

A greater range of shade-tolerance niches in nutrient-rich forests: an explanation for positive richness–productivity relationships?

David A. Coomes^{1,2*}, Georges Kunstler^{1,3}, Charles D. Canham⁴ and Elaine Wright⁵

¹Forest Ecology and Conservation Group, Department of Plant Sciences, University of Cambridge, Downing Street, Cambridge CB3 2EA, UK; ²Landcare Research, PO Box 40 Lincoln 7640, New Zealand; ³Cemagref – U.R. Mountain Ecosystems, 2, rue de la Papeterie, BP 76, 38402 St-Martin d'Hères Cedex, France; ⁴Cary Institute of Ecosystem Studies, Box AB, Millbrook, NY 12545, USA; and ⁵Department of Conservation, PO Box 13049, 3/137 Kilmore Street, Christchurch, New Zealand

Summary

1. A central concept in forest ecology is that differences in the growth rates and shade tolerances of tree species determine patterns of secondary succession. The most shade-tolerant tree species are the competitive dominants in late-successional forests, while species with fast growth rates persist through rapid establishment after disturbance. There is ample support for niche differentiation along the shade-tolerance axis, at least for temperate forests, but less thought has been given to the range of shade tolerances and growth rates encountered within a community and to how it might vary along environmental gradients.
2. We hypothesized that a wider range of growth rates and shade tolerances are found on nutrient-rich soils, because such soils not only support fast-growing species with high metabolic rates, but also species capable of tolerating the very deep shade cast by forest canopies growing where nutrients are plentiful. We test our hypothesis by quantifying light transmission through two neighbouring forests in southern New Zealand, one on phosphorus-rich alluvial soil and one on phosphorus-depleted marine-terrace soil, and comparing the growth rates of saplings on these contrasting sites.
3. Less light was transmitted to the forest floor on alluvial sites than on marine terraces (2.5% vs. 7.5% daylight, on average) and neighbourhood analyses within mapped stands indicated that large-leaved subcanopy species were responsible for intercepting that extra light. Sapling growth was strongly inhibited by shade in the understorey of the alluvial forests, but was less inhibited under the terrace forests.
4. Fast-growing subcanopy species were common on the alluvial sites and these species had characteristically soft leaves and high foliar-nutrient concentrations. Slow-growing shade-tolerant species were also abundant on these sites. Therefore, the interspecific variance in growth rates was greater on nutrient-rich sites, supporting our hypothesis of a greater range of shade tolerance niches on better soils. Of the five species found on both forest sites, all five had greater high-light growth rate on the alluvial sites.
5. *Synthesis:* A wider range of growth rates was observed in the nutrient-rich forests. This wider range may translate into a greater number of shade tolerance niches and thereby provides an explanation for the greater numbers of species commonly found on nutrient-rich soils when compared with neighbouring nutrient-poor sites.

Key-words: coexistence, forest dynamics, light transmission, niche differentiation, richness–productivity relationships, shade tolerance

*Correspondence author. E-mail: dac18@cam.ac.uk

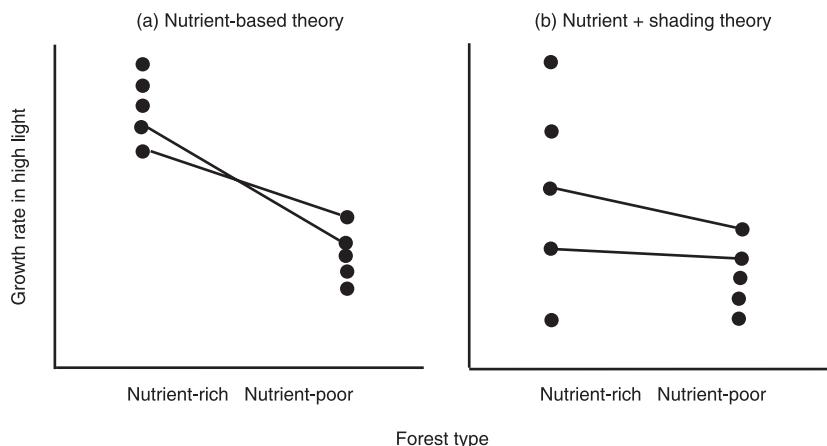


Fig. 1. Ideas regarding sapling growth within forests on nutrient-rich and nutrient-poor soils: (a) a conventional perspective is that species adapted to (mesic) nutrient-rich soils have faster growth rates than those associated with nutrient-poor soils; (b) an alternative perspective, tested in this paper, is that a greater range of growth rates is found on richer soils. Circles are species and lines indicate species common on both soil types.

Introduction

A central goal of ecology is to understand the mechanisms responsible for the coexistence of species, and niche differentiation during regeneration has long been regarded as an important explanation for the diversity of plant communities (Grubb 1977; Silvertown 2004). In forests, soil-type preferences and shade tolerance of juveniles are recognized as important axes of niche differentiation (Denslow 1987; Kobe 1996; Swaine 1996; Walters & Reich 1997; Clark *et al.* 1998; Greene *et al.* 1999; Lin *et al.* 2002; Svensson *et al.* 2004). Plants which are capable of surviving for long periods in deep shade have physiological and morphological traits that give rise to low whole-plant compensation points (Denslow 1987; Givnish 1988; Baltzer & Thomas 2007b), but these traits prevent the species from growing fast in full light (Abrams & Kubiske 1990; Walters & Reich 1996). This interspecific trade-off between survival in deep shade and growth in full light promotes coexistence by allowing species to specialize along gap–understorey gradients of light availability within forests (e.g. Hubbell & Foster 1992; Pacala *et al.* 1996; Kobe 1999; Kunstler *et al.* 2009). Trade-offs associated with soil fertility may also help to explain how many tree species coexist at the landscape level (Russo *et al.* 2005; Schreeg *et al.* 2005). Species which dominate on infertile soils capture and retain nutrients efficiently by having long-lived leaves, but these species have inherently low growth rates, because the long-lived leaves are highly sclerophyllous and have low assimilation rates per unit mass (Grime 1977; Reich *et al.* 1991; Lambers & Poorter 1992; Valladares *et al.* 2000). Such physiologically tolerant species are considered to be relatively unresponsive to nutrients and inherently slow growing on fertile soils, and so are out-competed on nutrient-rich soils (Chapin *et al.* 1993; Aerts & Chapin 2000). This trade-off between species competitiveness on nutrient-rich soils and tolerance on nutrient-depleted soil may contribute to compositional shifts along edaphic gradients (Grime 1977; Lambers & Poorter 1992; Russo *et al.* 2005).

The literature on trade-offs associated with shade and nutrient shortage is well established, but surprisingly little thought has been given to how the range of shade-tolerance niches may vary along gradients of soil fertility. Lusk &

Matus (2000) suggested that fast-growing species should dominate on nutrient-rich soils, because these species capitalize on the nutrients available to them by rapid height growth, giving them substantial advantages over neighbours with whom they compete for light. This idea is similar to that expressed in the plant strategy theory of Grime (1977). In contrast, Tilman (1988) and Keddy & McLennan (1990) have suggested that shade-tolerant species should dominate on nutrient-rich sites because they are superior competitors over the long term. Here we reason that the range of shade-tolerance niches among species is greater on nutrient-rich soils (when soil moisture does not limit productivity), because these soils not only support fast-growing species, with high light-compensation points (*sensu* Givnish 1988) and inability to tolerate shade, but also slow-growing species with low compensation points, which persist within the system by tolerating deep shade and regenerating beneath the fast-growing species. Conversely, we reason that the range of growth rates is smaller on nutrient-poor soils because seedlings growing under conditions of low nutrients tend to have higher whole-plant compensation points as a consequence of spending more carbon on competing for, and retaining, nutrients (Baltzer & Thomas 2007a). If our suggestion of a greater range of shade-tolerance strategies on nutrient-rich sites was supported by empirical evidence, then it would have implications for the received wisdom on trade-offs associated with soil-fertility gradients. Nutrient-rich sites would not necessarily be dominated by fast-growing species but instead by a spectrum of species with different growth rates: from slow-growing shade tolerators to fast-growing gap demanders (Fig. 1). This theory is straightforward, yet does not seem to have been described previously. We also predict that the range of light conditions beneath nutrient-rich forests should be greater than beneath nutrient-poor forests, because the former support a greater leaf area index, casting a deeper shade in places where the canopy is closed whilst allowing a similar percentage of light to the floor within tree-fall gaps.

Our hypotheses were as follows: (i) forest canopies on nutrient-rich soils cast, on average, deeper shade than those on nutrient-poor soils; (ii) a consequence of greater light interception on P-rich soils is that shading has a major effect on sapling growth, whereas the lesser extent of light inter-

ception on P-depleted soils means that shading has little effect on growth; (iii) fast-growing species will be highly responsive to nutrient supply whereas slow-growing species will be less responsive; and (iv) species associated with nutrient-rich soils will display a wider range of growth rates and shade tolerances than those associated with P-depleted soils. These hypotheses were tested by comparing sapling growth and canopy light interception in contrasting forest types growing on P-rich alluvial soils and P-depleted soils in southern New Zealand (Mark *et al.* 1988; Coomes *et al.* 2005). We quantified variation in light transmission in these forests using neighbourhood modelling of photosynthetically active radiation data within mapped stands and we compare the growth responses of 13 evergreen tree species to naturally occurring variation in light and nutrient supply. In an accompanying paper we demonstrate an interspecific trade-off between sapling growth in full light and seedling survival in shade for six tree species at our study site (Kunstler *et al.* 2009), confirming the well-established relationship between growth and shade tolerance (e.g. Hubbell & Foster 1992; Pacala *et al.* 1996; Walters & Reich 1996). Therefore, although we quantify growth rate in this article, we use the term 'shade-tolerance niche' to emphasize that growth rate and shade tolerance of species are interlinked and jointly determine a species' niche with respect to light.

Methods

STUDY AREA

Work was carried out in the southern region of Fiordland National Park, South Island, New Zealand ($46^{\circ}06'S$, $167^{\circ}30'E$) in evergreen forests that are classified as cool temperate rain forests, because rainfall (1600–2400 mm) exceeds potential evapotranspiration in every month of the year (LENZ environment data base; www.landcareresearch.co.nz/databases/lenz/). The climate is moderated by the influences of the surrounding oceans, so that the winters are mild with infrequent snowfall in the lowlands. Mean January and July temperatures are 12 and 5 °C, respectively (Ward 1988). We focus on comparing the vegetation on alluvial and marine terraces (see map in Appendix S1). Marine terraces were uplifted during the late Quaternary (Ward 1988; Wardle *et al.* 2004; Coomes *et al.* 2005) and form a chronosequence dating back 290 000 years. We sample from marine terraces created 80–120 thousand years ago during the last interglacial which support compositionally and structurally similar forests (Wardle *et al.* 2004; Coomes *et al.* 2005). Alluvial surfaces have formed alongside two large rivers and several smaller streams that intersect the marine terraces, some surfaces are about 24 000 years old and are depleted in phosphorus, whereas others surfaces are more recent and periodically refreshed by fresh alluvium. Coomes *et al.* (2005) reported that the alluvial surfaces are relatively rich in phosphorus compared with the marine terrace soils (total P \pm 1 SE of the mean: 87 ± 7.9 vs. 11 ± 0.36 g m $^{-2}$ within the top 15 cm of soil, of which 43% and 8% was in inorganic forms, respectively), but contain similar amounts of nitrogen (total N, 286 ± 10.1 vs. 307 ± 7.8 g m $^{-2}$). Soil N : P ratios suggest that phosphorus is increasingly limited on the marine terraces (5.7 ± 0.77 vs. 28.5 ± 0.81 , respectively), as commonly found in old, highly leached soils (Walker & Syers 1976; Vitousek & Farrington 1997; Richardson *et al.* 2004; Wardle *et al.* 2004). The forests differ markedly in composition and structure: the alluvial forest is slightly taller (height of tallest

trees = 24 vs. 20 m), more diverse (number of tree ferns, tall shrubs and trees = 30 vs. 21 species), dominated by angiosperm trees and has dense understorey layers of short angiosperm trees, tree ferns and ground ferns. In contrast, the P-depleted-terrace forests are shorter, with a simpler structure co-dominated by angiosperms and conifers with far fewer understorey plants (Coomes *et al.* 2005).

LIGHT TRANSMISSION — A NEIGHBOURHOOD MODEL

Measurements of light transmission were made in seven large mapped stands, three of which were in alluvial forests and four in terrace forests (Coomes *et al.* 2005). The mapped stands, 1.5–2.25 ha in size, were chosen to be representative of the forests following a preliminary survey of the area using reconnaissance plots, and were enumerated in the Austral summers of 2001/02 and 2002/03. All canopy tree stems > 10 cm in diameter at breast height (d.b.h.), all subcanopy (palatable) trees > 2.5 cm d.b.h. and all tree ferns > 2.0 m in height were mapped using an Impulse laser rangefinder (Laser Technology Inc., Tucson Way Centennial, CO), and their diameters recorded. Light levels were quantified using measurements of percent transmission of diffuse photosynthetically active radiation during May–June 2002 at a height of 135 cm above-ground level in plots spaced at 1-m intervals along permanent marked transects established in each of the stands (these plots form part of a seed dispersion study). Readings were taken on cloudy days, using quantum sensors (LI-1905B, LI-COR, Lincoln, NE), and were expressed as a proportion of light measurements taken in the centre of large forest clearings nearby (at least 20 × 20 m in size), in which a sensor connected to a data logger had been placed. The sensor in the clearing logged measurements every 10 s and averaged every 5 min; the 5-min average closest to the measurement time was used to calculate the proportion.

The percentage light transmission, Q , was related to local forest composition using the following function, selected after extensive exploration of alternative functions:

$$Q = \frac{a}{(1 + c_t BA_t + c_s BA_s + c_c BA_c + c_f BA_f)} \quad \text{eqn 1}$$

where BA_t , BA_s , BA_c and BA_f are the basal area of mapped tall angiosperms (> 12 m height), short angiosperms (< 14 m height), conifers and tree ferns found within a distance r of the light measurement location, and a , c_t , c_s , c_c , and c_f are parameters estimated by the regression (see list of species in Table S1 in Supporting Information), with a log-normal distribution for the error term. A series of alternative models were fitted to the data. The simplest model included a term representing the mean percentage of light transmission (model M1), the second model included a single basal-area term representing all woody plants within a distance r (model M2), and the third model included terms that allowed different functional groups to have different effects on light transmission, as shown in eqn 1 above (model M3). We tested radii (r) ranging from 2.5 to 10 m assuming that trees within a maximum radius of 10 m are the most important for light interception in closed forest.

SAPLING GROWTH IN RELATION TO LIGHT AND NUTRIENTS

Light and nutrient responses were characterized for the eight common species, six of which were found both on marine terraces and alluvial surfaces (Table 1). These species comprise 77% and 71% of basal area in the alluvial and terrace sites, respectively (taken from Appendix of Coomes *et al.* 2005). An additional five species of

Table 1. Mean foliar phosphorus and nitrogen concentrations (± 1 SE) of saplings of 13 tree species growing on P-rich alluvial terraces ('A') and P-depleted marine terraces ('T') in a temperate rain forest in southern New Zealand. All species, except *Fuchsia excorticata*, are evergreen. The numbers of saplings sampled is shown ('Repl'). The acronyms of species with sufficient replication for modelling are shown in bold

	Acronym	Repl.		Foliar P content ($\mu\text{g g}^{-1}$)		Foliar N content (mg g^{-1})	
		A	T	A	T	A	T
Conifers							
<i>Dacrydium cupressinum</i>	DACCUP	65	54	1179 \pm 50	623 \pm 29	10.8 \pm 0.24	8.9 \pm 0.23
<i>Podocarpus hallii</i>	PODHAL	42	57	1212 \pm 74	591 \pm 28	8.7 \pm 0.26	7.1 \pm 0.17
<i>Prumnopitys ferruginea</i>	PRUFER	9	54	1695 \pm 190	649 \pm 47	11.0 \pm 0.11	8.4 \pm 0.19
Tall angiosperms							
<i>Pseudowintera colorata</i>	PSECOL	59	10	1295 \pm 38	1035 \pm 104	12.0 \pm 0.24	12.1 \pm 0.86
<i>Weinmannia racemosa</i>	WEIRAC	27	49	790 \pm 35	453 \pm 24	8.5 \pm 0.31	6.6 \pm 0.13
<i>Nothofagus solandri</i> †	NOTCLI	0	39		823 \pm 33		10.0 \pm 0.20
<i>Nothofagus menziesii</i>	NOTMEN	41	40	1427 \pm 57	915 \pm 40	11.9 \pm 0.24	10.6 \pm 0.19
Short angiosperms							
<i>Carpodetus serratus</i>	CARSER	18	0	1637 \pm 147		14.6 \pm 0.77	
<i>Coprosma foetidissima</i>	COPFOE	5	0	2070 \pm 232		16.7 \pm 0.24	
<i>Coprosma lucida</i>	COPLUC	7	0	1331 \pm 67		12.3 \pm 0.18	
<i>Fuchsia excorticata</i>	FUCEXC	5	0	6459 \pm 813		35.9 \pm 0.13	
<i>Griselinia littoralis</i>	GRILIT	7	0	1715 \pm 211		9.4 \pm 0.81	
<i>Neopanax colensoi</i>	NEOCOL	6	0	1860 \pm 119		11.6 \pm 0.43	

†*Nothofagus solandri* var. *cliffortioides*.

subcanopy tree were sampled from large gaps in the alluvial sites and used for comparisons of growth rate in near-optimal conditions (some common species were also sampled from these gaps). These alluvial-site specialists comprised 18% and 0.1% of basal area in the alluvial and terrace sites, respectively. We would have liked to characterize the resource responses of these additional subcanopy species, but they are all heavily browsed by deer and are almost entirely absent from the browse layer of forests except in clearings around huts, where deer numbers are kept low by hunting activity. Around 40 saplings (between 0.5 and 5 m in height) of each of the 10 main species were sampled from alluvial and/or terrace forests (terraces T2–T4 shown in Appendix S1) during the Austral summer of 2001/02, and samples were collected across a light gradient from low (< 5% full sun) to high light (> 20% full sun). We sampled opportunistically, by walking tens of kilometres in search of saplings, in an attempt to sample from across the range of light in both forest types while avoiding recent tree fall gaps and plants that showed obvious signs of disease or physical damage. After a sapling was selected, its height was measured and two estimates of stem diameter were made at right angles to one another using callipers, at 10 and 135 cm from the ground. The terrace on which each sapling was growing was recorded (using the terrace numbering system of Ward (1988) which is shown in Appendix S1), and a note was made of the type of surface on which the sapling was rooted (forest floor, rotting log, tree-fern trunk, or mound – i.e. any other raised surface type) and of the predominant floor cover in the vicinity of the roots (moss, litter or soil). The sapling was cut at 10 cm above the ground surface and a disc was removed for tree ring analysis. Each disc was sanded with increasingly fine grades of grit (from 80 to 400 grit) until the growth rings were clearly observable, and individual ring widths were measured on a digital ring analyzer (0.005-mm resolution; Velmex Inc., Bloomfield, NY). The central growth ring of a sapling seldom coincides with the geometric centre of the disk, so growth measurements were taken along two perpendicular radii, and averaged. Radial stem growth was obtained by averaging the most recent 5 years of growth.

We used the concentrations of foliar nutrients as an indicator of the availability of soil nutrients to plants within a species; studies that have examined the relationship between concentrations of nutrients in leaves and soil often report positive correlations (e.g. Vitousek *et al.* 1995; Lusk & Matus 2000) although it is recognized that many other factors influence foliar nutrient concentrations (Vitousek *et al.* 1995). About 200 g of foliage was collected from each sapling and air-dried in the field. In the laboratory, these samples were dried at 70 °C for at least 3 days and ground samples were analysed for N and P content using a modified semi-micro Kjeldahl method (Blakemore *et al.* 1987) at the internationally accredited Environmental Chemistry Laboratory in Palmerston North, New Zealand. Light transmission through the crowns of neighbouring trees to the crowns of the saplings was estimated from hemispherical canopy photos taken with a digital camera (CoolPix 990, Nikon Inc., Tokyo, Japan), using the gap light index (GLI-% of full sun) developed by Canham (1988). Most saplings were shaded by trees that were much larger than themselves and under such conditions the height at which photos are taken is not critical (Canham *et al.* 1999). A standard tripod height of about 1.4 m was used, which was above the crown height of some saplings and below that of others. A few saplings were sampled from dense tree-fern patches, where light transmission varied greatly over a few vertical metres, and for these species the photo was taken at the top of the sapling's crown. Digital images were analysed for percentage light transmission over a growing season using GLI/C 2.0 software (Finzi & Canham 2000).

STATISTICAL ANALYSES OF RADIAL GROWTH DATA

The Michaelis–Menton equation was used as the basic function to describe the growth of each species (Wright *et al.* 1998):

$$G = \frac{\alpha}{(1 + \alpha/\beta L)} D^\phi + \epsilon, \quad \text{eqn 2}$$

where G is the radial stem growth (mm year^{-1}), D is the stem diameter in mm, L is light availability (0–100% of daylight), α and β are parameters describing the asymptotic growth in high light and the slope of the function at zero light, respectively, ϕ is a parameter which describes the changes in growth rate with tree size, and ε is the residual error term. This equation assumes that our light measurements are representative of growing conditions over the previous 5 years, which is not unreasonable given the slow turnover of trees in the Waitutu forests (Kunstler *et al.* 2009) and a sampling strategy that avoided recent tree fall gaps. We fitted models using generalized non-linear regression (*gnlr* function in the *gnlm* package of R). After preliminary exploration of the data set, we set ε to be normally distributed, with a mean of zero and variance that varied as a linear function of the predicted mean. The function often failed to converge because of the strong covariance between ϕ and the other parameters, so we determined the optimal value of ϕ by fitting regression models in which it had been fixed at a range of values between 0 and 1, and the likelihood of these models was then compared (see Pacala & Silander 1985). The minimum negative log likelihood was found to occur at $\phi = 0.55$ and this value was used in all subsequent modelling.

A series of alternative functions were fitted to see whether a simpler function than eqn 2 would be adequate to describe the data and the best function was determined by a standard model-comparison approach (Burnham & Anderson 2002). The first model (M1) was a ‘null model’ in which growth was unrelated to size, light or nutrient supply. Model M2 had only a mean growth rate for each species ($G = \mu_1$), M3 included the effect of size ($G = \mu_1 D^\phi$) with a single scaling parameter ϕ for all species, M4 included the effect of size with a different scaling parameter for each species, M5 included the effects of light without considering size ($G = \alpha L / (L + \alpha/\beta)$) and M6 included the effects light and size (as given in eqn 2). Next, we modified eqn 2 to include the effects of nutrients. Three alternative models were used to incorporate the effects of foliar P concentrations in the Michaelis–Menton function of growth: model M7 allowed α to be linearly related to P (i.e. $\alpha = \alpha_0 + \alpha_1 P$), M8 allowed β to be linearly related to P (i.e. $\beta = \beta_0 + \beta_1 P$) and M9 simultaneously modifying α and β . The same procedure was used to fit alternative models to describe the effects of foliar N concentrations on growth (model M10, M11, M12).

For each species, the alternative models were fitted and a series of maximum-likelihood values were obtained. We summed the log maximum likelihoods of the individual species to obtain the total log likelihood (log L) and then used this total to compare the performance of candidate models using the small-sample-size Akaike Information Criterion (AICc, Burnham & Anderson 2002).

Given that the nutrient statuses of alluvial and terrace forests are markedly different, and these differences are seen in the foliar nutrient concentrations, the observed effects of foliar nutrients on growth could be site effects, that is, it could be that there was no effect of foliar nutrient concentrations on growth within either the terrace or alluvial forests. To test this, we fitted models in which the value of α was allowed to vary between terrace types and compared this model to one in which α varied between terrace types and nutrients were also modelled, including all species represented by > 10 stems in both forest types.

ESTIMATION OF HEIGHT GROWTH FROM RADIAL GROWTH

The relationship between height H and diameter D was represented by a power function:

$$H = aD^b,$$

eqn 3

where a and b are estimated parameters. We linearized this function with a log transformation. Height and diameter are both subject to natural variation and measurement error, so Reduced Major Axis regression was used to fit the regression line for each species, using the *smatr* package in the R statistics platform. To examine the height growth of saplings we differentiated eqn 3 to give:

$$\frac{dH}{dt} = abD^{b-1} \frac{dD}{dt} \quad \text{eqn 4}$$

Since radial growth rate (G in eqn 2) is half diameter growth (dD/dt), combining eqns 3 and 4 gives:

$$\frac{dH}{dt} = 2abD^{b-1} \left[\frac{\alpha LD^\phi}{L + \alpha/\beta} + \varepsilon \right] \quad \text{eqn 5}$$

This function was used to calculate the height growth of saplings with stem diameters of 2.3 cm (the mean diameter of all the saplings sampled). Standard errors were then estimated using a bootstrapping approach. For each species, the data set containing information on growth, size and resource supply was sampled with replacement to produce a new data set with the same total number of samples as the original, then the best-fitting growth model was fitted to this bootstrapped data set to provide estimates of α , β and the variance of ε . Next, the resampled data were used to fit the allometric regression model for estimates of a and b (see eqn 3). This bootstrapping procedure was then repeated 25 000 times. For each bootstrap, we calculated height growth by substituting the parameter estimates into eqn 5, setting D as 2.3 cm, and drawing the values of ε at random from a normal distribution with the estimated variance.

Results

DETERMINANTS OF LIGHT TRANSMISSION

The multi-layered canopy of the alluvial forest transmitted less light to the forest understorey than that of the marine-terrace forests: mean light transmission values were 2.5% vs. 7.5%, respectively. The range of light conditions was larger in the alluvial site (0.05–0.95 quantiles of data: alluvial sites 0.2–32% vs. marine terrace sites 1.7–19%). We found that light interception was affected by the abundance of different functional groups of trees in the immediate neighbourhood of the sampling points (i.e. within 10 m of them). The best-fitting model was selected from three alternative functional forms and for four different radii, using AICc as a basis for comparison (Table 2). Light interception was related to the total basal area of trees in a circle of 10-m radius centred on the measurement (M1 and M2, Table 2). The inclusion of different parameters for the light interception of the four functional groups gave rise to a large drop in AICc (M2 vs. M3, Table 2, for all radii considered). The best-fitting model explained 39.5% of the deviance. For the same basal area, the small angiosperms cast the deepest shade, followed by tree ferns and conifers (Fig. 2a). Tall angiosperms cast very little shade for the same basal area in comparison with the three other functional groups (Fig. 2a). Thus, the differences in canopy composition of the alluvial forests vs. the terrace

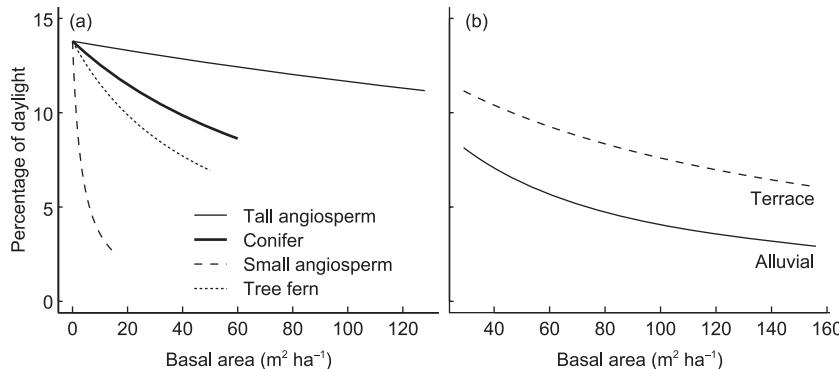


Fig. 2. Percentage of daylight transmitted through forest canopies as a function of (a) the basal area of short trees, tree ferns, conifers and tall angiosperm trees within 10 m of the survey point assuming that the basal area of other functional groups equals zero, and (b) the basal area of all trees and tree ferns in the alluvial and terrace forests, assuming stands of average composition. These curves are based on the predictions of model M3 in Table 2.

Table 2. Model selection statistics (Akaike's Information Criterion values; AICc) for three candidate models describing light interception as a function of basal area for four functional groups (tall angiosperm trees, short angiosperm trees, conifer trees and tree ferns), within circles of four different radii. Models are described in the analysis of 'determinants of light transmission' section of the text. Models were fitted by maximum-likelihood methods and the best-fitting model was identified as the one with the smallest AICc value (see Burnham & Anderson 2001)

Model	Description	Radius of circle (m)			
		2.5	5	7.5	10
M1	Mean*	10547.2	10547.2	10547.2	10547.2
M2	Basal area effect	10538.2	10472.3	10404.2	10352.2
M3	Basal area effect by functional groups	10216.7	10102.4	9992.3	9844.8

*AICc values do not vary with radius because the model does not use radius information.

forests (particularly the abundance of small angiosperms and tree ferns on alluvial sites) effectively explains the deeper shade cast in the alluvial than in the terrace forests (Fig. 2b).

RADIAL GROWTH OF SAPLINGS

Growth rates varied substantially among species and were non-linearly related to incident light. Functions that included the effects of size had much lower AICc values (i.e. were much better supported statistically) than functions that did not consider size (models M1, M2, M5 and M6 in Table 3), and a species-specific non-linear scaling function for the effects of size had a lower AICc than a nonlinear scaling function that did not distinguish species (model M3 vs. M4 in Table 3). Figures indicating goodness-of-fit are provided in Fig. S1. The species differed greatly in light-saturated growth rates and in the slope of growth response at low light (Table 4). Stem radial growth in 30% daylight was estimated to vary threefold among the eight species included in the analyses (Table 4), while the diameter growth at 1% of full light was found to vary 10-fold (Table 4); these estimates are based on saplings of 2.3-cm diameter which have average foliar P and N concentrations. Growth rates were close to, or at,

their maximum in 30% light for all species except *Nothofagus solandri* var. *cliffortioides*, which is a strongly light-demanding species, and showed no indication of saturating (Fig. 3). The predicted growth rates across all species in 1% daylight, which corresponds with the deepest shade found anywhere in either of the forests, varied from 26% to 76% of the maximum rates, depending on species (Fig. 3). There was no clear trade-off among species in growth rates in low vs. high light (rank-order correlation of species in 1% and 30% light; $\rho = -0.16$, $n = 8$, $P = 0.70$).

The average growth rate across all species was more than twice as high on alluvial sites than on terrace sites ($0.0598 \text{ mm mm}^{-1} \text{ year}^{-1}$ on the alluvial sites, compared with $0.0223 \text{ mm mm}^{-1} \text{ year}^{-1}$ on the terrace sites). Individual growth was strongly affected by intraspecific variation in foliar P concentrations (compare model M6 vs. M7 in Table 3). Phosphorous concentrations affected the light-saturated growth rates but not the slope of growth response under low light (M7, M8 and M9 in Table 3). Much of the variation in growth was related to the forest type from which the sapling was sampled. Including forest type in the regression models for the six species found in both forest types was strongly supported by the data ($AIC = 3662.8$ vs. 3700.6 for a model with only size and light effects). All but one of the species (*Pseudowintera colorata*) had slower growth rates and lower P concentrations on the terrace forests (significant at $P < 0.01$ when tested with Student *t*-tests).

We had additional information on plant nutrition in terms of foliar nutrient concentrations. Phosphorous concentrations in the leaves of saplings sampled from the P-depleted sites were found to be 44% lower than those in leaves from the P-rich sites, whereas N concentrations were only 15% lower (Table 1). Even though much of the variation in P concentration was explained by terrace type, introducing individual foliar P concentrations into the regression models resulted in a lower AICc than for models that simply included terrace type ($AIC_c = 3607.3$ vs. 3662.8), indicating that within-terrace variation in P nutrition had some influence on growth, especially in the alluvial sites. However, the effect was small and there was less support for a model containing both the effects of forest type and P ($AIC_c = 3614.8$). The predicted growth rates of saplings with low foliar P concentrations (i.e. 20th percentile of the range of concentrations observed) varied from 43% to 80% of those saplings with high foliar

Table 3. Model selection statistics (Akaike's Information Criterion values; AICc) for 12 candidate models describing the radial growth rates of saplings as a function of size, incident light and foliar N and P concentrations (a proxy for soil nutrient supply). Models were fitted by maximum-likelihood methods, and the best-fitting model was identified as that with lowest AICc value (see Burnham & Anderson 2001). The best-fitting model is highlighted in bold and the difference in AICc between each model and the best-fitting model is given (Δ_i). w_i are the Akaike weights, which provide an approximate probability that a given model is the best fitting of the candidate set

	N	AICc	Δ_i	w_i	Model
Without competition for resources					
Null	1	5191.6	586.2	0.0000	M1
Mean growth rate for each species	8	4917.5	312.1	0.0000	M2
Scaling function of size (common ϕ)	9	4783.7	178.3	0.0000	M3
Scaling function (ϕ for each species)	17	4781.0	175.6	0.0000	M4
Michaelis–Menton for effect of light					
Light (α , β)	16	4918.2	312.8	0.0000	M5
Light (α , β), size (ϕ)	17	4711.9	106.5	0.0000	M6
Adding phosphorus effects					
Light ($\alpha_0 + \alpha_1 P$, β), size (ϕ)	25	4605.4	0	0.7665	M7
Light (α , $\beta_0 + \beta_1 P$), size (ϕ)	25	4626.4	20.9	0.0000	M8
Light ($\alpha_0 + \alpha_1 P$, $\beta_0 + \beta_1 P$), size (ϕ)	33	4607.8	2.4	0.2315	M9
Adding nitrogen effects					
Light ($\alpha_0 + \alpha_1 N$, β), size (ϕ)	25	4618.6	13.2	0.0010	M10
Light (α , $\beta_0 + \beta_1 N$), size (ϕ)	25	4654.7	49.3	0.0000	M11
Light ($\alpha_0 + \alpha_1 N$, $\beta_0 + \beta_1 N$), size (ϕ)	33	4618.8	13.4	0.0009	M12

Table 4. Parameter estimates (± 1 SE) from modelling of stem radial growth as a function of diameter D , light L and foliar phosphorus concentration P. The regression model was $G = (\alpha_0 + \alpha_1 P) D^{\phi}/(1 + (\alpha_0 + \alpha_1 P)/\beta L)$, where α_0 , α_1 , ϕ and β are parameters, and ϕ was set at 0.55 for all species. The R^2 of the models for each species is given. Predicted growth rates of saplings ($D = 2.3$ cm) in 1% and 30% daylight (for saplings with average concentrations of P in their leaves) and for plants with relatively high and low foliar P concentrations (i.e. $P_L = 20$ th and $P_H = 80$ th percentile of the range of P concentrations observed) are given

Species	$\alpha_0 \times 10^2$	$\alpha_1 \times 10^2$	$\beta \times 10^2$	R	Estimated radial growth (mm year $^{-1}$)			
					$L = 1\%$	$L = 30\%$	$P = P_L$	$P = P_H$
Conifers								
DACCUP	4.2 ± 0.84	24.2 ± 4.77	3.5 ± 0.61	0.57	0.154	0.658	0.39	0.903
PODHAL	5.4 ± 0.62	10.1 ± 2.79	7.3 ± 3.3	0.53	0.216	0.445	0.353	0.542
PRUFER	6.1 ± 1.77	12.8 ± 5.3	2.5 ± 1.04	0.35	0.111	0.460	0.355	0.579
Tall angiosperms								
PSECOL	2.9 ± 0.92	7.8 ± 2.58	6.2 ± 3.7	0.35	0.183	0.372	0.299	0.446
NOTMEN	4.8 ± 1.98	19.7 ± 7.04	2.8 ± 0.76	0.28	0.132	0.646	0.46	0.798
WEIRAC	6.3 ± 1.27	4.9 ± 3.57	8.5 ± 8.44	0.15	0.228	0.423	0.377	0.472
NOTCLI	11.3 ± 4.17	19.3 ± 8.01	1.7 ± 0.38	0.66	0.089	0.811	0.669	0.91
Short angiosperms								
CARSER	12.1 ± 5.05	92.8 ± 38.5	13.2 ± 8.94	0.28	0.495	1.407	1.16	1.554

P concentrations (i.e. 80th percentile of the range of concentrations observed), depending on species. In this case, the rank order of species growth was similar for species with high and low foliar P concentrations ($\rho = 0.90$, $n = 8$, $P = 0.005$). Functions that modelled growth in terms of light, size and P explained between 15% and 66% of the variance (Table 4) and provided unbiased estimates of the data (see Fig. S1).

Growth was also affected by intraspecific variation in foliar N concentrations, but the fit of models including N was not as good as those including P (M7, M8, M9 vs. M10, M11, M12 in Table 3). Convergence failure occurred when we tried to fit

models that included the effects of both N and P, almost certainly because N and P are correlated ($\rho = 0.77$, $P < 0.0001$) and including both terms resulted in strong covariance among parameters. Because models including foliar P had greater explanatory power, we conclude that this is the nutrient that primarily limits growth on these sites. There were marked differences among species in their responses to nutrients and light (a model consisting of a single function to describe the growth of all species was far worse than a model consisting of separate functions for each species; difference in AICc of 345.3).

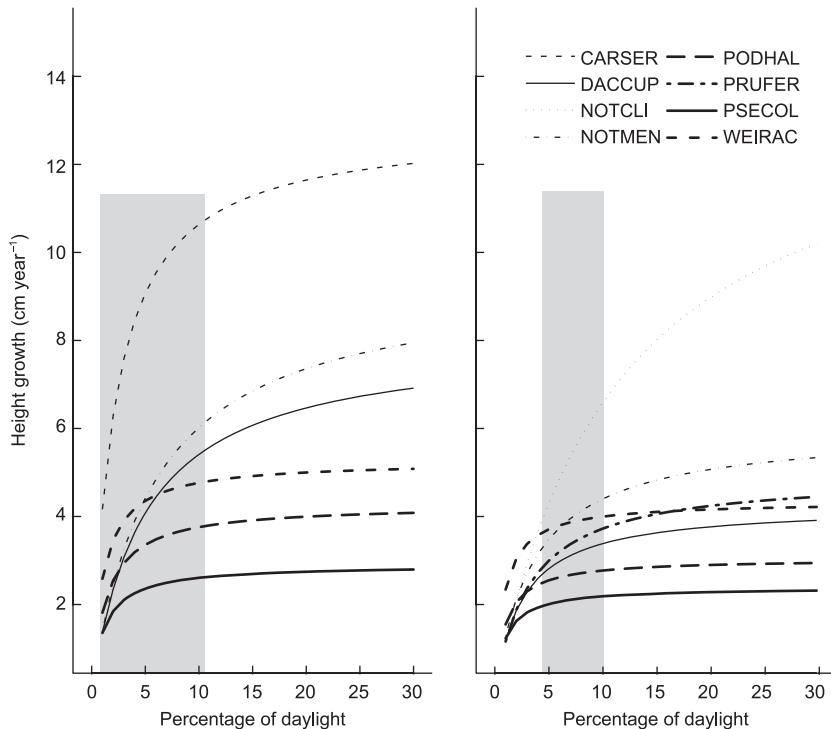


Fig. 3. Predicted height growth of eight tree species on the (a) alluvial sites or (b) terrace sites, plotted as a function of light. The grey bars indicate the percentage of daylight typically found on the forest floor, based on the 20th and 80th percentile of measurements taken in the two forest types.

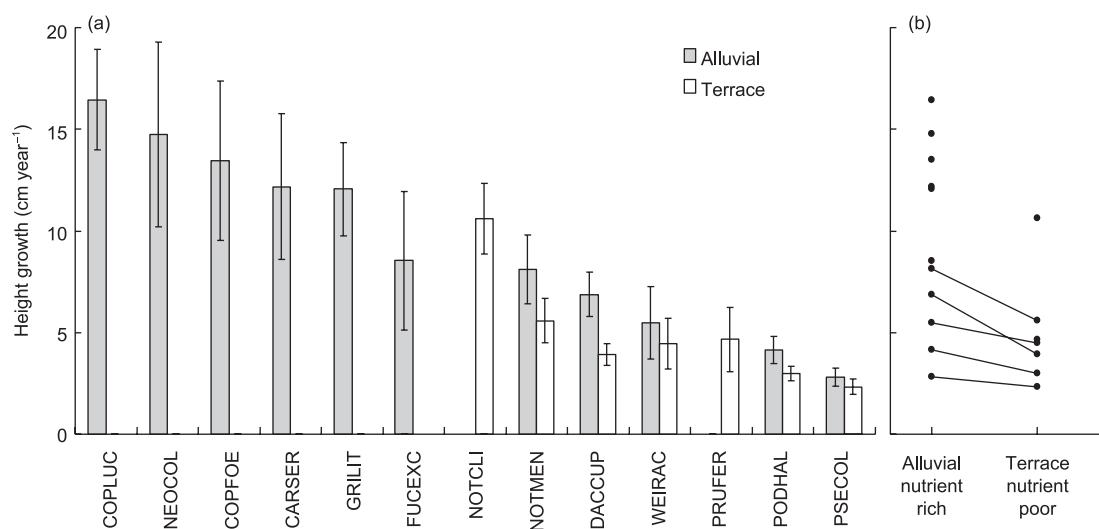


Fig. 4. (a) Height growth (\pm SE) of eight tree species growing on alluvial and/or terrace forests (based on predictions of a regression model with $L = 30\%$ daylight and P equal to the mean for the species concerned) and five species restricted to alluvial forests that were sampled only in large clearings, and (b) the data re-plotted in the same format as Fig. 1 to illustrate support for the shade-tolerance niche hypothesis.

HEIGHT–DIAMETER RELATIONSHIPS AND HEIGHT GROWTH CURVES

The relationships between height and diameter, which are required for the calculation of height growth from diameter growth, are provided in Appendix S2. Scaling functions accurately fitted the data, with no signs of bias (Appendix S2). The fastest height growth was observed in the short angiosperm species that are restricted primarily to alluvial forests; their average growth rate was about twice that of the other species in the study (Fig. 4). In the terrace forests, height growth was

typically about 75% of that in the alluvial forests and the ranking of growth rates was similar to that in the alluvial forests (Pearson $r = 0.95$; $P = 0.0007$; Fig. 4). The large standard errors for the growth estimates overlap among species and indicate that few differences would be significant if traditional inference tests were applied (Fig. 4). There was also a correlation between height growth and foliar P concentration in the alluvial forests but not in the terrace forests (Fig. 5); the fast-growing species associated with the alluvial soils have high foliar P concentrations and are responsible for the significant correlation for this soil type.

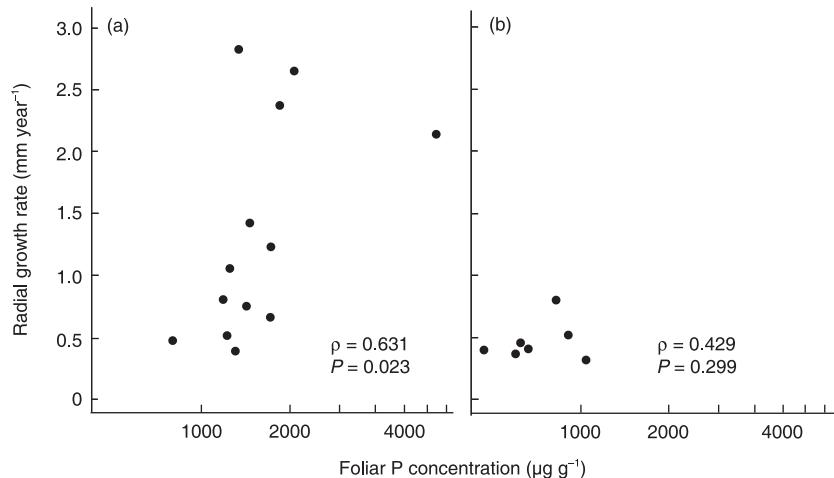


Fig. 5. Correlations between radial growth rate of species associated with (a) alluvial and (b) terrace forests and mean foliar P concentrations. Growth rates were predicted for saplings located in 30% daylight, using regression models.

Discussion

GROWTH RATES AND SHADE TOLERANCES

The temperate rain forest species in this study exhibited fivefold variation in high-light growth rates and we have evidence that this growth variation is negatively correlated with the shade tolerance of the study species, as shown previously for species in northern-hemisphere temperate forests (e.g. Kobe *et al.* 1995; Seiwa 2007). In a recent published article we found that species with low seedling mortality in shade had slow sapling growth rates in full light, based on data from six species growing on the alluvial and marine terraces of our field site (Kunstler *et al.* 2009). Additionally, the species' growth-rate rankings are broadly consistent with perceived wisdom on shade tolerances within New Zealand, based on observations of where seedlings establish: the six fastest-growing species shown in Fig. 4 are recognized as being 'seral', with *N. solandri* as a strongly light-demanding species (Wardle 1991; Bray *et al.* 1994), and *N. menziesii* as more shade-tolerant than *N. solandri* (Wardle 1984). *Dacrydium cupressinum*, which is next in rank in Fig. 4, persists for many years under partial shade but is regarded as one of the most light-demanding of the New Zealand conifers (Hill & Brodribb 1999; Wells *et al.* 2001). However, we note that our findings contrast with those of Enright *et al.* (1993), who reported *D. cupressinum* to be unresponsive to light at the seedling stage. Next in rank in Fig. 4 is *Weinmannia racemosa*, which has a slow growth rate suggesting shade tolerance. The literature provides conflicting views on the shade tolerance of this species; according to Smale & Smale (2003) the species is relatively intolerant of shade, but other authors consider the species as shade-tolerant (Allen & Rose 1983; Bellingham & Richardson 2006; Gaxiola *et al.* 2008) and stands of *Weinmannia*, comprised of stems of all sizes and ages, indicate an ability to regenerate in shade (Allen & Rose 1983; Lusk & Ogden 1992). Measurements of seedling mortality (Kunstler *et al.* 2009) indicate that this species is indeed tolerant of shade, consistent with the slow growth-rate measurement reported here. Next in rank are two slow-growing conifers,

both of which are regarded as shade-tolerant (Ogden & Stewart 1995; Carswell *et al.* 2007) and have flattened leaves capable of intercepting low-intensity light efficiently (Hill & Brodribb 1999). Finally, the slowest-growing of our species was *P. colorata*, which is known to grow in deep shade under tree-fern groves in our study sites (Coomes *et al.* 2005) and is widely accepted to be shade-tolerant (Wardle 1984; Wardle 1991; Smale & Smale 2003). Hence, the differences in high-light growth among species observed in this study equate to large differences in shade tolerance.

DEEPER SHADING ON RICHER SOILS

Forests growing on P-rich alluvial soils cast a deeper shade than those on P-depleted marine-terrace soils. This is largely attributable to the additional layer of subcanopy trees and tree ferns on alluvial soils (Fig. 2). The subcanopy trees and tree ferns comprised about 25.3% of the total basal area and brought the typical irradiance in the understorey down to 1–11.3% daylight (20–80th quantile) compared with about 5.0–10.6% daylight under the P-depleted terrace forests. Similar examples of lower light transmission on richer soils have been reported in other parts of the world (reviewed by Coomes & Grubb 2000), for example, along gradients of sandiness in central-northern United States (Tilman 1988) and in tropical rain forests on contrasting soil types in Malaysia (Palmiotto *et al.* 2004) and Amazonia (Coomes & Grubb 1996). Our neighbourhood analyses indicate that subcanopy species are particularly influential in reducing light transmission: the occurrence of large-leaved subcanopy angiosperms appears to be a characteristic of rain forests growing on nutrient-rich soils, both in temperate (Richardson *et al.* 2004) and tropical regions (Ashton & Hall 1992). The occurrence of these subcanopy trees can lead to a deeper shade because they have leaves closer to the ground (MacArthur & Horn 1969). In New Zealand and Hawaii, tree ferns form a dense layer on the relatively fertile soils, giving way to shorter, less dense ferns on the nutrient-poor soils (Vitousek 2004; Coomes *et al.* 2005). The shade tolerance of tree ferns 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). Similar trends towards smaller ground-layer plants on less fertile soils are reported for bamboos (Veblen 1989; Takahashi 1997). A physiological explanation for greater light interception by the alluvial forests is based on the fact that an economically viable leaf must produce enough carbon in its lifetime to pay for its construction and maintenance costs, as well as contribute towards the maintenance and production of stems, roots and seeds (Givnish 1988). A greater area of leaves per unit ground area can be supported on richer soils because the maintenance costs are reduced since trees need to allocate fewer resources to roots and below-ground processes when nutrients are plentiful (Tilman 1988; Whitehead *et al.* 2002). The construction costs of a leaf are also reduced because the leaves have lower mass per unit area (Coomes *et al.* 2005).

EFFECTS OF SHADING ON SAPLING GROWTH AND SURVIVAL

Light is usually considered as the principal resource limiting seedling growth in forest understoreys (Osunkoya *et al.* 1993; Bloor & Grubb 2003) and our analyses indicate this to be the case in the alluvial forests – average growth rate under typical understorey conditions was reduced to 41% of high-light growth. Working at the same alluvial sites, Gaxiola *et al.* (2008) showed that seedling growth increased substantially when light transmission to the forest floor was increased by removing tree fern fronds. In contrast, the effect of shading was less pronounced on the marine terraces; growth under typical understorey conditions was reduced to only 67% of high-light growth, primarily because the established forests cast less deep shade. Relatively weak impacts of shading on physiological performance have been reported in another study of podocarp-dominated forests on a nutrient-poor site in New Zealand. Whitehead *et al.* (2002) quantified the light-response curves of *D. cupressinum* foliage at various heights within a forest canopy and found that even the most shaded leaves were photosynthesizing at close to light-saturated rates. The resource-ratio hypothesis (Tilman 1988) provides a theoretical framework for understanding why competition for light is weak on nutrient-poor soils. Tilman (1988) argued that plants allocate a larger proportion of assimilate to foraging for nutrients when growing on poor soils and consequently produce relatively few leaves, resulting in a shift from above- to below-ground competition. Subsequent papers have suggested that changes in root and leaf morphology are also responsible for a shift from above- to below-ground competition on poor soils (Coomes & Grubb 2000). Experimental exclusion of the roots of mature trees is needed to confirm this hypothesis.

A GREATER RANGE OF SHADE-TOLERANCE NICHES ON RICHER SOILS

The range of high-light growth rates was greatest on the P-rich alluvial soils (Fig. 4), as we hypothesized (Fig. 1),

suggesting that there is also a wider shade-tolerance spectrum on these soils. The range was greatest on the alluvial soils because six fast-growing species were restricted to these soils, while several slow growing species were found on both sites. The fast-growing alluvial species have high foliage N and P concentrations (Fig. 5), short leaf life spans, high photosynthesis rates, high respiration rates (A. Gaxiola, unpublished data), and wide vessels in their xylem tissues capable of high rates of hydraulic conductivity (S. Russo, unpublished data). In these respects, they are archetypal fast-growing species adapted to abundant resource supply (Grime 1977; Reich *et al.* 1997; Aerts & Chapin 2000; McGlone *et al.* 2004) that capitalize on rapid height growth to compete asymmetrically with neighbours for light (Weiner 1984; Lusk & Matus 2000). However, such species generally do not cast deep shade (Canham *et al.* 1994) and as a result, shade-tolerant species can recruit beneath their canopies. This may explain why an extremely slow growing species – *P. colorata* – was common on the alluvial sites. It is these slow-growing plants that previous theories have conspicuously failed to mention. *Pseudowintera colorata*, a member of the Winteraceae (a basal lineage of angiosperms), is well-adapted to shade tolerance due to three features of its foliage: flat leaves that efficiently intercept light at low irradiance (Hill & Brodribb 1999; Feild *et al.* 2004), a pessimistic growth habit (*sensu* Kohyama & Grubb 1994) and secondary compounds that are repellent to ground-dwelling herbivores (McGlone & Clarkson 1993). The inability of *P. colorata* to respond to light is not unexpected since its xylem is comprised of narrow tracheids that place severe constraints on transpiration and growth rate (Pearce 2001). The tree fern *Dicksonia squarrosa* provides another example of deeply shade-tolerant species restricted to the alluvial soils. It has a height growth of only 4 cm year⁻¹ and hardly responds to light (Gaxiola *et al.* 2008).

Fewer opportunities for diversification along the shade-tolerance axis occurred on the nutrient-poor soils. It is well-known that species associated with nutrient-poor soils have long-lived leaves with low photosynthetic rates and slow growth rates (Grime 1977; Chapin 1980; Aerts & Decaluwe 1995; Reich *et al.* 1997; Aerts & Chapin 2000; Cordell *et al.* 2001; McGlone *et al.* 2004). In particular, the conifers (*D. cupressinum*, *Podocarpus hallii* and *Prumnopitys ferruginea*) were relatively slow growing and dominated on the poorer soils (Fig. 4). Bond (1989) argued that conifers generally have conservative traits that allow them to persist in extreme environments, including narrow conducting cells in the xylem and non-reticulate venation in their needles which preclude rapid transpiration, and tough leaves with relatively low photosynthetic capacities (Lusk & Matus 2000; Lusk *et al.* 2003). These traits result in inherently slow growth rates for seedlings and result in conifers being outgrown by angiosperms wherever resources are plentiful and asymmetric competition for light occurs. However, it is important to note that competition for light occurs even on the nutrient-poor soils of the marine terraces, just not as intensely as on the alluvial soils. In the shaded understorey (i.e. 5% daylight) on the marine terraces, the two light-demanding species, *N. solandri* and

D. cupressinum, grew at approximately 50% of the full-light rate, whereas the shade-tolerant species grew at approximately 88% of their maximum rates. These differences in light response have strong effects on community dynamics, as shown by individual-based simulation models (Kunstler *et al.* 2009). Similarly, Coomes & Grubb (2000) report that above- and below-ground competition inhibited the growth of saplings even on nutrient-starved forests in southern Venezuela.

Finally, species grew slightly faster on the alluvial sites, but this plasticity is slight in comparison to cross-species differences in growth rates (Fig. 4). Similarly, in Bornean rain forests, soil type had no consistent effect on shade tolerance – defined as the *x*-intercept of the relationship between growth and incident light – but species associated with nutrient-poor sites were less shade-tolerant than those from better soils in phylogenetically controlled comparisons (Baltzer & Thomas 2007a). Yamada *et al.* (2007) explored whether the strong preference of *Scaphium borneense* for sandy ridge tops in a Malaysian tropical rain forest could be related to demographic rates, but found it had rather similar growth and mortality rates on sandy and loamy soils; concluding that its performance relative to other species contributes to its rarity on better soils.

A GREATER RANGE OF SHADE TOLERANCE NICHES ON RICHER SOILS: AN EXPLANATION FOR DIVERSITY–PRODUCTIVITY PATTERNS?

It is often observed that forests on nutrient-rich soils support many more species of vascular plants than nearby forests on nutrient-poor soils (Wright 1992; Cornwell & Grubb 2003; Laanisto *et al.* 2008) and we observed this pattern in our comparison of alluvial versus marine-terrace sites (Coomes *et al.* 2005). Miller (2004) argued that environmental heterogeneity within riparian zones provided an explanation for their high species richness; such heterogeneity may contribute to diversity within our alluvial sites, where the just a positioning of terraces of different ages creates a complex mosaic of habitats. We have argued that the shade-tolerance spectrum is wider on nutrient-rich sites; could it be that this also contributes to greater species richness? The case advanced by us is that the wider spectrum of shade tolerances has created a greater niche-axis length, and that this allows a greater number of species to coexist. The published literature provides some support for this idea. Cornwell and Grubb (2003) contrasted nutrient-rich and nutrient-poor forests in Europe and found much greater richness of herbaceous plants on the nutrient-rich soils. Many of the extra species found on nutrient-rich sites were light-demanders, much in the same way as subcanopy alluvial species in our study were light-demanders. These observations agree with the well-established theory that nutrient-rich soils allow fast-growing species to proliferate – species with high metabolic rates that cannot tolerate shade (Chapin *et al.* 1993; Aerts & Chapin 2000). Intriguingly though, Cornwell & Grubb (2003) also noted that nutrient-rich soils support shade-tolerant herbs, many of which are absent on nutrient-poor sites. This observation is consistent with the theory that shade-tolerant

plants are less affected by competition for below-ground resources in nutrient-rich forests, allowing them to tolerate deep shade (see Coomes & Grubb 2000). Therefore, a wider spectrum of shade tolerances among European herbaceous plants in nutrient-rich forests is associated with greater species richness on these sites.

An unresolved question is why competition among the fast-growing light-demanding species does not lead to a few species rising to dominance at the expense of others on the nutrient-rich soils, as appears to occur in grassland systems (Grime 1977). Cornwell & Grubb (2003) suggest that heterogeneity within small-gap environments allows further niche differentiation among species, but this hypothesis remains untested and alternative explanations based around the concepts of frequency dependence and non-equilibrium cannot be ruled out (e.g. Wright *et al.* 2004). Also unclear is whether nutrient-rich forests are taller and therefore enable a greater differentiation among species in response to vertical gradients of light (Easdale *et al.* 2007). Leaving aside these uncertainties, our study suggests that nutrient-rich sites provide the opportunity for species of a wide spectrum of shade-tolerance to develop, and this may in turn contribute to the greater species richness found in nutrient-rich sites.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Table S1 List of species within each functional group used in the light analysis

Appendix S1 Map of Waitutu field site

Figure S1 Figure indicating goodness-of-fit of regression models

Appendix S2 Parameter estimates of the allometric diameter–height regressions of 13 species

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