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Host provenance effects on germination and establishment of two New Zealand mistletoes (Loranthaceae)

D. A. NORTON*‡, J. J. LADLEY* and A. D. SPARROW†

**Conservation Research Group, School of Forestry, and †Department of Plant and Microbial Sciences, University of Canterbury, Private Bag 4800, Christchurch, New Zealand*

Summary

1. The influence of host genotypes (provenances) on mistletoe establishment, or the susceptibility of different host provenances to mistletoe infection, has not previously been documented.

2. We quantified the germination and establishment of two New Zealand mistletoes [*Alepis flavida* (Hook. f.) Tiegh. and *Peraxilla tetrapetala* (L. f.) Tiegh.] on different provenances of their main host *Nothofagus solandri* (Hook. f.) Oerst. in a 'common garden' host experiment.

3. Germination was high for both species (96·9% for *A. flavida* and 97·4% for *P. tetrapetala*), but establishment was much lower (13·2 and 2·3%, respectively).

4. Deviance explained in statistical models of germination with respect to light, branch growth rate, host tree provenance and tree effects was lower than that explained in models of establishment (20·3 compared with 33·2% for *A. flavida*; 35·9 compared with 73·7% for *P. tetrapetala*).

5. While branch growth rate and host tree provenance were significant variables in the *P. tetrapetala* establishment model, the most significant effect for both species was due to individual trees within provenances (24·9 and 42·8% of total deviance, respectively, for *A. flavida* and *P. tetrapetala*).

6. Even when a range of factors are accounted for (including branch growth rate and host tree provenance), there is still a large degree of unpredictability in mistletoe establishment that reflects either inherent or environmental conditions associated with individual trees.

Key-words: *Alepis flavida*, establishment, germination, parasite, *Peraxilla tetrapetala*

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Introduction

The regeneration niche (Grubb 1977) of parasitic plants, especially mistletoes (mainly Loranthaceae, Misodendraceae and Viscaceae), differs from non-parasitic plants because of the parasites' dependence on a host for water, nutrients and carbon (Press & Graves 1995). As with most plants, establishment is the key limiting step in a mistletoe's life cycle, where it requires an appropriate disperser, the presence of a suitable host species, and deposition on a suitable branch (Norton & Reid 1997; Reid, Stafford Smith & Yan 1995). Unlike most ground-dwelling species, mistletoe seeds cannot simply fall to the ground, germinate and grow.

Mistletoe dispersal has been widely studied, with birds the primary dispersers (Godschalk 1983; Hawksworth & Wiens 1996; Ladley & Kelly 1996; Reid 1989). Birds remove the pericarp, usually by swallowing the fruit and voiding the seed, with the sticky viscin layer around the seed ensuring that it adheres to a branch. While seeds of many plant parasites germinate only in response to chemical signals from host plants (Musselman & Press 1995), mistletoe seeds germinate readily in almost all situations (Lamont 1983). However, successful establishment (development of the haustorial connection) appears best on fast-growing, narrow branches (Norton & Ladley 1998; Sargent 1995; Yan & Reid 1995). Furthermore, it appears that certain parts of a host tree are more suitable for establishment than others (Norton, Ladley & Owen 1997), reflecting differences in disperser behaviour (Dawson, King & Ehleringer 1990; Overton 1996), small-scale environmental heterogeneity such as irradiance and temperature (Botto-Mahan *et al.* 2000; Lichter & Berry 1991), and host branch growth rates (Norton & Ladley 1998).

Even in the presence of seed dispersers and suitable establishment sites, most mistletoes will establish

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‡Author to whom correspondence should be addressed. E-mail: d.norton@fore.canterbury.ac.nz

only on particular host species (Hawksworth & Wiens 1996; Hoffmann *et al*. 1986; Norton & de Lange 1999; Yan 1993). Where the same mistletoe species parasitizes different host species, host-specific mistletoe races can occur. Then, mistletoe establishment within a particular host race is good on their usual host species and poor on hosts parasitized by other races of the same mistletoe species (Clay, Dement & Rejmanek 1985; Glazner, Devlin & Ellstrand 1988; May 1971).

While spatial variations in the genotype of plant species have been widely documented (Loveless & Hamrick 1984), the influence of host genotypes (provenances) on mistletoe establishment, or the susceptibility of different host provenances to mistletoe infection, have not. Differences in host provenance susceptibility to infection could lead to the formation of mistletoe races on particular host provenances, especially as gene flow is limited between the spatially patchy mistletoe populations (H. Chapman & D.A.N., unpublished results). This could lead to speciation in much the same way as can result from host race formation on different host species (Norton & Carpenter 1998). If differences in susceptibility to mistletoe infection and hence adaptation of mistletoes to local host provenances occurs, then mistletoe establishment success would be higher on hosts of the source population and lower on hosts with different genotypes. As well as being a potential pathway for mistletoe speciation, host provenance differences in susceptibility to infection have implications for transplanting mistletoe seeds, for example for medicinal or conservation purposes (Grazi 1984; Norton & Reid 1997), as successful establishment will require the correct host genotype.

Integrating these observations leads us to conclude that, if mistletoe seed is available and birds have dispersed seed to a potential establishment site, and that establishment is on a correctly sized branch, then establishment is likely to be influenced by a combination of (i) the species and genotype of the potential host; (ii) the vigour of the host; and (iii) environmental conditions at the establishment site (we assessed irradiance because of its strong influence on microsite temperature). The objective of this study was to quantify the influence of these factors on mistletoe establishment for two New Zealand mistletoe species, to test the following hypotheses.

1. Mistletoe establishment is greatest on the host provenance that the mistletoe naturally occurred on and less on other host provenances.
2. There is a positive relationship between mistletoe establishment and growth rate of the host branch.
3. There is a positive relationship between mistletoe establishment and the light environment on the host branch.

Materials and methods

Our study involved a 'common garden' experiment in which all host plants were grown at the same site to minimize the effects of regional environmental factors. Our experimental design involved establishing seeds of the mistletoes *Alepis flavida* (Hook. f.) Tiegh. and *Peraxilla tetrapetala* (L. f.) Tiegh. (Loranthaceae) on different provenances of their principal host tree *Nothofagus solandri* (Hook. f.) Oerst. (Fagaceae) (Norton & de Lange 1999) which were growing in a *Nothofagus* provenance trial established in 1978 at Rangiora (43°19′ S, 172°34′ E, 46 m asl; Wilcox & Ledgard 1983). This trial had been established to quantify genetic variability within *Nothofagus* by planting 80 provenances of four *Nothofagus* species in a randomized-block experimental design. Seven *N. solandri* provenances, each represented by at least three trees, were used in our study (Table 1). Because of tree mortality prior to our study, it was not possible to include the blocks in the *Nothofagus* planting in the experimental design. However, the within-provenance host trees used came from different blocks. Seeds of *A. flavida* and *P. tetrapetala* were collected from two of the sites from which trees in the provenance trial had been sourced (Table 1). These were then planted on to host trees of this provenance and all other provenances at the Rangiora experimental site in a fully factorial manner.

Seeds of *A. flavida* and *P. tetrapetala* were collected in mid-April 1996. At each site, fruits from 30–40 plants were mixed and stored in a cool ice-box in the field, then overnight in a refrigerator until used the following day. Ten seeds were deployed on each of five randomly chosen branches on each tree present for each provenance. Seed deployment involved carefully squeezing the seeds out of the fruit skins and placing them on the branch. Care was taken to ensure that the seeds' viscin was wiped onto the host branch to ensure

Table 1. *Nothofagus solandri* provenance origins and mistletoe sources

Provenance	Latitude	Longitude	Altitude (m)	No. trees	Mistletoe source
Panekirikiri	38°50′	177°04′	600	4	
Desert Road	39°10′	175°46′	760	4	
Hut Creek	43°09′	171°43′	950	4	*Alepis flavida*
Coopers Creek	43°16′	172°04′	300	3	
Ohau	44°16′	169°49′	550	4	*Peraxilla tetrapetala*
Mavora Lakes	45°17′	168°12′	680	4	
Rowallan	46°01′	167°36′	220	3	

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good adhesion (Ladley, Kelly & Norton 1997). Different branches were used for the two mistletoe species. A total of 1301 *A. flavida* seeds and 1280 *P. tetrapetala* seeds were used. The trial was checked monthly or bimonthly to determine seed fate, with final measurements made after 25 months. At each visit, the state of each seed was assessed as germinated (when the hypocotyl had emerged); established (when the first set of small leaves appeared); or dead (see Powell & Norton 1994 for more details on these stages).

We used shoot extension during the 1996–97 growing season as a measure of host branch growth rate based on the distance from the 1996 basal bud scar to the base of the 1997 overwintering terminal bud. Irradiances at each branch were quantified using diazo photosynthetic paper (Friend 1961) following the methods described by Baars, Kelly & Sparrow (1998). The papers were put out for an 8-day period in August 1998, and the number of exposed papers counted. We calibrated diazo paper exposure over the same period at an open site by fitting a regression model of the number of papers exposed, measured photosynthetically active photon flux density (PPFD) using LI-COR quantum sensors), and used this regression to estimate PPFD for each branch.

The effects of light environment, host branch growth rate, host provenance and tree (within provenance) on germination and establishment of each species were tested by generalized linear models using S-PLUS version 4 statistical software (MathSoft Inc., Seattle, WA). Each model initially assumed a binomial error distribution for the response, which was the number of successful germination or establishment 'events' out of the 10 seeds per branch. For the predictors, light and branch growth rate (log-transformed) were treated as continuous variates, while provenance and tree were factors. Because predictors were not completely orthogonal, they were added to the model in the order: light, branch growth rate, provenance and trees within provenance, in order to make the test of provenance as conservative as possible. Model diagnostics indicated that assumptions of complete independence of events were not met, thereby invalidating use of χ^2 tests of significance. Instead approximate F tests were calculated using binomial deviance in the manner of sums-of-squares for standard ANOVA (M. Faddy, personal communication). F tests were calculated using an error term appropriate for the true replication of each effect: tree replication of provenance and branch replication of light, branch growth rate and tree. Spearman's rank correlation coefficients were used to compare the order of germination and establishment by provenances within each mistletoe species.

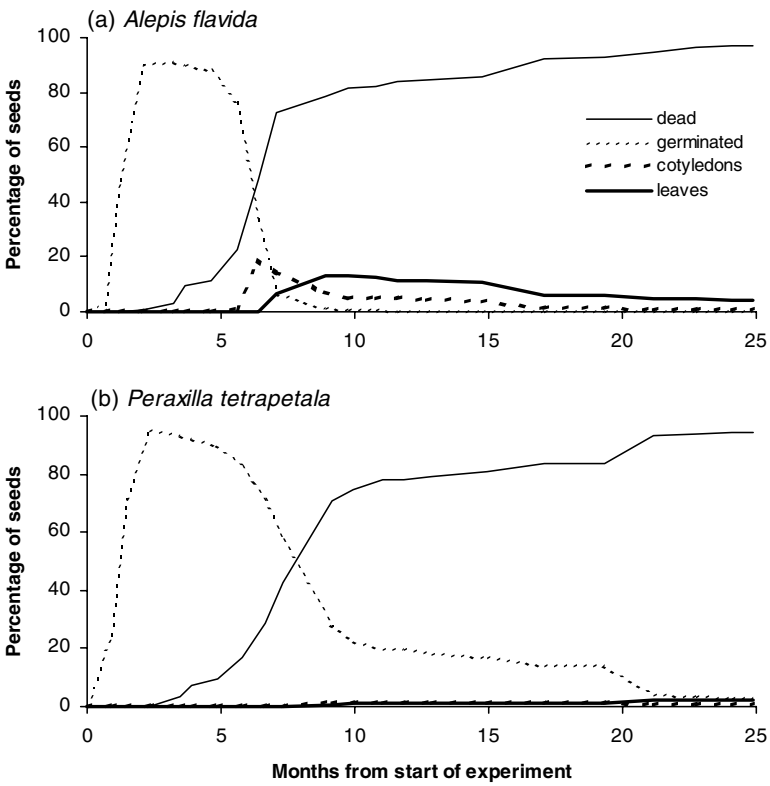

Fig. 1. Germination and establishment patterns for (a) *Alepis flavida* and (b) *Peraxilla tetrapetala* seeds. Germinated: germinated seeds with hypocotyl. Cotyledons: germinated seeds with cotyledons present. Leaves: established plant with true leaves. Dead: dead plant.

Results

OVERALL GERMINATION AND ESTABLISHMENT

Of the 1301 *A. flavida* seeds and 1280 *P. tetrapetala* seeds planted, 81 and 53, respectively, were lost from branches either through predation (possibly by birds) or because they fell off. These seeds were not included in the analyses, giving final sample sizes of 1220 and 1227, respectively, for the two species. Germination successes were 96·9% for *A. flavida* and 97·4% for *P. tetrapetala*. In contrast, the total number of seeds that established was only 13·2% for *A. flavida* and 2·3% for *P. tetrapetala*.

While the patterns of germination and establishment were similar for the two species, they differed in timing (Fig. 1). Both species showed a similar pattern in the onset of germination, with germinated seeds present 1 month after the start of the experiment, but the fate of the germinated seeds differed. For *A. flavida* almost all the germinated seeds had either developed further or died by the end of the tenth month, with the last seed still in the 'germinated' category recorded in month 14. In contrast, a few apparently live germinated seeds of *P. tetrapetala* were still present at the end of the experiment (25 months). Establishment also occurred sooner for *A. flavida* than for *P. tetrapetala*. The maximum number of seeds with cotyledons occurred in month 6, and the maximum number of established plants was recorded in month 9 for *A. flavida*. The comparable dates for *P. tetrapetala* were 12 and 24 months, respectively.

Table 2. Summary of analysis of deviance tables for the binomial generalized linear models for *Alepis flavida* and *Peraxilla tetrapetala* germination and establishment

	Alepis flavida			*Peraxilla tetrapetala*		
Variable	df	Percentage deviance	$P(F)$	df	Percentage deviance	$P(F)$
Germination						
Light	1	0·2	0·633	1	0·1	0·724
Log(branch length)	1	0·2	0·657	1	0·4	0·407
Provenance	6	5·1	0·471	6	20·7	<0·001
Tree in provenance	19	14·8	0·498	18	14·7	0·173
Residual	98	79·7		99	64·1	
Establishment						
Light	1	0·6	0·337	1	0·7	0·140
Log(branch length)	1	1·4	0·135	1	2·8	0·003
Provenance	6	6·3	0·206	6	27·4	<0·001
Tree in provenance	19	24·9	0·007	18	42·8	<0·001
Residual	98	66·8		99	26·3	

Significance of model effects is tested using an appropriate F test rather than the more usual χ^2 tests; see text for explanation.

While we assessed establishment based on the presence of the first pair of true leaves, many of the established *A. flavida* plants subsequently died. Mortality between month 9 (when the maximum number of established plants was present) and the end of the experiment (month 25) was *c.* 70% (Fig. 1). Mortality of established plants was very low for *P. tetrapetala*, probably reflecting the slower establishment in this species.

GERMINATION PATTERNS

The generalized linear models for both *A. flavida* and *P. tetrapetala* germination explained only a limited amount of the variance present (20·3 and 35·9%, respectively). Neither light nor branch growth rate was significant in either model. Provenance was significant in the *P. tetrapetala* model only (Table 2; 20·7% total deviance).

For *A. flavida*, germination was highest on the Desert Road provenance, lowest on Rowallan, and intermediate on Hut Creek, the source provenance for *A. flavida* seed, although germination was high (82·7–93·5%) for all provenances (Table 3). There was no obvious pattern in germination with distance from mistletoe source provenance (Hut Creek), with germination on Hut Creek hosts not significantly different from that on trees of any other provenances except Rowallan. For *P. tetrapetala*, germination was highest on Hut Creek, where all seeds germinated, and lowest on Desert Road, with the Ohau provenance, the source provenance for *P. tetrapetala* seed, second lowest; but again germination was high (88·4–100%) for all provenances (Table 3). There was no obvious pattern in germination with distance from the source provenance, with germination at Ohau not significantly different from all the other provenances except Hut Creek.

ESTABLISHMENT PATTERNS

The generalized linear models for both *A. flavida* and *P. tetrapetala* establishment explained more of the deviance than the germination models (33·2 compared with 20·3%; 73·7 compared with 35·9%, respectively). Light was not significant in either model, but branch growth rate was significant in the *P. tetrapetala* model, although the deviance explained was very small (2·8%). Provenance was also significant in the *P. tetrapetala*

Table 3. Mean germination/establishment and distance from the mistletoe source provenance ordered by germination/establishment success

Alepis flavida			*Peraxilla tetrapetala*		
Provenance	Mean germination/establishment (%)	Distance (km)	Provenance	Mean germination/establishment (%)	Distance (km)
Germination					
Desert Road	93·5[a]	560	Hut Creek	100·0[a]	200
Ohau	92·5[a]	200	Mavora	94·7[b]	180
Hut Creek	92·0[ab]	0	Coopers Creek	94·7[b]	220
Coopers Creek	90·7[abc]	40	Rowallan	94·7[b]	280
Panekirikiri	90·6[abc]	660	Panekirikiri	91·6[bc]	860
Mavora	87·5[bc]	380	Ohau	90·5[bc]	0
Rowallan	82·7[c]	480	Desert Road	88·4[c]	760
Establishment					
Coopers Creek	23·8[a]	40	Rowallan	2·7[a]	280
Mavora	17·5[b]	380	Desert Road	1·6[a]	760
Hut Creek	14·5[b]	0	Coopers Creek	1·3[a]	220
Ohau	14·5[b]	200	Mavora	1·1[a]	180
Desert Road	14·0[b]	560	Hut Creek	1·0[b]	200
Panekirikiri	11·9[b]	660	Ohau	0·0[c]	0
Rowallan	10·0[b]	480	Panekirikiri	0·0[c]	860

Germination/establishment is not significantly different between provenances with the same letters (based on paired χ^2 tests derived from the generalized linear models). The source provenance is underlined.

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model (27·4%), and trees in provenances was significant in both models (Table 2, 24·9 and 42·8% deviance, respectively, for *A. flavida* and *P. tetrapetala*).

For *A. flavida*, establishment was highest on the Coopers Creek provenance and lowest on Rowallan, and intermediate on the Hut Creek provenance, the source provenance for *A. flavida* seed (Table 3). There was no obvious pattern in establishment with distance from mistletoe source provenance (Hut Creek), with establishment on Hut Creek hosts not significantly different from any other provenance except Coopers Creek. For *P. tetrapetala*, establishment was highest on Rowallan, where all seeds established, and lowest on Ohau, the source provenance for *P. tetrapetala* seed, and Panekirikiri, where no establishment was recorded (Table 3). Again there was no obvious pattern in establishment with distance from the source provenance (Ohau).

There was no significant correlation in the order of provenances in germination and establishment for either *A. flavida* ($r = 0{\cdot}178$, $P = 0{\cdot}702$, $n = 7$) or *P. tetrapetala* ($r = -0{\cdot}036$, $P = 0{\cdot}939$, $n = 7$). Nor was there any significant correlation in the order of either germination ($r = -0{\cdot}464$, $P = 0{\cdot}294$, $n = 7$) or establishment ($r = -0{\cdot}107$, $P = 0{\cdot}819$, $n = 7$) between the two species.

Discussion

Our results showed little evidence for any significant effect on mistletoe germination, except host tree provenance for *P. tetrapetala*, although here the source host population had the second lowest germination percentage, making interpretation of the host provenance effect difficult. Total deviance explained in the statistical models is much less for germination than for establishment within each species, although explained deviance for *P. tetrapetala* germination (35·9%) is similar to that for *A. flavida* establishment (33·2%). The lack of a strong germination effect is consistent with the widespread observation that mature mistletoe seeds can germinate readily on most surfaces (Ladley & Kelly 1996; Lamont 1983; Yan 1993). Germination percentages observed here for individual host provenances (82·7–100%) are comparable to those in other studies (Hawksworth & Wiens 1996; Ladley & Kelly 1996; Lamont 1983; Norton & Ladley 1998; Yan 1993; Yan & Reid 1995). Yan & Reid (1995) did observe differences in germination between seed cohorts planted at different times, and suggested that environmental conditions at the time of planting could affect germination rates. However, the significant differences in *P. tetrapetala* germination among host provenances cannot be attributed to this effect, as the seeds were planted on the same date.

The total deviance explained in the establishment models was higher than in the germination models (33·2 compared with 20·3% for *A. flavida*; 73·72 compared with 35·9% for *P. tetrapetala*). For both species, the effect of trees within provenances and provenance was much stronger than the branch growth rate effect, with the latter significant only for *P. tetrapetala*. Light was not significant for either species, despite other studies suggesting that branch microclimate is important for mistletoe establishment (Botto-Mahan *et al.* 2000). A branch growth rate effect on seedling growth has been observed with naturally established *A. flavida* seedlings (Norton & Ladley 1998), where significantly higher mistletoe growth rates were observed on the fastest growing host branches. However, the branch growth rate effect in the present study was small compared to the effect of host provenance and trees within provenances.

Numerous studies have documented mistletoe host races on different host species, especially in the mistletoe genera *Arceuthobium* and *Phoradendron* (Clay *et al.* 1985; Glazner *et al.* 1988; Hawksworth & Wiens 1996; May 1971; Overton 1997). However, we are unaware of any studies of the formation of host races on different provenances of the same host species, or the susceptibility of different host provenances to mistletoe infection. We hypothesized that there might be differences in host susceptibility to mistletoe establishment relating to host provenance. However, this was true only for one species, *P. tetrapetala*. Furthermore, the provenance with the greatest establishment success (Rowallan) occurred 280 km from the source provenance (Ohau), while no establishment occurred on trees from the Ohau provenance. While geographical isolation does not necessarily equate with genetic distance, provenance studies (Wilcox & Ledgard 1983) and genetic data (Haase 1993) show the host species *N. solandri* to be genetically variable, with regional ecotypes present. Therefore differences in susceptibility to mistletoe infection between provenances are possible.

One explanation for the absence of a stronger provenance effect relates to the dramatic changes in plant distribution that have occurred between glacial and interglacial periods in New Zealand (McGlone, Mildenhall & Pole 1996). Major contractions and expansions in the range of the mistletoes and their host over the past 2–3 million years have probably limited the amount of genetic segregation that has occurred, and resulted in the absence of strong patterns in host provenance susceptibility to mistletoe infection. The lack of host specialization in two other New Zealand mistletoes, *Ileostylus micranthus* and *Tupeia antarctica*, has also been attributed to the dramatic climatic upheavals of the past 2–3 million years (Norton & de Lange 1999). However, the absence of a strong provenance effect may also be due to shortcomings in the experimental design. While a common garden experiment ensured that all host trees and mistletoes were subjected to the same environmental conditions, the conditions at the Rangiora study site may have favoured some host provenances over others. However, the absence of any significant correlation in the order

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of provenances in germination or establishment within and between mistletoe species suggests that any such effect was weak. Nonetheless, it may be helpful if future studies of host provenance effects on mistletoe establishment utilize reciprocal transplant experiments (Rödl & Ward 2002).

The only factor that was significant for establishment of both mistletoe species was the effect of trees within provenances. This was an unexpected result, although a significant tree effect was also found in two studies of mistletoe establishment on different-sized branches (Norton & Ladley 1998; Sargent 1995). Field-based studies have suggested that differences in establishment between trees may reflect aspects of bird behaviour (such as greater within-tree than between-tree dispersal; Overton 1994). However, by hand-planting mistletoe seeds we eliminated any between-tree disperser behaviour influence on mistletoe establishment. Between-tree differences may therefore reflect differences in tree quality from the perspective of the establishing mistletoe (for example, with respect to availabilities of key resources such as water and nutrients, or genetic differences relating to host resistance to mistletoe infection; Reid *et al*. 1995).

While our study was undertaken in a randomized host provenance trial in which differences between trees in terms of resource availability were assumed to be minimal (Wilcox & Ledgard 1983), the trial had not been actively managed for the preceding decade (N. Ledgard, personal communication). Intense competition over this period had led to poor growth and high mortality among many of the planted host trees. This may have led to differences in tree quality due to tree-scale variation in competition intensity, and may also have contributed to the weaker-than-expected host provenance effect. Incompatibility mechanisms can also prevent mistletoes from establishing on some host individuals while successfully establishing on others. The reasons for such mechanisms are poorly understood, but physical and chemical barriers may be involved (Hariri, Salle & Andary 1991; Sargent 1995). These may be present prior to mistletoe seed dispersal, or induced by the presence of the seed or by haustorial penetration (Reid *et al*. 1995). It may be that the large amount of deviance accounted for by trees within provenance in our study also reflected variations in tree susceptibility to mistletoe establishment, although we have no information on which to assess the specific mechanisms involved.

Explained deviance in both germination and establishment models was substantially greater for *P. tetrapetala* than *A. flavida*. *Alepis flavida* is shorter-lived, grows more quickly, and has a much wider range of hosts (Norton & de Lange 1999; Powell & Norton 1994). This species may be more flexible ecologically and hence less influenced by factors such as those we modelled – certainly, overall establishment was far greater for this species (13·2 compared with 2·3%).

The absence of a strong provenance effect may result from New Zealand's geological history, although it may also be partly due to our experimental design. However, the absence of either a branch growth rate or a light effect is more puzzling, and contrary to other studies (Lamont 1983; Norton & Ladley 1998; Sargent 1995). Our key finding was that the strongest influence on mistletoe establishment is a tree effect independent of provenance, an effect that other studies have also identified (Norton & Ladley 1998; Sargent 1995), but it is unclear what the causal mechanisms are. This result highlights the large degree of unpredictability in mistletoe establishment that reflects either inherent or environmental conditions associated with individual trees.

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