks of removing lianas from forests, it has been suggested that liana cutting should be limited only to those colonizing commercial tree species (Fredericksen 2000). Because lianas infrequently colonize the most abundant commercial tree species in this forest, *Anadenanthera colubrina*, the cost of this silvicultural treatment should be relatively low.

It appears that in Las Trancas there is no one major characteristic that facilitates or repels liana colonization. A combination of morphological factors may interact to influence liana attraction and possibly a related set of factors exist to determine intensity. However, frequent branch shedding; although represented by only three species (*Attalea phalerata, Syagrus sancona* and *Cecropia concolor*) may be the most important characteristic. *Attalea phalerata* and *Syagrus sancona* both had low colonization rates. *Cecropia concolor* on the other hand, despite being a common species in Las Trancas, tended to have few trees >20 cm dbh and was not well represented in this study which included only larger trees. However, observations of this species showed that liana colonization of this species were rare. Pioneers, in general, have been found to be effective at repelling lianas. Clark & Clark (1990) also found strong liana deterrence of liana colonization in *Cecropia* sp. Similarly, Pinard & Putz (1992) found that stem flexibility and long leaves, both of which are characteristics of *Cecropia* sp., were effective in deterring lianas in Malaysia.

Problems in predicting liana infestation are reflected in the literature where many factors have been proposed to influence liana colonization, the effect of vine infestation on tree growth, and the magnitude of gap creation on felling. Liana effects on tree species may vary due to different abilities to colonize trees. Tree characteristics such as liana anatomy and biomechanics may be important (Pinard & Putz 1992; Putz 1995; Putz 1984; Putz & Chai 1987). Twining, clasping and tendril climbing mechanisms are thought to influence liana colonization on certain tree species, and tree diameter and number of branch supports were important characteristics determining liana colonization in Malaysia (Pinard & Putz 1992).

Environmental aspects may also influence climber abundance. Appanah & Putz (1984) found twice as many lianas in wet, lowland areas as on upland sites. In addition, they concluded that lianas tend to be more abundant on alluvial and rich soil, perhaps because more natural gaps from treefalls form on these soils. Tree species that occur in these areas may have more lianas than in sites where lianas are less abundant. Riverine species in this study with a significant number of observations included *Aspidosperma cylindrocarpon, Capparis prisca, Cariniana ianeirensis, Gallesia integrefolia* and *Rollinia herzogii*. However, from this group, only *Aspidosperma cylindrocarpon* had liana colonization in classes 3 and 4 >60%. Therefore, the topographic position of Las Trancas may not be a significant factor in determining the degree of liana colonization.

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