

Effects of size, competition and altitude on tree growth

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Summary

1. Understanding the factors influencing tree growth is central to forest ecology because of the significance of growth to forest structure and biomass. One of the simplest, yet most controversial growth models, proposed by Enquist and colleagues, predicts that stem-diameter growth scales as the one-third power of stem diameter. Recent analyses of large-scale data sets have challenged the generality of this theory and highlighted the influence of resource competition on the scaling of growth with size.

2. Here we explore the factors regulating the diameter growth of 3334 trees of mountain beech (*Nothofagus solandri* var. *cliffortioides*) growing in natural single-species forests in New Zealand. Maximum-likelihood modelling was used to quantify the influences of tree size, altitude, the basal area of taller neighbours (B_L) and the basal area of all neighbours (B_T) on growth. Our interpretation of the models assumed that taller neighbours compete for light whereas all neighbours compete for nutrients.

3. The regression analyses indicate that competition for light has a strong influence on the growth of small trees, whereas competition for nutrients affects trees of all sizes. These findings are consistent with experimental manipulation studies showing that competition for light and nutrients inhibits the growth of small mountain beech trees, and fertilizer application studies showing that nitrogen limits the growth of large trees.

4. Tree growth declined with altitude. The regression analyses suggest that the intensity of light competition also declines with altitude, when trees with similar B_T and B_L values were compared along the gradient. These results are consistent with observations that trees become stunted and have more open canopies at high altitudes.

5. Our study is the first to build the effects of competition and environment into Enquist's model of tree growth. We show that competitive interactions alter the scaling of mean growth rate with size, whereas altitude does not influence the scaling of potential growth rate with size.

Key-words: Boltzmann–Arrhenius function, competition, elevation, facilitation, metabolic theory, non-linear mixed-effects model, quantile regression, temperature, Tilman vs. Grime debate, WBE theory

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Introduction

Trees in natural populations usually exhibit large variation in growth (e.g. Harper 1977). Understanding this variation in growth is central to forest ecology because of its significance to forest structure and biomass. One approach to understanding variation in tree growth is to derive mechanistic explanations for the potential maximum growth rate of trees and then

determine why and how the growth of individuals falls below this potential constraint. Enquist (2002) argued that because trees have an efficient transport system then whole-tree photosynthetic rate is simply related to the number of leaves on a tree, and so is mechanistically related to size by an invariant power law. Based upon this relationship, Enquist *et al.* (1999) argued that stem diameter growth dD/dt scales as $D^{1/3}$ (henceforth referred to as the Enquist growth model). Clearly the assumption that photosynthetic rate is only dependent upon leaf number, or size, is suspect because it is, of course, also limited by many other factors including the supply of water, light and nutrients (Coomes 2006; Reich *et al.*

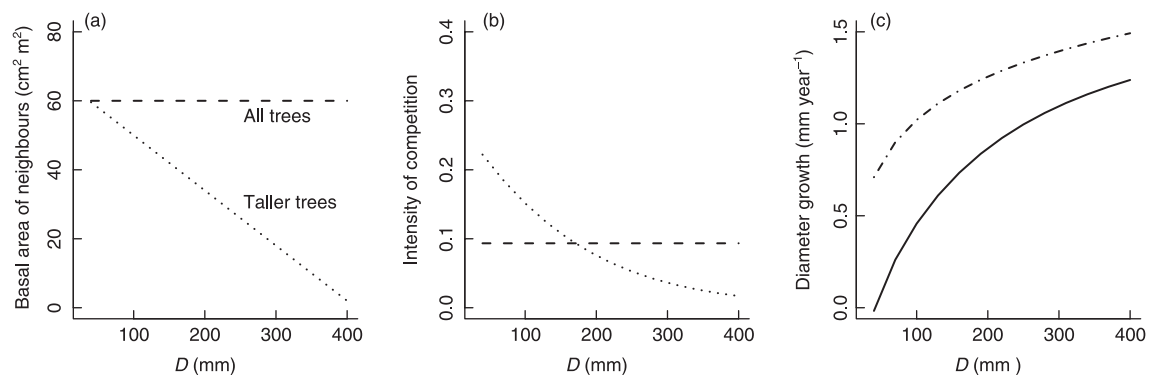


Fig. 1. A conceptual model of the ways in which growth varies with tree size, as a result of changes in competition with neighbours: (a) As the stem diameter D of a tree increases, there is a decrease in the basal area of taller neighbours (B_L) while the basal area (B_T) of all neighbours remains relatively constant; (b) the intensity of competition for light (....) decreases with size because trees are less likely to be overshadowed by taller neighbours, whereas the intensity of competition for nutrients (---) remains constant; (c) the difference between potential growth rate (no competitors) and mean growth rate (with competitors —) is greatest for small trees because the overall intensity of competition is greatest for small trees.

2006; Muller-Landau *et al.* 2006). In a recent paper, Muller-Landau *et al.* (2006) fitted growth curves to data from 1.7 million trees in 10 tropical forests. They showed that the scaling of mean diameter growth with size varied considerably among the forests, and was not described by a power law with slope of $1/3$. They argued that the changing supply of light with size exerted a strong influence on the scaling of growth: small trees were shaded by taller neighbours and grew slowly as a consequence, while larger trees were less affected by shading (see Weiner 1990). Therefore the Enquist growth model needs to be reconsidered, with the control of competition made more explicit (Coomes 2006).

Here we build upon these ideas using a data set of 3334 mountain beech trees (*Nothofagus solandri* var. *cliffortioides*) growing along an altitudinal gradient in New Zealand's Southern Alps. Our work explores three avenues not investigated by Muller-Landau *et al.* (2006) in their important tropical study. First, we consider whether the Enquist growth model represents an upper boundary relationship that occurs when nothing else is limiting except flow through the vascular network. The supply of resources to trees is spatially heterogeneous because gaps created by the death of large trees allow light to penetrate to the forest floor and sometimes result in the release of nutrients (Coomes & Grubb 2000), so tree growth in natural forests is immensely variable (Canham *et al.* 2004). We hypothesized that the diameter growth of trees uninhibited by competition scales with $D^{1/3}$, as the Enquist growth model predicts. We investigate this hypothesis by using quantile regression to fit an upper boundary curve to the size–growth distribution (Thomson *et al.* 1996; Cade *et al.* 1999; Cade & Guo 2000) and testing how similar it was to the curve predicted by the Enquist growth model.

Second, we use neighbourhood modelling to explore the ways in which competition for light and nutrients varies with tree size (Freckleton & Watkinson 2001;

Canham *et al.* 2004; Uriarte *et al.* 2004). The general form of our model is $G = \lambda D^\alpha l(B_L) n(B_T)$, where G is stem-diameter growth, B_L and B_T are the basal areas of larger neighbours and all neighbours, respectively, and $l(B_L)$ and $n(B_T)$ are functions that describe the competitive effect of such neighbours on growth. The function $l(B_L)$ is often regarded as defining the effect of competition for light because only taller neighbours are able to intercept light before it reaches the focal tree (Vanclay 1995; cf. Schwinning & Weiner 1998). By similar reasoning, $n(B_T)$ describes the effect of below-ground competition because nutrient-uptake by a plant depends upon the extent to which the fine roots of neighbouring plants have depleted the pool of available nutrients, and the roots of all neighbours compete for resources, not just the taller neighbours (Schwinning & Weiner 1998). Our hypothesis was that competition affects the growth of all trees, but that competition shifts from being mainly for light when the focal tree is small to being mainly for nutrients when the tree reaches maturity (Fig. 1).

Third, we examine the ways in which potential growth rate and competitive intensity vary with altitude. Grime (1977) has argued that competition is intense in productive sites, where the potential for rapid growth allows rapid pre-emption of resources, but decreases in intensity and importance in less productive ('stressed') sites. In contrast, Tilman (1988) has argued that plants respond plastically to changing rates of resource supply (Bloom *et al.* 1985; Gleeson & Tilman 1992), and consequently compete for light in nutrient-rich sites and for below-ground resources in nutrient-depleted sites. These contrasting views form the basis for one of the longest running debates in ecology (Craine 2005). Numerous authors have quantified changes in competitive intensity along environmental gradients using short-term removal experiments in herbaceous communities (Goldberg *et al.* 1999; Callaway *et al.* 2002; Maestre *et al.* 2005) but there have been remarkably few studies using long-lived individuals in forest

communities, and only one that has explicitly factored size into their design (Canham *et al.* 2004). As well as testing for how light competition varies with altitude we evaluate the Enquist growth model prediction that the size-dependence of growth, as defined by the scaling exponent α , does not vary with environment.

We examine diameter growth in mountain beech trees found in unmanaged stands which form naturally single-species forests on the eastern slopes of New Zealand's Southern Alps (Wardle 1984). Data collected from 246 permanent plots, spanning a 780-m altitudinal gradient, were used to evaluate the ways in which size, competition for light, and altitude interact to affect an individual's diameter growth. These monospecific forests are uniquely suitable for testing such relationships without the confounding effects of species turnover. Specifically we test the following hypotheses.

1. The Enquist growth model defines the upper rate of growth that occurs when competition is not limiting;
2. there is a shift in relative importance of competition for light and nutrients with ontogeny;
3. Trees are slower growing and less influenced by competition for light in high altitude forests, but the scaling exponent is unaffected by altitude.

Methods

STUDY AREA

The 200-km² study area (43°10' S, 171°35' E) has a mountainous terrain with peaks over 2000 m a.s.l. and valley bottoms down to 600 m a.s.l. altitude. Mountain beech (*Nothofagus solandri* var. *cliffortioides*; Nothofagaceae) is a light-demanding species and a member of one of the few ectomycorrhizal genera in New Zealand forests (Wardle 1984). The mountain beech forest in the study area is spatially heterogeneous because storms, earthquakes and pathogen outbreaks have patchily disturbed the stands over recent decades (Wardle & Allen 1983; Harcombe *et al.* 1998; Allen *et al.* 1999). This heterogeneity was beneficial for our neighbourhood modelling because it provided a wide range of neighbourhood basal area values. While the mean basal area of mountain beech trees per plot increases with altitude (Harcombe *et al.* 1998), the trees get shorter, and there is a substantial reduction in biomass per plot as a result (Harcombe *et al.* 1998). A weather station at 914 m altitude on the eastern edge of the study area has recorded a mean annual temperature of 8.0 °C, precipitation of 1447 mm year⁻¹, and irradiance of 4745 MJ m⁻² year⁻¹ (McCracken 1980). Monthly mean daily temperature is greatest in February (13.9 °C) and least in July (2.0 °C). Air temperature decreases by 0.71 °C, and rainfall increases by 21.9 mm year⁻¹, for every 100-m rise in altitude (based on 13 years of data; McCracken 1980). Rainfall increases from about 1200 mm year⁻¹ in the east to 2500 mm year⁻¹ in western parts of the study area (Griffiths & McSaveney 1983), and there is no evidence to suggest that rainfall

limits growth within the study area (Wardle 1984). There is compelling evidence from fertilizer and root-trenching experiments that nitrogen limits tree growth in our mountain beech forest (Davis *et al.* 2004; Platt *et al.* 2004), so we regard below-ground competition and competition for nutrients as being synonymous in this paper.

FIELD DATA

We utilized plots sampling 9000 ha of forest that included stands up to the natural tree line at 1400 m a.s.l. A total of 246 plots were established systematically along 98 compass lines in the mountain beech forest over the austral summers of 1970–71 and 1972–73 (Allen 1993; Allen *et al.* 1999; Coomes & Allen 2007). The origins of lines were randomly located points along stream channels (30–1000 m apart), and their compass directions were also chosen at random. Plots were then located at 200-m intervals along each line until the tree line was reached, giving rise to lines containing between one and eight plots (mean = 2.6). The altitude of a plot was based upon field measurements using a barometric altimeter. Each plot was 0.04 ha (20 × 20 m), and divided into 16 subplots (5 × 5 m). Within each plot, the diameter at breast height (d.b.h.) of each tree stem > 30 mm, and the subplot in which it was located, were recorded. Plots were re-enumerated during the austral summers that started in 1974 and 1993. All tree stems were tagged in 1974, and new recruits (> 30 mm d.b.h.) tagged in 1993. Hereafter, we refer to the nominal date for plot establishment as 1974, and utilize the surviving individuals in 1993 to characterize stem diameter growth. Trees that died between 1974 and 1993 tended to have slower growth rates than trees that survived (D.A. Coomes & R. B. Allen, unpublished data), so our approach overestimates the average growth rate of the population; this issue is not considered further in this paper. The vast majority of trees are single-stemmed and resprouting is uncommon.

Growth analyses were focused on the 3334 individuals in the four central 5 × 5 m subplots of the 246 plots. As the data set contained information about which square subplot a tree was located in, our competition indices were based upon summing basal areas within set subplots (Freckleton & Watkinson 2001). Given the close correlation ($r^2 = 0.74$) between stem diameter and height in mountain beech forests (Harcombe *et al.* 1998), taller trees are taken to be those with larger diameters. We calculated B_L by summing the basal area of stems that had diameters larger than the initial diameter of a target tree within a 15 × 15 m area centred upon the 5 × 5 m subplot containing the target tree. Values of B_L were calculated from diameter data collected in 1974 and 1993, expressed in standard units (cm² m⁻²) and averaged. We chose to use the mean of the 1974 and 1993 values because it is more representative of the neighbourhood conditions experienced by a tree over the course of the study than the value at either the start

or end of the study. The basal area of all neighbours B_T was calculated in the same way. Neighbourhood areas of 25 m² and 400 m² were also tried, but regression models had weaker explanatory power than ones based on an area of 225 m².

POTENTIAL GROWTH RATE

The Enquist growth model suggests stem diameter growth dD/dt is defined by the following power function:

$$dD/dt = \lambda_0 D^\alpha, \quad \text{eqn 1}$$

where D is the diameter at breast height, λ_0 is the scaling coefficient and α is the scaling exponent. Our first hypothesis, that the Enquist growth model defines a potential growth curve rather than the mean growth curve, was tested by using non-linear quantile regression (*nlsr* routine in the *quantreg* package of R) to fit the integrated form of the power function to our data set:

$$D_t = [D_0^{1-\alpha} + \lambda_0(1-\alpha)t]^{1/(1-\alpha)}, \quad \text{eqn 2}$$

where D_0 is the initial diameter at breast height, D_t is diameter recorded at the second enumeration, t is the time between measurements (19 years), λ_0 is the scaling coefficient and α is the scaling exponent. We used the integrated form of the power function because instantaneous growth rate (dD/dt) varies continuously and non-linearly with size (Muller-Landau *et al.* 2006). Quantile regression allowed us to fit curves through the middle of the data set by weighting regression on the 50th quantile, and to the 'upper boundary' (Cade & Guo 2000); the choice to define the upper boundary is arbitrary so we used the 95th and the 99th quantiles.

EFFECTS OF COMPETITION FOR LIGHT AND NUTRIENTS

Our second hypothesis, that mountain beech trees compete mainly for light as juveniles and for nutrients as adults, was tested by fitting alternative competition functions to the data (e.g. Canham *et al.* 2004; Uriarte *et al.* 2004). The effect of competition for light was modelled using the function:

$$\frac{dD}{dt} = \frac{\lambda_1 D^\alpha}{\left(1 + \frac{\lambda_1}{\lambda_2} e^{\lambda_3 B_L}\right)}, \quad \text{eqn 3}$$

where D is the stem diameter, B_L is the basal area of taller neighbours, and λ_2 and λ_3 define the competitive effect of taller neighbours on growth. B_L was the average of the values calculated from the 1974 and 1993 surveys. Note that $\lambda_1 D^\alpha / (1 + \lambda_1/\lambda_2)$ is the potential growth rate attained when trees are not subjected to competition. The logic behind this choice of function is explained in Appendix S1 (see Supplementary Material). Briefly, we assume that the amount of light

reaching a tree is determined non-linearly by the leaf area index (LAI) of taller trees around it (the Beer–Lambert law is used), and that the assimilation rate of the plant depends non-linearly on light availability (the Michaelis–Menten function is used). Based on these assumptions, λ_3 quantifies the amount of shade cast by taller neighbours (it is directly proportional to the light-extinction coefficient) while λ_2 quantifies the response of the target tree to light (it is the slope of the growth–light curve at zero light). The model contains four parameters to be estimated by regression analysis (α , λ_1 , λ_2 , λ_3).

We decided against developing a complex mechanistic model to describe the effects of below-ground competition because much remains obscure about the processes involved in taking up and retaining nutrients (e.g. Schwinning & Weiner 1998; Höglberg & Read 2006; Reich *et al.* 2006). Instead, the effects of competition for below-ground resources were modelled using the following simple function:

$$\frac{dD}{dt} = \frac{\lambda_1 D^\alpha}{(1 + \lambda_4 B_T)} \quad \text{eqn 4}$$

where B_T is the total basal area of all trees within a specified area around a target stem, and λ_4 and α are parameters to be estimated by regression. B_T was the average of the values calculated from the 1974 and 1993 surveys. This is a basic density-dependence function which predicts that growth declines towards zero with increasing B_T . An important distinction from the light model is that it assumes that the ability of a plant to capture nutrient depends on the total basal area of neighbours, rather than on the basal area of taller neighbours. Note that we tried increasing the flexibility of the response curve by including an extra parameter to raise B_T to a power, but these models failed to converge. When we fixed the exponent at different values and allowed the likelihood estimator to find the optimal value for the other parameters, we found that the models converged and the AICs of the models were worse, or very similar to, the AIC value of the model given (i.e. exponent set at 1).

Finally, the combined model of competition for light and nutrient that we chose, after extensive exploration of alternative models, was:

$$dD/dt = \lambda_1 D^\alpha / [(1 + \lambda_1/\lambda_2 e^{\lambda_3 B_L})(1 + \lambda_4 B_T)] \quad \text{eqn 5}$$

This model can only be fitted when trees of a wide range of sizes are considered because B_T is closely correlated with B_L for small trees (by definition $B_T = B_L$ for the smallest tree in the plot), but the two metrics are much less closely related for big trees (see Appendices S3 and S4).

The parameters in equations 1, 3, 4 and 5 were estimated by maximum likelihood methods (Canham *et al.* 2004). The integrated forms of the models were fitted using non-linear mixed-effects modelling (the *nlme* routine in R), which accommodated the covariance

associated with non-independent sampling (trees within plots) as a random intercept term (R Foundation 2006). For example, parameters λ_0 and α in equation 1 were estimated by fitting as:

$$D_t = [D_0^{1-\alpha} + \lambda_0(1-\alpha)\Delta t]^{1/(1-\alpha)} + \varepsilon + \varepsilon_t, \quad \text{eqn 6}$$

where D_0 and D_t are stem diameters in 1974 and 1993, Δt is the time interval, ε_t is a plot-level random term and ε is the residual error. Both random terms were assumed to be normally distributed, and analyses of residuals indicated that this assumption was valid.

The relative strength of alternative models (equations 1, 3, 4 and 5) were compared by their Akaike Information Criteria (AICs). AIC is defined as the $-2 \log(\text{maximum likelihood}) + 2(\text{number of parameters})$, and provides a quantitative measure that can be used to rank alternative models; the model with the smallest AIC is taken to be the 'best' of the set under consideration (Burnham & Anderson 2002). AICs were used to make these comparisons because the models are not nested.

EFFECTS OF ALTITUDE

Growth rates may decline with altitude because of reduced air and soil temperatures (an adiabatic effect), shorter growing seasons, increased exposure to wind, and reduced supply of nutrients. The effect of altitude on the potential growth rate parameter was ascertained by allowing λ_1 to become a quadratic function of altitude (A):

$$\lambda_1 = \lambda_{1A} + \lambda_{1B}A + \lambda_{1C}A^2. \quad \text{eqn 7}$$

The significance of altitude terms was tested by likelihood ratio tests, and by examination of standard error estimates (i.e. testing whether the parameter differed from zero by more than two times the standard error). Having incorporated the effects of altitude on potential growth rate, we proceeded to explore whether the scaling exponent or competition terms (i.e. α , λ_2 , λ_3 , or λ_4) varied with altitude. Each of these terms was made into a quadratic function of altitude, the models were refitted, and the statistical significance of adding altitude terms was tested using log-likelihood ratio tests. The change in AIC associated with adding the altitude terms is also given, for consistency.

If the fall in mean temperature with altitude is the main determinant of changes in growth rate (e.g. Benecke & Nordmeyer 1982; Richardson *et al.* 2005) then the Enquist growth model theory predicts that the Boltzmann–Arrhenius function provides a mechanistic explanation for changes in potential growth (Enquist *et al.* 2003):

$$\lambda_1 = \lambda_8 \exp(-E/kT) \quad \text{eqn 8}$$

where T is absolute temperature in Kelvin based on a lapse rate of 0.71 °C per 100 m altitude, E is the average

activation energy (*c.* 0.65 eV), and k is the Boltzmann constant (8.62×10^{-5} eV K⁻¹). The goodness of fit of the Boltzmann–Arrhenius function vs. the quadratic function of altitude was assessed by comparing AICs.

INTENSITY OF COMPETITION ALONG GRADIENTS

Several indices of competition intensity have been proposed in the literature, of which we selected to use the log-transformed performance ratio:

$$\ln \text{RR} = \ln(G_P/G_C), \quad \text{eqn 9}$$

where G_P is the potential growth of a plant growing without competitors and G_C is growth in the presence of competitors (Goldberg *et al.* 1999). Most studies of competition have involved inserting herbaceous plants into natural communities and comparing their growth with paired controls growing in isolation from competitors. In our study, it is the regression model that provides the mean and potential growth rates used to calculate $\ln \text{RR}$. The general form of the growth model is $G_C = \lambda D^\alpha l(B_L)n(B_T)$, where $l(B_L)$ and $n(B_T)$ are functions that describe the effects of competition for light and nutrients, respectively, and the potential growth rate is $G_C = \lambda l(0)n(0)D^\alpha$. Entering these growth functions into equation 9 we get:

$$\ln \text{RR} = \ln l(0)/l(B_L) - \ln n(0)/n(B_T). \quad \text{eqn 10}$$

We define $\ln l(0)/l(B_L)$ and $\ln n(0)/n(B_T)$ as being competition intensities for light and nutrients, respectively (henceforth ICL and ICN). The advantage of using $\ln \text{RR}$ is that it is simply the sum of ICL and ICN.

In order to explore how the mean ICL varied with altitude, we plotted ICL against A for all 3334 trees in the data and then fitted a smooth curve through the data using generalized additive models (the *gam* function in R, selecting the smoothing spline option with 6 d.f., and otherwise using default settings). This approach was also used to explore the ways in which mean ICL, ICN and $\ln \text{RR}$ varied with altitude and tree size. All curves fitted by *gams* were significantly different from flat-line relationships ($P < 0.00001$) unless otherwise stated. Note that simply inserting the mean value of B_L or B_T into ICN or ICL would give an incorrect estimate of the mean intensity of competition because of Jensen's Inequality (the function of a mean is not equal to the mean of a function).

Results

MEAN AND UPPER BOUNDARY GROWTH CURVES

Growth of mountain beech trees was significantly correlated with tree size ($r = 0.41$, $P < 0.00001$),

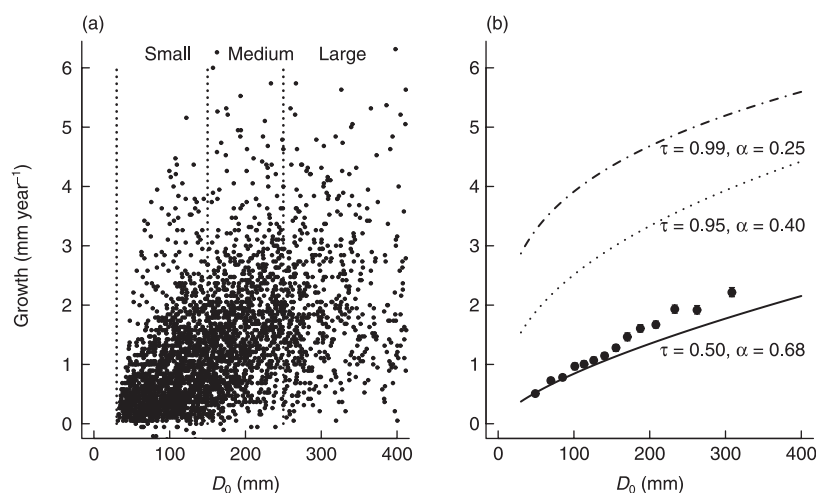


Fig. 2. (a) Diameter growth rate of individual trees, calculated as $(D_t - D_0)/\Delta t$ and plotted as a function of initial stem diameter (D_0). The diameter size-classes used in subsequent regression analyses ('small' < 150 mm, 'medium' 150–250 mm and 'large' > 250 mm) are shown; (b) the same data presented as mean growth rates (●) within 15 size classes (± 1 SEM), and scaling relationships fitted by quantile regression through the centre of the dataset ($\tau = 0.50$), and to the 'upper boundary' of the data set ($\tau = 0.95$ and 0.99). The scaling exponent (α) is also given for each of these regression relationships.

Table 1. Parameter estimates and standard errors for five models of stem diameter growth (dD/dt) for 3334 mountain beech trees. Models were fitted using maximum likelihood methods and the last column gives the Akaike Information Criteria (AICs) relative to the model with the lowest AIC (the final one). Burnham & Anderson (2002) state that models that differ by more than 10 from the best model are poorly supported

Model	Growth function	Parameter estimates (\pm SE)	AIC
Null	λ_0	$\lambda_0 = 1.11 \pm 0.030$	477
Power	$\lambda_0 D^\alpha$	$\lambda_0 = 1.11 \pm 0.016$, $\alpha = 0.52 \pm 0.023$	299
+ Light	$\lambda_1 D^\alpha / (1 + \lambda_1 / \lambda_2 e^{\lambda_3 B_L})$	$\lambda_1 = 0.94 \pm 0.19$, $\lambda_2 = 8.70 \pm 2.61$, $\lambda_3 = 0.042 \pm 0.0050$, $\alpha = 0.19 \pm 0.029$	10
+ Nutrients	$\lambda_1 D^\alpha / (1 + \lambda_4 B_T)$	$\lambda_1 = 0.23 \pm 0.035$, $\lambda_4 = 0.013 \pm 0.0026$, $\alpha = 0.48 \pm 0.022$	183
+ Light	$\lambda_1 D^\alpha$	$\lambda_1 = 1.01 \pm 0.19$, $\lambda_2 = 15.0 \pm 5.54$, $\lambda_3 = 0.048 \pm 0.0062$,	0
+ Nutrients	$[(1 + \lambda_1 / \lambda_2 e^{\lambda_3 B_L})(1 + \lambda_4 B_T)]$	$\lambda_4 = 0.0055 \pm 0.0017$, $\alpha = 0.20 \pm 0.030$	

although growth rates were immensely variable among individual trees of the same size (Fig. 2a). Quantile regression provides an indication of this variability. The average growth curve was estimated to be $dD/dt = 0.037 D^{0.68}$, using quantile regression weighted on the 50th quantile of the data set (i.e. $\tau = 0.50$). The 95% confidence interval for the scaling exponent, 0.63–0.73, did not overlap with the value of 0.33 predicted by the Enquist growth model. The scaling exponent of the upper boundary was 0.40 (95% CI = 0.29–0.51) when $\tau = 0.95$, and was 0.25 (95% CI = 0.16–0.35) when $\tau = 0.99$ (Fig. 2b). Clearly, the scaling exponent of the upper boundary was highly dependent on the value of τ chosen.

The influence of size on growth was also evident from maximum likelihood modelling. The power function was $dD/dt = 0.114 D^{0.52}$, and was a better fit to the data than the null model ($\Delta AIC = 178$, $P < 0.00001$). The scaling exponent was significantly different from that predicted by the Enquist growth model (0.52 ± 0.023 vs. $1/3$, $t = 8.29$, $P < 0.00001$).

COMPETITION FOR LIGHT AND NUTRIENTS

The growth function which included B_L and B_T was found to be the best fitting of all the models that we compared (i.e. it had the lowest AIC; Table 1). In other words, the regression analyses suggest that competition for both light and nutrients suppress the growth of trees in mountain beech forests. To illustrate the extent to which growth was reduced by competition for light and nutrients, we calculated the mean growth rate of small, medium and large trees for which B_L was less than $20 \text{ cm}^2 \text{ m}^{-2}$, between 20 and $40 \text{ cm}^2 \text{ m}^{-2}$, and greater than $40 \text{ cm}^2 \text{ m}^{-2}$ (upper row of Fig. 3), and for which B_T was less than $20 \text{ cm}^2 \text{ m}^{-2}$, between 20 and $40 \text{ cm}^2 \text{ m}^{-2}$, and greater than $40 \text{ cm}^2 \text{ m}^{-2}$ (lower row of Fig. 3). It can be seen that growth was strongly suppressed by neighbours in all size classes (Fig. 3); differences between classes were all statistically significant (t -tests, $P < 0.0001$).

The intensity of competition for light is given by $ICL = \ln(1 + 0.068 \exp(0.048 B_L))$. Tall trees have few taller neighbours, so the mean value of B_L decreases

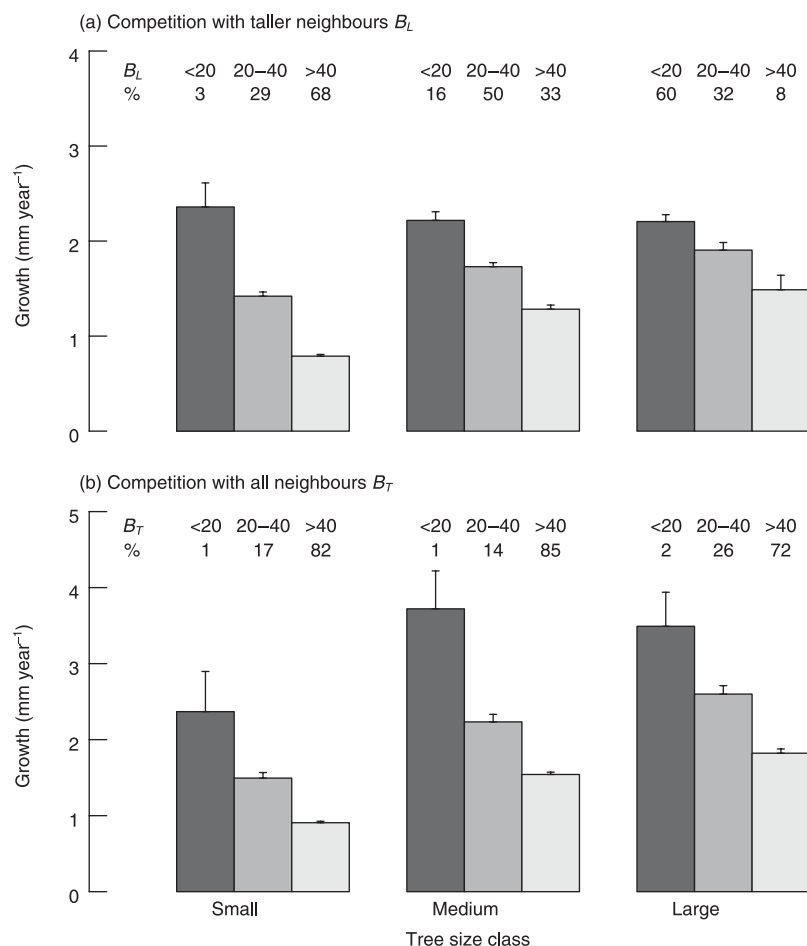


Fig. 3. Influences of taller neighbours (B_L) and all neighbours (B_T) on the diameter growth (mean \pm 1 SEM) of small (30–150 mm), medium (151–250 mm) and large (> 251 mm) diameter trees. B_L and B_T were separated into three classes (dark grey < 20, mid-grey 20–40 and light grey > 40 cm² m⁻²). The percentage of trees within a size class that experience each level of competition is given above the bar.

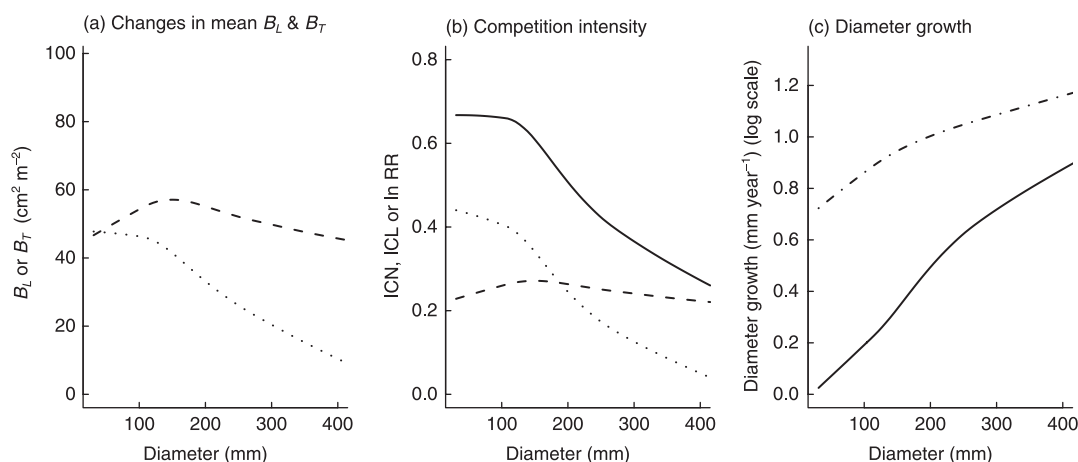


Fig. 4. Changes with tree diameter in (a) mean B_L (....) and B_T (---); (b) mean ICL (....), ICN (---) and ln RR (—) and (c) mean diameter growth (—) and potential diameter growth rate (.....). The curves in panels (a) and (b) were obtained by fitting generalized additive models.

with size (Fig. 4a), and this results in a decrease in mean ICL with size (Fig. 4b). The intensity of competition for nutrients is given by $ICN = \ln(1 + 0.0055 B_T)$. Mean ICN remains virtually constant with size because B_T varies little with size (Fig. 4a,b). The overall inten-

sity of competition ($\ln RR = ICN + ICL$) decreases with size as a result of the decreases in ICL (Fig. 4b). Finally, the mean growth curve is given by $\ln G_C = \exp(\ln G_p - ICL - ICP)$. The mean and potential growth curves are shown in Fig. 4(c). Note that the difference

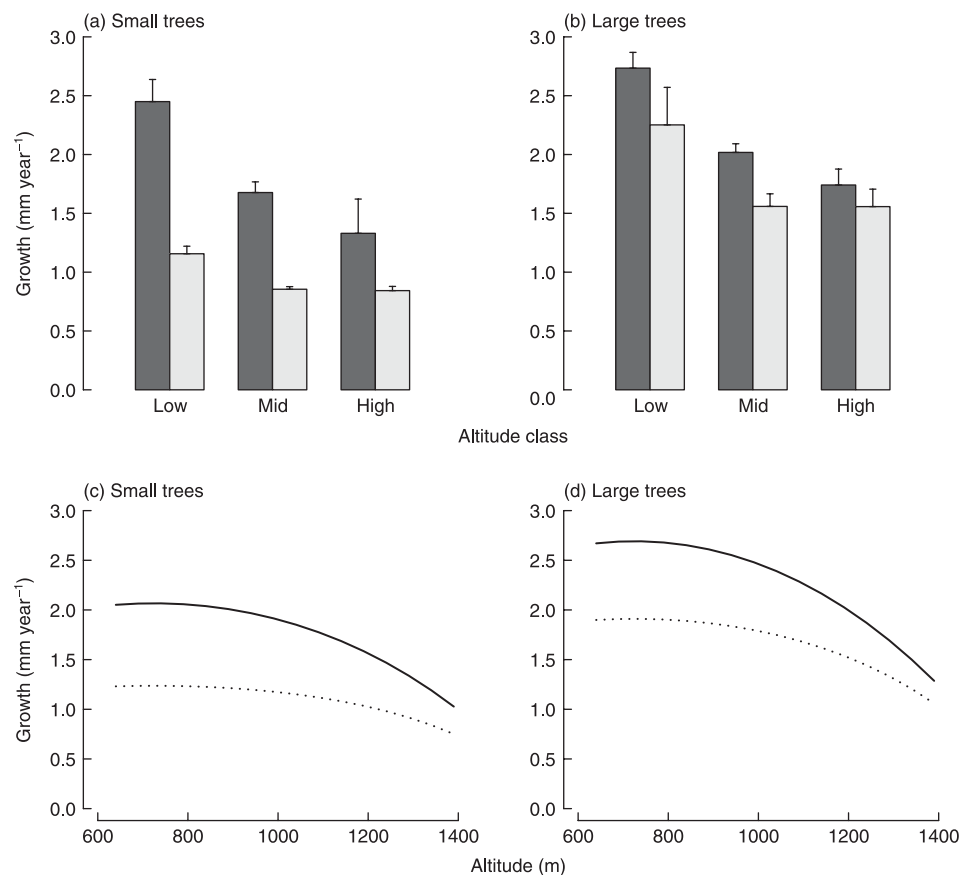


Fig. 5. Mean growth rates (± 1 SEM) of (a) small trees and (b) large trees in uncrowded and crowded neighbourhoods (black, $B_L \leq 30$ and light grey, $B_L > 30$ cm² m⁻²) at three altitudes ('low' 640–890, 'mid' 890–1240, and 'high' > 1240 m a.s.l.) compared with the predicted growth curves (c and d) from regression modelling (— $B_L \leq 30$ and $B_L > 30$ cm² m⁻²). Means were also calculated for medium-sized trees as well, but are omitted for clarity.

between potential and mean growth curves decreases with increasing size because competition for light is diminishing, resulting in the average growth curve having a steeper slope than the potential growth curve.

As a check on the validity of our regression modelling, we estimated the light extinction coefficient of mountain beech stands from parameter λ_3 in the best-supported model. As explained in the Appendix S1, $\lambda_3 = \nu B_i / A_i$ where ν is the light extinction coefficient, B_i is its stem basal area and A_i is the leaf area of a tree. For mountain beech trees growing at mid-altitude, the relationship between leaf biomass M_L (g) and basal area B_i (cm²) is given by $M_L = 15.2 B_i$ (Osawa & Allen 1993), and the relationship between leaf biomass (g) and leaf area (cm²) is given by $M_L = 176 A$ (Hollinger 1989), from which it follows that $B_i / A_i = 176 / 15.2$. The estimated value of λ_3 is 0.048 ± 0.0061 (Table 1), so we estimate ν to be $0.048 \times 176 / 15.2 = 0.56$, which is within the range of coefficients measured directly in several forest types (0.28–0.62; in Jarvis & Leverenz 1983).

GROWTH VARIATION WITH ALTITUDE

Growth rate declined with altitude (Fig. 5a,b), and the decline was modelled by allowing λ_1 in the combined growth model (eqn 4) to vary as a quadratic function of

altitude ($\Delta AIC = -120$, likelihood ratio test $L = 62$, d.f. = 2, $P = 0.0001$). The quadratic function forecasts that growth varies little from 640 to 740 m a.s.l. then declines steeply at higher altitudes. A quadratic relationship was found to be more effective at describing the decrease in growth with altitude than a linear relationship ($\Delta AIC = -5$), or the Boltzmann function ($\Delta AIC = -19$). Furthermore, we discovered that the Boltzmann–Arrhenius function was a poor choice of function to use when the temperate range is small (about 5.5 °C in our case) because E and λ_1 trade-off to give near-identical AIC values for a range of E -values (we tried values ranging from 0.50 to 0.75). The value of λ_8 for $E = 0.65$ was $2.52 \times 10^{-12} \pm 4.5 \times 10^{-13}$.

The non-overlapping error bars in Fig. 5 indicate that shading caused lower growth rates at all three altitudes (Fig. 5a,b; t -tests gave $P < 0.0001$), although the shading effect appears to be most marked in small trees at low altitudes. Comparison of alternative regression models revealed that neither the scaling exponent nor any of the competition terms (λ_2 , λ_3 or λ_4) were influenced by altitude, once altitude had been included in the growth model as a determinant of growth. In other words, making these parameters dependent upon altitude (equation 6) was not statistically significant (likelihood ratio tests, P -values > 0.05). Therefore the

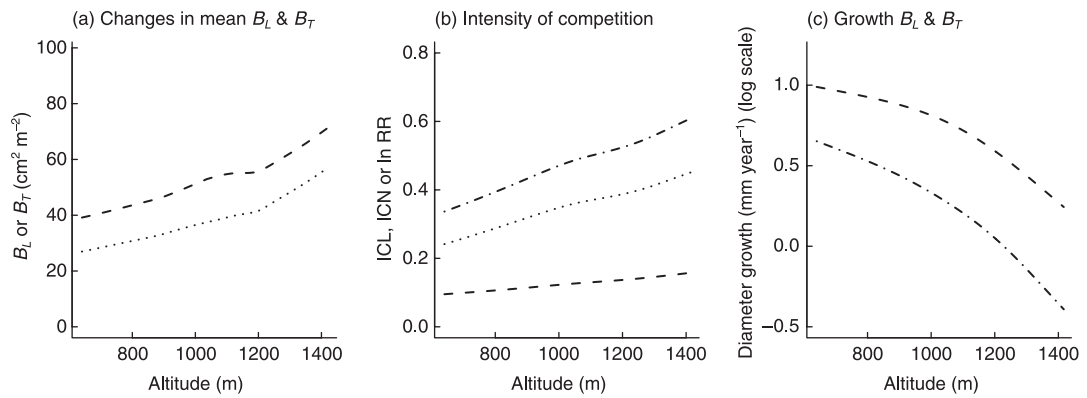


Fig. 6. Changes with altitude in (a) mean B_L (....) and B_T (---); (b) mean ICL (....), ICN (---) and $\ln RR$ (----) and (c) mean diameter growth (.....) and potential diameter growth rate (---). The curves in panels (a) and (b) were obtained by fitting generalized additive models.

most strongly supported growth function that included the effects of size, altitude and competition was:

$$\frac{dD}{dt} = \frac{\lambda_1 D^{0.22}}{\left(1 + \frac{\lambda_1}{15.9} e^{0.052 B_L}\right) (1 + 0.0025 B_T)} \quad \text{eqn 11}$$

$$\lambda_1 = 0.982 + 2.17 \times 10^{-4} A_1 - 1.21 \times 10^{-6} A_1^2,$$

where $A_1 = 0$ for the lowest altitude plot in the study area (i.e. $A_1 = A - 640$). The quadratic λ_1 function changes little from 640 to 800 m altitude (peaking at $A_1 = 729$ m) then decreases rapidly towards higher altitudes. However, λ_2 remains greater than zero at the tree line, so there is no indication of a switch from competition to facilitation. The means and standard errors of the parameter estimate were $\lambda_{1A} = 0.982 \pm 0.206$, $\lambda_{1B} = 2.17 \times 10^{-4} \pm 0.412 \times 10^{-4}$, $\lambda_{1C} = -1.21 \times 10^{-6} \pm 5.4 \times 10^{-7}$, $\lambda_2 = 15.9 \pm 5.67$, $\lambda_3 = 0.052 \pm 0.0063$, $\lambda_4 = 0.0025 \pm 0.0013$, and $\alpha = 0.22 \pm 0.030$. The predicted changes in growth with altitude and crowding for small trees ($D = 100$ mm) and large trees ($D = 300$ mm) are broadly consistent with the empirical data (Fig. 5d).

The intensity of competition for light is given by $ICL = \ln(1 + \lambda_1/15.2 \exp(0.052 B_L))$. If B_L were constant with altitude then ICL would fall by about 33% across the altitudinal gradient because of decreases in λ_1 . This effect is seen by comparing the upper and lower curves in Fig. 5(c,d), which were fitted without allowing B_L or B_T to vary with altitude: the difference in growth between the upper and lower curves is 0.7 mm year⁻¹ at low altitude but only 0.2 mm year⁻¹ at the tree line. However, B_L actually increases with altitude (Fig. 6a and Appendix S5) and this counterbalances the effects of the falling value of λ_1 . In fact, when ICL was calculated for all 3334 trees and plotted against altitude, there was an upward trend in the mean ICL with altitude (Fig. 6b). The intensity of competition for nutrients (ICN) is given by $\ln(1 + 0.0025 B_T)$. If B_N were constant with altitude then mean ICN would also remain constant because the index does not contain an altitude term, but B_T increases with altitude (Fig. 6a

and Appendix S5) and this results in an increase in mean ICN. As a consequence of increasing ICN and ICL, the overall intensity of competition ($\ln RR = ICN + ICL$) also increases with altitude (Fig. 6b). Finally, the difference between the potential and mean growth curves ($\ln G_C = \ln G_P - \ln RR$) increases with altitude because $\ln RR$ increases (Fig. 6c).

Discussion

THE ENQUIST GROWTH MODEL: AN UPPER CONSTRAINT ON GROWTH?

WBE theory has generated enormous controversy with its claim to have discovered a simple mechanistic basis for understanding many patterns and processes observed in natural systems (see Kozłowski & Konarzewski 2004; Li *et al.* 2005; Reich *et al.* 2006). In essence, the theory is founded on the idea that organisms have evolved optimized vascular transport systems that minimize the resistance to the flow of fluids within the organisms. Anatomical studies suggest that plants do indeed have transport systems structured to reduce hydraulic resistance (Anfodillo *et al.* 2006; Coomes *et al.* 2007; Weitz *et al.* 2006; but see McCulloh & Sperry 2005). The diameter-growth model of Enquist *et al.* (1999) considers the implications of an optimized transport system for tree growth, but does not recognize the importance of competition for resources as a determinant of tree growth. We contend that there is no empirical support for Enquist's growth model because the statistical analyses in the original paper were based on inadequate replication to reach reliable conclusions (Muller-Landau *et al.* 2006; Coomes & Allen, in press), because foresters have shown that power functions are not generally the best descriptors of tree growth (e.g. Vanclay 1995 and see Appendix S2), and because recent analyses have quite clearly demonstrated that growth does not scale as $D^{1/3}$ (Muller-Landau *et al.* 2006; Russo *et al.*, 2007, this paper).

An alternative hypothesis is that Enquist's growth model defines the potential growth of trees, instead of the mean growth rate, but we did not find strong support

for this hypothesis in the case for mountain beech trees (Fig. 1b and Table 1). The reality was that tree growth was immensely variable (Fig. 2a). The upper boundary was diffuse, and this uncertainty meant that the upper potential curve was ill-defined: for instance, simply choosing the 95th rather than the 99th quantile in the quantile regression analysis resulted in α changing from 0.25 to 0.40 (Fig. 2b). Also, the values of α estimated by the regression analyses depended greatly on the choice of function (Table 1). However, the alternative hypothesis cannot be rejected using evidence from just one species: further analyses may reveal that the scaling exponent is about 1/3 when averaged across species. Considerable differences among species are to be expected, not least because the scaling of mass to diameter varies between species (Niklas 2004). For example, the conclusion that $dD/dt \propto D^{1/3}$ is based on an assumption that $M \propto D^{8/3}$ but empirical studies show that species often deviate from this allometric relationship. Specifically, the mass-diameter relationships of 15 North American tree species have exponents ranging from 2.15 to 2.74, with an average of 2.48 (recalculated from Ter-Mikaelian & Korzukhin 1997). Thus, the growth curves of these species could have exponents that ranged from 0.26 to 0.85 even before other sources of uncertainty are considered (Li *et al.* 2005 and Russo *et al.* 2007). Some of these differences may result from violations of some assumptions of the branching models that are fundamental to WBE theory (Enquist *et al.* 2007). Therefore the potential growth rate curves of a large number of species need to be estimated before any conclusions can be reached about the generality of the alternative scaling theory.

CHANGES IN COMPETITION FOR LIGHT AND NUTRIENTS WITH SIZE

Forest ecologists universally appreciate the importance of light as a limiting factor for tree growth (e.g. Pacala *et al.* 1996; Smith *et al.* 1997; Herwitz *et al.* 2000; Canham *et al.* 2004; Uriarte *et al.* 2004; Wyckoff & Clark 2005). The light extinction coefficient of mountain beech was estimated to be 0.53. This equates with about 4% of light being transmitted through a canopy with a leaf area index of six, which is typical for mountain beech (Hollinger 1989). This diminution of light by the canopy is less than that commonly observed in many tropical and temperate forests (Coomes & Grubb 2000), but is still likely to have strong effects on the growth of subordinates, especially as mountain beech is a light-demanding species (Wardle 1984). Competition for light alters the shape of the growth curve because shorter trees are more deeply shaded, on average, than taller trees, and so are particularly strongly affected by light competition (Weiner 1990; Muller-Landau *et al.* 2006). This situation is likely to be universal in natural forests (e.g. Wyckoff & Clark 2005; Sheil *et al.* 2006), so a systematic deviation of the mean growth curve from $dD/dt \propto D^{1/3}$ will be observed generally (Coomes 2006).

The huge variability in growth rate observed in this study (Fig. 2) is typical of that reported elsewhere (e.g. Van Mantgem & Stephenson 2005), and reflects the ability of trees to alter metabolic rates in response to resource supply (Harper 1977; Grubb 1992; Reich *et al.* 2006). The ontogenetic growth of any particular tree in a natural population is unlikely to bear much resemblance to a scaling function because trees may spend long periods of time suppressed in deep shade followed by relatively brief interludes of fast growth in high light when openings are created above them by tree-fall events (e.g. Uhl & Murphy 1981; Wright *et al.* 2000).

Growth was also affected by competition for nutrients, and intense competition for nitrogen is known to occur in mountain beech forests: substantial increases in growth rate have been reported when trenches are cut around seedlings to isolate them from root competition with established trees (Platt *et al.* 2004), and nitrogen addition results in large increases in fine root and seed production (Davis *et al.* 2004). More generally, Coomes & Grubb (2000) have reported that root trenching results in increased growth rates in many forest types, and particularly when the seedlings are growing in relatively well illuminated forest understoreys. Many models of tree growth include sophisticated functions of light interception by neighbours (e.g. Pacala *et al.* 1996), but very few attempt to include competition for below-ground resources (Canham *et al.* 2004). Further progress will require the development of a mechanistic understanding of root competition and nutrient retention. We were not able to derive a mechanistic model without being speculative about the ways in which fine roots compete for nutrients, and plants recycle and store nutrients (Reich *et al.* 2006), and we are aware that competitive intensity may not be related to B_T in the way we have supposed (Weiner 1990; Schwinning & Weiner 1998). A mixture of experimentation and modelling is required to make further progress (Tilman *et al.* 2004).

CHANGES WITH ALTITUDE

Diameter growth rates declined with altitude, and this was associated with a shortening of growing season and reduction in mean summer temperatures (Wardle 1984). Physiological studies have also reported substantial losses of productivity with altitude in mountain beech stands, resulting from falls in both photosynthetic and respiration rates (Table 2). However, the Boltzmann–Arrhenius function did not adequately represent the fall in growth rate; the decline in growth rate above 1100 m was greater than predicted. Perhaps the Boltzmann–Arrhenius function adequately models the decline in growth with altitude that result from falling temperatures, but fails to capture the negative effects of mineral nutrient shortage or strong winds. For example, phosphorus availability is known to decline with altitude across our 246 mountain beech plots ($r = -0.29$, $P < 0.0001$; R. B. Allen, unpublished

Table 2. Estimated annual C balance ($\text{T C ha}^{-1} \text{ year}^{-1}$) for montane (1000 m a.s.l.) and subalpine (1320 m a.s.l.) mountain beech stands in the study area (adapted from data in Benecke & Nordmeyer 1982). Subalpine values are given as a proportion of montane values.

		Altitude (m)		Proportion
		1000	1320	
Whole plant	Photosynthesis	37.1	15.7	0.42
	Respiration	20.3	6.7	0.33
	Net growth	16.8	9.0	0.54
Growth allocation	Foliage	4.7	2.6	0.55
	Branch	4.9	1.7	0.35
	Stemwood	4.4	2.2	0.50
	Coarse roots	0.8	0.7	0.88
	Fine roots	2.0	1.8	0.90
	Total growth	16.8	9.0	0.54

data), and may contribute to slow growth at high altitudes. Alternatively, it may be that the metabolic response of plants to temperature variation is more complex than that encapsulated by the thermodynamics formula (Clarke 2004). Enquist *et al.* (1999) has suggested wood density variation might also contribute to changing growth rates. The wood density of mountain beech increase by 13% from the lowest to the highest elevation sites in the study area ($0.47\text{--}0.53 \text{ g cm}^{-3}$; Jenkins 2005), which is much less than the change in diameter growth rate.

The debate on changes in competition intensity with environmental gradients is one of the most protracted in plant community ecology (e.g. Grime 1977; Tilman 1988; Grace 1991; Goldberg *et al.* 1999; Craine 2005). Our analyses indicate that competition intensity increased with altitude, but this is exactly opposite to the trend we had expected. Previous studies of light-demanding *Nothofagus* species in Chile have indicated that competition has its strongest influence on stand dynamics at low altitudes (Pollman & Veblen 2004). Mountain-beech trees produce only about half as much wood and leaf biomass at high altitude than at mid-altitude, whilst producing a similar amount of root biomass (Table 2; Benecke & Nordmeyer 1982). As a result, high altitude trees are stunted, have open canopies, and allow more light to be transmitted to the forest floor (D.A. Coomes, unpublished data). Thus, while we anticipated that the intensity of competition for light would diminish with altitude, the analyses suggest the opposite. Why did our findings differ so markedly from our expectations?

Understanding why basal area increases with altitude may hold the key to resolving this paradox. The only reason that competition intensity increases with altitude is because mean basal area increases with altitude (Fig. 6); had basal area been invariant of altitude then our analyses would have predicted a decline in competition intensity with altitude (Fig. 5c,d). So why does basal area increase with altitude? One

possibility is that spatial variation in disturbance has created the observed pattern: many trees at low and mid-altitudes died after being damaged by snow storms in 1968 and 1972, whereas trees at high altitude were much less affected, and we know that the forest is in disequilibrium as a result of temporal variation in disturbance frequency (Wardle & Allen 1983; Allen *et al.* 1999; Coomes & Allen 2007). If differences in disturbance history are responsible for the observed increases in basal area with altitude, then resurveying the plots in, say, 100 years time might give the opposite trend! From this perspective it seems more logical to calculate competitive intensities with basal area kept constant. When this is done, the regression analyses are consistent with expectations: ICL declines with altitude whereas ICN stays constant, so competition for light is most intense at low altitude and competition for nutrients is most intense at the tree line. This fits with the idea that trees respond plastically to changing rates of resource supply by allocating more carbon to above-ground tissues when below-ground resources are relatively abundant, and allocating more carbon to roots when nutrients are scarce (Bloom *et al.* 1985; Tilman 1988; Gleeson & Tilman 1992). The key question is whether disturbance history really is the driver of the basal area trend, or whether it is underpinned by physiological processes. Further investigation is required into this issue.

Irrespective of whether competition intensity increases or decreases with altitude, when expressed in absolute terms, the effect of competition on growth was greatest at low altitude (Grace 1991): shading reduced the growth of small trees by about 7 mm year^{-1} at 640 m altitude but by only 2 mm year^{-1} at the tree line (Fig. 5c). These findings are broadly consistent with the theory of Grime (1977), that plants associated with productive habitats are inherently fast growing and their fast growth rates allow pre-emptive capture of resources from neighbours, while plants associated with 'stressed' sites have traits that allow them to survive harsh conditions, but also result in slow growth rate.

The fact that growth rates are slow in 'stressed' habitats means that competition may go undetected unless studies are well replicated and monitored over long time frames. This may explain why most studies in stressed habitats do not detect competitive interactions. Several recent experiments have reported that competitive interactions give way to facilitation interactions at high altitude (Callaway 1995; Brooker & Callaghan 1998; Callaway *et al.* 2002), and have brought to attention the hitherto neglected importance of facilitation in plant community dynamics. However, our study did not unearth fresh evidence of facilitation. We had anticipated that facilitation might be important in high-altitude forests of mountain beech because trees experience similar conditions to those in Callaway's study (Wardle 1984), but no evidence was found despite our analyses being based on high numbers of replicates. Given the nature of plastic above- and below-ground growth responses by tree species along gradients, we suggest resolving differences among studies may require comprehensive data on allocation patterns in trees. For example, reduced diameter growth near the tree line, upon the loss of neighbours, may reflect increased allocation of growth below-ground to capture soil resources.

Finally, the potential growth rate had the same scaling exponent at all altitudes ($\alpha = 0.22$). If potential growth rate is controlled by the design of the internal transport systems, then this finding suggests that the evolutionary design of the transport system is similar across the sequence. A recent study of the wood anatomy of mountain beech trees sampled at three altitudes showed that the vascular systems were all remarkably similar in structure, and that the scaling of vessel sizes within the trees was broadly consistent with the design that WBE theory predicts would minimize resistance to hydraulic flow (Coomes *et al.* 2006). Therefore our analyses support some aspects of scaling theory (West *et al.* 1997), but not Enquist's theory of tree growth.

Conclusions

Our study is the first to build the effects of competition and environment into Enquist's model of tree growth. We show that competitive interactions alter the scaling of mean growth rate with size, whereas altitude does not influence the scaling of potential growth rate with size. Ecologists need to include the effects of competition for light and nutrients and various types of disturbance into models of size-dependent processes, as these factors swamp out the potentially real effects that WBE theory might encapsulate (Tilman *et al.* 2004).

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Supplementary material

The following supplementary material is available for this article:

Appendix S1. Biological basis for the light competition function.

Appendix S2. Alternative growth models not described in main body of paper.

Appendix S3. Correlations between B_T and B_L .

Appendix S4. Changes in B_T and B_L with size.

Appendix S5. Increases in B_T and B_L with altitude.

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