

The hare, the tortoise and the crocodile: the ecology of angiosperm dominance, conifer persistence and fern filtering

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Summary

1 Angiosperm trees often dominate forests growing in resource-rich habitats, whereas conifers are generally restricted to less productive habitats. It has been suggested that conifers may be displaced by angiosperms except where competition is less intense, because conifer seedlings are inherently slow growing, and are outpaced by faster-growing angiosperm species. Here we investigate whether competition with ferns and deeply shading trees also contributes to a failure of conifers to regenerate in resource-rich habitats.

2 We examined how changes in soil nutrient availability and drainage affected vegetation along the retrogressive stages of a soil chronosequence in southern New Zealand. Vegetation composition shifted from angiosperm-tree dominance on ‘recent’ alluvial terraces (< 24 ky), via coniferous-tree dominance on older marine terraces (79–121 ky), to coniferous-shrub dominance on the oldest marine terraces (291 ky). Soil drainage deteriorated along the sequence, and $N : P_{\text{leaves}}$ and $N : P_{\text{soil}}$ indicate increasing P-limitation. Conifer species appear to be adapted to persistence on infertile and poorly drained soils.

3 The floor of the relatively fertile alluvial forests was deeply shaded (~1% light transmission) by dense groves of tree-ferns and ground-ferns, and by large-leaved subcanopy trees. Few seedlings of any type were found on the forest floor, even in tree-fall gaps, and establishment was restricted to rotting logs and tree-fern trunks. Angiosperms were particularly successful at colonizing these raised surfaces.

4 Less shade was cast by the conifer-dominated forests on infertile marine terraces (~5% light transmission), which lacked tall ferns. There were many opportunities for conifer establishment, with high seedling densities recorded on the forest floor and on logs. By contrast, angiosperm seedlings were mainly restricted to logs.

5 Our results suggest that several mechanisms act in concert to reduce regeneration opportunities for conifers in productive habitats. In particular, we suggest that tall ferns and deep shade are responsible for a restriction of regeneration opportunities in relatively productive forests in New Zealand, diminishing the opportunities for conifers to escape the competitive effects of fast-growing angiosperms. Thus ‘crocodiles’ may alter the outcome of the race between ‘hares’ and ‘tortoises’.

Key-words: chronosequence, competition, forest, light transmission, microsite, nutrients, PAR, podocarpaceae, regeneration, resource, retrogressive, safe sites

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Introduction

Angiosperms first appeared in the Early Cretaceous, and rapidly assumed dominance of most terrestrial ecosystems (Raven 1977; Bond 1989; Midgley & Bond 1991). Their diversification and rise to dominance was associated with the virtual elimination of gymnosperms (including coniferous trees) from the tropics, and a decrease in gymnosperm abundance in many other terrestrial ecosystems. Conifers are now generally dominant only at high latitudes, in subalpine forests, in arid regions and on nutrient-poor or poorly drained soils (Ellenberg 1988), but the mechanisms that led to this displacement remain controversial (e.g. Becker 2000). Bond (1989) argued that the faster growth rates of angiosperms during the early regeneration phase gave them a formidable competitive advantage over conifers, and resulted in their dominance at productive sites. Conversely, 'conservative' traits favoured conifer persistence in less productive habitats; for example, their tough, long-lived needles are advantageous on nutrient-poor soils (Grime 1979; Lusk *et al.* 2003; Richardson *et al.* 2004), and their narrow tracheids are less likely to cavitate when frozen, enabling persistence in boreal regions (Sperry & Sullivan 1992).

However, the faster early growth rates of angiosperms are not, by themselves, a sufficient explanation for the competitive displacement of conifers, because spatial or temporal refugia may allow 'inferior competitors' to escape the negative effects of competition (Rees *et al.* 2001). First, some tree species can escape the competitive effects of faster growing species by having greater shade-tolerance (Toumey & Korstian 1937; Augspurger 1984; Pacala *et al.* 1996). Some conifer species are known to tolerate deep shade, including *Prumnopitys ferruginea* in New Zealand (Brodrigg & Hill 1997), *Podocarpus nagi* in Japan (Kohyama & Grubb 1994), *Podocarpus nubigenus* in Chile, *Taxus baccata* in Europe (Bond 1989) and *Tsuga canadensis* in North America (Toumey & Korstian 1937); these species come to dominance in forests long after catastrophic disturbance (e.g. Enright & Ogden 1995). Secondly, 'inferior competitors' can persist by having superior colonization ability (Coomes & Grubb 2003). Thirdly, species with long-lived reproductive life stages may persist alongside superior competitors by taking advantage of opportunities for successful regeneration that arise infrequently in temporally variable environments (Chesson & Huntley 1997). For example, several species of conifer in New Zealand (mostly in the Podocarpaceae and Araucariaceae) are recognized as 'long-lived pioneers', which colonize extensively after catastrophic disturbance (such as volcanic ash deposition, landslide or earthquake) and then form conifer-dominated stands that persist for many hundreds or even thousands of years (Ogden & Stewart 1995). Pines in the northern hemisphere provide further examples of 'pioneer' conifer species, often associated with both primary and secondary succession (Christensen & Peet 1984; Richardson 2000; Walker &

del Moral 2003). When conifers do not fit the 'general rule' of exclusion from relatively productive habitats, a better understanding of the underlying escape mechanisms may help resolve the biogeographical patterns.

We argue that conifers are generally less abundant in productive habitats because such habitats usually provide fewer (or less frequent) opportunities to escape competition from faster growing angiosperm trees (Veblen *et al.* 1995). One possible hypothesis is that forests in productive sites cast deeper shade, and thereby provide fewer opportunities for conifers to escape faster growing angiosperms. Under such conditions trees in general may (i) allocate more resources to leaf production, and so have greater leaf area with which to capture light (Chapin 1980; Tilman 1988), (ii) grow taller and attain greater stem basal area, and so intercept more light with their trunks and (iii) have increased shade-tolerance, allowing shrubs and small trees to attain high densities in the forest understorey (Wright 1992; Burslem *et al.* 1996; Givnish 1999; Coomes & Grubb 2000). We argue that shade-tolerant species, in general, are able to establish on the forest floor of productive sites, but that light transmission is too low for seedlings to accrue height, and that they are either killed by other hazards (e.g. falling branches and animal activity) or do not gain a sufficient initial size advantage in the understorey to prevent overtopping by faster growing trees when a tree-fall gap forms above them.

Our alternative hypothesis is that conifers have fewer opportunities to escape angiosperm competitors in productive habitats, because increased competition from ground-layer plants restricts the numbers of microsites available for seedling establishment. Many studies indicate that shade-tolerant herbs and ferns can block the regeneration of certain species, and thus 'filter' which species are capable of regenerating (e.g. Takahashi 1997; Humphrey & Swaine 1997; Russell *et al.* 1998; George & Bazzaz 1999a, 1999b, 2003; Pages & Michalet 2003). Other studies have suggested that changes in the prominence of shade-tolerant herbs along productivity gradients could have important implications for forest dynamics (Veblen 1989). Combining these two lines of thought, could competition from shade-tolerant herbs and ferns operate as a differential filter on conifer and angiosperm seedlings in productive sites, and thereby contribute to a dearth of conifers in such locations?

The lowland temperate rain forests of New Zealand provide an excellent opportunity to explore the mechanistic basis for conifer distributions along productivity gradients, because many stands contain mixtures of conifer and angiosperm trees, sometimes in equal abundance (Wardle 1991; Enright & Ogden 1995; Ogden & Stewart 1995). Shade-tolerant ferns dominate the ground layer of these temperate rain forests, and suppress seedling establishment in some sites (June & Ogden 1975), although the effects of ferns on regeneration are not entirely negative for all species. Tree-ferns, in particular, may support large numbers of epiphytic seedlings on their trunks, and provide opportunities for

certain species to regenerate successfully (Pope 1926; Beveridge 1973; Newton & Healey 1989). However, little is known about trends in fern cover and morphology along environmental gradients, so their influences on seedling establishment at the landscape scale are poorly understood. If ferns do act as a regeneration filter, then the dynamics of 'tortoise-like' conifers and 'hare-like' angiosperms (*sensu* Bond 1989) could be influenced by indirect competition from 'crocodile-like' ferns. Here, we quantify the extent to which conifer abundance changes along a soil chronosequence in southern South Island, New Zealand. We address our first hypothesis by determining the ways in which tree and fern-layer composition and structure vary along the soil chronosequence, and what consequences these changes have on light transmission. We then address our second hypothesis by determining how seedling densities vary among sites, and if there is evidence that conifers have fewer opportunities to escape competition in productive habitats.

Materials and methods

STUDY AREA

The study area is situated in the south-west of the South Island, New Zealand, in the Waitutu Ecological

Region of Fiordland National Park (46.4° S 167.2° E; Fig. 1). The area is characterized by a series of 13 uplifted marine terraces on soft Tertiary rock, each of which is overlain by granite gravels (pebbles that were part of rocky beaches), separated by steep scarps, which are former sea cliffs that have eroded and collapsed under gravity (Ward 1988). Each terrace corresponds to a period of relatively high sea levels, and the youngest is a Holocene raised beach close to sea level, while the oldest lies 12 km inland at an elevation of 1040 m and is estimated to be at least 900 000 years old (Ward 1988). The terrace sequence is intersected by two large rivers, the Waitutu and the Wairaurahiri, and several smaller streams. The two large rivers are bordered by narrow alluvial terraces that range in width from 100 m to 1500 m (Fig. 1). Soils close to the rivers are regularly refreshed by fresh alluvial deposition, but surfaces further away are much older and are no longer refreshed (Hewitt 1988).

We chose to contrast three vegetation types growing along the sequence of alluvial and marine terraces (terrace numbers follow Ward 1988): forests bordering the rivers (alluvial sites, denoted by A in Fig. 1), forests located on terraces 2–4 (terrace sites: T) and shrublands located on terrace 6 (shrubland sites: S). Alluvial surfaces are less than 24 000 years in age, terraces 2, 3 and 4 have been dated at 79 000 years, 99 000 years and 121 000

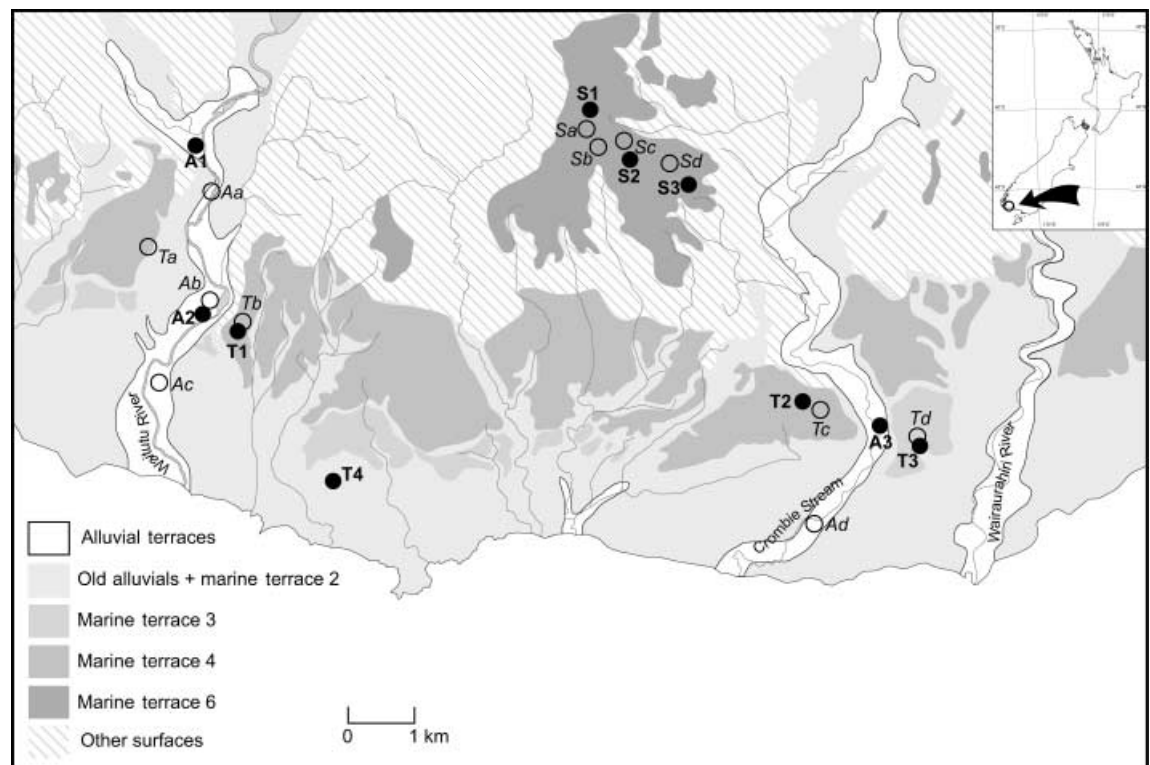


Fig. 1 Map of study area in south-western South Island, New Zealand, showing a sequence of marine terraces and alluvial surfaces (adapted from Ward 1988). About 13 marine terraces have been formed by uplift during the Quaternary (of which terraces 2, 3, 4 and 6 are identified), forming a chronosequence dating back about 900 ky. Streams have dissected the marine terraces and deposited alluvial surfaces; the youngest alluvial surfaces border the rivers shown, while marine terrace 2 has been extensively reworked by rivers during the penultimate and antepenultimate glaciation. Permanently marked plots have been established in the alluvial forests bordering rivers (prefixed with 'A'), in forests on terraces 2, 3 and 4 (prefixed with 'T'), and in shrublands on terrace 6 (prefixed with 'S'). Filled circles indicate the position of ten 1.5-ha plots (suffixed with numbers), and open circles indicate the locations of 12 clusters of four 0.04-ha plots (suffixed with lower-case letters).

years, respectively, and terrace 6 has been dated at 291 000 years (Ward 1988). The youngest marine terrace forms only a narrow non-continuous strip immediately next to the ocean, so was avoided in this study. Previous work has shown that the ecosystem properties of terraces 2–4 are non-distinguishable (Wardle *et al.* 2004), and the forests growing on them have similar structure. Elevation ranges from 300 m a.s.l. for terrace 6 to close to sea level for the alluvial terraces, so differences in air temperature may contribute to the differences in vegetation across the sites. However, these effects must be weak as the eroding escarpments around terrace 6 support large trees of all major species found lower in the terrace sequence.

The Waitutu terrace soils are generally silt loams, containing accumulations of quartzofeldspathic loess (Hewitt 1988; Mark *et al.* 1988), underlain by an apparently impermeable layer of consolidated granite pebbles at a depth of 40–100 cm. The terraces have only a slight slope, and annual rainfall is 1600–2400 mm (Ward 1988), so they are poorly drained, and the soils are often saturated. The climate is moderated by the influences of the surrounding oceans, so that winters are mild with snow infrequent in the lowlands. The mean January (summer) and July (winter) temperatures are 12 °C and 5 °C, respectively (Ward 1988).

CONIFER ABUNDANCE AND ITS ENVIRONMENTAL CORRELATES

Vegetation survey

'Small' (0.04-ha) and 'large' (1.5-ha) permanent plots were established in each vegetation type, and different selection criteria were applied when locating these plots. In alluvial forests, the small plots (at sites Aa–d, Fig. 1) were selected to be representative of the most recent alluvial deposits, where there was little humus development (< 1 cm depth); all these plots were within 30 m of the river. The large plots (A1–3) were selected to be representative of the whole alluvial surface, and included older surfaces with deeper humus and some podzol development. In the terrace forests (T), small and large plots were selected to be representative of the predominant vegetation. In the terrace shrublands, which are characterized as ombrotrophic bogs (Mark *et al.* 1988), the small plots were concentrated on slightly raised hummocks, which supported shrubs (*c.* 1–3 m tall) and short trees (< 6 m tall), and avoided the hollows, which are permanently wet and dominated by *Sphagnum* and non-woody plants. The large plots were representative of the surface as a whole.

The small permanent plots (20 × 20 m) were established in the austral summers of 2001/02 and 2002/03. In each of the vegetation types we selected four 1-ha sites, within each of which a cluster of four plots was established. On each 0.04-ha plot, all trees and tree-ferns with stems greater than 4.0 cm d.b.h. (diameter at breast height, 1.4 m) were tagged and their diameters measured with tape measures (Wiser *et al.* 2001). In addition, a full species list was recorded on each plot, using the

classification of Allan (1961) and Connor & Edgar (1987). Large plots (1.5 ha) were established in the austral summers of 2001/02 and 2002/03 (numbers in each vegetation type: A = 3, T = 4, S = 3; Fig. 1). Twenty-four sampling points were set out at 20-m intervals on a grid within each of the 100 × 150 m plots; at each of these points a PVC pipe was inserted into the ground, and these piezometers were visited sporadically to measure water-table depths (with a ruler). Light transmission and soil chemistry measurements were taken around these points (see below). All canopy trees of > 10 cm d.b.h. and all subcanopy (palatable) trees of > 2.5 cm d.b.h. in each large plot were mapped by triangulation from control points, using an Impulse 500 station (Laser Technology Inc., Colo., USA). Additionally, all tree-ferns > 2.0 m in height were mapped and their heights and diameters recorded. Vegetation was not mapped in the three large shrubland plots, but maximum vegetation heights were recorded within a 2-m radius of each piezometer.

Growth rates

Growth in each vegetation type was compared by stem increment measurements obtained by tree-ring analyses. No tree species was found on all three surfaces. In January 2003, we took cores from randomly selected trees of *Weinmannia racemosa* on alluvial plot Ac (24 stems), and on terrace forest plots T1, T2 and T3 (64 stems). We also took cores from randomly selected *Nothofagus solandri* var. *cliffortioides* growing on T1 and T3 (111 stems), and took discs in the vicinity of S1, S2 and S3 (44 stems). Cores were extracted at breast height, glued into mounts and sanded until the growth rings were clearly observable under a binocular microscope. The age of each tree was estimated from its rings, and growth was estimated by dividing stem radius by age.

Soil chemistry

Soil samples were taken in February 2002 at each of 24 sampling points in a subsample of large permanent plots on each vegetation type (A = 2, T = 4 and S = 2 plots). Soils were collected from three areas on the perimeter of a circle of 1-m radius centred on a sampling point, and pooled for analysis. After discarding identifiable fragments of litter, a 15 × 15 cm block of the F/H layer was cut with a knife from each of the three areas, and all three blocks were placed into a single polythene bag (*i.e.* were pooled for analysis). The depth of the F/H layer was measured in each hole with a tape measure. Next, three mineral soil samples (each 0–15 cm deep and 58 mm in diameter) were extracted from each of the three areas, and were placed together into a second polythene bag. Prior to analyses, soil samples were kept cool, and moist sieved (4 mm) to remove coarse organic debris, roots and stones. Each sample was split into two subsamples. One soil subsample was dried at 30 °C and used for measurement of pH (in water), total C and N (FP2000 CN analyser; LECO

Corp., Mich., USA), total P (ignition and dissolution in 0.5 M sulphuric acid), inorganic P (dissolution in 0.5 M sulphuric acid) and organic P (difference between total and inorganic pools), all according to Blakemore *et al.* (1987). The second subsample was adjusted to 60% water-holding capacity and used to measure aerobic net N mineralization: 10 g of the subsample underwent extraction in 100 ml 2 M KCl at day 0, and a further 10 g were placed into a 125-ml polypropylene container for incubation. Containers were covered with polyethylene (30 μ m), and put into plastic trays containing water. The trays and containers were put in polyethylene bags to maintain high humidity, and placed in an incubator at 25 °C for 56 days before extraction in 100 ml 2 M KCl. This system allows for gas exchange. Day 0 mineral N was subtracted from day 56 values to give aerobic potentially mineralizable N. Nitrate-N and ammonium-N were measured colorimetrically (QuikChem 8000; LaChat Instruments, Wisc., USA). All soil results are expressed per unit area of ground; we used the bulk densities of the FH and mineral layers to convert concentration measurements into per-unit area quantities.

Drainage characteristics

Capacitance meters (Omnilog Trutrack, Christchurch, New Zealand) were inserted into the soil at two grid intersections within each mapped stand, to log water-table fluctuations. The capacitance meters were installed within 1-m PVC tubes inserted as far into the ground as possible (they hit layers of boulders at 30–100 cm depth). They recorded water-table depth every 2 h for 4 months, after which time the data were downloaded onto a PC. These data were summarized by calculating the total numbers of days that the water table spent in each of three depth classes (0–20 cm, 20–40 cm, > 40 cm).

Foliar chemistry

Fully sunlit foliage samples of *Nothofagus menziesii*, *N. solandri* var. *cliffortioides* and *Weinmannia racemosa* were shot using a shotgun from the canopy of each small plot in which they were present, in summer 2001. The leaves were oven dried at 80 °C, ground, and analysed for total N and P using a modified semi-micro Kjeldahl method (Blakemore *et al.* 1987) at the Environmental Chemistry Laboratory in Palmerston North, New Zealand. Leaf areas were calculated with an ellipse equation based on leaf diameter and width measurements given in Allan (1961), and seed lengths (embryo, endosperm and testa) were obtained from Webb & Simpson (2001).

Statistical comparisons

Soil and light data were analysed using linear mixed effects models (LME) that explicitly take the hierarchical sampling design (i.e. samples in vegetation plots) into account within the random error terms (Crawley 2002). The statistical significance of the association between

vegetation type and soil properties was tested by adding vegetation type as a fixed effect, and using a likelihood ratio test (Crawley 2002). Furthermore, in order to establish whether differences among vegetation types were consistent among the plots selected, a variance component was used to compare the variation among vegetation types (σ_A^2) with variation among plots within vegetation types (σ_B^2), and with the residual variation within plots (σ_C^2), using the VARCOMP routine (S-PLUS 6.0, Insightful Corp., USA). The components are presented as σ_A^2/σ_C^2 (= vegetation-type variance ratio VarV) and σ_B^2/σ_C^2 (= plot variance ratio VarP); when the vegetation-type variance ratio greatly exceeds the plot variance ratio, the differences between surfaces are highly consistent among plots.

LIGHT TRANSMISSION ALONG PRODUCTIVITY GRADIENT

Light transmission measurements were taken at ground level and 1.4 m above ground level at the same 24 sampling points as used for soil chemical analyses. The percentage of photosynthetically active radiation (% PAR) transmitted through the tree and fern canopies was measured on cloudy days using paired quantum sensors (LI-1905B, Licor, Lincoln, Neb., USA) in April 2002. One quantum sensor was used to take instantaneous light measurements at ground level and then at 1.4-m height in the forest understorey (three instantaneous readings at each location), while another was connected to a logger (LI-1400, Licor) in a large forest clearing close to the stand, providing a continuous measure of incoming flux, which was logged every 10 s and averaged every 5 min. Each understorey reading was paired with an external reading taken within 2.5 min of it, and the ratio of these gave the percentage transmission of diffuse light (henceforth % PAR). These light measurements were analysed by LME models, as described in the soil section above. We omitted data from one plot, because the external reading contained periods of direct sunlight, which strongly biased percentage transmission calculations. In addition, light transmission was measured at ground level, at 1.4 m and immediately above the canopies of the 61 *Cyathea* and 49 *Dicksonia* tree-ferns that were found within nine 2-m-wide strips, separated by 500 m, orientated in an east–west direction across two alluvial terraces sites (A1 and Ac in Fig. 1). Our measurements of diffuse light transmission are well replicated spatially but do not fully represent the light environment (Canham *et al.* 1990). In particular, they do not provide information on the frequency of sunflecks, which can influence the photosynthetic responses of understorey foliage (Chazdon 1988; McDonald & Norton 1992; Whitehead *et al.* 2004).

SEEDLING ESTABLISHMENT PATTERNS

Within each of the small plots, 24 circular seedling subplots were established, each with an area of 0.75 m².

Within these, the number of stems of each vascular species was recorded in the following height classes: 16–45 cm, 46–75 cm, 76–105 cm, 106–135 cm and > 135 cm. Any plants < 16 cm tall were recorded as present but were not counted.

Seedling establishment patterns were also quantified in natural tree-fall gaps (numbers of gaps: A = 5, T = 9). All gaps had clearly identified 'gap-making' trees at advanced stages of decomposition (soft wood, covered in moss, small branches and twigs decomposed). The size of each gap was estimated from two perpendicular measurements, assuming an ellipsoidal shape. Seedlings were then counted in 15 × 15 cm quadrats on a 1 × 1 m grid that was laid out across the entire gap. The following were recorded for each quadrat: the height of the substrate above the general ground surface (to the nearest 10 cm), the number and species of seedlings (15–135 cm tall) and the occurrence of ferns within 50 cm of the quadrat. Because raised surfaces were infrequent, but important, sites for establishment, we sampled all surfaces > 80 cm off the ground at a higher density, using a 0.50 × 0.50 m grid, and estimated the total area of these raised surfaces using tape measures. Finally we recorded the species identity and establishment height of all saplings (> 135 cm tall and < 3 cm d.b.h) within the gaps. These data were analysed by comparing counts of seedlings and saplings in three substrate height classes (0–20 cm, 20–80 cm, 80 cm), using a generalized linear model (GLM), with Poisson errors, and treating gaps as replicates. For analyses of individual species, data from all gaps were pooled, and the frequency of seedlings on the forest floor (0–20 cm) and on raised surfaces (> 20 cm) was compared with the frequencies expected by chance (i.e. knowing the proportion of the gaps occupied by forest floor and raised surfaces) using a randomization test, based on 1000 draws.

Seedlings on tree-fern trunks (caudices) were recorded in transects at two alluvial forest sites (see above – there were few tree-ferns on the other surfaces). These transects totalled about 2 km in length and all seedlings on tree-

fern trunks (61 *Cyathea* and 49 *Dicksonia*) were counted, the seedling heights were measured and their species identified. All trees over > 4 m tall within 5 m of the transect lines were examined to see whether they had regenerated on tree-ferns – the criterion for epiphytic regeneration was that traces of tree-fern stem were visible embedded in the tree trunk.

Results

CONIFER ABUNDANCE AND ITS ENVIRONMENTAL CORRELATES

Low soil fertility and poor drainage on the marine terraces were associated with an increased dominance of conifers compared with the alluvial terraces (Fig. 2). There were lower densities of conifers in alluvial compared with terrace forest, both in the 0.04-ha plots (A = $21 \pm 38 \text{ ha}^{-1}$ and T = $545 \pm 38 \text{ ha}^{-1}$, GLM with log-link, $F_{1,31} = 93.1$, $P < 0.001$) and in the 1.5-ha plots (A = $15.8 \pm 9.0 \text{ ha}^{-1}$ and T = $468 \pm 97 \text{ ha}^{-1}$, $F_{1,5} = 4.6$, $P = 0.02$). The conifers comprised a lower proportion of basal area in alluvial forests within the 0.04-ha plots (A = 0.05 ± 0.03 and T = 0.57 ± 0.05 , GLM with arcsine-transformed data, $F_{1,31} = 55.1$, $P = 0.001$) and within the 1.5-ha plots (A = 0.063 ± 0.035 and T = 0.583 ± 0.031 , $F_{1,5} = 8.1$, $P < 0.0001$). There was no further increase in conifer dominance in the terrace shrublands (0.04-ha plots only; S = 0.58 ± 0.05 vs. T = 0.57 ± 0.05 , $F_{1,23} = 0.289$, $P = 0.77$), but a completely different set of conifer species dominated than those found in the terrace forests (Appendix).

The increasing dominance of conifers from A to T was associated with declines in tree growth rates, in total soil P and in soil net N mineralization rate. Thus the growth of *Weinmannia racemosa* was much slower in T than A (Table 1; $t = 4.2$, d.f. = 15, $P = 0.0008$). Although overall conifer dominance did not change between S and T, growth of *Nothofagus solandri* var. *cliffortioides* was slower on S (Table 1; $t = 7.2$, d.f. = 48, $P = 0.0001$).

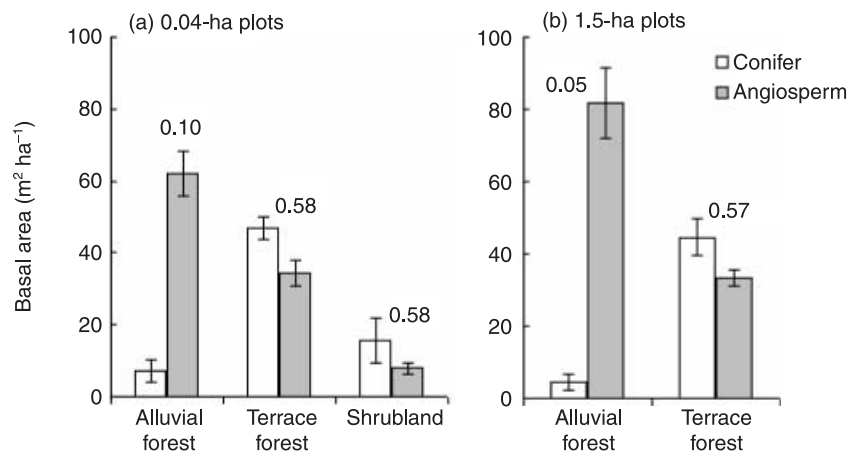


Fig. 2 Mean basal area (± 1 SEM) of conifers (open bars) and angiosperms (shaded bars) growing in alluvial forests (most productive), terrace forests, and terrace shrublands (least productive), estimated from data collected in (a) 0.04-ha plots and (b) 1.5-ha plots. Numbers above pairs of columns are proportions of conifers.

Table 1 Mean (± 1 SEM) growth rates of two tree species, and the chemical and drainage characteristics of soil under alluvial forest (A), terrace forest (T) and terrace shrubland (S). The sampling design for soil chemistry was hierarchical (20 samples within 1.5-ha plots, A = 2, T = 4 and S = 2), so analyses were made using a mixed-effects model, and statistical comparisons made by likelihood ratio tests (L , *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$). Superscript letters indicate significant differences among vegetation types (Student's t -tests, $P < 0.01$). The variance associated with vegetation types (VarV) and plots (VarP) are given as ratios of the residual variance. Water-table depths were measured with six capacitance probes in each vegetation type, every 2 h for 4 months

	Alluvial forest	Terrace forest	Shrubland	Variance ratios		Significance tests	
				VarV	VarP	L	P
Tree growth (mm yr⁻¹)							
<i>Weinmannia racemosa</i>	3.18 \pm 0.50 ^a	1.06 \pm 0.049 ^b					
<i>Nothofagus solandri</i> var. <i>cliffortioides</i>		2.27 \pm 0.112 ^a	0.20 \pm 0.017 ^b				
General soil properties							
pH	4.92 \pm 0.041 ^a	3.91 \pm 0.013 ^c	3.97 \pm 0.021 ^b	9.9	0.32	24	***
Total C (g m ⁻²)	6563 \pm 249 ^a	11757 \pm 357 ^b	10136 \pm 802 ^b	0.51	0.34	7.4	*
F/H layer depth (cm)	0.24 \pm 0.24 ^a	9.3 \pm 1.61 ^b	12.3 \pm 2.24 ^b	-0	0.27	6.5	*
Nitrogen							
N mineralization (g m ⁻²)	2.03 \pm 0.33 ^a	1.15 \pm 0.10 ^b	0.74 \pm 0.10 ^c	0.10	0.15	7.5	*
Total N (g m ⁻²)†	286 \pm 10.1	307 \pm 7.86	257 \pm 17.6	-0	0.25	2.1	NS
C : N ratio	24 \pm 0.80 ^a	39 \pm 0.547 ^b	39 \pm 0.80 ^b	2.7	0.66	19.5	**
Phosphorus							
Acid-digested P (g m ⁻²)	48 \pm 1.32	0.97 \pm 0.0057	0.58 \pm 0.014	2.6	3.6	6.9	*
Total P (g m ⁻²)†	87 \pm 7.9 ^a	11 \pm 0.36 ^b	8 \pm 0.5 ^b	6.4	5.0	9.7	**
C : P ratio	75 \pm 24 ^a	1031 \pm 43 ^b	1334 \pm 119 ^c	1.3	0.72	13.7	***
Organic : total P ratio	0.57 \pm 0.0403 ^a	0.92 \pm 0.0002 ^b	0.93 \pm 0.0042 ^b	2.0	0.64	17	***
N : P ratio	5.7 \pm 0.7692 ^a	28.5 \pm 0.811 ^b	38.7 \pm 2.74 ^c	1.6	0.9	14.4	***
Drainage							
Water in FH layer (g g ⁻¹)	237 \pm 24.0 ^a	412 \pm 15.0 ^b	537 \pm 21.1 ^c	0.42	0.26	20.8	***
Proportion of time water table spent in three depth classes							
0–20 cm	0.03 \pm 0.016	0.14 \pm 0.101	0.44 \pm 0.163				
20–40 cm	0.08 \pm 0.052	0.46 \pm 0.060	0.38 \pm 0.292				
40+ cm	0.89 \pm 0.068	0.40 \pm 0.104	0.17 \pm 0.101				

†P and N contents are comparable with those found in under coastal conifer forests (*Fitzroya cupressoides*) in Chile ($N = 98$ g m⁻², $P = 3.6$ g m⁻²), but much less than under European temperate forests ($N = 730$ g m⁻², $P = 280$ g m⁻²) (Ellenberg *et al.* 1986; Armesto *et al.* 1995).

There was a strong decrease in total soil P in A vs. T and S, with relatively small differences among plots within the vegetation types (high VarV and low VarP). The highest soil P was found in lower lying areas of the alluvial surfaces, which are regularly replenished with fresh alluvium; we found a negative association between soil surface height and total P in sites A1 (correlation, $r = -0.79$, $n = 23$, $P < 0.001$) and A2 (correlation, $r = -0.83$, $n = 21$, $P < 0.001$).

There was significant decline along the gradient (A > T > S) in net N mineralization rate, and a switch from NO₃ to NH₄. N mineralization was negatively associated with C : N_{soil}, which increased along the sequence as a result of a 150% increase in soil C (and greatly increased F/H layer depth) with relatively small changes in soil N (Table 1). There was a much greater decline in total P along the gradient than in total N, so the N : P ratio increased from 6 to 39 (Table 1). These results suggest that plants may become increasingly limited by P relative to N along the sequence. This is reflected in the foliar concentrations of P in fully sunlit canopy leaves of *Weinmannia racemosa* and *Nothofagus menziesii* in the terrace forests, which were 40% and 49%,

respectively, less than in the alluvial forests, whereas the foliar N concentrations were, respectively only 13% and 22% less (Table 2). Second, foliar P concentrations of *Nothofagus solandri* var. *cliffortioides* were 21% less in shrubland than in terrace forest, but the reduction in N concentrations was only 13% (Table 2).

Finally, the increased dominance of conifers along the sequence was associated with poorer soil drainage (Table 1). For most of the 4-month recording period, the water table was within 0–20 cm of the soil surface in the terrace shrubland, within 20–40 cm in the terrace forest and below 40 cm depth in the alluvial forests (Table 1; differences among sites tested by GLM with binomial errors; $F_{4,24} = 8.0$, $P = 0.0002$).

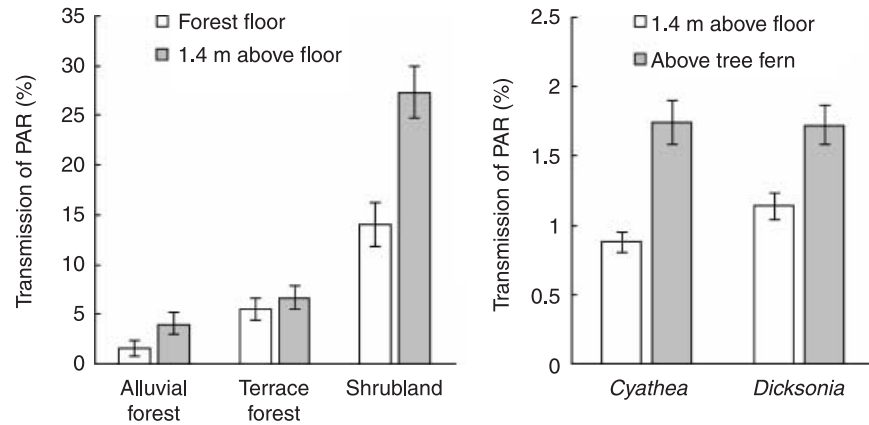
LIGHT TRANSMISSION ALONG PRODUCTIVITY GRADIENT

Effects of trees

The increase in conifer dominance along the sequence (A < T = S) was associated with decreased light interception by the forest canopy. Transmission of light to

Table 2 Mean foliar concentration (± 1 SEM) of phosphorus and nitrogen, taken from the leaves at the top of canopies in alluvial forest (A), terrace forest (T) and terrace shrubland (S) representing a fertility gradient (A > T > S). All comparisons between vegetation types are statistically significant at $P = 0.001$ (tested by Student's t -tests)

	Forest	Nitrogen (mg g ⁻¹)	Phosphorus (mg g ⁻¹)	N : P ratio
Canopy-top leaves				
<i>Nothofagus menziesii</i>	A	1.32 \pm 0.02	0.146 \pm 0.007	9.0 \pm 0.568
	T	1.15 \pm 0.01	0.088 \pm 0.007	13.1 \pm 1.56
<i>Weinmannia racemosa</i>	A	0.79 \pm 0.02	0.092 \pm 0.009	8.6 \pm 1.06
	T	0.62 \pm 0.01	0.047 \pm 0.003	13.1 \pm 1.05
<i>Nothofagus solandri</i> var. <i>cliffortioides</i>	T	0.98 \pm 0.03	0.073 \pm 0.003	13.4 \pm 1.97
	S	0.85 \pm 0.02	0.058 \pm 0.002	14.6 \pm 0.85

**Fig. 3** (a) Mean (± 1 SEM) percentage transmission of photosynthetically active radiation (PAR) through the canopies of alluvial forests, terrace forests, and terrace shrublands, recorded with quantum sensors placed at 1.4-m above the ground, and at ground level, under cloudy conditions; (b) mean (± 1 SEM) percentage of incoming PAR recorded above and below the crowns of *Cyathea smithii* and *Dicksonia squarrosa* (tree-fern species restricted to the alluvial forests). The outside PAR readings averaged 294 $\mu\text{mol m}^{-2} \text{s}^{-1}$.**Table 3** Comparison of the physiognomy, light transmission and regeneration of angiosperm-dominated alluvial forest (most productive), conifer-dominated terrace forest and conifer-dominated terrace shrubland (least productive)

	Alluvial forest	Terrace forest	Terrace shrubland
Forest physiognomy			
Height of tallest trees (m)	24	21	5
Maximum height of tree-ferns (m)	14	6	–
Mean height of ground-ferns (cm)	130	50	< 10
Tree-fern density (ha ⁻¹)	610	19	Absent
Leaf size distribution of angiosperm trees			
< 225 mm ² Nanophyll*	6	6	2
225–2025 mm ² Microphyll	8	6	1
> 2025 mm ² Mesophyll†	10	3	0
Mean light transmission (%)	1.5	4.6	29
Regeneration			
Seedling densities (m ⁻²)	0.25	3.2	0.44
Vegetative reproduction	Uncommon	Common	Dominant

*Smallest leaf = 6 mm², so includes two picophyll species.

†Includes notophyll and mesophyll species.

1.4 m above the forest floor increased along the sequence (Fig. 3a; A = 4.0 \pm 1.07, T = 6.7 \pm 1.15 and S = 27 \pm 2.6% PAR, LME modelling tested with a likelihood ratio test, $\chi^2 = 17.9$, d.f. = 2, $P < 0.0001$). The gradient of light transmission was correlated with a decline in

forest stature (Table 3), and a decline in the species richness of angiosperm trees, particularly in the sub-canopy layer: of the 22 short (i.e. < 10 m) angiosperm tree species of the alluvial forests only 10 were present in the terrace forests, and all were uncommon, whereas

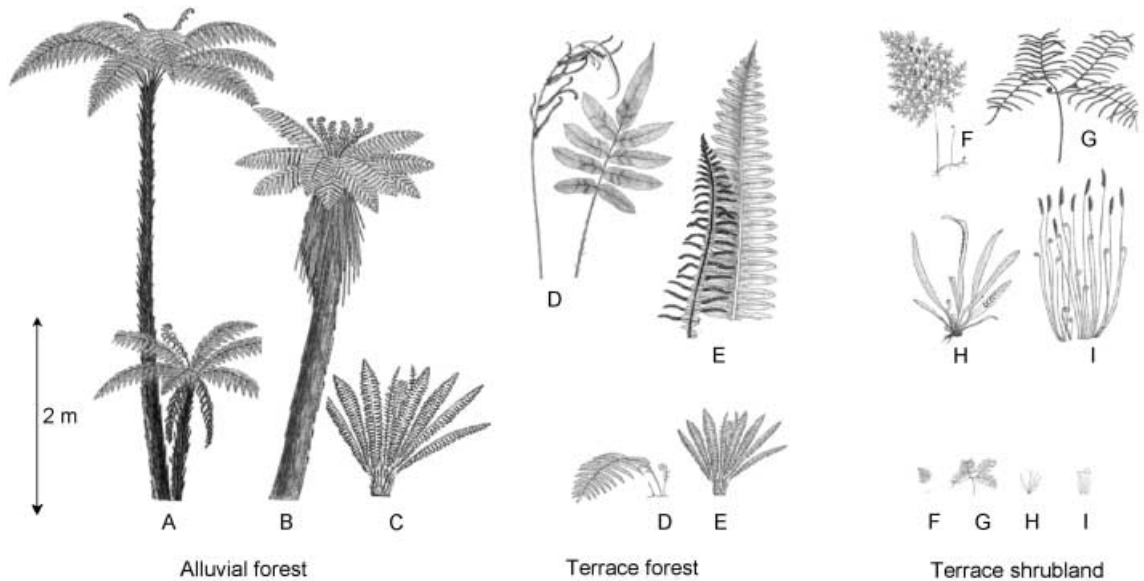


Fig. 4 Dominant fern species of alluvial forest (most productive), terrace forest and shrubland (least productive), drawn approximately to scale, with insets showing the fronds in greater detail (including fertile fronds for *Blechnum*). The species are: A, *Dicksonia squarrosa*; B, *Cyathea smithii*; C, *Blechnum discolor*; D, *B. procerum*; E, *B. discolor* (again); F, *Hymenophyllum multifidum*; G, *Gleichenia dicarpa*; H, *Grammitis billardierei*; and I, *Schizaea fistulosa* (drawings modified from Wilson 1994).

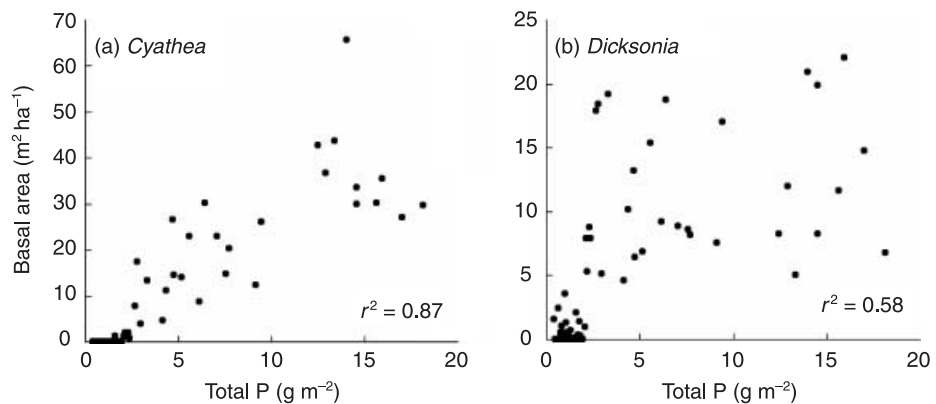


Fig. 5 Relationships between total soil P content (g m^{-2}) and basal area of tree-ferns (a) *Cyathea smithii* and (b) *Dicksonia squarrosa* within 15 m of the sampling point. Non-linear regression curves, fitted by mixed-effects modelling, are (a) $BA = 83 / (1 + 18.1 / (P - 1.16))$ and (b) $BA = 16 / (1 + 5.68 / (P - 0.59))$, where BA is basal area and P is total soil P, and plot was included as a random term. There was stronger support for this three-parameter model than simpler models that were compared using AIC tests.

the two short tree species that were found only on the marine terraces were also uncommon (Appendix). Most of the subcanopy species were mesophylls (leaf area $> 2025 \text{ mm}^2$), whereas most of the canopy trees were microphylls (leaf area $225\text{--}2025 \text{ mm}^2$), so the loss of subcanopy species was associated with a shift towards smaller leaf sizes in the terrace forests (Table 3).

Effects of ferns

Tree-ferns and tall *Blechnum* ferns formed a dense ground layer in the alluvial forests, but ferns were shorter in the terrace forests, inconspicuous in the shrublands (Fig. 4) and intercepted little incoming light. Tree-ferns attained their highest densities on alluvial surfaces,

especially where the soil contained high levels of P (Fig. 5). These P-rich patches were relatively low lying (see above), and appear to be regularly refreshed with alluvial deposits. *Dicksonia* tolerated lower P concentrations than *Cyathea*, and was found in low densities in the terrace forests, where *Cyathea* was absent. Higher densities of tree-ferns were recorded on the 0.04-ha plots than on the 1.5-ha plots (*Cyathea* = $551 \pm 85 \text{ ha}^{-1}$ vs. $328 \pm 91.3 \text{ ha}^{-1}$, respectively, and *Dicksonia* = $431 \pm 70 \text{ ha}^{-1}$ vs. $285 \pm 38.4 \text{ ha}^{-1}$, respectively) because the small plots were located on the youngest alluvial surfaces. Tree-fern densities were not responsive to local crowding by canopy trees (i.e. basal area of trees within 15 m of the sampling point). The forest floor beneath the tree-ferns was more heavily shaded than elsewhere

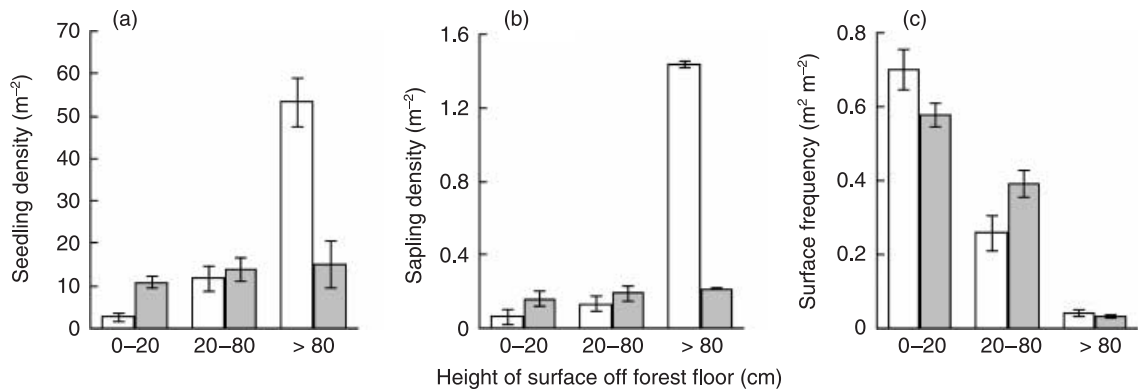


Fig. 6 Comparison of establishment and regeneration on the forest floor (0–20 cm), on slightly raised surfaces (20–80 cm), and on large logs (> 80 cm off ground) in alluvial (open bars) and terrace forests (filled bars): (a) density of seedlings, (b) density of saplings, and (c) frequency of surface types.

in the alluvial forests, with only $0.88 \pm 0.074\%$ transmission of PAR to the ground under *Cyathea* and $1.14 \pm 0.097\%$ under *Dicksonia* (Fig. 3b); shade was significantly deeper under *Cyathea* (Wilcoxon rank test, $Z = 2.0$, $P = 0.046$). Comparison of above- and below-frond readings indicated that the tree-ferns intercepted about half of the incoming radiation (*Cyathea*, 51%; *Dicksonia*, 44%); they cast deep shade because their megaphyll fronds arch out near horizontally, maximizing light interception (Fig. 4). In the alluvial forests a further fern species, *Blechnum discolor*, occurred in 56% of seedling subplots within the small plots and in 94% of seedling plots within five tree-fall gaps. *Blechnum discolor* typically reached 1.3 m height, and had dense ‘shuttlecocks’ of fronds that cast dense shade (Fig. 4). The fern layer cast deep shade onto the forest floor, intercepting about 61% of the incident radiation (Fig. 3a; average $4.0 \pm 1.2\%$ PAR above, $1.5 \pm 0.61\%$ PAR below, $Z = 4.7$, $P < 0.0001$).

A shorter fern species, *Blechnum procerum*, dominated the ground layer of the terrace forest (in 93% of seedling plots), where it spreads rhizomatically, sending up highly dissected fronds from beneath the ground (Fig. 4). *Blechnum discolor* also occurs, but at a much lower frequency than on the alluvial soils (being present in 5% of seedling plots), and is much shorter (rarely attaining 75 cm height vs. 135 cm on the alluvial soils). The fern layer in terrace forests intercepts about 20% of the incoming light (Fig. 3a; average $5.7 \pm 1.7\%$ PAR above, $4.6 \pm 0.14\%$ PAR below, $Z = 4.7$, $P < 0.0001$).

In the terrace shrubland, *Gleichenia dicarpa* was the tallest fern species, often reaching around 30 cm, but was found on only 13% of seedling plots. It is also rhizomatous, and has very open fronds, which intercept little light (Fig. 4). The other shrubland ferns are diminutive, all holding tiny fronds nearly vertically, and intercepting little light (Fig. 3a). The percentage PAR at ground level averaged $16 \pm 1.2\%$, while at 1.4-m height it averaged $29 \pm 1.5\%$ ($Z = 6.9$, $P = 0.001$), with much of the light interception resulting from the high density of woody plants in the ground layer (see above).

The changes in fern architecture and density were associated with less light penetration to the forest floor of A compared with T or S (LME model, likelihood ratio test, $\chi^2 = 18$, d.f. = 1, $P = 0.0001$). Virtually complete cover of tall ferns in the alluvial forests appeared competitively to suppress shorter fern species, with fewer subplots containing short ferns in alluvial forests than in the terrace forest (0–15 cm size class, A = $63 \pm 4\%$ vs. T = $98 \pm 2\%$, $Z = 7.1$, $P < 0.0001$; 16–45 cm size class, $38 \pm 3\%$ vs. $69 \pm 2\%$, $Z = 7.5$, $P < 0.0001$).

SEEDLING ESTABLISHMENT PATTERNS

In the alluvial forests, seedling densities were extremely low, both in the understorey (only $0.25 \pm 0.051 \text{ m}^{-2}$ in 0.04-ha plots) and on the forest floor in tree-fall gaps ($2.66 \pm 0.97 \text{ m}^{-2}$ in gap-centred plots). Establishment in these forests was almost entirely on two types of raised surfaces: rotting logs and tree-fern trunks. Seedling density was much greater on rotting logs than on the forest floor (Fig. 6a; $F_{2,12} = 58.0$, $P < 0.0001$), as were sapling densities (Fig. 6b; $F_{2,12} = 5.3$, $P = 0.02$). Although surfaces over 80 cm high occupied about 3% of gap areas (Fig. 6c), they contained 31% of all seedlings and 47% of all saplings. Most species had significantly more seedlings and saplings on raised surfaces than predicted by chance (Table 4); the only exception to this was the angiosperm *Pseudowintera colorata*, which grows in deep shade under tree-ferns and does not rely on raised surfaces. *Cyathea smithii* had an average of 1.2 seedlings per trunk, and *Dicksonia squarrosa* had an average of 2.4 seedlings per trunk, corresponding to densities of 0.039 m^{-2} and 0.067 m^{-2} of ground area (based on tree-fern densities in the 1.5-ha plots). The vast majority of epiphytic seedlings were small-seeded angiosperms, *Weinmannia racemosa* (74%), *Pseudopanax simplex* (12%) and *Coprosma foetidissima* (5%), while another 13 species of angiosperm tree were represented by a total of 1–3 seedlings on the 109 tree-ferns sampled. Only one conifer seedling was found growing epiphytically. Examination of mature trees for signs of embedded

Table 4 Microsite preferences of regenerating trees in tree-fall gaps in alluvial and terrace forests. The total numbers of seedlings (n) enumerated and the proportion of those seedlings located on raised surfaces are given for common species (c = coniferous); the proportions are compared with those expected under the null hypothesis that plants are equally likely to establish on raised surfaces as on the forest floor, and randomization tests were used to determine whether these proportions were significantly higher (+) or lower (-) than the null expectation (** $P < 0.001$, * $P < 0.01$, * $P < 0.025$, ns not significant)

	Seed length† (mm)	Seedlings			Saplings		
		n	Prop	P	n	Prop	P
Alluvial forest							
<i>Carpodetus serratus</i>	1–1.7	10	(+) 0.63	**	25	0.28	ns
<i>Coprosma foetidissima</i>	5.5–7.5	25	(+) 0.61	**	43	(+) 0.84	***
<i>Nothofagus menziesii</i>	4.5–6.3	81	(+) 0.96	**	80	(+) 0.90	***
<i>Pseudowintera colourata</i>	2.6–3.6	10	(-) 0.10	*	15	0.20	ns
<i>Weinmannia racemosa</i>	1.1–1.5	68	(+) 0.96	**	8	(+) 0.88	***
Null hypothesis‡			0.30			0.30	
Terrace forest							
<i>Coprosma foetidissima</i>	5.5–7.5	9	0.76	ns	11	0.55	ns
<i>Dacrydium cupressinum</i> (c)	3.2–3.8	7	0.71	ns	10	0.50	ns
<i>Metrosideros umbellata</i>	2.0–3.0	32	(+) 0.89	***	–	–	
<i>Nothofagus menziesii</i>	4.5–6.3	23	(+) 0.67	***	7	0.14	ns
<i>Podocarpus hallii</i> (c)	6.5–8.5	46	0.32	ns	102	0.44	ns
<i>Prumnopitys ferruginea</i> (c)	11–17	145	0.39	ns	–	–	
<i>Weinmannia racemosa</i>	1.1–1.5	9	(+) 0.83	*	22	(+) 0.82	**
Null hypothesis‡			0.42			0.42	
Alluvial forest							
Angiosperms		200	(+) 0.77	***	188	(+) 0.71	***
Conifers		8	0.58	ns	4	1.00	ns
Null hypothesis‡			0.30			0.30	
Terrace forest							
Angiosperms		93	(+) 0.72	***	86	(+) 0.60	***
Conifers		198	0.39	ns	113	0.45	ns
Null hypothesis‡			0.42			0.42	

†Taken from Webb & Simpson (2001), including seed case.

‡The proportion expected under the null hypothesis is the area of raised surfaces as a proportion of ground area.

tree-ferns in their trunks showed that 60% of *Weinmannia* had regenerated epiphytically.

There were many more opportunities for establishment in the understorey of the terrace forest (average seedling density within 0.04-ha plots, $A = 0.25 \pm 0.051 \text{ m}^{-2}$ vs. $T = 3.2 \pm 0.68 \text{ m}^{-2}$; $Z = -4.8$, $P < 0.001$) and to a lesser extent in gaps (estimated seedling density within gaps, $7.1 \pm 0.89 \text{ m}^{-2}$ vs. $12.1 \pm 0.70 \text{ m}^{-2}$). In contrast to the alluvial sites, densities of seedling and saplings were no greater on raised sites than on the forest floor (Fig. 6a, $F_{2,8} = 0.54$, $P > 0.20$; Fig. 6b, $F_{2,8} = 0.15$, $P > 0.20$, respectively). When individual species were examined, none of the conifers showed any preference for establishing on raised surfaces, but three angiosperm species showed statistically significant preferences for raised surfaces (Table 4). Two of these angiosperms are small-seeded (*Metrosideros umbellata* and *Weinmannia racemosa*) and may be restricted to litter-free patches provided by the raised surfaces (Lusk & Kelly 2003).

The number of conifer seedlings was significantly lower in alluvial than in terrace forests (as a percentage of all seedlings, $A = 3.1 \pm 1.8\%$ vs. $T = 31.2 \pm 3.7\%$, $Z = -4.4$, $P < 0.001$); this is unsurprising given the differences in canopy composition between the two terraces. The percentage of conifer seedlings was remarkably

similar to the percentage of conifer basal area in the terrace forests (seedlings 31.2% vs. adults 31.0%, $\chi^2 = 0.23$, d.f. = 1, $P = 0.97$); there were too few seedlings in the alluvial forests to make such a comparison with any statistical confidence (seedlings 3.1% vs. adults 6.7%, binomial test, $\chi^2 = 2.45$, d.f. = 1, $P = 0.12$).

Within the shrubland communities, the numbers of stems counted in the 'seedling' tiers were an order of magnitude greater than in the terrace forests ($38 \pm 0.6 \text{ m}^{-2}$ vs. $3.2 \pm 0.68 \text{ m}^{-2}$; $Z = -3.88$, $P < 0.001$). However, few of these stems were actual seedlings, because many species regenerate vegetatively. True seedlings were found in only 14% of 216 subplots, with an average density of $0.442 \pm 0.048 \text{ m}^{-2}$. Many seedlings (27%) were of species never found as adults on the shrublands (especially *Nothofagus menziesii*), and presumably dispersed from forest margins on the edge of the terrace.

Discussion

CONIFER ABUNDANCE AND ITS ENVIRONMENTAL CORRELATES

The depletion of P along the early part of the chronosequence is consistent with an accumulating body of

evidence that P is weathered and leached without replacement during soil development along chronosequences around the world (Walker & Syers 1976; Crews *et al.* 1995; Vitousek & Farrington 1997; Vitousek *et al.* 1998; Chadwick *et al.* 1999; Richardson *et al.* 2004; Wardle *et al.* 2004). This process may be particularly rapid in high-rainfall areas of New Zealand (Smith & Lee 1984; Richardson *et al.* 2004), where P is lost with virtually no replenishment of nutrients from aerial deposition (Miller 1961; Verhoeven *et al.* 1987; Meurk *et al.* 1994). P depletion contributed to the substantial changes in the stoichiometry of C : N : P in plants and soils (Tables 1 & 2), and the resulting increase in P limitation is likely to have had major consequences (Koerselman & Meuleman 1996; Elser *et al.* 2000; Tessier & Raynal 2003; Wardle *et al.* 2004). One reason why conifers (specifically Podocarpaceae) may be advantaged on P-depleted soils is that they have long-lived leaves relative to their angiosperm associates (Lusk 2001; Richardson *et al.* 2004), and thus make more efficient use of nutrients (Monk 1966; Grime 1979; Vitousek 1982; Berendse & Aerts 1987). Recent evidence suggests that conifers may also acquire P more efficiently than angiosperms from the soil (Richardson *et al.* 2004; cf. Enright & Ogden 1995). However, although podocarps are heavily infected with endomycorrhizal associates (Baylis *et al.* 1963; Russell *et al.* 2002), which efficiently take up phosphate, the majority of angiosperm species in mixed lowland rain forests are also heavily infected (Hurst *et al.* 2002).

The abundance of conifers on older terraces was also associated with poor soil drainage, a property that has received little attention from ecosystem ecologists working on chronosequences (but see Mark *et al.* 1988; Kitayama *et al.* 1997). Reduced stature on poorly drained soils results from an inability of plants to transport oxygen to deep anchoring roots, without which woody plants are unable to grow tall (Crawford *et al.* 2003). Lowering the water table on ombrotrophic mires in the northern hemisphere results in aeration of the upper organic layer, and brings about an increase in soil temperature, decomposition rate and nutrient availability (e.g. Silins & Rothwell 1999), all of which facilitate the survival of trees that gradually invade (e.g. Lees 1972; Macdonald & Lin 1999). The prevalence of conifers in waterlogged sites, both in New Zealand and in other temperate forests (Crawford 1987), would appear to result from various morphological and biochemical adaptations. For example, *Taxodium distichum* develops knee roots containing ventilating tissues that carry oxygen to submerged parts, *Pinus* species develop large cavities in the steles and *Picea* species have shallow rooting systems that spread out above the anaerobic region (Crawford 1987). The podocarps on the older terraces were shrubs with many stems, which could improve aeration of roots via aerenchyma (Crawford *et al.* 2003). In terms of biochemical tolerance to anoxia, little seems to be known about whether conifers have low metabolic rates in their roots

or export carbohydrates from their roots (Crawford *et al.* 2003).

LIGHT TRANSMISSION ALONG THE PRODUCTIVITY GRADIENT

The difference in light transmission among vegetation types (from ~1% of incoming PAR on the alluvial forest floor to ~5% of incoming PAR in terrace forests) is sufficient to have profound effects on seedling survival (Osunkoya *et al.* 1993; Kobe *et al.* 1995; Coomes & Grubb 1996; Bloor & Grubb 2003). The few studies of shade tolerance for New Zealand forest trees suggest light-compensation points of between 1% and 4% (Wardle 1991); in northern temperate forests only a minority of species can maintain a positive carbon balance in less than 2% light (Pacala *et al.* 1996), depending upon nutrient supply from the soil (Coomes & Grubb 2000).

One possible explanation for the deeper shade cast on fertile soils is that trees allocate more resources to leaves when nutrients are plentiful (Tilman 1988; Huston 1994; Whitehead *et al.* 2004); this idea requires testing for the Waitutu chronosequence. A second explanation is the presence of subcanopy angiosperm trees (Table 3), which were predominantly mesophylls (*sensu* Raunkiaer 1934; Richardson *et al.* 2004). A third explanation for differences in light transmission was the presence of tall, dense ferns on the relatively fertile soils, giving way to shorter, less dense ferns on the nutrient-poor soils (Fig. 4, Table 3). Ferns dominate the ground layer in many New Zealand rain forests, particularly where soils and air are reliably moist (Lehmann *et al.* 2002), and their shade tolerance allows them to persist under evergreen canopies, unlike many herbs in temperate deciduous forests that take advantage of light penetrating to the floor before trees flush their leaves in spring (Ellenberg 1988). The height of ferns across the vegetation types was closely associated with P availability: tree-ferns dominate in P-rich patches of the alluvial forests, and tall *Blechnum discolor* dominate on older alluvial surfaces, both of which cast deep shade, whereas ferns were much shorter on the terraces, and had highly dissected fronds, which intercepted little light. Similarly, trees ferns are replaced by much shorter ferns on P-limited older sites in Hawaii (Vitousek 2004). The trends toward smaller ground-layer plants is consistent with patterns recorded for bamboos in South America (Veblen 1989) and south-east Asia (Takahashi 1997), whereas a scarcity of herbs is a general feature of infertile soils, both in the tropics (Gentry & Emmons 1987; Coomes & Grubb 1996) and in northern temperate forests (Grubb 1987; Cornwell & Grubb 2003). Herbs proliferate in clearings on fertile soils in North America and Europe, where they grow more quickly than tree seedlings because they invest more resources into resource-capturing tissue and less into structural tissues (Tilman 1982; Bond 1989), but are less abundant in gaps on infertile soils (Ellenberg 1988; Gilliam & Roberts 2003; de Grandpré *et al.* 2003).

The seminal work of Bond (1989) recognized the importance of resource competition in determining the geographical displacement of conifers, and built a case for conifers being excluded from productive sites because of their relatively slow growth as seedlings. We suggest that conifers in New Zealand are further disadvantaged in relatively productive habitats by three additional mechanisms: (i) shading in the forest understorey is so deep as to prevent shade-tolerant conifers from escaping competition from angiosperms, (ii) ground-ferns restrict seedlings to raised surfaces and (iii) tree-ferns provide sites for angiosperm seedlings to establish.

Firstly, few seedlings of any species were found to establish in the understorey of alluvial forests, presumably because establishment was blocked by shading from the multilayered forest canopy, dense tree-fern layer and near continuous cover of *Blechnum discolor* (Fig. 4). In contrast, a substantial seedling bank was found in terrace forests (Fig. 6a). Such seedling banks provide shade-tolerant species with a competitive advantage by allowing them to accrue height slowly in the absence of gap formation; this initial height advantage can be critically important when it comes to competition with faster growing seedlings in tree-fall gaps (Canham 1989; Burns 1993; Tanner *et al.* in press), particularly in fertile soils when competition for light is intense (Keddy *et al.* 1997). Several conifer species are tolerant of deep shade, but our results suggest that the limited opportunities for seedling-bank formation in the nutrient-rich sites may disadvantage shade-tolerant tree species, both angiosperm and conifer, pushing the system in favour of tree species whose seedlings grow relatively rapidly on logs in tree-fall gaps.

Secondly, seedlings fail to regenerate through the dense ferns on the ground in the alluvial forests, even in tree-fall gaps where herb cover becomes even greater (Midgley *et al.* 1995; George & Bazzaz 2003): this blocking effect of ferns might disadvantage conifers because of their relatively large seed sizes. In the alluvial forests, hardly any seedlings established under ferns, and seedling densities were 22 times greater on raised surfaces (> 80 cm) than on the forest floor. Small-seeded species produce many more seeds than larger-seeded species (Rees 1995; Coomes & Grubb 2003), and thereby have a greater seed rain onto the few raised surfaces available for establishment. Small-seeded angiosperms require raised surfaces for establishment, as shown by the three smallest seeded species regenerating preferentially on logs in terrace forest (Table 3), whereas all the larger-seeded species (including conifers) were equally able to regenerate on the ground (and would therefore be more affected by microsite restriction). Similar results are reported from Chilean forests, possibly because raised surfaces provide litter-free sites for the establishment of small seedlings, and provide a good substrate

for root penetration (Christie & Armesto 2003; Lusk & Kelly 2003). Ground-layer plants can have profound effects on forest dynamics, as illustrated by Takahashi's (1997) work on two conifer species in northern Japan; *Abies sachalinensis* regenerates on both the ground and elevated sites, and dominates forests in which bamboo is scarce, whereas *Picea glehnii* regenerates mostly on raised surfaces, and dominates in forests with dense bamboo understories. By analogy, we speculate that podocarps are disadvantaged by dense fern cover in the relatively fertile lowland forests of New Zealand, contributing to their scarcity.

Thirdly, tree-ferns acted as a filter on regeneration by allowing only small-seeded angiosperms to establish on their trunks. About 12% of all seedlings in the alluvial sites were situated on these trunks. Establishing on a vertical surface must present challenges for seedlings, and this is presumably a reason why the small seeds of *Weinmannia* preferentially establish there, whereas larger-seeded podocarps are absent. Several other studies from New Zealand have noted the importance of tree-fern stems as microsites for the establishment of small-seeded species (Pope 1926; Wardle 1966; Veblen & Stewart 1980). Beveridge (1973) envisaged tree-ferns as a serial species that came to dominate early successional stands, blocking conifer regeneration while allowing epiphytic regeneration of the various angiosperm species which eventually overtopped and suppressed the tree-ferns. In Jamaica, Newton & Healey (1989) have also found that small-seeded *Clethra occidentalis* relies locally on *Cyathea pubescens* stems as a site for regeneration.

The filtering effects of ferns in the New Zealand forests are less subtle than those reported by George & Bazzaz (1999a, 1999b, 2003) for forests in north-eastern USA. They showed that ferns reduced the regeneration success of seedlings, and found that some tree species were more affected than others, leading them to propose that the patchiness of fern cover was responsible for spatial heterogeneity in tree regeneration success, with potentially important implications for species coexistence. In contrast, we found that tall ferns formed a nearly continuous cover in the alluvial forests of New Zealand, and that very few seedlings could regenerate through this fern layer. We suggest that the filtering effect of ferns results primarily from the differential ability of tree species to establish on raised surfaces, rather than their differential ability to establish within different fern patches. However, we note that most of the seedlings found on the alluvial forest floor were of *Carpodetus serratus*, *Coprosma foetidissima* or *Pseudowintera colorata*, and that these short tree species are occasionally observed to recruit successfully through the *Blechnum* layer (i.e. a filtering effect as envisaged by George & Bazzaz 1999a).

The argument that regeneration opportunities for conifers are often more restricted in relatively productive sites is supported by a number of previous studies (Read & Hill 1988; Veblen *et al.* 1995). In the Andes,

Araucaria araucana (Araucariaceae) is able to establish under open canopies of *Nothofagus antarctica*, which resprouts after fire in drier areas (Burns 1993; Veblen *et al.* 1995). However, in the more mesic Chilean forests, *Araucaria* seedlings do not establish under closed stands of *N. antarctica* or *N. dombeyi*, but rely on large tree-fall gaps (Veblen 1982). Similarly, *A. araucana* grows under *N. antarctica* or *N. dombeyi* in relatively open Argentinian forests, taking advantage of small gaps as they arise (Burns 1993), but opportunities for regeneration are more limited on mesic sites where *N. dombeyi* grows faster and forms a denser canopy (Veblen *et al.* 1995). *Fitzroya cupressoides* seedlings are commonly found in the understorey of forests in Chilean mountains, but at lower altitudes in Chile they are less frequent at lower altitudes, and are increasingly restricted to areas of large disturbance (Donoso *et al.* 1993; Veblen *et al.* 1995). The same observation has been made for podocarps in South Africa (Midgley *et al.* 1995) and Tasmania (Read & Hill 1988). Together, these various strands of evidence suggest that competition from ground-layer herbs and ferns reduces regeneration opportunities in relatively productive habitats, and contributes to the relatively low abundance of conifers in such habitats.

Conclusions and future research

Our results suggest that modern angiosperms dominate many productive habitats because several mechanisms act in concert to reduce regeneration opportunities for conifers. The argument that angiosperms gain an advantage against New Zealand's conifers by having small seed size and tolerance of shade is consistent with recent palaeoecological evidence that identifies these traits as setting the angiosperms apart from Early Cretaceous conifers (Feild *et al.* 2004). Research is needed to identify the escape mechanisms that are employed by those conifers that can persist on relatively productive sites. For example, manipulation experiments are required to quantify the extent to which seedlings are out-competed by ground-ferns, and to discover whether tree-ferns facilitate regeneration by allowing epiphytic establishment, while simultaneously competing with those seedlings for resources. *Dacrycarpus dacrydioides* dominates expanses of forest on the relatively fertile alluvial floodplains in New Zealand (Wardle 1991; Duncan 1993), and there is substantial evidence to suggest that such conifers persist as 'pioneer' species that regenerate after catastrophic disturbance (Wardle 1991; Wells *et al.* 2001). The reasons why podocarps have colonization advantages after catastrophic disturbances are not entirely resolved. In the forests examined here, conifers are relatively large-seeded, and consequently produce fewer seeds per unit area, and so do not have a colonization advantage in that respect. However, podocarp seeds have a pseudo-aril, which facilitates long-distance dispersal by birds (Wardle 1991), and this attribute may provide a colonization advantage. Addi-

tionally, it is suggested that the conservative physiology of conifers may allow them to tolerate the inhospitable conditions on fresh alluvial surfaces, volcanic ash deposits and landslide successions (Ogden & Stewart 1995; Richardson 2000). The long lifespan of southern conifers is likely to be important in allowing persistence from one rare catastrophic disturbance event to the next (Enright & Ogden 1995; Veblen *et al.* 1995; Lusk & Smith 1998; Loehle 2000; Lusk & Del Pozo 2002), consistent with 'storage-effect' models (Chesson & Huntley 1997); a single catastrophic disturbance every thousand years may be sufficient to maintain conifers as dominant elements in forests (Wells *et al.* 2001).

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Appendix

Mean (± 1 SEM) basal areas ($\text{cm}^2 \text{m}^{-2}$) of tree species and tree-ferns in alluvial forests, terrace forests and shrublands (recorded on 16, 16 and nine plots of 0.04 ha, respectively). Taxonomy follows Allan (1961), except that for Podocarpaceae, which follows Connor & Edgar (1987)

Species	Family	Alluvial forest	Terrace forest	Terrace shrubland
Tall angiosperms trees				
<i>Nothofagus menziesii</i>	Fagaceae	24.118 \pm 5.047	11.317 \pm 2.912	
<i>Weinmannia racemosa</i>	Cunilnaceae	21.351 \pm 2.334	8.268 \pm 0.896	
<i>Metrosideros umbellata</i>	Myrtaceae		6.156 \pm 1.753	
<i>Nothofagus solandri</i> var. <i>cliffortioides</i>	Fagaceae		7.890 \pm 3.171	6.230 \pm 0.653
Short angiosperm trees				
<i>Griselinia littoralis</i>	Cornaceae	4.364 \pm 1.682	0.016 \pm 0.016	
<i>Carpodetus serratus</i>	Escalloniaceae	4.053 \pm 1.186		
<i>Fuchsia excorticata</i>	Onagraceae	2.541 \pm 0.860		
<i>Meliccytus ramiflorus</i>	Violaceae	0.860 \pm 0.403		
<i>Pseudopanax edgerleyi</i>	Araliaceae	0.621 \pm 0.274		
<i>Elaeocarpus hookerianus</i>	Eleocarpaceae	0.507 \pm 0.372	0.030 \pm 0.030	
<i>Coprosma rotundifolia</i>	Rubiaceae	0.318 \pm 0.083		
<i>Schefflera digitata</i>	Araliaceae	0.212 \pm 0.110		
<i>Pennantia corymbosa</i>	Icacinaceae	0.187 \pm 0.113		
<i>Pseudowintera colourata</i>	Winteraceae	0.179 \pm 0.056	0.016 \pm 0.016	
<i>Myrsine australis</i>	Myrsinaceae	0.115 \pm 0.067	0.063 \pm 0.029	
<i>Coprosma foetidissima</i>	Rubiaceae	0.070 \pm 0.032	0.068 \pm 0.032	
<i>Pseudopanax simplex</i>	Araliaceae	0.036 \pm 0.022	0.082 \pm 0.029	
<i>Pseudopanax crassifolius</i>	Araliaceae	0.018 \pm 0.018	0.031 \pm 0.022	
<i>Aristolelia serrata</i>	Elaocarpaceae	0.012 \pm 0.012		
<i>Coprosma ciliata</i>	Rubiaceae	0.012 \pm 0.008		
<i>Neomyrtus pedunculata</i>	Myrtaceae	0.012 \pm 0.008	0.037 \pm 0.016	
<i>Pittosporum eugenioides</i>	Pittosporaceae	0.010 \pm 0.010		
<i>Pseudopanax colensoi</i>	Araliaceae	0.009 \pm 0.009		
<i>Coprosma rigida</i>	Rubiaceae	0.008 \pm 0.008		
<i>Coprosma colensoi</i>	Rubiaceae	0.007 \pm 0.007	0.005 \pm 0.005	
<i>Myrsine divaricata</i>	Myrsinaceae	0.003 \pm 0.003	0.059 \pm 0.037	
<i>Cyathodes juniperina</i>	Epacridaceae		0.002 \pm 0.002	
<i>Dracophyllum longifolium</i>	Epacridaceae			1.846 \pm 0.973
<i>Leptospermum scoparium</i>	Myrtaceae			4.304 \pm 1.429
Conifers				
<i>Dacrydium cupressinum</i>	Podocarpaceae	4.061 \pm 2.200	26.092 \pm 2.835	
<i>Dacrycarpus dacrydioides</i>	Podocarpaceae	0.510 \pm 0.510		
<i>Prumnopitys ferruginea</i>	Podocarpaceae	0.445 \pm 0.444	7.332 \pm 1.215	
<i>Podocarpus hallii</i>	Podocarpaceae	0.032 \pm 0.031	12.112 \pm 2.451	
<i>Halocarpus biformis</i>	Podocarpaceae			7.678 \pm 0.855
<i>Lepidothamnus intermedius</i>	Podocarpaceae		0.148 \pm 0.088	4.371 \pm 2.382
<i>Prumnopitys taxifolia</i>	Podocarpaceae		0.025 \pm 0.025	
Tree-ferns				
<i>Cyathea smithii</i>	Cyatheaceae	59.622 \pm 12.43		
<i>Dicksonia squarrosa</i>	Dicksoniaceae	44.585 \pm 9.686	0.994 \pm 0.623	