

LIANE DISTRIBUTION WITHIN NATIVE FOREST REMNANTS IN TWO REGIONS OF THE SOUTH ISLAND, NEW ZEALAND

Summary: To determine the susceptibility of different forest types to lianes, and to investigate which ecological factors are limiting for lianes, a field survey covering 28 naturally forested sites in Golden Bay (Northwest Nelson) and on Banks Peninsula (Canterbury) was carried out. Results from Detrended Canonical Correspondence Analysis of liane species abundance data in relation to tree and shrub species abundance data and abiotic site variables, showed that the liane community composition was highly correlated with the composition of the tree and shrub community. Forest remnants with introduced lianes in the canopy were characterised by high soil pH, low altitude and high mean temperatures. Native lianes were more widespread geographically and showed a wider ecological tolerance range than introduced lianes. Native liane species were found in both early successional and mature forest, whereas introduced lianes occurred more often with early-successional vegetation. Forest canopy height was also an important factor affecting liane distribution and abundance. Both climbing mechanism and liane stem longevity seemed to affect the height of canopy accessible to lianes. The three twining lianes with longer-lived woody stems (*Muehlenbeckia australis*, *Parsonsia* spp. and *Ripogonum scandens*) reached higher host canopies than a twiner with herbaceous stems (*Calystegia tuguriorum*), a tendril climber (*Passiflora mollissima*), and a hook climber (*Rubus cissoides*). The susceptibility of individual tree and shrub species to canopy invasion by lianes was affected both by the light environment of the potential host, and the architectural properties (height and support availability) of the host.

Keywords: disturbance; introduced lianes; light; native forest remnants; native lianes; soil pH; support availability; liane distribution.

Introduction

Lianes are climbing woody plants which rely on other plants for physical support; several species are considered serious adventive weeds of native forest in New Zealand (Webb *et al.* 1988; Timmins and Williams, 1991; Baars and Kelly, 1996). In this paper we examine physical and biological factors which affect liane distribution. Although lianes occur in most plant communities world-wide, they are most common in highly heterogeneous light habitats (Castellanos, 1991), thriving where there are areas of abundant light. Such conditions are characteristic of disturbed habitats (Putz, 1984a; Hegarty and Caballé, 1991). Large-scale disturbances often lead to rapid invasion by lianes; for example LaRosa (1983) found that clear-felling in Hawaiian forests caused rapid development of dense *Passiflora mollissima* infestations. Rainfall, altitude, soil pH and nutrient levels are all important factors determining liane distribution in tropical regions (Hegarty and Caballé, 1991; Putz and Chai, 1987). In southern mixed hardwood forest in the USA, lianes were associated with sites that had high levels of phosphorus, potassium, and exchangeable bases, and high pH values (Collins and Wein, 1993).

Availability of suitably-sized support is a major factor limiting liane access to the canopy because lianes are not self-supporting (Putz and Holbrook, 1991). In the Knysna Forest, South Africa, aspects of forest architecture which affect support availability, rather than abiotic factors such as light levels and soil nutrients, were the primary determinants of liane distribution (Balfour and Bond, 1993). Climber abundance was negatively associated with canopy height. In high canopies there were fewer low supports available; support availability is greatest where there is regeneration of young vegetation following disturbance in a forest. As the tree canopy becomes taller and more continuous, lianes must climb higher to reach the light. Some climbing mechanisms (such as twining) seem to be more effective at reaching high canopies than others (e.g. tendril climbing; see Discussion).

Lianes are generally not distributed at random on their potential host trees (Campbell and Newberry, 1993), suggesting that trees are not equally likely to host lianes (Putz, 1984b; Hegarty, 1991). The susceptibility of individual trees to invasion by lianes is determined by the habitat of the host and by host architecture. Early-successional trees of disturbed habitats in the tropics often have

flexible branches and fast growth rates, with large compound leaves or leaf-like branches; these characteristics help them to remain free of lianes by denying them a reliable attachment (Putz, 1984a). Bark characteristics and stem diameter of host plants can also limit ascent (Collins and Wein, 1993). Flaking bark (e.g. in kauri, *Agathis australis*: Ecroyd, 1982, p 30) offers some protection against bole lianes which use adventitious roots. The skirt of dead fronds around New Zealand treefern trunks may similarly protect against lianes and epiphytes by denying them support and establishment sites (Page and Brownsey, 1986).

Little is known about the associations between lianes, particular forest types or host species, and abiotic variables in New Zealand. Therefore the aims of this study were:

- 1) To investigate the effects of abiotic site characteristics such as disturbance, soil pH, slope, aspect, and light availability on liane distribution within South Island forest remnants in Golden Bay (Northwest Nelson) and Banks Peninsula (Canterbury).
- 2) To determine whether native and introduced liane species show different distributions in relation to the above site characteristics.
- 3) To determine whether the climbing mechanism used by a liane affects its height and spread within the forest canopy.
- 4) To find out whether particular tree species differ in their susceptibility as potential liane hosts.

Materials and methods

Sites

A field survey was carried out to determine liane distribution in 28 naturally forested sites in two regions of the South Island; Golden Bay and Banks Peninsula. Two regions were used to give a wider range of climate and soil conditions than could be surveyed in any single region. Eighteen sites were used in Golden Bay and 10 on Banks Peninsula (Fig. 1). At each site, four randomly located 10 m x 10 m plots were measured. Within each plot, a range of abiotic and biotic variables were measured, as detailed below. In large forest remnants, plots were randomly located in both edge and interior habitats, but many of the smaller remnants had little definite interior habitat. For the analysis all plots were analysed together, to determine how vegetation composition varied across both regions.

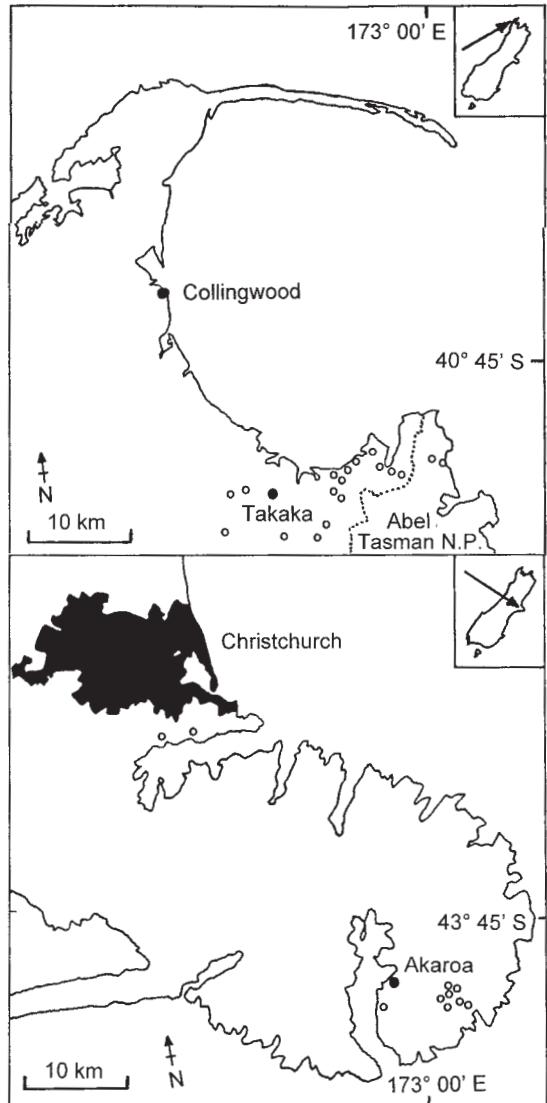


Figure 1: Distribution of study sites (each site = four survey plots) within (a) Golden Bay and (b) Banks Peninsula. The inset map shows the location of each main map on the South Island. Abel Tasman N.P. = Abel Tasman National Park.

Three broad forest types were recognised; early-mid successional broadleaf forest, mature podocarp-broadleaf forest, and beech (*Nothofagus* spp.) forest. About two-thirds of the plots were in early- to mid-successional forest remnants ranging in size from 1 - 20 ha. The remaining one-third of the

plots were evenly distributed between beech and podocarp-broadleaf forest ranging in size from 1 ha remnants to large tracts of native forest. All three vegetation types were found in both Golden Bay and Banks Peninsula, although there were regional differences in the overall species composition of the remnants surveyed. There were also regional differences in geology and climate. Most Golden Bay soils are derived from limestone bedrock or from alluvial silt, although some sites close to Abel Tasman National Park had soils derived from granite. Soils on Banks Peninsula are derived from igneous bedrock and loess (Wilson, 1992). Annual rainfall in Golden Bay ranges between 1600-2400 mm per annum on the eastern side of the bay, and reaches 3200 mm per annum towards the mountain ranges in the west (Wards, 1976). Annual rainfall on Banks Peninsula ranges between 600-800 mm per annum near Christchurch and between 700-2000 mm per annum around Akaroa, with high altitude areas receiving the highest rainfall (Wilson, 1992).

Abiotic variables

The slope of each plot was calculated using a clinometer, and the aspect determined with a compass. For analysis the aspect was converted into $\sin(\text{aspect})$, i.e. east/west, and $\cos(\text{aspect})$, or north/south, components. Drainage was estimated on a 7 point scale from 1 (swamp) through 2 (level) to 7 (ridge). Evidence of recent local habitat disturbance was scored, if present, as minor (walking track, snowbreak; score = 1), moderate (treefall, river; score = 2) or major (forest edge, road; score = 3) weighted by nearness (0 = absent to 3 = very close) giving a "disturbance" score from 0 to 9. Soil pH was recorded from 3 cm \times 3 cm \times 3 cm samples of topsoil (starting just below the loose litter layer) collected from the centre of each plot. Since the samples could not be immediately tested, they were sieved and put to dry in sunlight on the same day to reduce biological activity which could alter soil pH. Oven drying was rejected because of the potential effect of heat on organic matter and hence pH. Once the samples were air-dry, they were sealed in air-tight plastic bags which were kept in a cool dark place until the pH could be measured from a suspension of 10 ml dried soil in 50 ml distilled water. This was agitated gently for 10 minutes before the pH was measured using an electric probe standardised against a buffer of pH 6.

Light availability beneath the forest canopy was measured using ammonium diazo paper light sensors (Friend, 1961; Young and Whitehead, 1981; Turton,

1985). These booklets of light-sensitive paper in plastic petri dishes bleach in proportion to total accumulated light received. The sensors were exposed for a period of one week, after which they were retrieved and developed over a concentrated ammonia solution, to determine the number of pages bleached by exposure to light. Five diazo sensors were used per plot; four were arranged within each plot at the corners of a 5 m \times 5 m square, and the fifth was placed in the open as close to the other four as possible. The diazo sensors were attached to 20 cm stakes using Blu-tack. A small number of diazo sensors were destroyed by possums (*Trichosurus vulpecula* Kerr). The sensors were calibrated by exposing some in the open for different time intervals up to one week next to a Li-Cor quantum light sensor attached to a Li-Cor Li1000 data logger. The number of papers bleached was regressed against the cumulative irradiance recorded by the datalogger. These values from the regression were then used to determine the average irradiance for each site relative to full sunlight, as measured by the sensor in the open nearby (% RI).

Plot altitude, latitude and distance inland from the coastline were estimated from 1:50,000 topo maps; plot mean annual temperature was then calculated from these data using the equations in Norton (1985). Rainfall varies much more than temperature over short distances, so we did not attempt to estimate rainfall from isohyets.

Biotic variables

To determine the composition of the tree and shrub communities, all individuals greater than 50 cm in height were counted for all tree and shrub species present in the 10 \times 10 m plot. Plant nomenclature follows Allan (1961), Moore and Edgar (1976), Connor and Edgar (1987), and Webb *et al.* (1988). To determine the liane community composition, all individuals greater than 50 cm tall were counted. However, in many liane species, a proportion of the stems is produced by clonal extension of larger individuals (genets). In these species field determination of genet identity is impossible without extensive excavation (Hegarty and Caballé, 1991). Therefore, independently climbing stems that were firmly rooted at the base were recorded as separate individuals (following Putz, 1983; Hegarty and Caballé, 1991; and Balfour and Bond, 1993). Lianes were identified to species except for *Parsonsia capsularis* and *Parsonsia heterophylla* which were combined due to difficulties in discriminating seedlings of these two species.

Liane-host relationships

To investigate the relationship between lianes and their hosts, the following measurements were made wherever a tree or shrub within a plot supported a liane: the tree species and its height; the liane species, the height it achieved within that particular host, and the amount of host canopy it covered. Canopy coverage was estimated within 10% canopy coverage classes (1 = 1-10% of the canopy and 10 = 91-100%). Where a liane did not reach the host canopy, only the height achieved by the liane was recorded.

Analysis

Detrended correspondence analysis (DCA) as implemented in CANOCO (Version 2.1; Ter Braak, 1988) was used to ordinate abundance data for tree and shrub species (excluding lianes) in order to summarise the floristic composition of the 112 plots surveyed. The scores of the first four axes from this ordination (Trees1 - Trees4) were then added to the

abiotic data to form the set of canonical variables used to ordinate liane species abundance data using detrended canonical correspondence analysis (DCCA). Data from 104 plots were used for the DCCA, because light readings were not obtained from 8 plots.

Relative height and cover data for the six most commonly occurring liane species were analysed as generalised additive models (GAM) (Hastie and Tibshirani, 1990) using S-Plus (Statistical Sciences Inc., 1993). Both relative height and cover models were fitted against two predictors: host species as a factor and \log_e (height of the host) as a variable. Relative height data were fitted using a normal error distribution with an identity-link function. Cover data were fitted using a Poisson error distribution with a log-link function. Cubic splines (df approx. = 4) were used as smoothing functions for non-linear data, but were removed from the model where the responses were found to be not significantly different from linear.

The susceptibility of the 20 most common trees to infestation by lianes was calculated by testing whether these trees were more likely to act as hosts

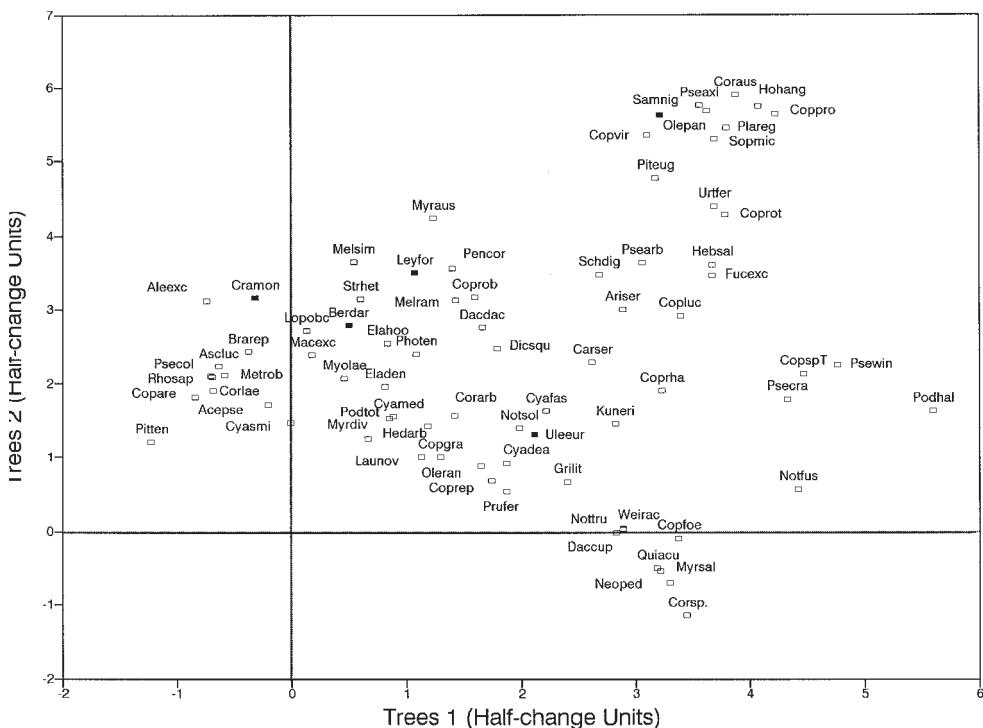


Figure 2: Tree and shrub species positions on the first two DCA ordination axes on data from 112 plots. One half change unit indicates a 50% change in the floristic composition of a site. Filled symbols indicate introduced species. Species codes consist of the first three letters of the genus name plus the first three letters of the species name; a full listing is given in Appendix 1.

for lianes than would be expected at random. All liane species were grouped together for this analysis, since the main interest was in the overall susceptibility of the 20 tree species to infestation by lianes. A χ^2 test was performed on the tree species by liane presence/absence contingency table to determine whether the distribution of lianes was independent of host species. Pearson residuals were used to determine the susceptibility of particular tree or shrub species to infestation by lianes. Pearson residuals ($N_{\text{obs}} - N_{\text{exp}} / \sqrt{N_{\text{exp}}}$) give the degree to which the observed value in a particular cell deviates from that expected by a random process. Although there is no exact statistical test for a Pearson residual, its significance can be tested approximately against the square root of χ^2 with one degree of freedom. Pearson residuals were ranked in order of decreasing susceptibility to lianes, with high positive values indicating high susceptibility and high negative values indicating low susceptibility.

Results

Detrended Correspondence Analysis of tree and shrub abundance

The two largest gradients identified by DCA analysis of site tree and shrub composition and abundance (here called Trees1 and Trees2) explained 8.3% and 6.5% respectively of the variance in the self-supporting vegetation over all 112 sites. The distribution of tree and shrub species along the two axes suggests the presence of both a temperature and a disturbance gradient within the vegetation (Fig. 2). Trees1 separated warmer-site (northerly or lowland) species such as *Rhopalostylis sapida*, *Alectryon excelsus* and *Ascarina lucida* (on the left), from cooler-site species such as *Nothofagus* spp., *Podocarpus hallii* and *Quintinia acutifolia* on the right. Temperature was the environmental variable with the strongest correlation with Trees1 (Fig. 3). Four of the five naturalised tree and shrub species can be found on the top-left of the ordination plot, along with a number of native early successional broad-leaved species such as *Meliccytus ramiflorus*, *Myrsine australis* and *Pittosporum eugenioides*. This suggests a successional and/or fertility gradient diagonally from upper left to lower right. The strongest environmental correlations with this upper left - lower right gradient were soil pH, which was highest at upper left, and sine(aspect), with easterly aspects at upper left (Fig. 3). The presence of infertility-tolerant *Nothofagus* spp at lower right reinforces this conclusion.

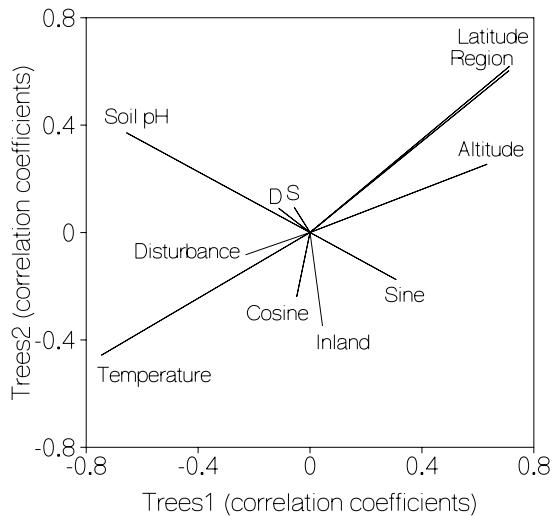


Figure 3: Correlation coefficients between environmental variables and the DCA ordination axes from tree and shrub data from 112 plots. The two non-significant variables are indicated only by letters for slope (S) and drainage (D); all other variables were significantly correlated with one or both axes.

Detrended Canonical Correspondence Analysis of liane abundance

Seventeen liane species, including five introduced species, were found in the plots. The most common were *Parsonsia* spp., *Muehlenbeckia australis*, *Ripogonum scandens*, and *Calystegia tuguriorum* (Table 1). *Rubus cissoides* was common on Banks Peninsula, and *Passiflora mollissima* (introduced) in Golden Bay.

Axis 1 and Axis 2 from the DCCA ordination of liane species abundance over 104 sites (Fig. 4a) explained 10.0% and 6.3% respectively of the variance in the liane species data. The environmental and floristic data used as canonical variables explained 28.6% and 21.6% of the variance in the species-environmental relationships along the same two axes. The plot of the canonical environmental variables reveals that Soil pH and Trees2 had the highest correlations with Axis 1 from the DCCA ordination of liane species abundance data, while Temperature, Altitude, Latitude/Region and Trees1 had the highest correlations with Axis 2 (Fig. 4b). Trees1 and Trees2 were rotated 120° and reversed relative to the liane DCCA axes and were highly correlated with both axes. Some of the environmental variables were intercorrelated; in particular Region and Latitude, and less strongly Altitude and Temperature were correlated with each

Table 1: *Liane distribution, and inferred site tolerances based on ordination positions, for all species found in the survey (excluding Rubus fruticosus, found in only one Golden Bay site), grouped by most common successional stage of forest. Parsonsia spp. = P. heterophylla and/or P. capsularis. Introduced vines are marked *.*

Species	% of vines found in Golden Bay	% of vines found on Banks Peninsula	Climbing mechanism	Successional stage of forest	Soil fertility (pH)	Light availability
<i>Clematis vitalba</i> *	2.18	0	Petioles	Early	High	Moderate
<i>Lonicera japonica</i> *	1.19	0	Twining	Early	High	Moderate
<i>Passiflora mollissima</i> *	13.86	0	Tendrils	Early	High	Moderate
<i>Senecio mikanioides</i> *	1.39	0	Scrambling	Early	High	Moderate
<i>Passiflora tetrandra</i>	3.76	0.86	Tendrils	Early	High	Moderate
<i>Calystegia tururiorum</i>	8.71	11.08	Twining	Early-mid	Medium	High
<i>Parsonsia</i> spp.	19.80	26.99	Twining	Early-mid	Medium	Moderate (-low)
<i>Clematis foetidissima</i>	3.56	4.83	Petioles	Mid	Medium	High
<i>Muehlenbeckia australis</i>	17.43	20.17	Twining	Mid	Medium	Moderate
<i>Ripogonum scandens</i>	11.88	9.66	Twining	Mid	Medium	Low
<i>Rubus schmidelioides</i>	0	1.42	Hooks	Mid	Medium	High
<i>Rubus cissoides</i>	1.00	20.45	Hooks	Late	Low	High
<i>Clematis paniculata</i>	2.57	4.26	Petioles	Late	Low	High
<i>Metrosideros diffusa</i>	8.90	0.28	Adventitious roots	Late	Low	Low
<i>Metrosideros perforata</i>	1.00	0	Adventitious roots	Late	Medium	Low
<i>Rubus australis</i>	2.77	0	Hooks	Late	Low	Low

other (negatively in the case of Temperature). Soil pH showed some negative correlation with Region; most soils in eastern Golden Bay are derived from limestone and have a higher pH. The average soil pH over all Golden Bay sites was 6.42 ± 0.96 (mean \pm 1 SD), compared to an average soil pH of 5.95 ± 0.85 over all sites on Banks Peninsula. This difference is however too small to account entirely for the high correlation that soil pH had with the liane DCCA axes (Fig. 4b).

Liane distribution

The five introduced liane species *Clematis vitalba*, *Lonicera japonica*, *Passiflora mollissima*, *Rubus fruticosus* and *Senecio mikanioides* formed a distinct cluster at the bottom-right of the DCCA ordination along with the native species *Passiflora tetrandra* (Fig. 4a). All five exotic species were recorded only in Golden Bay; *Clematis vitalba* and *Passiflora mollissima* are present on Banks Peninsula, but did not occur in the study sites from that region. Relating these vegetational gradients to the ordination diagram of environmental correlates (Fig. 4b) shows that sites with introduced lianes in the canopy were generally characterised by high soil pH, warmer and lower altitude sites, nearness to coast, low sine(aspect) i.e. westerly aspects, and

combined Trees1 and Trees2 scores indicating (after allowing for axis rotation) predominantly early-successional vegetation.

The other native liane species can be divided loosely into two groups, one (including *Rubus schmidelioides*, *Calystegia tururiorum* and *Muehlenbeckia australis*) on the upper right of Fig. 4a also associated with disturbed or regenerating forest species (mapping to the upper centre of the DCA plot, Fig 2), and the other towards the lower left (including *Metrosideros* spp, *Rubus australis* and *Ripogonum scandens*) associated with late successional or mature forest. Unexpectedly, *Parsonsia* spp., which are very shade-tolerant (Baars and Kelly, 1996), were grouped nearer the disturbed-site species. However, the optimum position of *Parsonsia* is not well resolved because seedlings were present in most plots, which will tend to place the species in the centre of the ordination plot. If the sampling had been restricted to only mature *Parsonsia*, a different result may have been found. A number of native species were common to both Golden Bay and Banks Peninsula, causing some overlap in the DCCA ordination of sites (Fig. 4c). The *Metrosideros* species were a characteristic floristic feature of many Golden Bay sites, especially undisturbed forest, although *Metrosideros diffusa* can also be found on Banks Peninsula (Wilson, 1992). *Rubus cissoides* and

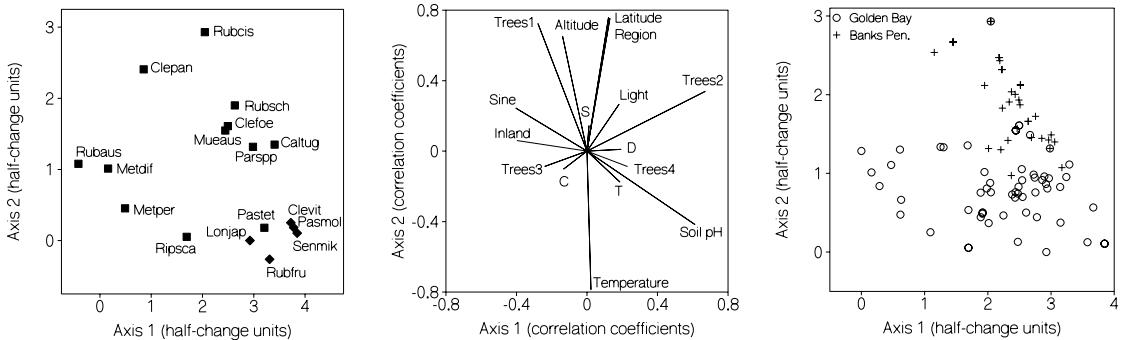


Figure 4: Ordination diagrams from the DCCA of liane species abundance data on 104 plots. (a) Species positions on the first two axes. Introduced species are shown as diamonds. Species codes: (*Caltug*) *Calystegia tuguriorum*; (*Clefoe*) *Clematis foetidissima*; (*Clepan*) *C. paniculata*; (*Clevit*) *C. vitalba*; (*Lonjap*) *Lonicera japonica*; (*Metdif*) *Metrosideros diffusa*; (*Metper*) *M. perforata*; (*Mueaus*) *Muehlenbeckia australis*; (*Parspp*) *Parsonia heterophylla* and/or *P. capsularis*; (*Pasmol*) *Passiflora mollissima*; (*Pastet*) *P. tetrandra*; (*Ripsca*) *Ripogonum scandens*; (*Rubaus*) *Rubus australis*; (*Rubcis*) *R. cissoides*; (*Rubfru*) *Rubus fruticosus*; (*Rubsch*) *R. schmidelioides*; (*Sennmik*) *Senecio mikanioides*. (b) Correlation between the canonical variables used as input and the resultant first two ordination axes. Variables which were not significantly correlated with either Axis1 or Axis2 are indicated only by letters for slope (S), drainage (D), cosine aspect (C) and disturbance (T). All other variables were significantly correlated with one or both axes. (c) Plot positions on the first two axes.

Table 2: Significance levels for GAM fitted relationships between liane height and cover, and host height, for six liane species. Models with numerator degrees of freedom (df) = 1 were not significantly different from linear. The remaining models have had smoothing functions fitted and their df are rounded to the nearest whole number.

(a) relative height of liane on host versus absolute height of host

Liane species	Host species			Log _e (Hostheight)		
	df	χ ²	P (χ ²)	df	χ ²	P (χ ²)
<i>Calystegia tuguriorum</i>	13	1.222	ns	1	0.468	ns
<i>Muehlenbeckia australis</i>	15	1.951	P<0.05	4	2.954	P<0.05
<i>Parsonia</i> spp.	14	3.713	P<0.001	4	2.371	ns
<i>Passiflora mollissima</i>	6	1.750	ns	1	4.666	P<0.05
<i>Ripogonum scandens</i>	18	3.157	P<0.001	4	19.352	P<0.001
<i>Rubus cissoides</i>	9	4.469	P<0.001	4	3.278	P<0.05

(b) cover of liane on host versus absolute height of host

Liane species	Host species			Log _e (Hostheight)		
	df	χ ²	P (χ ²)	df	χ ²	P (χ ²)
<i>Calystegia tuguriorum</i>	13	39.29	P<0.01	4	15.27	P<0.01
<i>Muehlenbeckia australis</i>	15	37.04	P<0.01	4	26.70	P<0.001
<i>Parsonia</i> spp.	14	61.57	P<0.001	4	59.05	P<0.001
<i>Passiflora mollissima</i>	7	14.02	ns	4	23.08	P<0.001
<i>Ripogonum scandens</i>	18	114.76	P<0.001	4	66.03	P<0.001
<i>Rubus cissoides</i>	9	37.08	P<0.001	1	17.48	P<0.05

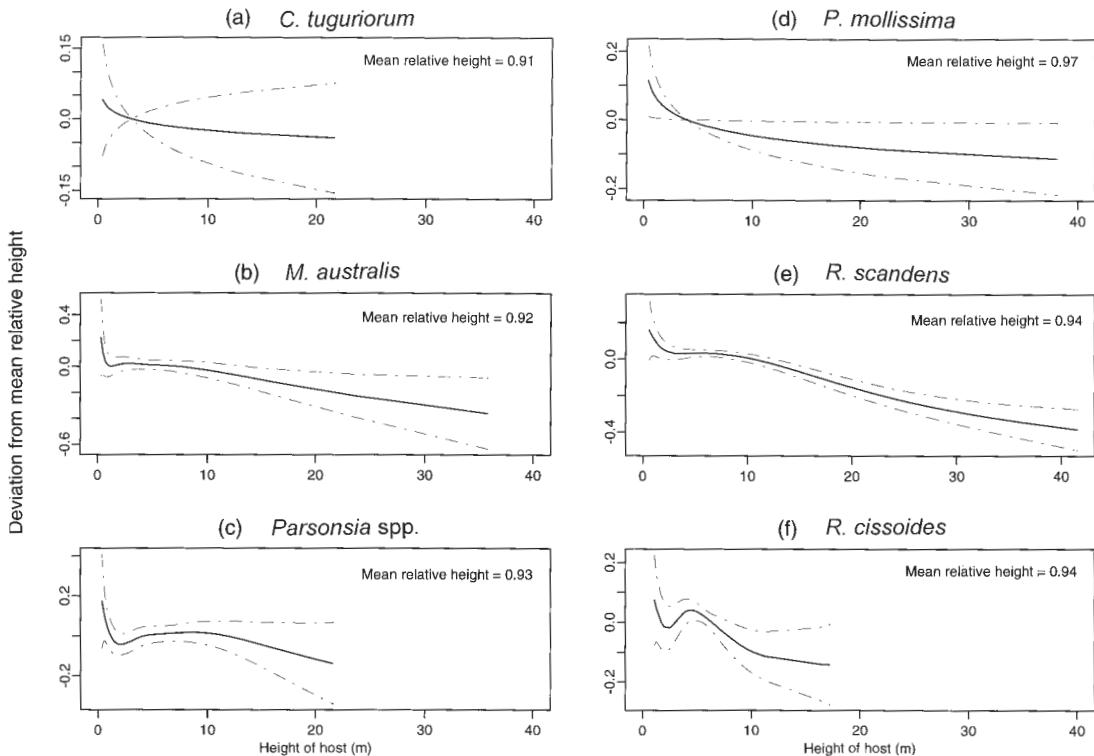


Figure 5: GAM fitted relationships between relative height of liane on host and absolute height of host for six liane species. The dot-dash lines are $2\times$ standard error curves. For significance tests see Table 2a. Note varying scales on the y - axis.

Rubus schmidelioides were a distinctive feature of Banks Peninsula sites.

The apparent site tolerances for each liane species, inferred from their positions on the ordination, are listed in Table 1 (excluding *Rubus fruticosus* which was found in only one plot). Rather than as definite conclusions, these are presented as hypotheses to test experimentally, especially since some variables in the observational data were collinearly confounded.

Liane-host interactions

Relative height of lianes on hosts

Host species identity was significant for the relative height achieved by *Muehlenbeckia australis*, *Parsonsia* spp., *Ripogonum scandens* and *Rubus cissoides*, but not for *Calystegia tuguriorum* or *Passiflora mollissima* (Table 2a), indicating that both *Calystegia tuguriorum* and *Passiflora mollissima* are less specific in their requirements in

terms of supporting species than the other four liane species. The ordination resulting from the liane species abundance DCCA suggested that these two species were more indicative of disturbed or regenerating forest (see previous section), which usually had low canopy heights, perhaps partly explaining their non-significant response to host identity. The relative height responses to different host heights showed some variation between the six liane species (Fig. 5). Where a liane was the same height as its host, it had a relative height value of 1. *Calystegia tuguriorum* and *Passiflora mollissima* showed responses which were linear (indicated by intersecting $2\times$ standard error curves). The height achieved by *Calystegia tuguriorum* and *Passiflora mollissima* relative to that of their host declined only slightly as host heights increased, while *Muehlenbeckia australis*, *Ripogonum scandens*, and *Rubus cissoides* were more strongly affected. *Muehlenbeckia australis* and *Ripogonum scandens* were progressively less likely to reach the canopy of their hosts where hosts were taller than 10 m; while

Rubus cissoides had an optimum host height of 4.5 m and was unlikely to reach canopies over about 7 m. *Parsonsia* spp. were relatively insensitive to host height up to at least 15 m.

Cover of lianes on hosts

All six liane species investigated covered a significantly lower proportion of their host canopy as host height increased (Table 2b), but the change was largest in *Calystegia tuguriorum*, *Passiflora mollissima* and *Rubus cissoides* (Fig. 6). *Muehlenbeckia australis*, *Parsonsia* spp. and *Ripogonum scandens* showed a much more consistent amount of host canopy coverage over all host heights, although there were few data for hosts taller than 15 m (Fig. 6). The identity of the host species was a significant factor contributing towards host canopy coverage for five species. The only liane for which host species identity was not significant was *Passiflora mollissima* (Table 2b).

Host susceptibility

A χ^2 association analysis between the 20 tree and shrub species most commonly encountered during sampling and the presence of lianes in their canopy gave an overall χ^2 value of 201.45 ($P < 0.001$, $df = 19$). This indicated that some species were more likely to act as hosts for lianes than would be expected by chance. Pearson residuals (Table 3) provided an indication of host susceptibility. By this analysis, *Laurelia novae-zelandiae*, *Fuchsia excorticata*, *Kunzea ericoides* and *Meliccytus ramiflorus* ae highly susceptible to infestation by lianes; all but *Laurelia novae-zelandiae* have low canopies and are common in regenerating forest. *Coprosma rotundifolia*, *Urtica ferox*, *Olearia rani* and *Coprosma grandifolia* are less likely to be liane hosts. Species which are less susceptible to infestation by lianes are commonly found beneath an established forest canopy as shrubs, or seedlings (e.g. *Hedycarya arborea*). Two

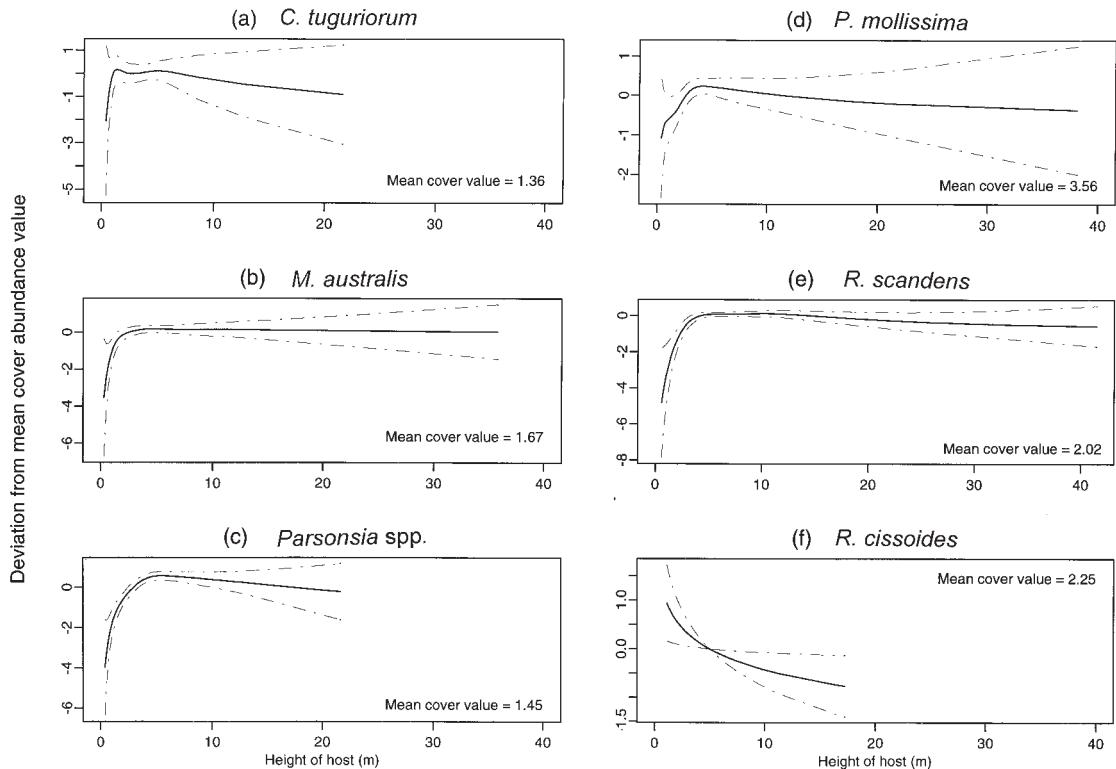


Figure 6: GAM fitted relationships between cover of liane on host and absolute height of host for six liane species. The dot-dash lines are 2x standard error curves. For significance tests see Table 2b. Note varying scales on the y-axis.

species with low susceptibility to infestation by lianes (*Rhopalostylis sapida* and *Brachyglottis repanda*) possess large leaves.

Table 3: Susceptibility of hosts to lianes ranked according to Pearson residuals. High positive values denote high susceptibility to liane infestation, large negative values denote low susceptibility.

Species	Pearson residual	$P(\sqrt{\chi^2})$
<i>Laurelia novae-zelandiae</i>	6.473	$P < 0.001$
<i>Fuchsia excorticata</i>	5.936	$P < 0.001$
<i>Kunzea ericoides</i>	3.965	$P < 0.001$
<i>Meliclytus ramiflorus</i>	3.104	$P < 0.01$
<i>Podocarpus totara</i>	2.989	$P < 0.01$
<i>Coprosma robusta</i>	0.673	ns
<i>Pennantia corymbosa</i>	0.638	ns
<i>Pseudopanax arboreus</i>	0.312	ns
<i>Ascarina lucida</i>	-0.176	ns
<i>Myrsine australis</i>	-1.315	ns
<i>Cyathea dealbata</i>	-1.511	ns
<i>Coprosma rhamnoides</i>	-2.112	$P < 0.05$
<i>Rhopalostylis sapida</i>	-2.256	$P < 0.05$
<i>Hedycarya arborea</i>	-2.275	$P < 0.05$
<i>Macropiper excelsum</i>	-2.288	$P < 0.05$
<i>Brachyglottis repanda</i>	-2.448	$P < 0.05$
<i>Coprosma rotundifolia</i>	-2.663	$P < 0.01$
<i>Urtica ferox</i>	-2.748	$P < 0.01$
<i>Olearia rani</i>	-2.996	$P < 0.01$
<i>Coprosma grandifolia</i>	-3.544	$P < 0.001$

Discussion

The distribution of lianes in relation to biotic and abiotic variables

The two axes from the DCA ordination of tree and shrub vegetation (Trees1 and Trees2) were significantly correlated with Axis 1 and Axis 2 from the DCCA ordination of liane species abundance data. Both the floristic composition of the tree and shrub vegetation, and the environmental variables which affect this composition, influence the abundance and distribution of lianes. The DCCA indicates that the most significant influences on liane distribution were the tree and shrub vegetation, latitude/region (Golden Bay or Banks Peninsula), altitude, temperature, and soil pH. Light, east/west aspect and distance inland had smaller but still-significant effects.

Differences between the two regions studied were probably mainly due to soil composition, climate, and historical factors. Climatic differences included mean temperatures, oceanicity (measured

as distance from coast), and rainfall (not measured). Temperature had a large correlation with Axis 2 of the DCCA, but was confounded with Region and Altitude, so the results must be interpreted with caution. The effect of a west-east aspect component (Aspect Sine) is most likely to be due to the effects of morning and afternoon sun. This would have different effects in summer and winter. In summer, west faces would experience maximum irradiation during the hottest part of the day. Where frost occurs in winter, east-facing slopes will receive the sun first and would therefore be expected to be most susceptible to photoinhibition damage (Ball, 1994).

Soil parent material and mean pHs also varied between regions. The widespread distribution of most native liane species indicates an ability to tolerate some variation in soil nutrient and pH levels, although some native lianes were more often found on more-acidic soils. The introduced liane *Clematis vitalba* is abundant on most alkaline soils in England, especially shallow soils over chalk and to a lesser extent limestone (Kennedy, 1980). However, *Clematis vitalba* grows in soils of a wider pH range in New Zealand than in Europe. West (1992) showed that soil samples taken from areas in New Zealand which were infested with *C. vitalba* came from a variety of different parent materials but most were of recent origin, with a high base saturation, indicating a high level of fertility. No information was found on the soil preferences of *Lonicera japonica* and *Passiflora mollissima* in New Zealand, although LaRosa (1984) found that *Passiflora mollissima* grew in a wide range of soil types on Hawaii. Results from the present study indicate that all five introduced liane species encountered during the field survey (*Clematis vitalba*, *Lonicera japonica*, *Passiflora mollissima*, *Rubus fruticosus* and *Senecio mikanioides*) were found mainly on soils with a high pH, indicative of higher fertility (Barbour *et al.*, 1987), but also were positively correlated in this study with early-successional vegetation. Disturbance, as well as allowing the establishment of early-successional plants, reduces root competition for nutrients and may increase relative base availability.

Increases in liane density following disturbance are well documented (Teramura *et al.*, 1991; and references therein). Robertson *et al.* (1994) found that colonisation by exotics (including *Lonicera japonica*) within forest remnants in Philadelphia, USA was limited primarily by low light intensity, and secondarily by the low incidence of landscape-scale physical disturbance. In Hawaii, disturbance of native or alien ground vegetation,

particularly by feral pigs, increases colonisation and establishment of *Passiflora mollissima* and subsequent growth of this liane increases proportionally to the increased light intensity found in most disturbed areas (LaRosa, 1992). Baars and Kelly (1996) showed that five native and introduced liane species varied from very shade-tolerant (native *Passiflora* spp.) to much less tolerant (*Passiflora mollissima*, *Muehlenbeckia australis*). However, in this study direct estimates of disturbance were not significantly correlated with liane species presence (Fig 3b). Light intensity in the plots was significantly correlated, but was still relatively unimportant. The same plot shows that inferred past disturbance (from Trees1 and Trees2 scores) was associated with higher soil pH and higher frequency of introduced vines. These contrasting results show the difficulty of measuring factors which are important to plant establishment, but transient. For example, light availability will increase after disturbance, but the increase may be relatively short-lived as early-successional species occupy space. Therefore, disturbances or high light intensities which may have been important in the establishment of these lianes, may no longer be obvious when surveying older specimens of long lived lianes. In such cases observational studies need to be backed up with experimental work (Baars and Kelly 1996).

The strong clustering of the introduced liane species on the DCCA ordination (Fig. 4a) indicates that the introduced liane species were most often associated with more fertile soils (higher-pH) and earlier seral vegetation in New Zealand. This agrees with earlier work that disturbance assists invasion by these exotic plants. Interestingly, *Passiflora tetrandra* was closely associated with the exotics, suggesting it also has a “weedy” growth strategy, while *Muehlenbeckia australis* (shown by Baars and Kelly 1996 to have similar light requirements and growth rates to the exotic liane species) was placed further away on the ordination diagram. However, the fact that Region has such a strong influence on the ordination diagram means this result must also be treated with caution. *M. australis* occurred widely in both regions, while the exotic lianes were recorded only in plots from Golden Bay (Table 1). It is not known to what extent this absence from Banks Peninsula plots reflects chance historical factors rather than the ultimate physiological limits of the exotic lianes.

Climbing mechanics and ascent into the canopy

The mechanism by which a liane climbs (e.g. twining, tendrils, adventitious roots, hooks, or

scrambling) partly determines which part of the vertical structure of a community a liane can reach (Putz and Holbrook, 1991). Twining around saplings or smaller diameter trees is an efficient method of ascent, but requires longer stems than climbing with clinging roots or adhesive tendrils, since there is always a lateral component to any increase in height (Putz and Holbrook, 1991); in low-light environments this may contribute to an energy balance problem for twiners. Carter and Teramura (1988) suggested that a low availability of small-diameter objects to provide support may restrict twining lianes to early and mid-successional areas characterised by smaller diameter shrubs and trees. However, twiners are capable of easily climbing thin bare stems up to 10cm diameter (Hegarty, 1989). Where suitably-sized supports are available, twining branches effectively resist slipping or breaking under the weight of the main stem. Tendrils, on the other hand, are often fragile. The majority attach by coiling around supports beside or below the extending liane shoot, and so are better for oblique rather than vertical ascent (Hegarty and Caballé, 1991). Such a method of climbing is ideal for traversing the sides and tops of trees and shrubs. The flexibility of tendrils decreases chances of the liane stem breaking as the supports sway in the wind (Hegarty, 1989). Putz and Holbrook (1991) suggest that tendril lianes are more suited to treefall gaps and forest edges where large numbers of small diameter supports more commonly occur. Results from research in West Africa, Australia and the Neotropics has revealed that the successional trend after forest disturbance is for tendril lianes to predominate in young regenerating stands, but for twiners and bole lianes to increase in relative abundance through time (Putz et al., 1989). Hooks allow vertical ascent, although the support they provide is limited by their number, strength, size and architecture. Scrambling lianes and hook lianes may be more common in early successional habitats owing to a need for dense vegetation (Putz and Holbrook, 1991), although Hegarty and Caballé (1991) found that lianes with hooks are found in both young and older, taller forests.

In this study, both the relative height achieved and the amount of host canopy covered by all six species investigated in detail decreased with increasing host height. Four of the six (*Calystegia tuguriorum*, *Muehlenbeckia australis*, *Parsonsia* spp. and *Ripogonum scandens*) were twiners; *Passiflora mollissima* climbs using tendrils and *Rubus cissoides* utilises hooks (Table 1). The woody twiners *Muehlenbeckia australis*, *Parsonsia* spp. and *Ripogonum scandens* reached taller canopies than the herbaceous twiner

Calystegia tuguriorum. *Passiflora mollissima* and *Rubus cissoides* also appear to be restricted to low forest canopies. For *Passiflora mollissima*, this trend probably reflects an early stage of invasion in New Zealand rather than a less effective climbing mechanism. Williams & Buxton (1995) have found that introduced *Passiflora* species in New Zealand tend to be most common on low scrub between stands of trees, whereas in Hawaii, *Passiflora mollissima* is capable of climbing at least 20 m into the canopy (LaRosa, 1984). Bird (1915) noted that *Rubus cissoides* tended to grow on low shrubs, mainly on forest edges. Some results from this study agree with this, with both relative height and cover data suggesting a maximum height of about 4.5 m, although there was little evidence of a strong association between *Rubus cissoides* and early-successional vegetation (Fig 3). Other species of *Rubus*, which also climb using hooks, may attain considerable heights. *Rubus australis* for instance, is capable of reaching heights in excess of 20 m (Bird, 1915).

Lianes are often dislodged from the forest canopy and many lianes also have relatively short-lived stems (Putz, 1990). Therefore, the increased stem-replacement costs faced by lianes as hosts grow taller may limit the height to which lianes may climb. Stem replacement may also become progressively more difficult if taller hosts have a more closed canopy casting deeper shade. Where liane stems are shorter-lived than the canopy trees this may lead to a progressive decrease in the relative abundance of lianes with stand age and stand height. In this study, *Parsonsia* spp. were relatively unaffected by host height (Fig. 5) which is consistent with their extreme shade tolerance (Baars and Kelly, 1996) allowing growth even in tall dense canopies. Both *Parsonsia* spp. and *Muehlenbeckia australis* form long-lived, thick cable-like stems up to 15 cm in diameter. *Muehlenbeckia australis* reached well into the canopy of hosts up to about 18 m but rarely occurred in hosts taller than this. By contrast, the herbaceous twiner *Calystegia tuguriorum* has shorter-lived, structurally weaker stems and it was rarely found on hosts taller than 9 m (Fig. 5). *Ripogonum scandens* probably has intermediate stem longevity, with woody stems reaching a maximum diameter of 2 cm, although the maximum age of individual stems is not known. MacMillan (1972) gives a maximum height of 18 m for *Ripogonum scandens* which is consistent with this study showing decreasing relative height over about 15 m (Fig. 5), but *Ripogonum* was still found in hosts up to 40 m tall. Therefore stem longevity and shade tolerance are associated with the height distributions of the lianes in this study.

Host susceptibility

Canopy height and openness

The results from this study tend to agree with the observation that low, shorter-lived canopies are more susceptible to invasion by lianes. Such canopies often have higher light, better support availability, and are not old enough to have had significant liane losses from the canopy. *Fuchsia excorticata*, *Kunzea ericoides* and *Meliccytus ramiflorus* are low trees which are common in regenerating scrub or forest, and were found to be highly susceptible to infestation by lianes. *Podocarpus totara* was susceptible because many of the trees encountered were relatively short. Less susceptible trees and shrubs were often taller, or in more deeply shaded positions, either as subcanopy species or as seedlings beneath the forest canopy. Understorey shrubs and seedlings should be less susceptible as hosts to lianes due to their light environment rather than their architecture. An exception to this is *Parsonsia* spp., which can be found growing in dense shade (Baars and Kelly, 1996), utilising understorey shrubs such as *Coprosma rotundifolia* and *Coprosma rhamnoides* as hosts, even though the Pearson residuals for these species indicated a low overall susceptibility to lianes (Table 3). Turning to height, most susceptible species were short, but *Laurelia novae-zelandiae* trees were taller (around 20 m), and this species was the most susceptible of all that were analysed. These trees were almost exclusively utilised as hosts by *Ripogonum scandens*, which can grow to considerable heights (see above), especially in established forest.

Defence mechanisms against lianes

Some of the native species that were found to be less susceptible as hosts have a relatively unbranched form and large leaves (e.g. *Brachyglottis repanda*) and may utilise these as a defence against lianes through regular leaf shedding, thus denying lianes a reliable point of attachment. Peñalosa (1982) found that the majority of supports encountered by lianes within rainforest, Veracruz, México, were leaf petioles. Where the majority of initial attachment points for lianes are leaf petioles, large and compound leaves would be an effective defence mechanism against lianes, provided these leaves were shed before a liane located further attachment points on the same host. Similarly, the architecture of palm leaves allow them to thrive in liane-infested areas within tropical forests. New palm leaves (sword leaves), which may be up to 20 m long in some tropical species, emerge from the terminal bud, grow vertically, and

then gradually spread out and lean over. These sword leaves often slice through liane tangles, rending holes in the leafy fabric, and then spread out in their newly open form-fitting gap. Lianes that succeed in reaching a palm tree's crown are generally shed along with the fronds (Putz, 1980). The native palm *Rhopalostylis sapida* had a low susceptibility to liane invasion of the canopy. Leaves of this palm may reach 3 m in length.

Only one treefern was included in Table 3: *Cyathea dealbata* showed a trend for low susceptibility to liane invasion in the sites that were sampled, but this was not statistically significant. *Cyathea dealbata* tends to shed its dead fronds, whereas most other New Zealand treefern species retain a persistent skirt of dead fronds or stipes, especially when young. It has been suggested that these skirts may act to keep treefern crowns free from invasion by lianes (Page and Brownsey, 1986) and that susceptibility to lianes may be an important factor limiting the distribution of *Cyathea dealbata* in habitats where lianes are common. Treeferns, like palms, can be killed by lianes smothering the single growing point, but this is not often seen. Our evidence suggests that *Cyathea dealbata* is not particularly susceptible to liane invasion, although the mechanism for this resistance is not clear, and we would predict that the other New Zealand species of treefern would be even less susceptible by virtue of their persistent skirts.

Conclusions

This study is largely observational, and cannot provide the certainty of good experimental data. However it does suggest likely patterns which can then be tested by experiments. From this broad survey, both site characteristics and the ecological characteristics possessed by the lianes themselves determine the distribution of lianes within forest remnants (Table 1). The geographical location, temperature, successional age of the forest, and soil pH, were important factors contributing towards overall liane abundance. The introduced liane species (*Clematis vitalba*, *Lonicera japonica*, *Passiflora mollissima*, *Rubus fruticosus* and *Senecio mikanioides*) were restricted in this dataset to warm, fertile forest sites in Golden Bay. Canopy height is a major factor limiting liane success, as indicated by relative height and cover data for six common liane species. Higher forest canopies are limiting for lianes due to the increased stem replacement costs for liane species without long-lived stems (Hegarty, 1991). In this study

species with longer-lived stems seemed to be capable of reaching higher canopies. Another possible factor was limited availability of suitably-sized supports. Peñalosa (1982) found that small-diameter supports were common in tropical rainforest, but it is not known whether this is also the case for forests in New Zealand. Overall, lianes which used adventitious roots to climb (see Table 1) were more characteristic of mid-successional to mature forest, while lianes which utilised tendrils, petioles or hooks were generally more characteristic of early successional forest (Table 1). The native liane species as a group showed a wider range of ecological preferences than the introduced lianes. The introduced liane species are dependent on human activity for long-distance dispersal (Williams and Buxton, 1995; West, 1992), and their limited distribution may be partly due to limited dispersal rather than environmental constraints. Where introduced lianes have become established in disturbed or regenerating forest, their often-faster growth rates (Baars and Kelly, 1996) will enable them to smother the canopy leading to a loss of structural integrity and species richness within native forest remnants.

Acknowledgements

We thank the numerous landowners who gave permission to work in reserves under their management; the Royal Forest and Bird Protection Society (Canterbury Branch) for the Stocker Scholarship, which partially funded this research; and two anonymous referees for helpful comments on the manuscript.

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- Appendix 1: Species names for all trees and shrubs recorded in the plots and shown in Figure 2:*
(Acepse) *Acer pseudoplatanus*; **(Aleexc)** *Alectryon excelsus*; **(Ariser)** *Aristolotelia serrata*; **(Ascluc)** *Ascarina lucida*; **(Berdar)** *Berberis darwinii*; **(Brarep)** *Brachyglottis repanda*; **(Carser)** *Carpodetus serratus*; **(Copare)** *Coprosma areolata*; **(Copfoe)** *C. foetidissima*; **(Coppgra)** *C. grandifolia*; **(Copluc)** *C. lucida*; **(Copropro)** *C. propinqua*; **(Coprep)** *C. repens*; **(Coprha)** *C. rhamnoides*; **(Coprobb)** *C. robusta*; **(Copropt)** *C. rotundifolia*; **(Copspt)** *Coprosma* species "T"; **(Copvir)** *C. virescens*; **(Coraus)** *Cordyline australis*; **(Corarb)** *Coriaria arborea*; **(Corsp.)** *Coriaria* sp.; **(Corlae)** *Corynocarpus laevigatus*; **(Cramon)** *Crataegus monogyna*; **(Cyafas)** *Cyathodes fasciculata*; **(Cyadea)** *Cyathea dealbata*; **(Cyamed)** *C. medullaris*; **(Cyasmi)** *C. smithii*; **(Dacdac)** *Dacrydium dacrydioides*; **(Daccup)** *D. cupressinum*; **(Dicsqu)** *Dicksonia squarrosa*; **(Dodvis)** *Dodonea viscosa*; **(Eladen)** *Elaeocarpus dentatus*; **(Elahoo)** *E. hookerianus*; **(Fucexc)** *Fuchsia excorticata*; **(Grilit)** *Griselinia littoralis*; **(Hebsal)** *Hebe salicifolia*; **(Hedarb)** *Hedycarya arborea*; **(Hohang)** *Hoheria angustifolia*; **(Kuneri)** *Kunzea ericoides*; **(Launov)** *Laurelia novae-zelandiae*; **(Leyfor)** *Leycesteria formosa*; **(Lopobc)** *Lophomyrtus obcordata*; **(Macexc)** *Macropiper excelsum*; **(Melsim)** *Melicope simplex*; **(Melram)** *Melicitytus ramiflorus*; **(Metrob)** *Metrosideros robusta*; **(Myolae)** *Myoporum laetum*; **(Myraus)** *Myrsine australis*; **(Myrdiv)** *M. divaricata*; **(Myrsal)** *M. salicina*; **(Neoped)** *Neomyrtus pedunculata*; **(Notfus)** *Nothofagus fusca*; **(Notsol)** *N. solandri*; **(Nottru)** *N. truncata*; **(Olepan)** *Olearia paniculata*; **(Oleran)** *O. rani*; **(Pencor)** *Pennantia corymbosa*; **(Photen)** *Phormium tenax*; **(Piteug)** *Pittosporum eugenioides*; **(Pitten)** *P. tenuifolium*; **(Plareg)** *Plagianthus regius*; **(Podhal)** *Podocarpus hallii*; **(Podtot)** *P. totara*; **(Prufer)** *Prumnopitys ferruginea*; **(Psearb)** *Pseudopanax arboreus*; **(Psecol)** *P. colensoi*; **(Psecrea)** *P. crassifolium*; **(Pseaxi)** *Pseudowintera axillaris*; **(Psewin)** *P. colorata*; **(Quiacu)** *Quintinia acutifolia*; **(Rhosap)** *Rhopalostylis sapida*; **(Samnig)** *Sambucus nigra*; **(Schedig)** *Schefflera digitata*; **(Solavi)** *Solanum aviculare*; **(Sopmic)** *Sophora microphylla*; **(Strhet)** *Streblus heterophyllus*; **(Uleaur)** *Ulex europaeus*; **(Urtfer)** *Urtica ferox*; **(Weirac)** *Weinmannia racemosa*.