

Host associations of lianas in a south-east Queensland rain forest

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ABSTRACT. Lianas are abundant in tropical forests around the world, yet little is known about their ecology. In this study we report the results of a survey of ten common liana species on 27 host tree species in Cooloola National Park, Queensland, Australia. We found significant associations between some liana and tree species. Our results indicate that host tree diameter was important in explaining liana presence or absence. Host tree fruit type was correlated with the presence or absence of different liana types. Tendrillar and root-climbing lianas tended to occur most often on mid-sized, fleshy-fruited trees, and on smaller, non-fleshy-fruited trees. The presence of stem twining lianas tended to decrease with increasing tree diameter for both fleshy- and non-fleshy-fruited trees, although this effect was more pronounced for fleshy-fruited trees. In general, lianas were most prevalent on trees possessing intermediate levels of bark roughness and flakiness. Although we established associative patterns between liana species and these host characteristics, the model suggested that other unidentified variables may also be important in determining presence or absence of liana species.

KEY WORDS: rain-forest dynamics, tree bark, tropical ecology, vines

INTRODUCTION

Lianas (woody climbers) play an important role in the ecological dynamics of rain forests. They may contribute significantly to physical structure of forests by binding trees together and closing canopy gaps (Richards 1996) and their biomass and leaf area comprise a large proportion of the primary productivity of rain forests (Hegarty & Caballé 1991). Liana leaves contribute 5–20% of

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their total above-ground biomass, compared with 1–2% for tree leaves (Hegarty & Caballé 1991). While primary productivity and abundance of lianas is high in all rain forests, they can have an even greater presence in both early successional and disturbed forests (DeWalt *et al.* 2000, Hegarty 1990). In addition to impacting rain forest structure, lianas compete with trees for light, space and water, often having a negative effect on individual trees (Perez-Salicrup & Barker 2000). Putz (1984a) has shown that lianas can contribute to tree mortality and reduced growth, and can increase the frequency at which canopy gaps are formed.

The potential negative effects of lianas on tree hosts may have evolutionarily driven some species of tree to exhibit characteristics that reduce their suitability as liana hosts (Allen *et al.* 1997). Tree species display a diversity of bark types that can be broken down into two components: variation in the topography of bark and variation in the rate at which that bark is shed. Lianas may be unable to climb trees with smooth bark because those trees lack attachment sites for their climbing structures (Putz 1980). Lianas may be unable to climb trees with rapidly shed bark because, although potentially well secured to the bark, they are only anchored as long as the bark remains on the host tree.

Lianas have evolved a number of climbing mechanisms that allow them to circumvent host species' adaptations designed to repel lianas. These include stem rootlets, specialized tendrils on leaves or stems, and various twining growth forms that maximize lianas' ability to ascend smooth or branched trunks. Host size may be important in determining the presence of lianas because lianas with twining and tendril adaptations are limited to hosts with relatively small trunk and branch diameters (Pinard & Putz 1992, Putz 1984b). All liana species, except those that climb by attaching directly to hosts' bark, should be excluded from large trees unless they entered that host when it was still small enough to climb, climbed up another liana already present in the host, or climbed into the hosts' crown from a neighbouring tree (Putz 1984b).

Although some tree species may have adaptations that limit their suitability as liana hosts, their relationship with seed dispersers may increase their chances of hosting lianas. Frugivorous birds are important dispersers of rain-forest seeds, and are attracted to fleshy, edible fruits. Thus, frugivorous birds are more likely to be found in the canopies of fleshy-fruited trees and are more likely to deposit seeds from fleshy-fruited lianas under these trees. Therefore, the fruit type of host trees and lianas may play a role in liana establishment.

Although lianas are common in most of the world's rain forests, there is a paucity of information on their biology and ecology (Hegarty & Clifford 1991). In this study we tested whether a set of liana species was associated with particular host species and tested the hypothesis that morphological characteristics of host and liana species were associated with these patterns. Specifically, we expected to find that (1) tree species with very smooth and/or flaky bark would host lianas less frequently than trees with rough and/or stable bark, (2)

tree species with fleshy fruits that appeal to frugivorous birds would be more likely to host fleshy-fruited lianas than trees with dry or inedible fruits, and (3) individual trees with a large dbh would be effective at repelling lianas with twining mechanisms, while dbh would be irrelevant for lianas that have specialized adherence structures.

METHODS

The study was conducted in evergreen subtropical rain forest, in Cooloola National Park, Queensland, Australia (25°56'S, 153°5'E). At the nearest weather station 8 km E of study sites, mean monthly temperature ranges from 17–25°C with an annual rainfall of 1428 mm and a mild dry season in July and August. Rain forest is distributed patchily on Quaternary siliceous sand formations that typically have poor drainage and limited nutrient availability (Webb & Tracey 1975). Selective logging has occurred in Cooloola forests for over 150 y, but all study sites have been protected from human disturbance since 1971 and are now included in the national park. There are approximately 40 species of canopy and subcanopy trees in the forest (T. Male, *pers. obs.*).

During 1998 we surveyed trees along transects in three rain-forest areas found in the northern 10 km of the park. Elevation, soil and topography were similar in all areas and although tree species abundance differed on a local scale, species composition was similar with almost all species being found in each area. At least three transects of 500 m or longer were surveyed in each area. They were placed at random locations in the forest and extended along randomly selected compass bearings.

Along transects, we measured the diameter at breast height (dbh) of each tree whose crown was visible enough to allow us adequately to survey liana abundance. If the tree's dbh was > 15 cm, we identified the tree species and its fruit type (fleshy or dry), and examined the crown for the presence or absence of 10 species of common lianas. A liana species was counted as being present in the crown if there was at least one stem of the liana species in contact with any of the branches of the tree bearing living foliage. We made no effort to count the number of individual lianas of each species in a crown and each was scored as 'present' or 'absent'. After collecting data on 1000 trees we examined additional trees to increase representation of rarer species.

In March 1999 two observers unfamiliar with the tree species devised a system of ranking trunk roughness and bark flakiness on subjective scales from 1 to 5 (with 1 being the smoothest or least flaky). Each observer then independently assigned a roughness and flakiness value (recorded by a third observer who also identified the tree species) for each of five trees of each of the 27 species. These trees were selected by randomly picking five from the trees used to categorize liana presence/absence. These rankings were averaged to calculate a mean roughness and mean flakiness for each tree species.

In order to analyse host associations we assigned the 10 liana species to four

different climbing categories modelled after the classification of Hegarty & Clifford (1991). Species classed as tendrillar climbers possessed special tendrils that wrap around narrow branches and leaf stems of host trees. Tendrillar climbers included: *Cissus hypoglauca* A. Gray, *Cissus sterculiifolia* (Benth.) Planch. and *Flagellaria indica* L. Root climbers, species that used adventitious roots to adhere to hosts' trunks, were represented by *Piper novae-hollandiae* Miq. Stem twiners attached by physically twining around branches and small trunks. Lianas in this category were: *Morinda jasminoides* A. Cunn., *Millettia megasperma* (F. Muell.) Benth., *Melodinus australis* Maiden & Betche and *Marsdenia glandulifera* C. T. White. Scrambling climbers, *Melodorum leichhardtii* (F. Muell.) Diels and *Coelospermum paniculatum* F. Muell., loosely twine their stems around supporting structures. Eight of the ten lianas have fleshy fruits that are eaten by various bird species (Cooper & Cooper 1994; T. Male *pers. obs.*). *Millettia megasperma* has large, woody seeds with no assisted dispersal mechanism, and *Marsdenia glandulifera* has non-fleshy fruits.

Statistical analysis

We carried out a principal components analysis (PCA) on the proportion of individuals of each tree species that hosted each liana species. We graphically summarized the results of the principal components analysis using a biplot showing scaled versions of the first two sets of principal component loadings and the first two sets of principal component scores (ter Braak 1995). The biplot jointly represents liana type (loadings) and tree species (scores) and is capable of showing relationships between them (for a more detailed explanation see ter Braak (1995)).

We performed statistical analysis on each of the four liana categories. Pearson's chi-square tests were used to test presence/absence of each liana type vs. fruit type, bark roughness and bark flakiness of the host tree. The chi-square analyses allowed for the determination of whether or not liana presence/absence was related to each explanatory variable separately.

Because chi-square analysis provides no information on the nature of the relationship or on the effects of possible interactions among the explanatory variables we modelled liana presence/absence as a function of dbh, fruit type, and bark characteristics using logistic regression. Because initial analyses gave strong evidence that the relationship between dbh and liana presence/absence was quadratic we modelled dbh using orthogonal polynomials. This reduced multicollinearity and the unstable parameter estimates it produces. Once a series of logistic regression models was fitted we compared models using the Akaike Information Criterion (AIC; Burnham & Anderson (1998) provide an accessible introduction to AIC in ecological modelling). AIC is computed in logistic regression as the deviance plus a penalty term that corrects for the inclusion of more parameters in a model. This penalty term equals twice the number of parameters in the model. In general, smaller AIC values indicate better models.

We modelled the presence/absence of lianas separately for each liana type. Because the original roughness and flakiness classifications were averages of subjective ordinal rankings we rounded these values to the nearest integer and treated them as ordinal categorical predictors. There were 16 combinations of roughness and flakiness values but some combinations had no observations associated with them. For example, no tree species had a roughness value of 3 and a flakiness value of 1. This made the direct modelling of interactions between roughness and flakiness impossible. There were six different combinations of roughness and flakiness values shared by at least one tree species. These six combinations are shown in Table 1. We used these six combinations as six levels of a single categorical variable denoted hereafter by the term *bark*. Interactions between roughness and flakiness are incorporated indirectly in this new categorical variable. Fruit type is also a categorical variable with two values (0 or 1) indicating fleshy or non-fleshy, while dbh is a continuous variable. The data were inadequate to model the presence/absence of scrambling climbers so logistic regression analyses presented below exclude this liana type.

Table 1. Combined roughness/flakiness factor levels 1–6 and their corresponding roughness and flakiness values.

Roughness/Flakiness value	Roughness Value	Flakiness Value
1	1	1
2	1	3
3	2	1
4	2	2
5	2	3
6	3	3

To determine if there was an interaction between roughness and flakiness, we fitted models with these bark characteristics included as two separate categorical variables with no interaction between them. We compared the goodness of fit from these models with those from models with the single bark characteristic variable described above which incorporates an interaction term. Large decreases in AIC values indicated the presence of a significant interaction between roughness and flakiness.

All statistical analyses were done using the S-Plus statistical computing package (MathSoft, Data Analysis Products Division, Seattle, Washington, USA).

RESULTS

We surveyed a total of 1123 individual trees comprising 27 species with 13–84 trees per species (Table 2). In total, we documented the presence of 1439 lianas. The number of liana species of those surveyed that occurred on any individual tree ranged from 0–6 (mean = 1.28, SD = 1.32; Table 3).

The biplot (Figure 1) produced from PCA illustrates the main tree species/liana type associations seen in Table 3. It shows that tendrillar climbers, stem twiners and scrambling climbers were associated with one another, but not

Table 2. Twenty-seven tree species surveyed for presence/absence of ten liana species, and their respective families.

Species	Family
Trees	
<i>Acmena hemilampra</i> (F. Muell.) Merr. & L.M. Perry	Myrtaceae
<i>Agathis robusta</i> (F. Muell.) F.M. Bailey	Araucariaceae
<i>Archidendron lovelliae</i> (F.M. Bailey) I.C. Nielsen	Fabaceae
<i>Archontophoenix cunninghamiana</i> H. Wendl. & Drude	Palmae
<i>Backhousia myrtifolia</i> Hook	Myrtaceae
<i>Beilschmiedia obtusifolia</i> (Meisn.) F. Muell.	Lauraceae
<i>Beilschmiedia elliptica</i> C.T. White & W. D. Francis	Lauraceae
<i>Canarium australasicum</i> (Bailey) Leenh.	Burseraceae
<i>Cryptocarya glaucescens</i> R. Br.	Lauraceae
<i>Cryptocarya macdonaldii</i> B. Hyland	Lauraceae
<i>Diospyros fasciculosa</i> (F. Muell.) F. Muell.	Ebenaceae
<i>Endiandra discolor</i> Benth.	Lauraceae
<i>Elaeocarpus eumundi</i> F.M. Bailey	Tiliaceae
<i>Euroschinus falcata</i> Hook. f.	Anacardiaceae
<i>Flindersia australis</i> R. Br.	Rutaceae
<i>Halfordia kendack</i> (Montr.) Guillaumin	Rutaceae
<i>Litsea leefeana</i> (F. Muell.) Merr.	Lauraceae
<i>Lophostemon confertus</i> (R. Br.) Peter G. Wilson & J.T. Waterh.	Myrtaceae
<i>Mischocarpus pyriformis</i> (F. Muell.) Radlk.	Sapindaceae
<i>Planchonella laurifolia</i> (A. Rich.) Pierre	Sapotaceae
<i>Podocarpus elatus</i> Endl.	Coniferae
<i>Polyscias elegans</i> (C. Moore & F. Muell.) Harms	Araliaceae
<i>Rhodamnia acuminata</i> C.T. White	Myrtaceae
<i>Sarcopteryx stipata</i> (F. Muell.) Radlk.	Sapindaceae
<i>Schizomeria ovata</i> D. Don	Cunoniaceae
<i>Syzygium luehmannii</i> (F. Muell.) L.A.S. Johnson	Myrtaceae
<i>Syzygium oleosum</i> (F. Muell.) B. Hyland	Myrtaceae
Lianas	
<i>Cissus hypoglauca</i> A. Gray	Vitaceae
<i>Cissus sterculiifolia</i> (Benth.) Planch.	Vitaceae
<i>Coelospermum paniculatum</i> F. Muell.	Rubiaceae
<i>Flagellaria indica</i> L.	Flagellariaceae
<i>Marsdenia glandulifera</i> C. T. White	Asclepiadaceae
<i>Millettia megasperma</i> (F. Muell.) Benth.	Fabaceae
<i>Melodinus australis</i> Maiden & Betche	Apocynaceae
<i>Melodorum leichhardtii</i> (F. Muell.) Diels	Annonaceae
<i>Morinda jasminoides</i> A. Cunn.	Rubiaceae
<i>Piper novae-hollandiae</i> Miq.	Piperaceae

with *Piper novae-hollandiae*, the only root-climbing species. The first two sets of scores and their associated loadings explained 89% of the variation. The distance of the symbols from the origin indicates that tendrillar climbers exhibited more variability than other liana types. This variation is derived from the high prevalence of tendrillar climbers on some hosts and complete absence from a number of other hosts. Scrambling climbers showed the least variability in part because their rarity minimized the statistical difference between their abundance on host species.

As a general rule, species to the right of the vertical axis have fewer lianas than species to the left of the vertical axis. Tendrillar climbers tended to occur in roughly equal amounts in tree species to the left of the vertical axis. Similar

Table 3. Host species, number surveyed, and proportion with each of 10 liana species (because a tree can host more than one liana, row totals may exceed 1.0). Liana species are: FI (*Flagellaria indica*), CH (*Cissus hypoglauca*), CS (*Cissus sterculiifolia*), PN (*Piper novae-hollandiae*), MG (*Marsdenia glandulifera*), MM (*Millettia megasperma*), MJ (*Morinda jasminoides*), MA (*Melodinus australis*), CP (*Coelospermum paniculatum*) and ML (*Melodorum leichhardtii*).

Tree species	n	FI	CH	CS	N	MG	MM	MJ	MA	CP	ML
<i>Acmena hemilampra</i>	45	0.47	0.33	0.11	0.13	0.13	0.11	0.13	0.04	0.11	0.00
<i>Agathis robusta</i>	35	0.03	0.03	0.00	0.00	0.03	0.00	0.00	0.00	0.00	0.00
<i>Archidendron lovelliae</i>	21	0.33	0.29	0.19	0.19	0.10	0.00	0.05	0.00	0.00	0.10
<i>Archontophoenix cunninghamii</i>	50	0.06	0.02	0.00	0.02	0.06	0.06	0.04	0.00	0.00	0.00
<i>Backhousia myrtifolia</i>	55	0.36	0.15	0.05	0.02	0.15	0.18	0.04	0.07	0.05	0.04
<i>Beilschmiedia obtusifolia</i>	60	0.42	0.25	0.22	0.18	0.08	0.15	0.07	0.08	0.07	0.10
<i>B. elliptica</i>	17	0.47	0.29	0.00	0.00	0.12	0.00	0.24	0.12	0.00	0.12
<i>Canarium australasicum</i>	46	0.52	0.37	0.17	0.17	0.09	0.09	0.15	0.09	0.07	0.09
<i>Cryptocarya glaucescens</i>	24	0.29	0.13	0.00	0.04	0.13	0.21	0.08	0.00	0.04	0.00
<i>C. macdonaldii</i>	64	0.34	0.36	0.05	0.13	0.17	0.19	0.09	0.09	0.03	0.05
<i>Diospyros fasciculosa</i>	58	0.34	0.24	0.12	0.17	0.17	0.22	0.10	0.03	0.07	0.05
<i>Endiandra discolor</i>	33	0.42	0.21	0.24	0.12	0.06	0.00	0.18	0.03	0.03	0.03
<i>Elaeocarpus eumundi</i>	19	0.32	0.16	0.21	0.11	0.05	0.21	0.16	0.11	0.00	0.05
<i>Euroschinus falcata</i>	43	0.58	0.33	0.33	0.26	0.07	0.09	0.12	0.12	0.07	0.07
<i>Flindersia australis</i>	13	0.15	0.00	0.00	0.23	0.00	0.15	0.00	0.00	0.00	0.00
<i>Halfordia kendack</i>	51	0.29	0.16	0.20	0.02	0.10	0.06	0.08	0.02	0.00	0.02
<i>Litsea lefeana</i>	39	0.49	0.31	0.15	0.03	0.18	0.13	0.08	0.08	0.15	0.05
<i>Lophostemon confertus</i>	37	0.05	0.05	0.00	0.08	0.05	0.03	0.00	0.00	0.00	0.00
<i>Mischocarpus pyriformis</i>	35	0.43	0.40	0.26	0.06	0.11	0.06	0.09	0.09	0.03	0.03
<i>Planchonella laurifolia</i>	48	0.54	0.33	0.08	0.13	0.08	0.04	0.04	0.06	0.04	0.06
<i>Podocarpus elatus</i>	18	0.44	0.33	0.33	0.39	0.22	0.17	0.11	0.06	0.06	0.06
<i>Polyscias elegans</i>	37	0.43	0.14	0.03	0.05	0.14	0.14	0.05	0.05	0.05	0.08
<i>Rhodamnia acuminata</i>	45	0.33	0.09	0.04	0.04	0.18	0.00	0.00	0.02	0.02	0.07
<i>Sarcopteryx stipata</i>	33	0.33	0.12	0.21	0.15	0.18	0.06	0.09	0.00	0.00	0.00
<i>Schizomeria ovata</i>	84	0.49	0.29	0.10	0.11	0.20	0.04	0.17	0.10	0.01	0.06
<i>Syzygium luehmannii</i>	59	0.36	0.24	0.15	0.24	0.05	0.10	0.08	0.07	0.07	0.00
<i>S. oleosum</i>	54	0.41	0.17	0.13	0.11	0.17	0.15	0.17	0.09	0.09	0.00
Total lianas present		416	250	138	128	135	111	101	64	49	47

conclusions can be drawn for stem twiners and scrambling climbers. The biplot does not provide all the information on liana occurrence. For example, it is not apparent in the biplot that tendrillar climbers tended to be much more common than scrambling climbers (Table 3). However, the plot does capture the overall picture of the relationships among liana types, among tree species, and between liana type and tree species.

The biplot also shows that some species, such as *Agathis robusta* and *Archontophoenix cunninghamii*, had similar principal component scores (for the first two modes of variation). Further, the location of the species relative to the liana type symbols indicates the tendency of a liana type to be present or absent from a tree species. *Agathis robusta* and *Archontophoenix cunninghamii* clearly had little association with any liana type. *Piper novae-hollandiae*, the sole root-climber, tended to occur on *Podocarpus elatus*, *Euroschinus falcata* and *Syzygium luehmannii* much more than on species in the lower quadrants of the biplot such as *Beilschmiedia elliptica* and *Cryptocarya glaucescens*.

Pearson's chi-squared test of liana presence/absence vs. fruit type, roughness

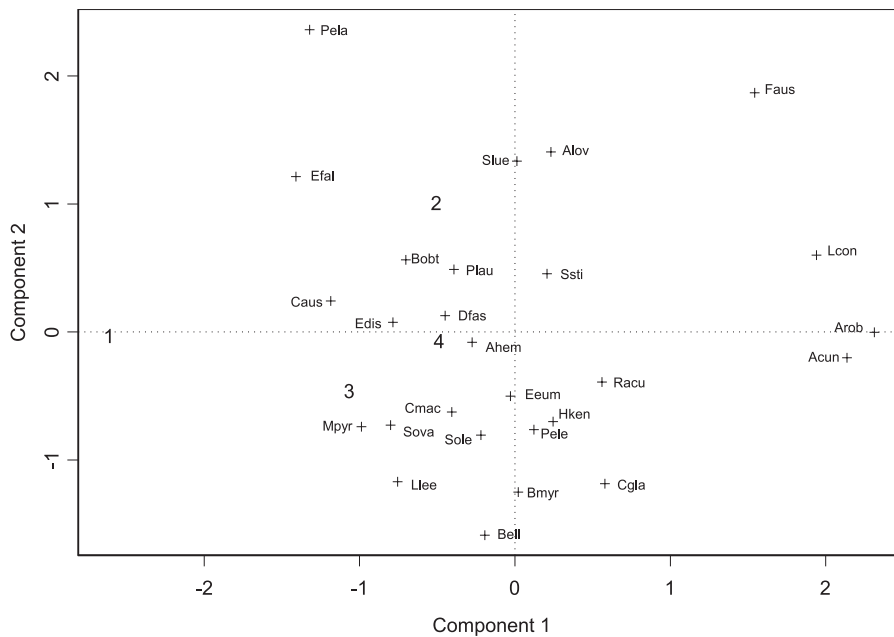


Figure 1. Principal components analysis biplot of vine types and tree species. The numbers refer to the four major types of vines: tendrillar climbers (1), root climbers (2), stem twiners (3) and scrambling climbers (4). The tree species are identified by the first letter of the genus followed by the first three letters of the species name (Table 2). The first component explained 77.5% of the variability and the second component explained 11.5% of the variability. Coordinates for tree species are principal component scores rescaled to have unit variance. Coordinates for vine types have been scaled so that the euclidean distances from the origin represent standard deviations.

and flakiness yielded distinct results for individual liana types (Table 4). For all liana types, there was a positive association between fleshy-fruitedness and presence of lianas.

Tendrillar climbers, *P. novae-hollandiae*, and scrambling climbers were associated with roughness values in a distinct pattern. Significantly more lianas than expected were observed at roughness value 2 (medium roughness), while at roughness values 1 and 3, fewer lianas were observed than expected. Stem twiners increased with roughness in a linear fashion, with smooth species hosting fewer lianas than expected, and rougher species hosting more lianas than expected. Tendrillar climbers and root climbers were associated with flakiness in the same manner as they were associated with roughness. There was no evidence of an association between flakiness and stem twiners or scrambling climbers.

Table 4. Pearson's chi-square test of liana type presence/absence vs. fruit type, roughness, and flakiness of host tree species.

Test performed	χ^2 statistic	degrees of freedom	P
Tendrillar climbers vs. fruit type	41.6	1	<0.0001
Root climbers vs. fruit type	5.84	1	0.015
Stem twiners vs. fruit type	11.0	1	0.001
Scrambling climbers vs. fruit type	4.11	1	0.043
Tendrillar climbers vs. roughness	35.2	2	<0.0001
Root climbers vs. roughness	10.05	2	0.007
Stem twiners vs. roughness	9.21	2	0.01
Scrambling climbers vs. roughness	14.5	2	0.001
Tendrillar climbers vs. flakiness	23.7	2	<0.0001
Root climbers vs. flakiness	20.2	2	<0.0001
Stem twiners vs. flakiness	0.70	2	0.704
Scrambling climbers vs. flakiness	4.26	2	0.119

Tendrillar climbers

The results of the model-building exercise suggested:

- (1) The presence/absence of tendrillar climbers was related to tree dbh in a quadratic manner.
- (2) There were interactions between the roughness and flakiness categories.
- (3) There were interactions between dbh and the type of fruit produced by a tree species.
- (4) There was no evidence of an interaction between dbh and the bark roughness and flakiness categories.

Because there were no detectable interactions between the bark-characteristic variable and the other predictors in the model, the interpretation of the coefficients associated with the bark characteristics was fairly straightforward (Table 5). For example, we were an estimated $\exp(-1.667) = 0.189$ times as likely to see a tendrillar climber on a tree with roughness level 1 and

Table 5. Estimated coefficients in logistic regression model for tendrillar climbers, root climbers and stem twiners. The variable 'Bark' refers to the combined roughness/flakiness variable. SE = standard error.

Coefficients	Tendrillar climbers		Root climbers		Stem twiners	
	Value	SE	Value	SE	Value	SE
Intercept	-0.3	0.2	-2.1	0.3	-0.9	0.2
DBH (linear)	-3.1	3.2	11.8	3.5	0.006	0.004
DBH (quadratic)	-12.5	3.7	-10.8	4.0		
Fruit type (non-fleshy)	-0.9	0.3				
Bark (level 2)	-1.7	0.8	-6.2	6.1	-1.7	1.1
Bark (level 3)	0.4	0.2	0.2	0.4	0.6	0.2
Bark (level 4)	0.7	0.2	0.3	0.4	0.3	0.2
Bark (level 5)	0.4	0.2	-0.3	0.5	0.5	0.3
Bark (level 6)	0.6	0.2	-0.4	0.4	0.7	0.3
Dbh(linear) \times Fruit type	-19.2	8.2				
Dbh (quadratic) \times Fruit type	22.0	7.0				
FCODE(1)					0.5	0.6
FCODE \times DBH					-0.03	0.02

flakiness level 3 (bark level 2) as we were to see one on a tree with roughness and flakiness levels of 1 (the reference bark level). We can compare the odds for other combinations as follows: we were an estimated $\exp(0.691 - 0.375) = 1.37$ times more likely to see a tendrillar climber on a tree with roughness level 2 and flakiness level 2 (bark level 4) than on a tree with roughness level 2 and flakiness level 3 (bark level 5). Overall, lianas tend to occur most on trees with bark roughness level of 2 and flakiness level of 2. Smoother and/or flakier bark was associated with lower levels of liana occurrence. There were few lianas on trees with roughness levels of 1.

Graphically displaying the results of the logistic regression model clearly illustrated an interaction between dbh and fruit type. For fleshy-fruited trees, there appears to be an increasing probability of occurrence of a tendrillar climber as dbh increases to about 60 cm, followed by decreasing probability at larger dbh values (Figure 2). In contrast, the estimated probability of liana occurrence in non-fleshy-fruited trees was highest for trees smaller than 60 cm dbh (Figure 2). The width of the standard error bands at the higher dbh values indicates that the effect of dbh on liana occurrence may not be quadratic in non-fleshy-fruited trees. The standard error bands are much wider at larger

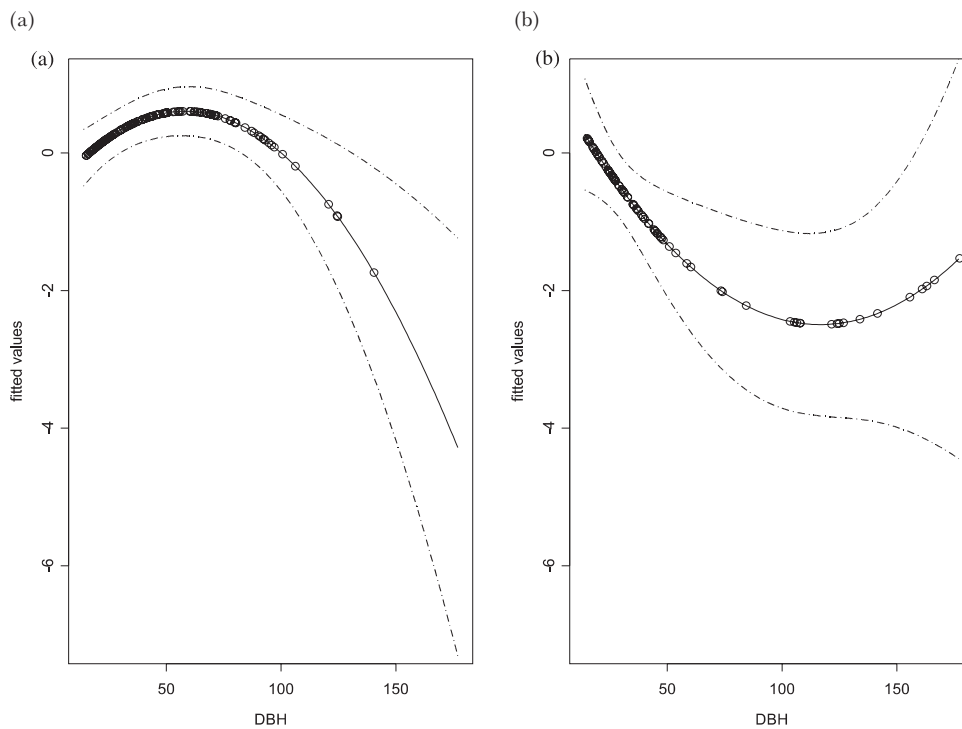


Figure 2. Fitted values of logits from a logistic regression analysis of tendrillar climbers versus diameter at breast height (dbh) of (a) fleshy-fruited trees and (b) non-fleshy-fruited trees. The solid lines represent the fitted regression functions. The dots are fitted values. The dashed lines represent $2 \times$ error bands. Results are from trees with roughness and flakiness values of 3. Results from other roughness/flakiness levels were similar to the displayed patterns and are therefore not shown.

dbh values, in part due to the small sample sizes associated with larger-diameter trees.

Root climbers

The overall findings were:

- (1) The presence of a quadratic effect due to dbh.
- (2) The presence of an interaction between roughness and flakiness.
- (3) The absence of an interaction between dbh and bark characteristics.
- (4) Fruit type was not an important predictor of liana presence.

The negative coefficients from the model-building exercise on bark levels 2, 5 and 6 indicate that root climbers tended to occur less often on trees with these bark characteristics relative to the reference level (Table 5). The coefficients associated with bark levels 3 (roughness level of 2 and flakiness level of 1) and 4 (roughness level of 2 and flakiness level of 3) indicate that root climbers tended to occur more often on trees with these bark characteristics. Therefore, *Piper novae-hollandiae* tended to be associated with medium levels of roughness and low to medium levels of flakiness.

The fitted values for linear and quadratic dbh illustrated an increasing probability of *Piper novae-hollandiae* occurrence as dbh increases to about 100 cm, with a decreasing probability at higher dbh values, a similar pattern to that of tendrillar climbers. This pattern was similar for fleshy and non-fleshy-fruited trees.

Stem twiners

The overall findings were:

- (1) The absence of a quadratic effect due to dbh.
- (2) The presence of an interaction between roughness and flakiness.
- (3) The presence of an interaction between dbh and fruit type.
- (4) The absence of an interaction between dbh and bark characteristics.

Lianas tended to be rare on smoother, less flaky bark (bark level 1) or smooth, very flaky bark (bark level 3). Lianas tended to prefer bark levels 3 (roughness level 2 and flakiness level 3) and 6 (roughness level 3 and flakiness level 3). The preference for level 6 was quite different from the other two categories of lianas (Table 5).

Lianas tended to decrease with increasing dbh (Figure 3). This tendency was greater for fleshy-fruited trees than for non-fleshy-fruited trees (Figure 3), hence the significant interaction.

DISCUSSION

Our results showed that there are a number of clear and consistent associations between liana species and potential host species. Several tree species almost

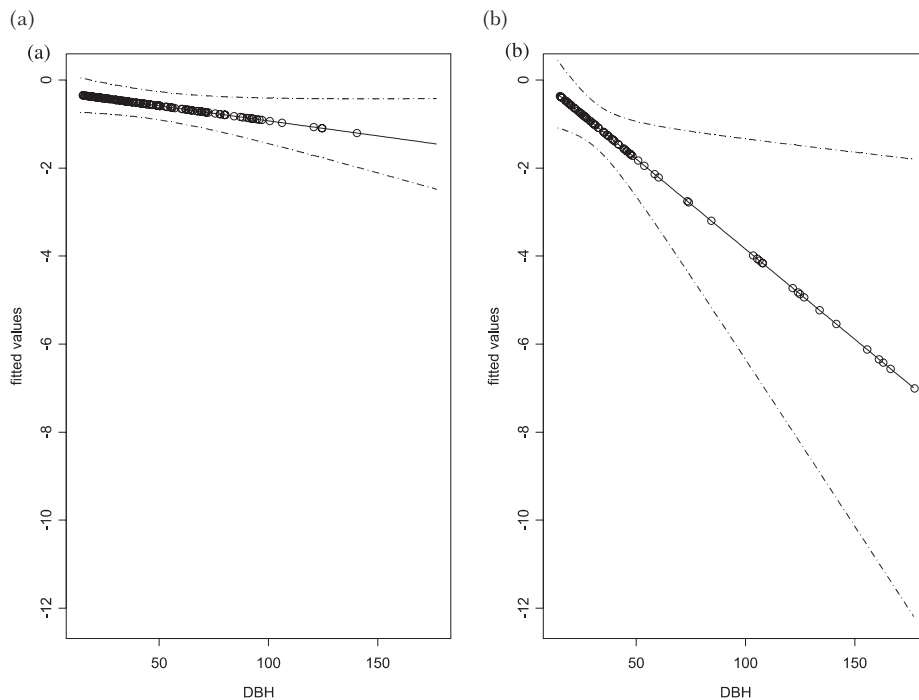


Figure 3. Fitted values of logits from a logistic regression analysis of stem twiners versus diameter at breast height (dbh) of (a) fleshy-fruited trees and (b) non-fleshy-fruited trees. The solid lines represent the fitted regression functions. The dots are fitted values. The dashed lines represent $2 \times$ error bands. Results are from trees with roughness and flakiness values of 3. Results from other roughness/flakiness levels were similar to the displayed patterns and thus are not shown.

never hosted lianas, such as *Agathis robusta*, *Lophostemon confertus* and *Archontophoenix cunninghamii*. Conversely, some trees hosted lianas with great frequency, in particular, *Podocarpus elatus*, *Euroschinus falcata* and *Canarium australasicum*. In addition, the biplots indicated that strong relationships exist between individual liana species and tree species. We found evidence that tree diameter, bark roughness and flakiness, host fruit type, and liana climbing type all contributed to this pattern.

Diagnostic procedures included checks of residuals for patterns and checks for overdispersion (analogous to non-constant variance in multiple linear regression). In a data set of this size some observations did have more influence on the fitted models than others but none stood out as being clearly aberrant.

Based on the results of the logistic regression, dbh and fruit type appear to be strong factors in determining presence/absence of various liana types on tree species. Tendrillar climbers had the highest probability of being found on mid-sized, fleshy-fruited trees. For trees that had non-fleshy fruit, these lianas were found most often on small trees, with the probability dropping rapidly as size increased. Smaller trees offer lower, smaller branches that tendrils may easily encircle, possibly explaining the high numbers of tendrillar climbers found on both fleshy- and non-fleshy-fruited trees at this stage. The dichotomy

arises with mid-sized trees, where fruit type becomes an important correlate with liana frequency. However, caution is necessary in interpreting these results. Although there was a lack of an interaction between dbh and bark characteristics, additional data at larger diameters could potentially lead to a finding of such an interaction.

Root climbers had a similar pattern to tendrillar climbers with regards to dbh. This was a surprising result, as root climbers, with their adventitious roots, can climb directly up a tree trunk regardless of size. Because dbh did not appear to have interactions with other factors, this pattern may have been due to an unexplored variable. The role of fruit type remains unclear for root climbers because of the conflicting results between the univariate and logistic regression analyses, a result which also suggests the possibility of effects due to another variable or due to undetected interactions.

Stem twiners appeared to associate with hosts differently than all other liana types. They matched our hypothesis that larger trees would host fewer liana species because of the constraints on substrate size for these lianas; however, this relationship was linear rather than quadratic, and was stronger for trees bearing fleshy fruits than for those bearing non-fleshy fruits. Only two of the four stem twiners have bird-dispersed, fleshy fruit. Therefore, the importance of fruit type in this model was most likely reliant upon these two lianas (*Melodinus australis* and *Morinda jasminoides*).

We hypothesized that tree bark roughness and flakiness (bark characteristics) would influence the presence or absence of liana species on their host because trees with rougher bark would provide a more conducive surface for lianas to climb, and because trees with flaky bark would be much more adept at shedding lianas. Our survey of lianas in individual tree crowns likely counted both lianas that had originally climbed trees and lianas that entered tree crowns from neighbouring trees, as there is no way to determine the origin of a liana after the fact. However, even with this noise in the data, we found strong associations between bark characteristics and liana presence. Roughness and flakiness values seemed to interact strongly with the highest number of lianas occurring at intermediate combinations of roughness and flakiness. Therefore, both factors seemed to have a strong influence on liana frequency, especially for tendrillar climbers and root climbers. For stem twiners, roughness seemed to be more important than flakiness, although neither component was a major factor in determining liana presence.

This study has documented several variables that contribute to establishing the ecological niche of lianas in south Queensland rain forests. Although this study has established the presence of associative patterns between liana distribution and dbh, roughness/flakiness, and fruit type, the modelling exercises suggest some patterns that are not fully explained by these variables. One such variable not explored in this study that may contribute to liana frequency is the sequence of colonization. Early colonizers may facilitate a path for later

colonizers by providing a more accessible substrate on which to climb (Pinard & Putz 1992). Long-term observational studies on colonization patterns may help identify new variables responsible for these patterns.

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