Size-dependence of growth and mortality influence the shade tolerance of trees in a lowland temperate rain forest

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Summary

1. A trade-off between growth in high-light and survival in low-light of species is often proposed as a key mechanism underpinning the dynamics of trees in forest communities. Yet, growth and survival are known to depend on plant size and few studies have analysed how this trade-off can vary between juvenile life stages and the potential consequences of the trade-off for the differences in regeneration rate between species in mixed forests.

2. We quantified growth and mortality for two different juvenile life stages – seedlings and saplings – of seven tree species common in temperate rain forests in New Zealand using data from field studies. We found strong evidence that the ranking of species for survival in shade and growth in full light was affected by size. There was a trade-off between seedling survival in low light and sapling height growth in high light, but no trade-offs were observed when considering other combinations of life stages (seedling growth vs. seedling survival, seedling growth vs. sapling survival, or sapling growth vs. sapling survival).

3. We ran simulations with an individual-based forest dynamics model – SORTIE/NZ – to explore how the trade-off drives the differences in tree species regeneration success in gaps vs. under closed forest conditions. These simulations indicate that because species' ranks in shade tolerance varied with life stage, regeneration success was not predicted from knowledge of tree performance at a single life stage. For instance, high-light sapling growth was a strong determinant of regeneration success in forest gaps, but seedling growth was also influential. Under closed forest, regeneration success was primarily limited by low-light mortality at the seedling stage, but seedling growth and sapling survival were also influential.

4. *Synthesis.* Growth-survival trade-offs can be strongly affected by the size of the individual analysed, resulting in completely different rankings of the shade tolerance of species across different juvenile life stages. Performance of both seedlings and saplings influenced regeneration success, highlighting the need to consider growth-survival trade-offs and the shade-tolerance strategies of tree species over a large range of juvenile sizes.

Key-words: growth, growth-survival trade-off, mortality, saplings, seedlings, shade tolerance, size effect, SORTIE/NZ

Introduction

Interspecific differences in shade tolerance are often cited as a key mechanism underpinning species coexistence and successional patterns in forest communities (Pacala *et al.* 1996; Nakashizuka 2001; Rees *et al.* 2001). In the last decade,

several studies in North American temperate forests have proposed that shade tolerance, as measured by the ability of juveniles to survive in low light, trade-offs against juvenile growth in high light at the species level (Kobe *et al.* 1995; Wyckoff & Clark 2002; Lin *et al.* 2002). The trade-off has also been observed in some lowland tropical rainforests (i.e. Hubbell & Foster 1992), but very few species are light-demanding; the vast majority are so shade-tolerant that they are virtually

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indistinguishable in their survival and relative growth rates (Hubbell 2005).

The importance of plant size has rarely been included in analyses of growth-survival trade-offs among long-lived plants (Baraloto *et al.* 2005a) but could be critically important. It has long been appreciated that shade tolerance of trees may vary with size (Givnish 1988). Having discovered a rank reversal in the hierarchy of shade tolerance with size for tree species of south-central Chile, Lusk (2004) has gone so far as to say that the size of individuals chosen for studies will 'shape scientists' answers' to questions about shade-tolerance strategies in forests. Size may affect the performance of a species under closed forest canopy because the constraints on growth and survival change during ontogeny, or because the physiological performance of a tree in low-light conditions changes with size, or some combination of both factors. For instance, small individuals usually have relatively high mortality rates, because they experience a low-light availability, a higher probability of herbivore damage and have a relatively low tolerance and/or resilience to damage (Harcombe 1987; Nakashizuka 2001; Lusk 2004), but their ability to tolerate shade may be relatively high because the ratio of photosynthetic to non-photosynthetic biomass is greatest for seedlings, so their maintenance costs are low (Waring 1987; Givnish 1988; Messier *et al.* 1999; Kneeshaw *et al.* 2006). These contrasting observations of size effects on survival under closed canopies show that the ranking of species performance in low vs. high-light conditions is likely to be affected by size of juveniles. We hypothesize that interspecific differences in mortality will be strongest at the seedling stage, whereas differences in growth will be more pronounced at the sapling stage. As a result, the growth-survival trade-off is likely to be stronger between seedling survival and sapling growth than between other combinations of juvenile life stages.

A trade-off between high-light growth and low-light survival is often assumed to drive succession and promote coexistence of tree species (Kobe 1999; Nakashizuka 2001; Lin *et al.* 2002; Baraloto *et al.* 2005a), but any changes in the rankings of growth and survival with respect to size could affect these processes. For example, a species could have a low regeneration success under closed canopy despite having high survival in low-light at the seedling stage if it has lower low-light survival at the sapling stage. Individual-based forest simulation models provide a tool for exploring the link between size-dependent demography and community-level processes, by allowing a quantitative analysis of the implications of changes in growth and survival with size, light conditions, and competition among individuals of all sizes.

In this study, we analyse the factors influencing the growth and mortality of seedlings and saplings using field data collected on seven canopy tree species in lowland temperate rain forests of southern New Zealand. We relate growth and mortality to size and light availability. Based on these observations we test the hypotheses that (i) the ranking of species for mortality in shade and growth in full light are affected by the size of the individual, (ii) there is a growth-survival trade-off between the seven study species, and (iii) the trade-off occurs principally

between seedling survival and sapling height growth, because the largest differences in low-light survival and high-light growth occur in those life stages. Then, we run simulations analysing the implications of the observed size-dependent trade-offs for the ranking of the success of canopy recruitment among the species in low vs. high-light conditions using SORTIE/NZ, a spatially explicit individual tree model of forest dynamics that has been recently parameterized for New Zealand lowland temperate rain forest.

Methods

STUDY AREAS AND SPECIES

Our research was conducted in the southern region of Fiordland National Park, South Island, New Zealand (46.4°S, 167.2°E). The area is characterized by a series of uplifted marine terraces intersected by two large rivers, and several smaller streams, which are bordered by alluvial terraces (Ward 1988). In the alluvial terraces (alluvial sites), the soils are replenished by fresh alluvial deposition, but surfaces further back from the river on the marine terraces (terrace sites) were deposited during the last glaciation and early Holocene, and are not replenished (Hewitt 1988). The soils on the terrace sites contain very little phosphorus in comparison with the alluvial sites, and the N : P ratios of leaf and soil samples indicate that phosphorus levels are sufficiently low to limit plant productivity in the terrace sites (Wardle *et al.* 2004; Coomes *et al.* 2005). Our study was conducted in a study area including both alluvial sites and terrace sites.

Seven canopy species are present in the terrace sites: the conifer *Dacrydium cupressinum* constitutes the largest proportion of basal area (see Appendix S1 in Supporting Information). The conifers *Prumnopitys ferruginea* and *Podocarpus hallii*, and the angiosperms *Weinmannia racemosa*, *Nothofagus menziesii*, *Nothofagus solandri* var. *cliffortioides* and *Metrosideros umbellata* comprise most of the remaining basal area (see Fig. S1). In the understoreys of these sites, there is a sparse cover of the ferns *Blechnum procerum*, *B. discolor* and *Hymenophyllum* species (Coomes *et al.* 2005). *Nothofagus menziesii* and *W. racemosa* are the dominant canopy trees in the alluvial sites and *D. cupressinum* and *Prumnopitys ferruginea* represent a minor component of total basal area (see Fig. S1). Alluvial sites are further characterized by a high abundance of subcanopy trees (including angiosperm species such as *Carpodetus serratus*, *Grisilinea littoralis*, *Fuchsia excorticate* and tree ferns species such as *Cyathea smithii* and *Dicksonia squarrosa*) and a dense layer of ground-ferns (dominated by *B. discolor*) (Coomes *et al.* 2005). Our growth and survival field studies and our simulations focus on six dominant species in terrace sites (*M. umbellata* was only included in the seedling growth and survival analysis because data were missing for the sapling life stage, and consequently this species was not include in our SORTIE/NZ simulations).

FIELD STUDIES OF SEEDLING GROWTH AND MORTALITY

In February–March 2003, 1 m^2 quadrats were established around patches of seedlings on the forest floor. The quadrats were distributed in sufficient numbers to include approximately 1000 seedlings for each of the seven most common species, and were stratified across a range of light levels. A total of 10 456 seedlings between 5 and 100 cm in height were labelled with aluminium tags, with the bulk of the

Table 1. The range of initial heights, percentage dead and percentage of seedlings with apparent marks of herbivory for seven tree species growing on nutrient-rich alluvial sites (A) and nutrient-poor terrace sites (T) in a temperate rain forest of southern New Zealand. The numbers of seedlings surveyed is shown (n), and the acronym for species names are given

Species	Acronym	Initial height (cm)	n		Mortality %		Herbivory %	
			A	T	A	T	A	T
Conifers								
Dacrydium cupressinum	DACCUP	5–98	168	1334	7.7	14	0.6	0.8
Podocarpus hallii	PODHAL	5–94		729		20		1.9
Prumnopitys ferrunginea	PRUFER	5–77	584	1609	15	25	33	25
Angiosperms								
Weinmannia racemosa	WEIRAC	5–54	611	782	26	36	52	30
*Nothofagus solandri**	NOTCLI	5–45		1598		50		15
Nothofagus menziesi	NOTMEN	5–71	1062	1005	40	39	47	28
Metrosideros umbellata	METUMB	5–42		974		18		9.2

*var. *cliffortioides*.

samples falling in the small size classes (Table 1). In quadrats where there were less than 25 seedlings of a particular species, we labelled all seedlings, but in denser stands we labelled a randomly chosen subsample of 25 seedlings of each species. Each seedling was identified by species, and a mark of white paint was made on the stem 2 cm above the root collar. Seedling heights were measured as the stretched distance from the painted mark to the apical bud. All seedlings were subsequently re-surveyed in January 2005, with each seedling being recorded as either alive or dead. Heights were also re-measured on the living seedlings. Any evidence of browsing by red deer (*Cervus elaphus*) was identified and recorded. All remaining seedlings missing after a thorough search were recorded as dead. The temperature and precipitation during the 2 years of study were similar to the long-term mean over 52 years (according to Invercargill Airport weather station – 46.4°S 168.3°E. – NIWA's CliFlo data base 1 October 2008). The mean annual temperature in 2003 and in 2004 were 9.8 and 9.5° C, respectively (long-term mean 9.8° C; range 8.8–10.7° C) and the mean annual rainfall were 1040 and 1357 mm, respectively (long-term mean precipitation 1104 mm; range 802–1446 mm).

Our study of seedling growth and survival was based on a survey of naturally established seedlings that had established under a suite of different soil fertility and substrate conditions. To avoid any confounding effects because of this variability of local conditions, both site fertility (fertile alluvial sites vs. low fertility terrace sites) and substrate type (elevated substrate vs. forest floor) are included in the analyses to control their effects in the comparison of species performance. We recorded the soil fertility in two categories: fertile alluvial sites and low fertility terrace sites. We recorded the substrate type of each seedling as either ground (G, i.e. forest floor with exposed mineral soil, or a layer of moss, or a mixture of leaf litter), or elevated substrate (E, i.e. elevated organic substrates, created by deposition of bark around the base of canopy trees or partially decomposed logs covered with moss or litter). An elevated substrate was defined as a surface > 20 cm above the forest floor. In the alluvial sites the vast majority of seedlings establish on elevated surfaces because dense *B. discolor* ground-ferns reduce seedling establishment on the ground (Coomes *et al.* 2005). The density of seedlings was very low and only four species present in the canopy had enough seedlings to be analysed (*N. menziesii*, *W. racemosa*, *D. cupressinum*, *P. ferrunginea*). Elevated surfaces are the only substrate type in which seedlings establish in alluvial sites and it was thus only possible to analyse growth and mortality on this substrate.

We took hemispherical canopy photos at 1.2 m above the centre of each quadrat to quantify the light available over the growing season (at a height of 1.35 m). Digital images were taken with a Nikon CoolPix digital camera, and were analysed using GLA 2.0 software (Frazer *et al.* 1999). The software estimates average light transmission over a growing season from the hemispherical photos, by integrating the direct-beam and diffuse radiation transmitted through the canopy over the course of a day, and over all days within a pre-defined growing season (Canham 1988a). Light intensities were reported as the percentage of above-canopy light that reaches each quadrat. The mean percent of full light in the quadrats was 6.53% (ranging from 1% to 27.9%); note that this value is not representative of the light environment of the forest as plots were selected to represent a broad range of light conditions. The percentage of full light available was not correlated with average seedling height within quadrats (Sperman's rank correlation ρ = 0.015, *P*-value = 0.1674).

Mortality and height growth of seedlings were analysed using maximum likelihood methods (see Appendix S2 for details of likelihood functions, optimization methods and model comparison techniques). We also include in these analyses substrate type (elevated substrate vs. forest floor) and site fertility (fertile alluvial sites vs. low fertility terrace sites) to avoid any confounding effects. This allows us to compare species performance in low vs. high light while controlling for these factors. The Weibull function was used to develop a model of annual probability of mortality for each tree species. The general model of probability of mortality (*P*) is:

$$p = m_{max}e^{-aH^b}e^{-cL^d} \qquad \text{eqn 1}$$

where *H* is the height of the seedling in cm, *L* is the light available to the seedling (% of full sun), m_{max} is the maximal annual probability of mortality, *a* and *b* are parameters describing the effect of size and *c* and *d* are parameters describing the effect of light. A series of alternative models were fitted to the data available for each species. The simplest model included a mean probability of mortality for each species ($P = m$), the second model included the effect of size ($p = m_{max}e^{-aH^b}$) and the third model included both light and size effects (see eqn 1). Next we modified eqn 1 to include the effects of substrate type (recall that seedlings establish only on elevated substrates in the alluvial sites), by allowing m_{max} to have different values for forest floor ($m_{max F}$) and elevated ($m_{max E}$) surfaces. We used the same approach to include soil fertility with different values in the alluvial sites and in the terrace

sites. Finally, we fitted a model including both the substrate type and the site fertility effect (with three different parameters: two for the two different substrates in the terrace sites $m_{max\,FT}$ and $m_{max\,ET}$ and one for the elevated substrate in the alluvial sites $m_{max\,EA}$). The alternative models were compared using the Akaike Information Criterion corrected for small sample sizes (AICc).

A Michaelis–Menton equation was used to model annual height growth for each tree species (see Wright *et al.* 1998; Coomes & Allen 2007; Coomes *et al.* 2009). We fitted several alternative models based on the following general model:

$$\frac{dH}{dt} = \frac{\alpha L}{(L + \alpha/\beta)} H^{\phi} \qquad \text{eqn 2}$$

where H is the height of the seedling (in cm), L is the light available for the seedling (% of daylight), α and β are parameters describing the asymptotic growth in high light and the slope of the function at zero light, respectively, and ϕ is a parameter which describes the changes in growth rate with tree size. A series of alternative models were fitted to the data available for each species. The simplest model included only a mean growth rate for each species ($dH/dt = \mu$), the second model added the effect of size ($dH/dt = \mu H^{\phi}$), the third included the effects of light without considering size ($dH/dt = \alpha L/(L + \alpha/\beta)$), and the fourth model included both light and size effects (see eqn 2). As with mortality, we also examined models in which eqn 2 was modified to include the effects of substrate type and soil fertility. We allowed α in the Michaelis–Menton function to have different values for forest floor (α_G) and elevated surface (α_F), and used the same approach to include soil fertility with different values in the alluvial sites and in the terrace sites. The growth model was estimated for seedlings that lacked any sign of damage by deer. We restricted our analysis to seedlings < 60-cm tall because few species had individuals taller than this limit.

FIELD STUDIES OF SAPLING GROWTH

We used high light sapling growth rates reported by Coomes *et al.* (2009). The growth estimation is described in detail in Coomes *et al.* (2009), but can be briefly summarized as follows. Sapling radial growth models were estimated with tree ring measurements on saplings (defined as individuals > 100 cm in height and < 10 cm d.b.h.) collected across a gradient from low (1.03% full sun) to high light (36% full sun) in the Waitutu study area. For each sapling, light availability, leaf P content and radial growth was measured (see Appendix S3). Growth models based on the Michaelis–Menton equation (including light, leaf P content and size effects) were estimated. Diameter-to-height allometric relationships were used to convert these estimates into height growth (see Appendix S3). *Metrosideros umbellata* was lacking from the analysis in Coomes *et al.* (2009) because its growth rings were not discernible under a binocular microscope. Bee *et al.* (2007) reported the radial growth of *M. umbellata*, but they measured growth with callipers instead of analysing tree rings (Coomes *et al.* 2009), making the comparison difficult. In the trade-off analysis we use the estimated height growth in 30% of full light for saplings with stem diameters of 2.3 cm (approximately 3 m in height) for the six remaining species. We compared seedling and sapling predicted growth at 30% of full light because this corresponds to the highest light level observed in large gaps in these forests.

FIELD STUDIES OF SAPLING MORTALITY

Sapling mortality was analysed with data collected on 560 plots extracted from the National Vegetation Survey (NVS) (Wiser *et al.*

2001). Plots were recensused at varying intervals ranging from 2 to 28 years between 1969 and 2004. Within each plot, each woody stem > 3 cm in d.b.h. was tagged and identified to species and its diameter recorded to the nearest millimetre. Only plots < 600 m in elevation were selected, to select ecological conditions similar to the Waitutu study area. Plots with evidence of disturbance events affecting the stand between the two censuses were excluded from the analysis. We defined saplings as individuals < 10 cm of d.b.h. For each of the seven species analysed we estimated a mean annual probability of mortality (i.e. no light or soil effects) with a maximum likelihood estimation taking in account the varying census intervals. We attempted to use the approach developed by Kobe *et al.* (1995), to take into account the effect of light availability (through its recent growth history) but it was not possible to measure tree rings of dead individuals in a system with such slow growth rates. In addition, no light data were available for the NVS plots. It is thus not possible to predict sapling survival precisely in low-light conditions. Our estimates represent survival under the range of light experienced by saplings in the permanent plots. Nevertheless, the permanent plots are mainly established within closed forest (average basal area = 76 m² ha⁻¹), with predominately shaded understorey condition. According to the light transmission model presented in Coomes *et al.* (2009), this basal area corresponds to a light level of 8.9% of full light in the terrace sites.

INDIVIDUAL BASED SIMULATION MODELLING

Our model, SORTIE/NZ, was implemented using the SORTIE-ND software (www.sortie-nd.org), an open-source platform for spatially explicit simulation of forest dynamics. SORTIE-ND is a descendant of the earlier SORTIE model (Pacala *et al.* 1996). We have parameterized our model only for the terrace sites because crucial parameters such as tree-fern demography are currently lacking for the alluvial sites. The basic elements of the simulation are sub-models that predict seedling recruitment, seedling and sapling mortality, seedling and sapling growth, adult tree growth and mortality, and sub-models that predict local availability of light and dynamics of substrate types on the forest floor. The seedling and sapling components of the model are based on the empirical functions described in this paper and in Coomes *et al.* (2009). Appendix S4 outlines the methods for parameterizing the other functions in the model. Given that *M. umbellata* was lacking from the analysis in Coomes *et al.* (2009), no sapling growth model was available for this species, and SORTIE/NZ simulations were run only for the six remaining species.

We used SORTIE/NZ to examine how the ranking of species growth and mortality at the seedling and sapling stage affects the ranking of species regeneration success in both large forest clearings (high light) and shaded understorey conditions (low light). It is generally assumed that trade-offs between high-light growth and low-light survival drive species differences in tree recruitment dynamics in low vs. high-light conditions (Lin *et al.* 2002; Baraloto *et al.* 2005a). Species' ranks in high-light growth are assumed to explain differences in species recruitment in high-light conditions, whereas species' ranks in low-light survival presumably explain differences in species recruitment under closed canopy. However, if species' ranks in growth or survival change dramatically between life stages, then including species differences only for some of the life stages in the simulation can lead to erroneous predictions about the recruitment success of species. We designed our simulations to explore the ways in which rank in growth or survival influences the recruitment success of species and to analyse the consequences of ignoring life-stage-specific parameters for the model's predictions about the recruitment success of species.
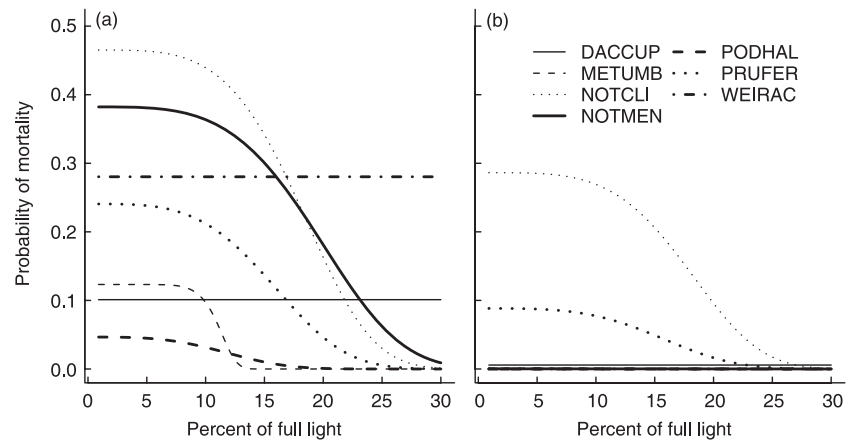
Fig. 1. Predicted probability of mortality as a function of percent of full light based on the best fitting model selected for each species (Table 2), for seedlings (a) 15 cm or (b) 50 cm in height, growing on the terrace sites. Species acronyms are listed in Table 1.

Table 2. Comparison of six alternative models, using Akaike's Information Criterion (AICc), describing the mortality and height growth rates of seedlings of seven woody species from southern New Zealand (species acronyms are listed in Table 1). Models that include the effects of plant size and light on mortality or growth are given as eqns 1 and 2, respectively, and more complex models incorporating the effects of substrate types and of site fertility are described in the text. The alternative models were fitted for each species using maximum likelihood methods. The best fitting model is given a ΔAICc value of zero (in bold), and the difference in AICc between this model and all others is reported. It was impossible to fit the models indicated by '–' because of insufficient numbers of seedlings of those species on the alluvial sites

	DACCUP	METUMB	NOTCLI	NOTMEN	PODHAL	PRUFER	WEIRAC
Seedling mortality							
Constant rate	65.4	127.5	21.8	134.8	335.8	54.3	82.0
Size	**0.0**	16.0	15.4	30.1	2.2	13.8	**0.0**
Size and light	3.3	1.9	**0.0**	16.2	**0.0**	6.6	0.9
Size and substrate	1.1	14.7	16.6	32.1	4.2	10.9	1.4
Size and site fertility	2.0	–	–	19.3	–	6.7	2.0
Size, light and substrate type	4.4	**0.0**	1.5	21.9	2.0	4.0	2.7
Size, light and site fertility	5.1	–	–	**0.0**	–	**0.0**	6.0
Size, Light, substrate and site	8.5	–	–	22.5	–	8.1	6.7
Seedling growth							
Constant	73.1	17.2	**0.0**	9.3	63.2	**0.0**	**0.0**
Size	21.9	19.1	1.9	1.9	7.5	2.0	2.0
Size and light	7.1	1.2	2.6	4.2	9.3	4.1	4.0
Size and substrate type	15.5	14.0	2.4	3.5	**0.0**	1.7	2.9
Size and site fertility	22.8	–	–	**0.0**	–	4.0	2.2
Size, light and substrate type	**0.0**	**0.0**	2.9	5.8	2.0	3.8	4.9
Size, light and site fertility	7.9	–	–	2.3	–	6.1	4.3
Size, light, substrate and site	3.8	–	–	6.4	–	5.0	5.7

For high-light conditions the simulation was initiated without any pre-existing adults, whereas for low-light conditions the simulation began with a closed forest canopy. In this latter case, the initial density, tree diameter distribution and spatial distribution were simulated to be similar to our mapped forest stands on the terrace sites (see Appendix S4 for details). We ran these two types of simulations starting with populations of 1000 seedlings per ha for each species. The simulation was based on a 1-ha grid. We initially ran simulations in which the seedlings and saplings of each species had distinct growth and mortality functions, as described in this article. We then ran simulations in which we simplified the model by giving (i) all seedlings the same growth function, (ii) all saplings the same growth function, (iii) all seedlings the same mortality function, and (iv) all saplings the same mortality function while retaining the other species-specific functions. The identical growth and mortality models used functions based on average parameter values for the six species, thus allowing us to test a model in which we ignored species differences in growth or survival at a given life stage. We repeated the simulations ten times

with different random spatial positions of the initial seedling population, and report for each simulation for each species the time course of the total basal area of trees reaching the forest canopy (defined in SORTIE/NZ as occurring when d.b.h. > 10 cm). Given that we wanted to focus on the fate of one cohort of seedlings, we did not allow mature trees to produce any seeds in the simulations (i.e. we set their fecundity to zero). In the case of the simulation initiated with mature forest, we allowed adult trees to grow and die using functions parameterized from the NVS (see Appendix S4 for details).

Results

SEEDLING MORTALITY

The probability of mortality fell rapidly with increasing size for all species (Table 2 and Fig. 1). Mortality of most species decreased with increasing light availability, with the notable
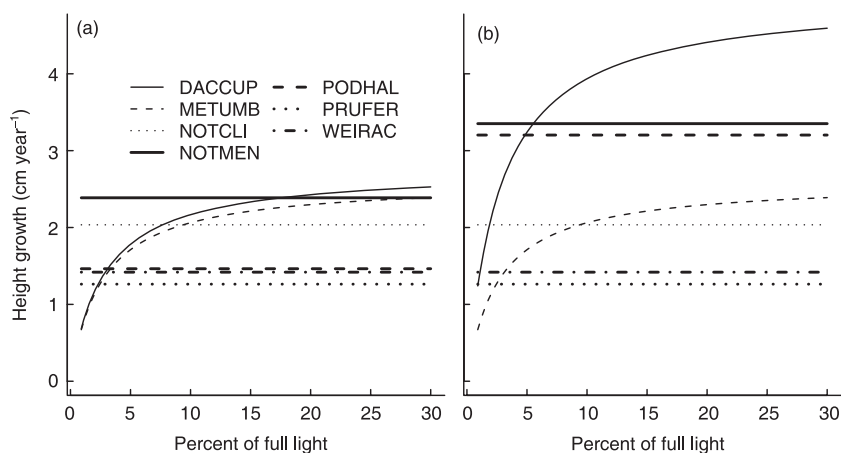
Fig. 2. Predicted height growth as a function of percent full light, based on the best fitting model selected for each species (Table 2) for seedlings (a) 15 cm or (b) 50 cm in height, growing on the terrace sites. Species acronyms are listed in Table 1.

exceptions of *D. cupressinum* and *W. racemosa* (Table 2). Probabilities of mortality at low light levels clearly differed among species for seedlings 15 cm in height, with very high probability of mortality for some species (Fig. 1a). The annual probability of mortality in shade, estimated for seedlings 15 cm in height, was low (< 0.15 year^{-1}) for *D. cupressinum*, *Podocarpus hallii*, and *M. umbellata*, but much higher for *N. solandri*, *N. menziesii*, *Prumnopitys ferruginea* and *W. racemosa* (> 0.20 year^{-1}), (Fig. 1a). In contrast, for seedlings 50 cm in height, the probability of mortality was very low at all light levels (< 0.15 year^{-1}) and differences among species were small, except that *N. solandri* experienced high mortality in low light, even at this size (Fig. 1b). The magnitude of the effects of size and light differed among species, resulting in size-dependent cross-overs of the ranking of species mortality in low light. For instance, *Prumnopitys ferruginea* had the fourth highest probability of mortality in low light when 15 cm tall but only the second highest probability of mortality in low light when 50 cm tall (Fig. 1).

HEIGHT GROWTH OF SEEDLINGS

Seedling height growth of only two of the species – *D. cupressinum* and *M. umbellata* – responded to light (Table 2). The differences in height growth rates among species were generally small for seedlings 15 cm in height (Fig. 2a). In contrast, more important differences occurred among the species for seedlings of 50 cm height (Fig. 2b). The height growth in 30% of light of *D. cupressinum*, *Podocarpus hallii*, and *N. menziesii* was about three fold higher than the growth of *Prumnopitys ferruginea* and *W. racemosa*. The effect of size resulted in changes in species' ranks for height growth between 15 and 50-cm tall seedlings. *Podocarpus hallii* had the fifth greatest height growth in 30% of light when 15 cm tall, but the third greatest when 50 cm tall. Inversely, *M. umbellata* had the second height growth in 30% of light when 15 cm tall, but only the fourth greatest when 50 cm tall.

SAPLING GROWTH AND MORTALITY

Sapling mortality was much lower than at the seedling stage (Table 3 and Fig. 1), with annual probability of mortality at

Table 3. Sapling height growth in 30% of full light (with 95% confidence intervals), taken from Coomes *et al.* (2009), and sapling probability of mortality, estimated with repeated-measure data taken from permanent plots within the National Vegetation Survey of New Zealand (no light effect). The number of samples used to estimate growth and mortality are given (n). Species acronyms are listed in Table 1

Species	Height growth (cm year^{-1})	n	Probability of mortality (year^{-1})	n
NOTCLI	10.6 (8.0–14.8)	39	0.0104	475
NOTMEN	5.5 (3.7–7.9)	81	0.0136	476
PRUFER	4.6 (2.6–8.9)	63	0.0091	116
WEIRAC	4.4 (2.7–7.3)	76	0.0108	4730
DACCUP	3.9 (3.0–5.0)	119	0.0058	388
PODHAL	2.9 (2.3–3.8)	99	0.0063	334
METUMB	No data		0.0095	135

the sapling stage lower than 1.5% for the seven species. The two species with the lowest probability of mortality were *D. cupressinum* and *Podocarpus hallii*, whereas the two species with the highest probabilities of mortality were *N. solandri* and *N. menziesii*. The probability of mortality of *N. solandri*, which was the highest at the seedling stage (Fig. 1), was intermediate at the sapling stage and close to the probability of mortality of *W. racemosa*, *Prumnopitys ferruginea* and *M. umbellata* (Table 3). According to the sapling height growth in 30% of full light reported by Coomes *et al.* (2009) (see Table 3), species differed clearly in their growth; however the ranking of the species was strikingly different from the ranking at the seedling stage. *Nothofagus solandri* had the highest height growth at the sapling stage (Table 3) whereas its ranking for growth was intermediate at the seedling stage (Fig. 2).

GROWTH-SURVIVAL TRADE-OFF

Interspecific comparisons of survival of 15-cm tall seedlings in low light with height growth of 15-cm tall seedling in full light, or comparisons of sapling survival with either 15-cm tall
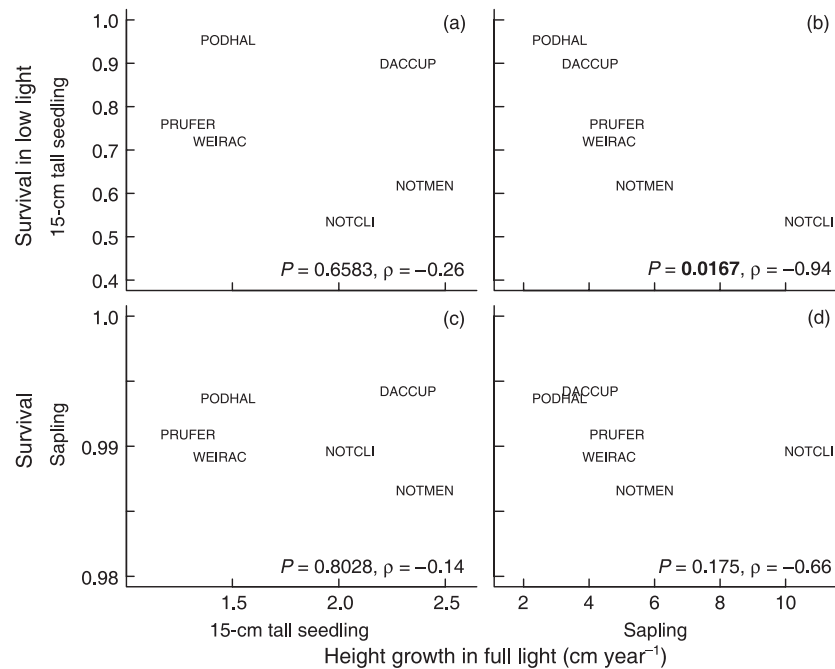
Fig. 3. Growth-survival trade-offs among tree species growing on P-depleted terrace sites in southern New Zealand: (a) trade-off between small seedling (15 cm tall) survival in low light and small seedling (15 cm tall) height growth in high light, (b) trade-off between small seedling (15 cm tall) survival in low light and sapling height growth in high light, (c) trade-off between sapling survival (no light effect) and small seedling (15 cm tall) height growth in high light, and (d) trade-off between sapling survival (no light effect) and sapling height growth in high light. Sapling height growth predictions are for stems 2.3 cm in diameter at 10 cm above the ground (equating to approximately 300 cm height) in high-light conditions (percent of full light = 30%) (see Coomes *et al.* 2009), sapling survival predictions are based on estimation from National Vegetation survey plots (with no light effect). Predictions of growth in high light (percent of full light = 30%) and survival in low light (percent of full light = 1%) for a 15-cm-tall seedling are based on the best estimated model for each species (Table 2). The Spearman's rank correlation coefficients and the *P*-value of the tests are given for each trade-off. Species acronyms are listed in Table 1.

seedling height growth in full light or with 3-m tall saplings growth in full light did not show significant trade-offs (based on Spearman's rank correlation see Fig. 3a,c and d). In contrast, the comparison of survival of 15-cm tall seedlings in low light with growth of 3-m-tall saplings in full-light did show a significant trade-off (Fig. 3b). The interspecific variation in sapling survival was extremely low in comparison with seedling survival. Note that these comparisons were made with the predictions of the best supported models for the terrace sites for each species.

sortie/nz simulations

Regeneration success of species (i.e. the basal area accumulation of the species in the > 10 cm diameter classes) depended strongly on initial light conditions (Fig. 4a,b). When all the species-specific parameters described above were included in the simulator, *N. solandri* was the first species to reach 10 cm d.b.h. in high-light conditions and rapidly accumulated basal area (Fig. 4a), whereas *D. cupressinum* and *N. menziesii* accumulated basal areas later during the simulations (Fig. 4a). In low-light conditions, the dynamics were quite different (Fig. 4b): *D. cupressinum*, *N. menziesii* and *Podocarpus hallii* were the only species to regenerate, reaching substantial basal areas by the end of the 300-year simulation, whereas hardly any *N. solandri* regenerated in low-light conditions (Fig. 4b).

Ignoring species differences in growth rate at the seedling or sapling stages illustrates the importance of including both life stages for predicting species regeneration success (Fig. 5a,b and Fig. S4.1 and S4.2). Under high-light conditions, ignoring species differences in sapling growth functions resulted in far lower basal area of *N. solandri* stems reaching the canopy within 300 years (Fig. 5a and Fig. S4.1), whereas the opposite effect was seen for slow-growing species such as *Podocarpus hallii*, *W. racemosa* and *Prumnopitys ferruginea*. Differences in sapling growth rate thus had important effects on regeneration success in high light. Ignoring species differences in growth at the seedling stage also resulted in higher basal area of these slow-growing species, but the effects were less pronounced, indicating that growth differentiation in the seedling stage was less influential than in the sapling stage (Fig. 5a and b). For slow-growing species such as *Podocarpus hallii* and *W. racemosa*, regeneration success in low light was strongly constrained by seedling and sapling growth (Fig. 5b).

Species differences in survival both at the seedling and the sapling stages influenced regeneration success in the shaded understorey. Ignoring species differences in mortality at the seedling stage greatly increased the predicted regeneration success of *N. solandri* in the shaded understorey (Fig. 5d and Fig. S4.2): otherwise there was very little canopy recruitment of this species because of its high seedling mortality (Fig. 5d). On the other hand, the regeneration success of *N. menziesii*
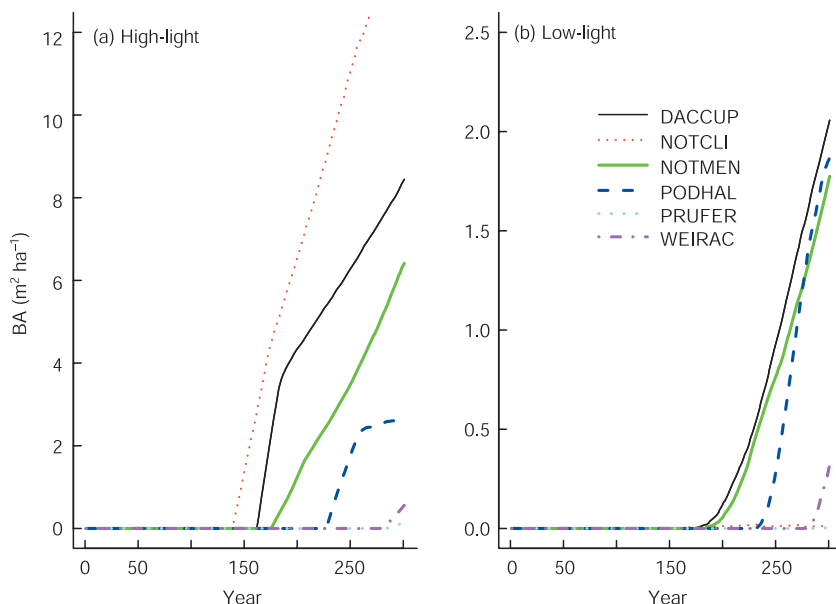
Fig. 4. Output of the SORTIE/NZ simulations showing time courses of the cumulative basal area of adult trees (i.e. those > 10 cm d.b.h.) over 300 years of simulation, using different functions for growth and mortality of each species at the seedling and sapling stages. Only the basal area of trees that started the simulation as seedlings are included in the basal area predictions, hence the values are all zero initially. The mean basal areas of 10 replicates are given, for simulation in which (a) there were no adult trees initially, resulting in high-light conditions for regenerating plants and (b) there was an established forest initially, resulting in low-light conditions for regenerating plants. Species acronyms are listed in Table 1.

was more constrained by its high sapling mortality than by its seedling survival (Fig. 5d).

Discussion

EFFECTS OF PLANT SIZE ON LOW-LIGHT MORTALITY

Mortality decreased with seedling size, and interspecific variation in mortality was far greater among 15-cm tall seedlings than 50-cm tall seedlings in deeply shaded sites. Saplings had even lower rates of mortality. Our estimates of sapling survival are not specific to very low light levels (i.e. 1%), because no light data were available for this analysis. Nevertheless, the average light levels of the plots used in this analysis were < 10%, and this light level is unlikely to explain the strong decrease of mortality observed for saplings in comparison to seedlings. The same convergence in shade tolerance with increasing size has been shown for North American tree species (Kneeshaw *et al.* 2006). Changes in the low-light mortality of seedlings with size can be interpreted in the context of the ability of a seedling to maintain a positive carbon balance. For instance, it has been proposed that onto-genetic shifts in several important traits related to carbon balance (such as crown plasticity and the ratio of photosynthetic to non-photosynthetic biomass) can lead to a decrease in shade tolerance with size of an individual (Canham 1988b, Messier *et al.* 1999; Kneeshaw *et al.* 2006). At the population level it is generally accepted that the probability of mortality of a juvenile tree decreases with size (Harcombe 1987; Peet & Christensen 1987), because this ontogenetic decrease of shade tolerance is offset by an increase in light availability with tree size, since smaller trees occur, on average, in deeper shade than larger trees.

The effects of size on shade tolerance are not only related to carbon balance traits and light availability. Indeed, in the terrace sites, differences between the average light available

for 15- and 50-cm tall seedlings is probably small. Results from related studies at these sites (Coomes *et al.* 2005) indicate that there is no detectable difference in light availability between the forest floor and 1.4 m above the floor in the terrace site. Thus, variation in light is unlikely to explain the decrease in the probability of mortality with size. The conceptual mortality models developed by Manion (1991) and Pederson (1998) present an alternative framework in which to analyse the effects of size on survival in low light. Under those models, mortality in low-light conditions does not result directly from carbon limitation, but from shade weakening the ability of the individuals to withstand external stress. It is generally considered that small individuals are more sensible to disturbances by external stresses such as damage, herbivory or pathogens than larger individuals (Metcalfe & Grubb 1997; Lusk 2004). For instance, Clark & Clark (1991) reported that the annual probability of mortality due to litterfall – which is an important agent of physical damage in New Zealand forests (Gillman & Ogden 2001) – decreases with tree size in tropical rain forests. In addition, frequency of herbivory by large mammals, which is high for small seedlings according to our observations, is likely to decrease with size as saplings escape the browsing layer. Shade tolerance would thus be linked to the ability of shaded small seedlings to mobilize carbohydrate reserves to withstand damage (Canham *et al.* 1999; Lusk & Piper 2007), and variation of external stress has the potential to affect the shade tolerance of the species (see Long *et al.* 2007 for an example based on variation of herbivory pressure). Variation of low-light survival with size would thus be driven by the carbon balance of the individual (decreasing with size), the average light conditions experienced by the individual (increasing with size), the size of the storage space to accumulate reserve (increasing with size), and the impact of external stress (decreasing with size). Given the large impact of external stresses (herbivory, physical damages, etc.) and the small space available to accumulate reserve for small seedlings,
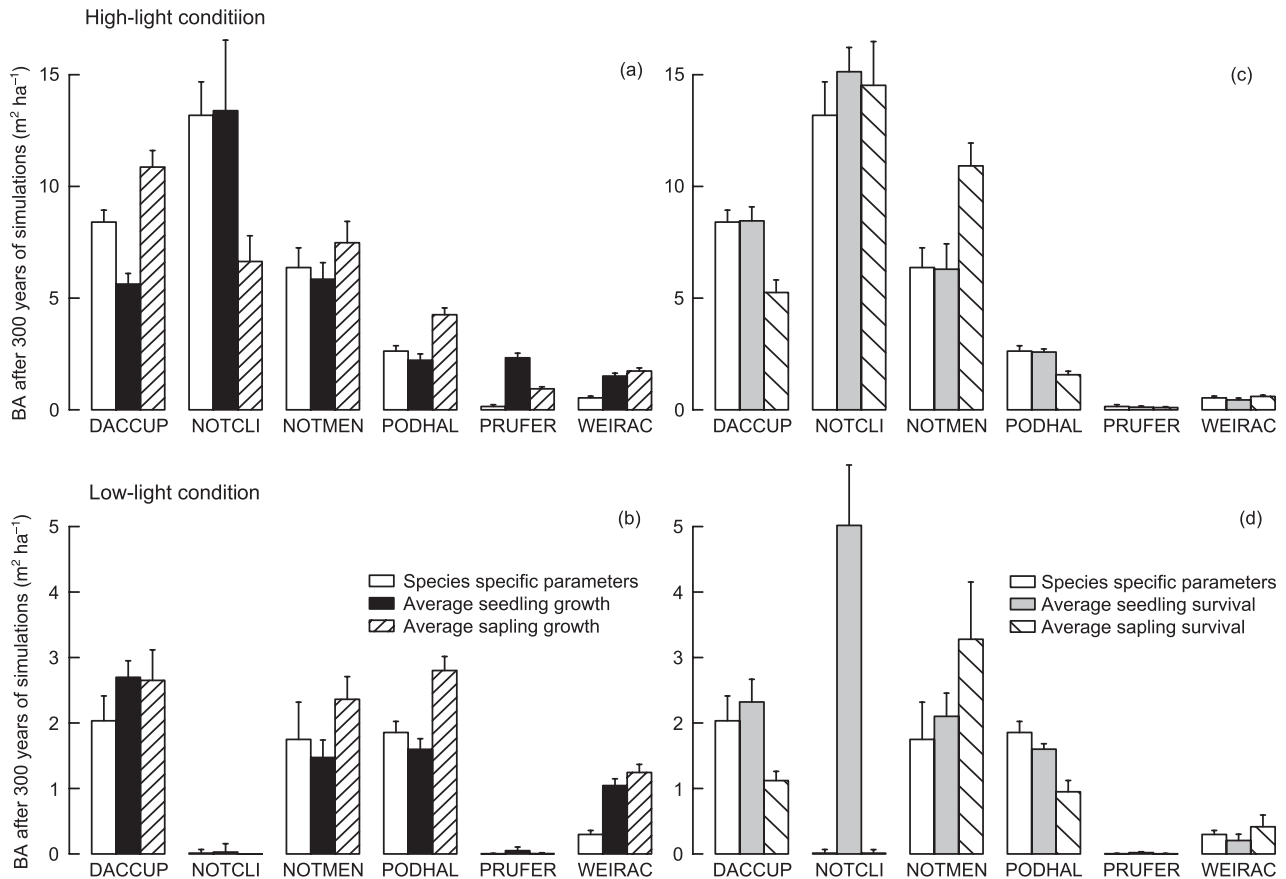
Fig. 5. Basal area of mature trees of six species after 300 years of SORTIE/NZ simulation (mean and standard error of 10 replicates) in which there were no adult trees initially, resulting in high-light conditions for regenerating plants (a and c), and in which there was an established forest initially, resulting in low-light conditions for regenerating plants (b and d). We compared simulations where seedlings and saplings of each species had distinct growth and survival functions (Species specific parameters) either with simulations where species differences in growth were ignored at the seedling (Average seedling growth) or at the sapling (Average sapling growth) stages (panels a and b) or with simulations where species differences in mortality were ignored at the seedling (Average seedling mortality) or at the sapling (Average sapling mortality) stages (panels c and d). Only the basal area of trees that started the simulations as seedlings are shown. Species acronyms are listed in Table 1.

species differences in shade tolerance are likely to be the most amplified at this stage (see also Delagrange *et al.* 2004).

EFFECTS OF PLANT SIZE ON HIGH-LIGHT GROWTH

In contrast to mortality, height growth generally increased from the seedling to sapling stage, but the magnitude of this increase differed among species, resulting in size-dependent cross-overs of the ranking of species growth in full light. For instance, *Podocarpus hallii* had the fifth greatest height growth rate in full light when 15 cm tall, third greatest when 50 cm tall, but had the slowest height growth at the sapling stage (approximately 300 cm in height). As reported in other field studies (Coomes 1995; Sipe & Bazzaz 1994; Canham *et al.* 1999), even if light does have a statistically significant effect, the actual magnitude of the growth response to light availability of small seedlings is small. The positive effect of size on growth resulted in greater differences among tree species height growth in high light at the sapling stage than at the seedling stage.

Why are the interspecific differences among high-light growth less clear at the small seedling stage than at the sapling stage?

This could be due to the high sensitivity of most seedlings to a myriad of factors such as drought, herbivory and pathogens, which reduce seedling investment in growth relatively to survival and blur interspecific distinctions in growth responses to light. An alternative explanation is that the initial reserve provided by the seed can give an initial height growth advantage for 15-cm tall seedlings of shade-tolerant large-seeded species (for instance this could be the case for *D. cupressinum*) that is quickly compensated in larger size classes by the fast growth rate of shade-intolerant species in high-light conditions (Coomes & Grubb 2003; Baraloto *et al.* 2005b; Niimemets 2006).

EFFECTS OF SIZE ON THE GROWTH–SURVIVAL TRADE-OFF

Our study demonstrates that the strength of the growth–survival trade-off is dependent on the size of target individuals. We found a significant interspecific trade-off between small-seedling survival in shade and sapling height growth in full light, but the trade-off was not observed when we considered the height

growth rates of small seedlings rather than saplings, or sapling survival rather than seedling survival. A size-dependent cross-over of the ranking of species performance in low or high light has been reported by other studies (Clark & Clark 1992; Svenning 2000; Davies 2001; Lusk 2004; Baraloto *et al.* 2005a), but to our knowledge no studies have specifically analysed the size effect on the growth-survival trade-off. Our findings are consistent with the hypotheses that interspecific differences in low-light survival are greatest for small seedlings (consistent with Kneeshaw *et al.* 2006), while interspecific differences in full-light height growth are greatest for saplings (Pacala *et al.* 1994 and Cole & Lorimer 2005).

The position of species within the growth-survival strategy space depended greatly upon which life stages were being compared. For instance, *D. cupressinum* had low growth at the sapling stage but high growth at the seedling stage. These changes of tree performance rank with ontogeny are likely to be common for long-lived perennial organisms such as trees, but relatively few studies have explored this question (see 'ontogenetic trade-off' of Baraloto *et al.* 2005a).

IMPLICATIONS OF SIZE-DEPENDENT TRADE-OFFS FOR TREE RECRUITMENT

Studies reporting trade-offs between high-light growth and low-light survival usually assume that the trade-off results in important consequences for tree recruitment dynamics (Lin *et al.* 2002; Baraloto *et al.* 2005a), but few studies have proceeded to test this assertion by integrating the dynamics of the species over different life stages and taking into account differences in growth and survival in each stage. In principle, strong performance of a species at one life stage could be cancelled out by weak performance at later stages.

Our simulations with SORTIE/NZ integrated demography over the different life stages and accounted for the process of light competition (recall that the light transmission sub-model of SORTIE is a simplification of reality and that our results are dependent on these simplifications). Results of the simulations show that the six New Zealand tree species clearly differed in their dynamics in high- vs. low-light conditions (*M. umbellata* was not included in these simulations). For instance, *N. solandri* was the most successful species in high-light conditions, but unsuccessful in low-light conditions. This species is generally considered to be shade-intolerant (Wardle 1984), and has rapid growth in high-light conditions, but low survival as a seedling in deep shade. In contrast, the regeneration of *Podocarpus hallii*, *W. racemosa* and *Prumnopitys ferruginea*, which are generally regarded as species with high or intermediate shade tolerance (Stewart & Veblen 1982; Lusk & Ogden 1992; Duncan 1993; Lusk & Smith 1998; Smale & Smale 2003), was largely restricted to understorey conditions. These results are in agreement with the classical vision of the impact of growth-survival trade-offs on forest dynamics: species positions along the trade-off drive their ability to recruit in high or in low light. The most shade-tolerant tree species, located at the high low-light survival end of the trade-off, regenerate mostly under closed canopy, whereas shade-intolerant species, located at the fast high-light growth end of the trade-off, regenerate mostly in gaps. However, our SORTIE/NZ simulations for other species show that the classical view of the impact of growth-survival trade-off on forest dynamics is overly simplistic. Species ranks varied with life stage; as a result, regeneration success in high-light could not be predicted from knowledge of sapling growth alone. For instance, despite its slow sapling growth *D. cupressinum* was the second most successful species in high-light conditions because of its high seedling growth, in agreement with intermediate shade tolerance reported by previous studies (Lusk & Smith 1998; Smale & Smale 2003). This clearly shows that ignoring species differences in growth or survival at a given life stage can lead to large errors in prediction of species regeneration success. In addition, regeneration success under a closed canopy was primarily limited by low-light mortality at the seedling stage, but seedling growth was also influential. For instance, despite its poor low-light seedling survival *N. menziesii*, which has been generally considered to be of intermediate shade tolerance in comparison with *N. solandri* (Stewart & Rose 1990; Runkle *et al.* 1995; Runkle *et al.* 1997), was the second most successful species in low-light conditions, mostly because of its fast low-light seedling growth.

Classical trade-off theory suggests that the regeneration strategy of a species is defined by its high-light growth rate, because a plant's ability to survive in shade is closely negatively correlated with its high-light growth rate and this trade-off acts to stretch species out along a shade–tolerance axis. Here we show that, because growth and survival are heavily influence by size, the classical trade-off is only evident when comparing specific life-history stages, namely the survival of seedlings and the growth of saplings. Furthermore, we show, as previously suggested by Baraloto *et al.* (2005a) that the size-dependent nature of these demographic rates has important influences on the regeneration success under high- and low-light conditions, blurring traditional distinctions in the shade tolerance of species.

Acknowledgements

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