Light environments occupied by conifer and angiosperm seedlings in a New Zealand podocarp–broadleaved forest

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Abstract: Interaction between conifers and angiosperms in New Zealand's podocarp–broadleaved forests is a topic of enduring interest. We aimed to determine if the often discontinuous regeneration of the podocarps *Dacrydium cupressinum* and *Prumnopitys ferruginea* can be attributed to their seedlings' tolerating less shade than those of angiosperm canopy trees and/or to occupying a narrower range of light environments. We quantified the light environments (% diffuse light availability) naturally occupied by large seedlings (50–200 cm tall) of these two conifers and five co-occurring angiosperms, in an old-growth podocarp–broadleaved forest in the central North Island of New Zealand. Randomisation was used to compare the mean and variance of the light environments occupied by each species with those of the distribution of light environments in the forest understorey. The 10th percentiles of distributions were also calculated as an indicator of the deepest shade tolerated by each species. These parameters showed *D. cupressinum* to be essentially randomly distributed in relation to light availability, like the angiosperm *Beilschmiedia tawa*. Although this was also true of the mean light environment of the other conifer, *P. ferruginea*, there was marginally significant evidence that this species was underrepresented at the shadiest microsites. In contrast, the angiosperms *Elaeocarpus dentatus* and *Weinmannia racemosa* showed strongly non-random patterns, occupying significantly brighter minimum and mean light environments than would be expected by chance. It therefore seems unlikely that the discontinuous population structures of podocarps in many forests result from an intolerance of shade at the large seedling stage. Furthermore, the similarity of the ranges of light environments occupied by *D. cupressinum* and *P. ferruginea* suggests that reported differences in population structure and successional position of these species are not attributable to differences in seedling shade tolerance.

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Introduction

Interactions between conifer and angiosperm trees have attracted attention worldwide in recent decades (Bond 1989; Becker 2000; Coomes et al. 2005). This international interest is pre-dated by a long-standing local debate about the dynamics of conifer–angiosperm interactions in New Zealand, where the two lineages coexist, in varied mixtures, over much of the landscape (e.g. McKelvey 1963; Wardle 1963; Beveridge 1973; Ogden 1985; Ogden & Stewart 1995). Whereas canopy angiosperms such as *Beilschmiedia tawa*[1] and *Weinmannia racemosa* often have all-sized populations in old mixed stands, podocarps such as *Dacrydium cupressinum* usually show a restricted size- or age-range, suggesting that their regeneration requires

rather specific conditions (Wardle 1963; Herbert 1980; Lusk & Ogden 1992; Smale et al. 1997 – but see Lusk & Smith 1998). Such population structures have usually been attributed to periodic regeneration in openings created by major disturbances (Ogden & Stewart 1995), and one recent study has in fact demonstrated establishment of *D. cupressinum* cohorts after major earthquakes in South Island forests (Wells et al. 2001). Yet growth of *D. cupressinum* seedlings is reported to be slow and relatively unresponsive to light intensity (Enright et al. 1993; Ebbett & Ogden 1998) – traits typically found in shade-tolerant late-successional species (e.g. Kobe et al. 1995; Baltzer & Thomas 2007). In a similar vein, Smale & Kimberley (1986) showed that seedling mortality rates of the podocarps *D. cupressinum* and *Prumnopitys*

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[1] Plant names follow Allan Herbarium (2002–2006).

ferruginea in a central North Island forest approximated those of their shade-tolerant angiosperm associate *B. tawa*, although the actual light environments of seedlings were not quantified.

Ecologists have debated the most meaningful ways of quantifying species shade tolerance. Although measuring seedling or sapling survival in low light has been advocated as a rigorous way of comparing shade tolerance of coexisting species (e.g. Kobe et al. 1995), survival data are hard to come by, and furthermore the outcome will depend on exactly what light environment species are compared in. Estimating the whole-plant compensation point by monitoring growth across a range of light environments may be a more unequivocal way of comparing species' shade tolerance (Baltzer & Thomas 2007). Alternatively, inferences can be made by quantifying the distribution of light environments naturally occupied by established juveniles (e.g. Lusk et al. 2008). To date there are very few such data for podocarps and their angiosperm competitors in New Zealand forests. Assessments of species' relative shade tolerance have therefore depended to a large degree on interpretation of indirect evidence (population structures, growth rates) and on subjective or semi-quantitative assessments.

Here we report data on the light environments occupied by large seedlings of two of the most widespread New Zealand podocarps (*D. cupressinum* and *P. ferruginea*), plus five common angiosperm tree associates, in an old-growth central North Island forest. These two podocarps are widely regarded as the most shade tolerant of New Zealand conifers (Beveridge 1973; Ogden & Stewart 1995). We quantified the frequency distribution of light environments occupied by large seedlings of each species, and compared several distribution parameters with those of the overall distribution of light environments in the forest understorey. We aimed to determine if the discontinuous regeneration of podocarps in many forests can be attributed to their having higher seedling light requirements, and/or occupying a narrower range of light environments, than most of their angiosperm canopy associates.

Materials and methods

Study area

Fieldwork was carried out in April 2005 in the Mokaihaha Ecological Area (38°11' S, 176°06' E, altitude c. 650 m a.s.l.) on the Mamaku Plateau, central North Island. Terrain is hummocky. Soils are yellow-brown loams formed from Mamaku ignimbrite c. 7400 years old, overlain by airfall tephra from the Taupo eruption c. 1800 years ago (Scott 1991). Annual precipitation in the area averages c. 2000 mm (NIWA 2003) and a mean annual temperature of 12.4°C has been recorded at the Tokoroa meteorological station about 20 km to the south-west (New Zealand Meteorological Service 1983).

The forest of the area is mainly unlogged (Nicholls 1991), with a typical old-growth mosaic of closed-canopy stands and tree-fall gaps in varied stages of regrowth. The podocarps *Dacrydium cupressinum* and *Prumnopitys ferruginea* occur throughout as scattered emergents. On knolls the canopy is formed mainly by *Beilschmiedia tawa*, *Ixerba brexioides* and *Weinmannia racemosa*, with fewer *Elaeocarpus dentatus*. Hollows are dominated by smaller trees and shrubs such as *Melicytus ramiflorus* and *Coprosma grandifolia*, and the tree fern *Dicksonia squarrosa*. Seedlings up to 2 m tall of all the above-named species were common in the old-growth forest mosaic, but larger juveniles of *D. cupressinum* were more localised.

Sampling

A pair of LAI-2000 Canopy Analyzers (Li-Cor, Lincoln, Nebraska, USA) was used to compare light environments occupied by large seedlings (50–200 cm tall) of seven common tree species with the overall distribution of light environments available in the forest understorey. The LAI-2000 quantifies diffuse light availability, equivalent to percentage canopy openness within a quasi-hemispherical (148°) field of view. Diffuse light availability is calculated by expressing measurements made within the forest as percentages of values recorded simultaneously outside the forest in a large clearing. Measurements with the LAI-2000 have been shown to be closely correlated with spatial variation in photosynthetic photon flux density within a stand (Machado & Reich 1999).

Sampling points were spaced at random intervals (25–30 m apart) on transects run through the forest, including both knolls and hollows. Diffuse light availability was quantified at 125-cm height above each of 110 randomly chosen points. At every second point, the nearest juvenile of each of the study species was located, and canopy openness was quantified immediately above the top of its crown. Thus, light environments of 55 juveniles were sampled for each of seven species: the conifers *Dacrydium cupressinum* and *Prumnopitys ferruginea*, and the angiosperms *Beilschmiedia tawa*, *Elaeocarpus dentatus*, *Ixerba brexioides*, *Melicytus ramiflorus*, and *Weinmannia racemosa*, all referred to henceforward by genus only.

Data analysis

Diffuse light availability measurements were log-transformed, and the back-transformed mean and variance were used to quantify the distribution of light environments occupied by juveniles of each species. The same approach was used to calculate the mean and variance of the overall distribution of light environments in the forest understorey, obtained from the random sample points. This approach offered two main advantages. First, light environment distributions were approximately log-normally distributed, so the geometric mean provided a more useful measure

of central tendency than the arithmetic mean. Second, responses of juvenile tree survival and growth are more closely related to a logarithmic scale of light availability than to an arithmetic scale (Kobe et al. 1995; Poorter 1999). This is in keeping with the expectation that the difference between (for example) 1 and 2% canopy openness has more physiological significance for plants than the difference between 21 and 22%. We used the log-variance of the light environments occupied by a species as a measure of niche breadth, with species occupying a wider range of light environments having greater variance.

We used resampling procedures to determine if species were significantly non-randomly distributed in relation to diffuse light availability. Three distribution parameters were examined: the geometric mean, log-variance, and 10th percentile, the latter intended as a measure of the deepest shade in which each species was typically found. We randomly resampled 55 points from the 110 random sample points located throughout the forest and calculated the three parameters for this sample. We repeated this process 10 000 times to generate the distributions of the geometric mean, log-variance, and 10th percentile that would be expected from a random sample of this size. We then calculated the empirical geometric mean, log-variance, and 10th percentile for each species and compared these values with those expected from a random sample of the same size. For each parameter, we calculated the probability of a randomly generated value exceeding the empirical value (Table 1). Thus, a species with a low P-value for its geometric mean would tend to be found on average in higher light environments than would be expected by chance. A two-tailed test is appropriate for the geometric mean, as it is biologically feasible that a species could occupy shadier environments on average than would be expected by chance. However, a one-tailed test seems more appropriate for the variance and 10th percentile parameters. Analyses were carried out using the statistical package R (Free Software Foundation, Inc.).

Results

The forest understorey light environments were log-normally distributed in the range 0.3 to > 24% (Fig. 1). All seven species also occupied an approximately log-normal distribution of light environments.

Geometric mean light environments occupied by *Dacrydium* and *Prumnopitys* (Fig. 2) did not differ significantly from the forest understorey mean (Table 1), as was also the case for the angiosperms *Beilschmiedia* and *Melicytus*. Two other angiosperms (*Elaeocarpus* and *Weinmannia*) were on average found in significantly higher light environments than would be expected by chance (Table 1), and *Ixerba* showed marginal evidence of a bias towards high light environments on average.

There was little interspecific variation in the log-variance of light environments (Fig. 2), and the variance of no species differed significantly from that of the forest understorey (Table 1).

Although there was only modest interspecific variation in the 10th percentile of the distribution of light environments (Table 1), this parameter did permit a more detailed distinction among species than was possible using the geometric mean. The 10th percentile of the light environments occupied by *Beilschmiedia* and *Dacrydium* did not differ significantly from that of the forest understorey, suggesting that no part of the forest was too dark for survival of their seedlings. *Ixerba*, *Melicytus*, and *Prumnopitys* had marginal P-values of 0.03–0.05, indicating that their seedlings tended to be underrepresented in the shadiest parts of the understorey. *Elaeocarpus* and *Weinmannia* had highly significant P-values, showing a strong under-representation in deep shade.

Discussion

The average understorey light availability of 1.5% at Mamaku (Fig. 2) was similar to figures reported for other old-growth rainforests on mesic sites with moderate fertility (Chazdon & Fetcher 1984; Brown & Parker 1994; Coomes et al. 2005). Although soils on the Mamaku Plateau are regarded as relatively infertile, they have been rejuvenated to some extent by airfall tephras within the last 2000 years (Scott 1991) and they supply enough

Table 1. Results of resampling tests for non-randomness of seedling distributions in relation to understorey light environments in an old-growth podocarp–broadleaved forest at Mamaku, New Zealand. P-values are the proportion of 10 000 values randomly generated from the forest understorey light environments that exceed the empirical value for each species. P-values < 0.05 for the geometric mean and 10th percentile indicate that a given species tends to occur in brighter light environments than would be expected by chance.

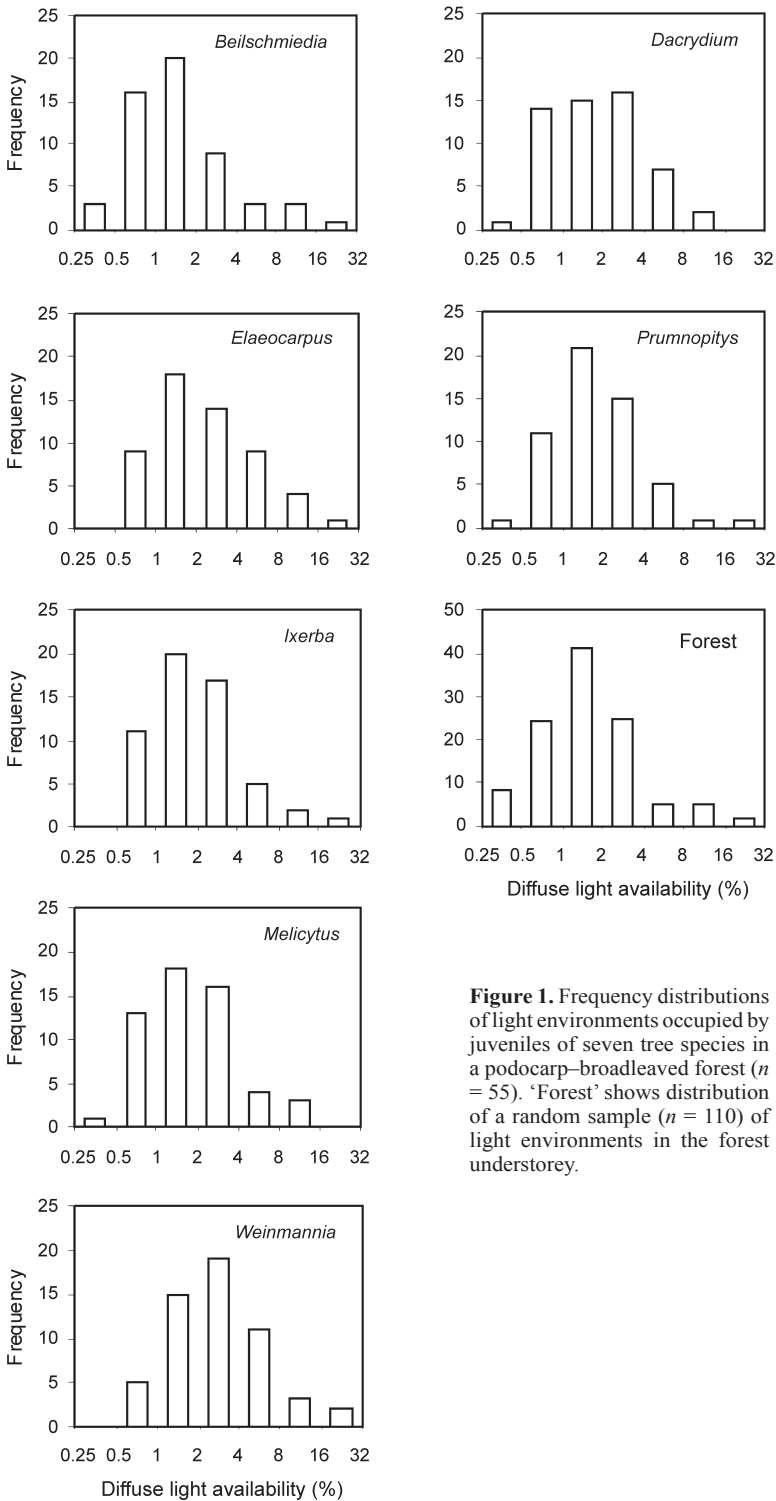| Species	Geometric mean (P)	Log variance (P)	10th percentile	
			% light	P
Beilschmiedia	0.62	0.27	0.6	0.23
Elaeocarpus	<0.0001	0.35	0.9	<0.0001
Ixerba	0.07	0.80	0.7	0.03
Melicytus	0.19	0.68	0.7	0.05
Weinmannia	0	0.78	1.0	0
Dacrydium	0.21	0.83	0.6	0.23
Prumnopitys	0.17	0.88	0.7	0.05
Understorey			0.6	

Figure 1. Frequency distributions of light environments occupied by juveniles of seven tree species in a podocarp–broadleaved forest (*n* = 55). 'Forest' shows distribution of a random sample (*n* = 110) of light environments in the forest understorey.
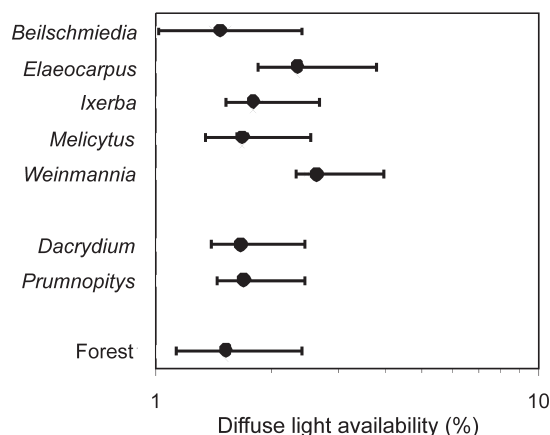
Figure 2. Geometric mean and log-variance (error bars) of light environments occupied by juveniles of seven tree species in a podocarp–broadleaved forest. 'Forest' shows distribution of a random sample of forest understorey light environments.

nutrients to support a forest canopy 25–30 m tall, with emergents attaining 40 m.

Neither of the podocarps showed any strong bias towards high-light environments. Seedling *Dacrydium* and *Prumnopitys* occupied similar ranges of light environments to the angiosperms *Melicytus* and *Ixerba* (Fig. 1; Table 1), although there was some evidence that *Beilschmiedia* was better represented at the shadiest microsites than any other species (Figs 1 and 2). *Beilschmiedia* dominates the understoreys of late-successional stands on mesic lowland sites throughout much of the North Island (Knowles & Beveridge 1982; West 1995) and is regarded as very shade tolerant. The angiosperms *Elaeocarpus* and *Weinmannia* showed evidence of being less shade tolerant than the podocarps, being the only two species whose seedlings showed strong biases towards high-light environments (Table 1; Fig. 2). The association of small-seeded *Weinmannia* with relatively open environments (Fig. 2) might partly reflect its disproportionate occurrence on fallen logs and other elevated substrates for establishment (Stewart & Veblen 1982; Lusk & Ogden 1992; Coomes et al. 2005), as these substrates are associated to some degree with recent canopy gaps. However, the high-light bias of *Elaeocarpus* is not subject to any such doubts, as this large-seeded species is not dependent on elevated substrates, and its behaviour at Mamaku is congruent with an earlier study showing saplings of this species to be significantly more common in tree-fall gaps than under closed canopies (Lusk & Ogden 1992).

There was little evidence of interspecific variation in niche breadth. On a log scale, the variance of light environments occupied by *Dacrydium* and *Prumnopitys* fell within the range seen among the five angiosperm

species (Fig. 2). We therefore found no convincing evidence that large seedlings of podocarps occupy a narrower range of light environments than their angiosperm associates.

Given the ability of their seedlings to survive at <1% light availability (Figs 1 and 2), why then do these conifers regenerate discontinuously on most sites? In old-growth stands at Horopito in Tongariro National Park, *Prumnopitys* and especially *Dacrydium* showed discontinuities of several hundred years in their age structures, whereas the angiosperms *Weinmannia* and *Elaeocarpus*, which our data suggest to be only moderately shade tolerant as seedlings, had all-aged populations (Lusk & Ogden 1992). It has been claimed that some podocarps, including *Dacrydium*, become markedly more light-demanding at the sapling stage (Beveridge 1973). Although the whole-plant light compensation point of all plants should increase with increasing size (Givnish 1988; Lusk et al. 2008), it is not clear a priori why this increase should be especially marked in *Dacrydium*.

On face value, our data are not consistent with the traditional view that *Prumnopitys ferruginea* is the most shade tolerant of New Zealand podocarps. As juveniles of *P. ferruginea* occupied almost exactly the same range of light environments as those of *Dacrydium* (Fig. 2, Table 1), it is unlikely that observed differences in population structures and successional position (Beveridge 1973; Herbert 1980; Lusk & Ogden 1992; Duncan 1993) can be attributed to differing seedling shade tolerance. Light requirements of the two species might diverge at later ontogenetic stages, with *Dacrydium* becoming markedly more light-demanding as it grows larger. Differences in seed size might also influence successional behaviour: these two species differ 80-fold in seed mass (Wardle 1991), and *P. ferruginea*'s late arrival in some successional sequences may reflect lower vagility, as dispersal of this large-seeded species depends to a great extent on a single vector, the pigeon *Hemiphaga novaeseelandiae* (Clout & Hay 1989). In contrast, the smaller seeds of *Dacrydium* are dispersed by a variety of bird species. However, dispersal seems less relevant to differences in population structure in old-growth forests (Lusk & Ogden 1992), and the regeneration modes of these two species in old stands remain poorly understood (Ebbett & Ogden 1998).

Although serving as a preliminary field assessment of the relative light requirements of the seven species, our measurements have some limitations. Carbohydrate reserves presumably enable juvenile trees to persist for some time in light environments where their net carbon gain is negative (Kobe 1997), and given the dynamic nature of forest light environments, our instantaneous measurements therefore probably overestimate the range of light levels that plants can really tolerate. As the LAI-2000 takes no account of the solar track, it does not distinguish between the north and south sides of canopy gaps, which will differ considerably in direct irradiance

even when diffuse light availability is similar, and it is possible that species respond differentially to positions within gaps (Runkle et al. 1995).

Despite these limitations, our data showed pattern in the distribution of some species in relation to light availability, and evidence of interspecific variation in species' light requirements. They also suggest that the general inability of podocarps to regenerate continuously and develop all-aged populations in mixed forests on productive sites cannot be attributed to their seedlings tolerating less shade than those of angiosperm associates. We hope that these findings will contribute to continuing efforts to unravel the dynamics of New Zealand podocarp–broadleaved forests (Carswell et al. 2007), as well as broader inquiries into the mechanisms determining habitat and landscape partitioning between conifers and angiosperms.

Acknowledgements

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