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Interspecific relationships among growth, mortality and xylem traits of woody species from New Zealand

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Summary

1. Wood density is considered a key functional trait influencing the growth and survival of woody plants and has been shown to be related to a slow–fast rate-of-living continuum. Wood density is, however, an emergent trait arising from several vascular properties of wood, including the diameter and frequency of xylem conduits.

2. We aimed to test the hypotheses that there is a set of inter-related trade-offs linked to the different functions of wood, that these trade-offs have direct consequences for tree growth and survival and that these trade-offs underlie the observed correlations between wood density and demographic rates. We evaluated the covariation between xylem anatomical traits among woody species of New Zealand and whether that covariation had the potential to constrain variation in wood density and demographic rates.

3. Several xylem traits were strongly correlated with each other, but wood density was not correlated with any of them. We also found no significant relationships between wood density and growth or mortality rate. Instead, growth was strongly related to xylem traits associated with hydraulic capacity (conduit diameter and a conductivity index) and to maximum height, whereas mortality rate was strongly correlated only with maximum height. The diameter and frequency of conduits exhibited a significant negative relationship, suggesting a trade-off, which restricted variation in wood density and growth rate, but not mortality rate.

4. Our results suggest, for woody species in New Zealand, that growth rate is more closely linked to xylem traits determining hydraulic conductance, rather than wood density. We also found no evidence that denser woods conferred higher survival, or that risk of cavitation caused by wide conduits increased mortality.

5. In summary, we found little support for the idea that wood density is a good proxy for position along a fast–slow rate-of-living continuum. Instead, the strong, negative relationship between vessel diameter and frequency may constrain the realized diversity of demographic niches of tree species in New Zealand. Trade-offs in function therefore have the potential to shape functional diversity and ecology of forest communities by linking selection on structure and function to population-level dynamics.

Key-words: functional traits, New Zealand forests, phylogenetic comparative methods, trade-offs, tree maximum height, tree diameter growth rate, tree mortality rate, vessel and tracheid properties, wood density

Introduction

Wood density is regarded as a key functional trait influencing the growth and mortality of woody plants. Wood density is conventionally defined as dry mass divided by fresh

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volume, so that, all else being equal, woody species producing denser wood should have slower volume growth than species producing lighter wood. This prediction is supported by studies in tropical forests showing that wood density is negatively correlated with diameter growth rate across species (Putz *et al.* 1983; Enquist *et al.* 1999; King *et al.* 2006b; Osunkoya *et al.* 2007). Wood density in angiosperms is related to the thickness and number of fibres per unit cross-sectional area (Carlquist 1975). As fibres convey strength to wood, denser wood is more resistant to damage from falling debris (Poorter *et al.* 2008), wind storms and buckling under the tree's own weight (Putz *et al.* 1983; Lawton 1984; King 1986), and wood-boring arthropods and pathogens (Bultman & Southwell 1976), which are significant causes of tree mortality. Consequently, studies in tropical forests also report a positive correlation between wood density and survival rate across species (Putz *et al.* 1983; King *et al.* 2006b Osunkoya *et al.* 2007). Thus, several lines of evidence suggest that wood density is related to position along a slow–fast rate-of-living continuum: species with denser wood tend to have slower growth, higher survival and greater shade tolerance, whereas species with lighter wood tend to have faster growth, lower survival and lower shade tolerance (Smith & Tumey 1982; Lawton 1984; King 1986; King *et al.* 2005; Chave *et al.* 2006; King *et al.* 2006b). The aim of this study is to examine the extent to which trade-offs in function involving wood density and xylem traits are in fact related to growth and mortality rates of woody plant species.

Wood density, is an emergent feature of wood that results from a combination of several xylem traits, including conduit (vessel or tracheid) diameter and frequency and fibre density. Wood density tends to increase with decreasing conduit diameter and frequency and with increasing fibre density (Carlquist 1975). Although high wood density may confer a direct survival advantage, the often-reported relationship between wood density and growth rate could arise from other xylem traits that are correlated with density, but are linked more directly to hydraulic attributes of wood. The diameter of angiosperm vessels, for example, is positively correlated with growth rate, because wider vessels allow greater rates of transpiration and photosynthesis (Castro-Diez *et al.* 1998; Denne, Cahalan & Aebischer 1999; Brodribb & Feild 2000; Stratton, Goldstein & Meinzer 2000). The wider vessels often associated with lighter woods can, however, increase the risk of cavitation (breakage of the water column within the xylem), causing water conduction to decline if cells become embolized (air-filled) and leading, in extreme cases, to tree death (Tyree & Sperry 1989; Tyree, Davis & Cochard 1994; Davis, Sperry & Hacke 1999; Hacke *et al.* 2001). A trade-off between hydraulic conductance and resistance to embolism may therefore underlie the relationship that wood density has with growth and mortality rate, although a comparative phylogenetic analysis did not find evidence for this trade-off (Maherali, Pocknan & Jackson 2004).

Negative relationships between species' xylem traits can arise when they are under opposing selection due to trade-offs in function related to hydraulic conductance, cavitation-risk and mechanical constraints (Carlquist 1975; Baas *et al.* 2004; Sperry, Meinzer & McCulloh 2008; Chave *et al.* 2009). For example, an increase in wood density should reduce the space in the stem that is available to the hydraulic pathway (lumen fraction), leading to higher resistance to water conductance and reduced photosynthetic capacity (Carlquist 1975). Lumen fraction itself is determined by conduit diameter and frequency, which are often found to be negatively correlated: if conduits are too wide and frequent, they may be easily embolized, but if they are too narrow and infrequent, hydraulic capacity is severely reduced (Chave *et al.* 2009). Furthermore, given stem diameter and wood of a particular density and modulus of elasticity, there is a critical height above which a tree will buckle under its own weight, and this biomechanical limitation is considered to be a determinant of a tree's maximum height (Greenhill 1881; McMahon 1973; King 1981). Consistent with these trade-offs in function, tree species with taller maximum heights generally have lighter wood to reduce buckling risks (Thomas 1995) and faster growth and higher mortality rates (King, Davies & Supardi 2006a).

Our aim in this study is to test the hypotheses that there is a set of inter-related trade-offs linked to the different functions of wood, that these trade-offs have direct consequences for tree growth and survival and that these trade-offs underlie the observed correlations between wood density and demographic rates. Specifically, we evaluated the covariation between xylem anatomical traits among species and whether that covariation had the potential to constrain variation in higher-order traits, such as wood density and demographic rates. To our knowledge, this is the first large-scale comparative test of these ideas outside of tropical forests. We related wood densities and xylem properties to data on growth and mortality rates collected over 36 years in natural forests of New Zealand. To account for other factors known to influence demographic rates, we modelled growth and mortality for juvenile and adult trees of each species, taking account of local neighbourhood interactions, which enabled us to relate wood densities and vascular properties to estimates of species' maximum growth and survival capacities.

Materials and methods

WOOD PROPERTIES

In New Zealand forests are dominated by *Nothofagus* (Southern beech; Nothofagaceae) and conifer (Podocarpaceae and Cuppressaceae) species, in association with a diverse group of hardwoods (Wardle 1991). We selected 39 species for study (34 angiosperms and 5 podocarps; Table S1), comprising all species for which we could obtain data on wood properties. We measured the following wood properties for each species: wood density (g cm^{-3}), conduit (vessel or tracheid) diameter (μm) and number of conducting cells (vessels or tracheids) per mm^2 (conduit frequency). Wood density was measured using air-dried wood samples archived in the Allan Herbarium at Landcare Research, New Zealand: each sample (one per species) was weighed to ± 0·001 g and its volume measured by submerging it into a container of water on a scale and measuring the change in recorded weight. The conventional method of calculating wood density is dry mass divided by fresh volume, rather than the dry volume used here. We compared our dry volume wood density estimates to fresh volume estimates using two independent data sets that shared species with our data set. The dry and fresh volume estimates were significantly correlated (D. A. Coomes, unpublished data: $N = 12$; $r = 0{\cdot}56$, $P < 0{\cdot}05$; I. A. Payton, unpublished data: $N = 28$, $r = 0{\cdot}71$, $P < 0{\cdot}05$; Pearson correlations). Wood densities of smaller-statured species (shrubs and some small trees) were largely sampled from branch samples, whereas those for canopy trees were from trunk cores.

The remaining wood properties were measured from published scanning electron micrographs (SEM) of each species (one image per species) taken using a Cambridge SIIa microscope (Meylan & Butterfield 1978). The wood samples used for these micrographs were collected from mature trees growing naturally in their native habitats within their normal distributional range. For most species, cores were removed at waist height from the outside of large trees following bark removal using a 25-mm diameter core borer, so that the micrographs are representative of sapwood. For smaller-stature trees and shrubs, coring was not possible without excessive damage to the tree, and so wood samples taken from branch segments were used (B. Butterfield, pers. comm.). A small cube (*c.* 5 mm on a side) with cleanly cut surfaces was prepared from each wood sample, and SEMs were made from the transverse face. These published SEM images were scanned into a computer, and vessel and tracheid diameters and numbers were measured from these images using ImageJ software (Abramoff, Magelhaes & Ram 2004). The diameters of all conduits fully visible on each micrograph were averaged, thereby accounting for differences between early- and latewood vessels. We developed a conductivity index based on the Hagen–Poiseuille law of laminar flow, which states that the hydraulic conductivity per unit pressure gradient of a bundle of pipes (k_{h}) equals $[\pi\rho/128\eta]$ $[\sum d_i^4]$ for $i = 1$ to n conduits in the bundle, where ρ is the density of the fluid, d_i is the diameter of each conduit in the bundle and η is the viscosity of the fluid. Formally, k_{h} is the proportionality constant between flux and the pressure gradient causing the flux (Tyree & Ewers 1991). The conductivity index that we used was the product of the number of conduits per mm^2 and the fourth power of the weighted mean diameter of conduits (μm^2). We estimated lumen fraction (F) as the product of conduit area and frequency. The estimated maximum height attained for each of the species for which demographic rates were estimated was collected from the literature (Wardle 1991; Poole & Adams 1994; Wilson 1994) and the New Zealand Plants Databases (Landcare Research 2006).

Wood traits can vary substantially within trees and species (Nogueira *et al.* 2005; Nogueira, Fearnside & Nelson 2008), although wood densities estimated from stem cores and branch segments can be highly correlated (Swenson & Enquist 2008). Nevertheless, this variation is often overwhelmed by interspecific differences, which we aimed to quantify. In our study, analyses restricted to data from canopy trees vs. shrubs and small trees largely showed the same patterns as analyses using all species; therefore, the latter are presented here.

ESTIMATES OF MEAN OBSERVED GROWTH AND MORTALITY RATES

Growth and mortality rates of woody plant species were estimated from permanent plot data archived in the National Vegetation Survey (NVS) databank (Wiser, Bellingham & Burrows 2001). We used species with at least 100 trees, which amounted to 54 and 59 species for growth and mortality rates respectively (Table S1). This increased our sample size from 39 species (for which we had wood traits) to 54 and 59 species for examining relationships between maximum height and growth and mortality rates respectively. Between 1969 and 2004, permanently marked 20 × 20 m (400 m^2) plots were established in a stratified random design in watersheds throughout New Zealand. Each 20 × 20 plot was divided into 16·5 × 5 m quadrats. Within each plot, each woody stem > 30 mm in diameter at breast height (diameter) was tagged, identified to species, and its diameter to the nearest 1 mm and quadrat were recorded. We extracted data for those plots that had been measured at least twice.

The observed mean diameter growth rate (G; mm year^{-1}) of a species was calculated as the change in diameter (D; mm), divided by the intercensus interval (t; years): $G = (D_t - D_0)/t$. We estimated the instantaneous mortality rate λ (year^{-1}) of each species using the survival function (the probability that a tree will survive to time t, $S(t) = \mathrm{e}^{-\lambda t}$) assuming that λ remained constant over time and did not vary among individuals (Appendix S1). We estimated λ by minimizing the negative log of its likelihood function (Appendix S1). For species that had at least 100 juvenile or adult trees, we estimated growth and mortality rates separately (juveniles: 30–200 mm and adults: ≥200 mm in diameter).

GROWTH RATES OF TREES WITH FEW TALL NEIGHBOURS

We modelled instantaneous diameter growth rates ($\mathrm{d}D/\mathrm{d}t$) of individual trees as a function of diameter (D), temperature (T in kelvin) and the basal area of taller trees in the immediate neighbourhood (A), using the following relationship (Coomes & Allen 2007):

$$\frac{\mathrm{d}D}{\mathrm{d}t} = \left[\frac{\beta}{1 + \beta \mathrm{e}^{\lambda_3 A}/\lambda_2}\right]\left[\mathrm{e}^{\frac{E(T-T_0)}{kTT_0}}\right][D^{\alpha}]. \qquad \text{(eqn 1)}$$

The term within the third set of brackets specifies the size dependence of growth assuming that growth is a power function of diameter (Enquist *et al.* 1999; Muller-Landau *et al.* 2006). The terms within the second set of brackets model the temperature dependence of growth using the Arrhenius–Boltzmann equation, where E is the activation energy of metabolic processes (*c.* 0·65 eV), k is the Boltzmann constant ($8{\cdot}62 \times 10^{-5}$ eV K^{-1}) and T_0 is the mean temperature across all plots in the NVS data (282 K). The terms within the first set of brackets define the influences of neighbouring trees on growth: we used a nonlinear function that assumes that the amount of light intercepted by taller neighbours is exponentially related to their summed basal area (based on the Beer–Lambert law and the Michealis–Menton function, assuming that the basal area is directly proportional to leaf area; Coomes & Allen 2007). We calculated whether trees were taller than the target tree by estimating the height of each tree from its diameter, using species-specific diameter–height allometries (Russo, Wiser & Coomes 2007). Based on this neighbourhood function, a tree growing at average temperature without competitors would have a growth rate of $\beta/(1 + \beta/\lambda_2)D^{\alpha}$. We estimated the basal area of taller neighbours of each tree in the central four 5 × 5 m quadrats (these are the target trees for which growth was modelled) using the sum of the basal areas of taller trees in the nine quadrats (comprising a 15 × 15 m area) surrounding and including the quadrat in which the target tree was located (Coomes & Allen 2007).

Integration of the growth function gives an expression predicting a tree's diameter at time t (D_t) from its initial diameter (D_0; eqn 3 of

Appendix S1); it was this integrated function that was fit to our data set. We assumed that individual deviations from the predicted final diameter for tree i, ε_i, were log-normally distributed and depended on the length of the intercensus interval in y, t_i, which varied among trees, thereby scaling error variance by time. For each species, we minimized the negative log-likelihood function of this growth model using the Nelder–Mead simplex search algorithm in R (The R Core Development Team 2006). The fitted values for parameters in eqn 1 were then used to predict each species' growth rate under standardized size and neighbourhood conditions. We selected values of A in the 15th percentile of neighbourhood overtopping basal area (lower percentiles were strongly influenced by outliers). We made these predictions for juveniles ($D = 100$ mm and $A = 25$ m^2 ha^{-1}) and adults ($D = 200$ mm and $A = 5$ m^2 ha^{-1}), using the mean temperature across all trees in the data.

MORTALITY RATES OF TREES WITH A HIGH DENSITY OF OVERTOPPING NEIGHBOURS

We modelled individual mortality probability in the time interval during which a tree was observed as a function of its diameter (D) and neighbourhood (A) at the beginning of that interval (Appendix S1). A tree's instantaneous mortality rate was modelled as:

$$m(D) = [\delta D^{\eta}]\left[\frac{1}{1 + \lambda_1 A^{\lambda_2}}\right]. \qquad \text{(eqn 2)}$$

The term in the first and second sets of brackets describe the size dependence of mortality and the effects of neighbours respectively. The basal area of taller neighbours in surrounding subplots was calculated in the same way as for the growth model; the two parameters were constrained such that $\lambda_1 > 0$ and $\lambda_2 < 0$ (Coomes & Allen 2007). This approach assumes that over the census interval during which mortality was estimated, a tree grows with respect to its diameter following the predicted relationship for its species, as fit in Russo, Wiser & Coomes (2007).

The parameters for each species were estimated by minimizing the negative log of the likelihood function of the survival function (eqns 6 and 7 in Appendix S1). Parameter estimates were then used to obtain the predicted instantaneous mortality rate of a tree with particular neighbourhood and diameter values. We used values of A in the 85th percentile of neighbourhood basal area of overtopping trees for juveniles and adults. We compared mortality of juveniles at $D = 100$ mm and $A = 80$ m^2 ha^{-1} and adults at $D = 200$ mm and $A = 64$ m^2 ha^{-1} at the mean temperature across all trees in the data.

STATISTICAL AND PHYLOGENETIC METHODS

Pearson correlation tests were used to quantify relationships among wood properties, and between wood properties and demographic rates, both across species and using phylogenetically independent contrasts (PICs) (Felsenstein 1985). Variables were log-transformed to improve normality. Because multiple tests of correlation were performed, we report calculated probabilities and indicate whether each would be considered statistically significant after a correction for multiple comparisons (Holm 1979).

We assembled an hypothesis of the phylogenetic relationships among the 59 species in our data using an unpublished phylogeny (S. J. Wagstaff, A. Wilton, M. Cochrane and G. Barker, unpublished manuscript), published genus-level phylogenies and sister–taxon relationships based on currently accepted alpha taxonomy of woody plant species of New Zealand (Fig. S1). As the phylogenetic tree was a composite from multiple sources, we lacked data on branch lengths and so used Grafen's branch lengths (Grafen 1989). Our phylogeny was not fully bifurcating for the genera *Coprosma* and *Olearia*. As detailed in Appendix S2, for analyses involving polytomies (between maximum height and juvenile mean observed growth and mortality rates), we generated 1000 random resolutions of the phylogenetic tree, calculated independent contrasts and performed a Pearson correlation for each. We report the mean correlation coefficient and the maximum probability value from these 1000 random trees (distributions are shown in Fig. S2). We used the R package *ape* for all phylogenetic comparative analyses.

We examined how wood vascular properties that were found to be significantly and strongly negatively correlated [i.e. conduit diameter (D) and frequency (N); Fig. 1a] jointly affected wood density and growth and mortality rates of angiosperms using a statistical model. A trade-off between vessel diameter and frequency implies that certain combinations of these traits are not favoured in nature, which could limit the possible variation in wood density or demographic rates. To examine this possibility, we fit a statistical model:

$$\log(R) = a\log(N) + b\log(D) + c, \qquad \text{(eqn 3)}$$

where R is either wood density or mean juvenile observed growth or mortality rate of tree species and a, b and c were fitted parameters. A strong relationship between predictors can result in multicollinearity, which does not reduce the predictive power of the overall model, but can reduce the interpretability of individual parameter estimates. We therefore restricted interpretation to the overall model fit, and took a significant fit to imply that the trade-off between conduit diameter and frequency constrained variation in the response variable. This model was fit using two regression methods, ordinary least squares (OLS) and phylogenetic generalized least squares (PGLS) (Martins & Hansen 1997; Freckleton, Harvey & Pagel 2002; Appendix S3), and their relative fits to the data were compared using Akaike's information criterion (AIC). Among alternatives tested, the AIC was always lower for the OLS model, implying a weak phylogenetic signal, and so only results from the OLS models are presented (Table S2).

Results

RELATIONSHIPS AMONG WOOD TRAITS

Several pairs of wood properties were significantly correlated among New Zealand's woody species, both across species and using PICs (Fig. 1, Fig. S3). Across species, lumen fraction was the only xylem trait that had any relationship with wood density, but the correlation was weak and non-significant (Fig. S3d). The correlation was stronger, however, when angiosperms were analysed alone ($r = -0{\cdot}44$, $P = 0{\cdot}0009$, $N = 34$). Species with higher conduit frequency had significantly narrower conduits (Fig. S3a) and greater lumen fractions (Fig. S3b). Higher conductivity indices were significantly associated with wider conduits (Fig. S3c) and greater lumen fractions (Fig. S3d).

Correlations based on PICs were consistent with those across species, with the exception of two correlations involving lumen fraction (Fig. 1b,d). For conduit frequency, the significant correlation across species was driven primarily by the inclusion of podocarps: the relationship was not significant

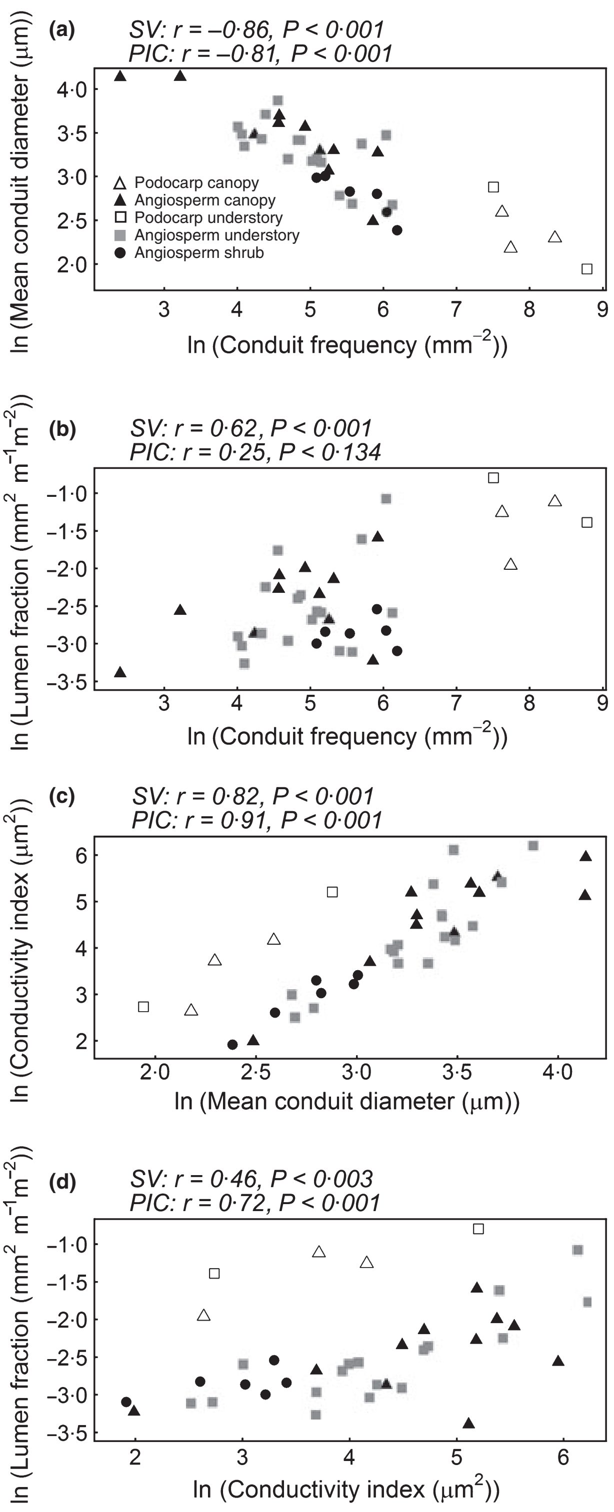

Fig. 1. Statistically significant relationships, after correction for multiple comparisons, between the five wood properties of New Zealand tree species examined in this study: (a) mean conduit diameter and frequency, (b) lumen fraction and conduit frequency, (c) conductivity index and conduit diameter and (d) lumen fraction and conductivity index. Correlation statistics for species' values (SV) and phylogenetically independent contrasts (PICs) are above each panel. Relationships are plotted on natural log scales. Symbols: triangles, canopy trees; squares, understory trees; circles, shrubs; filled symbols, angiosperms; open symbols, conifers. See also Fig. S3.

across angiosperm species alone ($r = 0{\cdot}28$, $P = 0{\cdot}113$, $N = 34$), which was consistent with the results based on PICs. For conductivity index, the five podocarp species tended to maintain a higher lumen fraction at a given conductivity index than did angiosperms. When the podocarps were removed, the relationship was closer to the result based on PICs ($r = 0{\cdot}72$, $P < 0{\cdot}001$, $N = 34$).

Significant negative correlations among wood traits suggest the possibility of interspecific trade-offs between conduit diameter and frequency (Fig. 1a), but not between conductivity index and wood density (Fig. S3c), nor lumen fraction and wood density (Fig. S3d). Based on our statistical model (eqn 3), *c.* 29% of the variation in wood density could be explained by vessel diameter and frequency, although after accounting for multiple comparisons, the model was not statistically significant ($F_{2,31} = 6{\cdot}467$, $P = 0{\cdot}004$, $R^2 = 0{\cdot}29$; Fig. 2). Model comparison favoured retention of both vascular properties in the model over a model with only vessel frequency or diameter ($\mathrm{AIC}_{\mathrm{full}} = -23{\cdot}51$, $\mathrm{AIC}_{\mathrm{frequency}} = -20{\cdot}55$, $\mathrm{AIC}_{\mathrm{diameter}} = -14{\cdot}41$).

RELATIONSHIPS AMONG WOOD TRAITS AND GROWTH AND MORTALITY RATES

Across species, the observed mean juvenile growth rate was significantly correlated with predicted juvenile growth rate in high light. Similarly, the observed mean juvenile mortality rate was significantly correlated with predicted juvenile mortality rate in shade. The correlations were weaker for adult rates (Fig. S4).

Across species, juvenile (30–200 mm in diameter) growth rates were significantly correlated with several wood properties, but not with wood density (Fig. S5). A faster growth rate

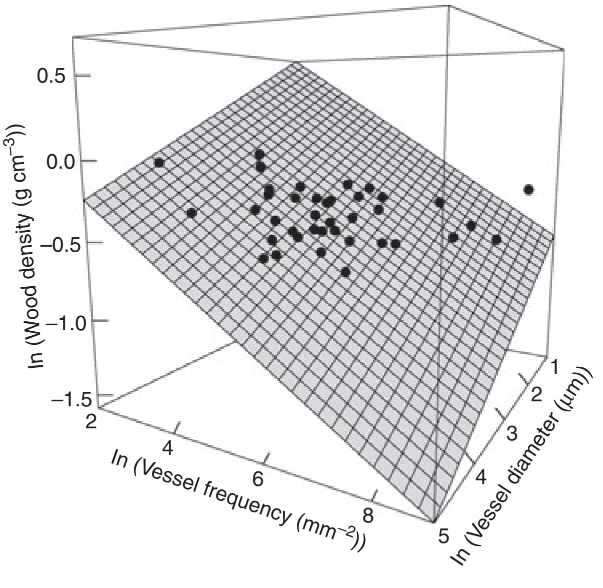

Fig. 2. Relationship of wood density (g cm^{-3}) with vessel frequency (mm^{-2}) and diameter (μm) for New Zealand angiosperm tree species. Black points are observed values. The plane is a fitted surface based on eqn 3. All axes are plotted on natural log scales.

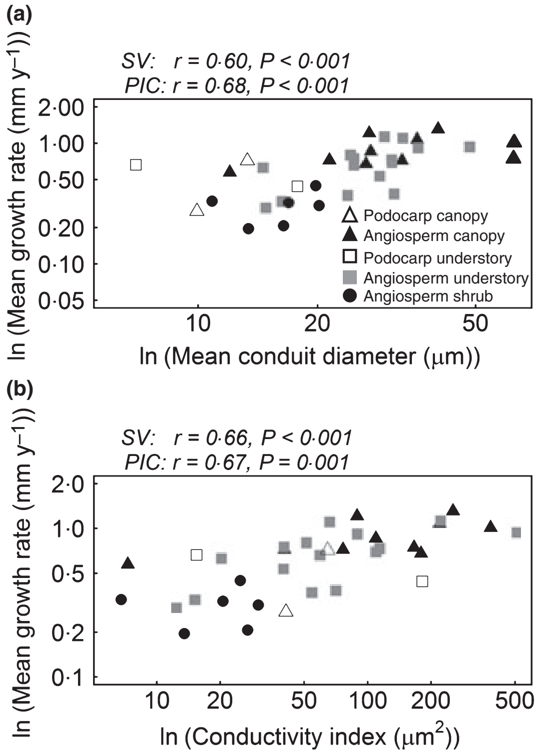

Fig. 3. Statistically significant relationships, after correction for multiple comparisons, between the five wood properties examined in this study with juvenile growth rates of New Zealand tree species: observed mean diameter growth rate and (a) conduit diameter and (b) conductivity index. See Materials and methods for details. Symbols: triangles, canopy trees; squares, understory trees; circles, shrubs; filled symbols, angiosperms; open symbols, conifers. Correlation statistics for species' values (SV) and phylogenetically independent contrasts (PICs) are above

was significantly associated with wider conduit diameter (Fig. 3a) and larger conductivity index (Fig. 3b). Across species, the relationship between growth and lumen fraction was not significant (Fig. S5e), which was likely due to its nonlinearity. Indeed, the correlation across species using only angiosperms was stronger, but still not significant ($r = 0{\cdot}45$, $P = 0{\cdot}010$, $N = 30$). For adults (≥200 mm in diameter), no estimate of growth rate was significantly correlated with any wood trait (Table S1). Similarly, across species, neither predicted mortality rate in shade nor observed mortality rate of juveniles or adults was significantly correlated with any wood trait (Table S3, Fig. S6). Correlations between wood traits and growth and mortality rates based on PICs paralleled the results across species.

We evaluated the extent to which strong negative relationships between wood traits might constrain interspecific variation in growth and mortality rates. For the trade-off between vessel diameter and frequency, the model explained a substantial portion of interspecific variation in growth rates ($F_{2,28} = 16{\cdot}3$, $P < 0{\cdot}001$, $R^2 = 0{\cdot}54$; Fig. 4a), but not mortality rates ($F_{2,29} = 0{\cdot}2436$, $P = 0{\cdot}785$, $R^2 = 0{\cdot}02$; Fig. 4b).

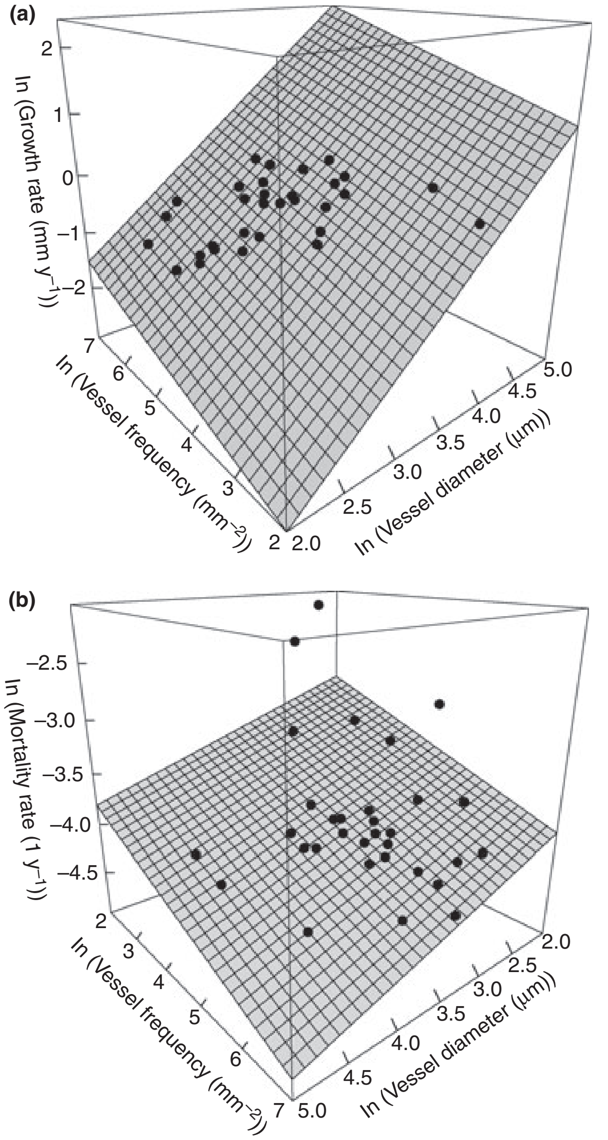

Fig. 4. Relationships of juvenile observed mean growth (a) and mortality (b) rates with vessel frequency (N; mm^{-2}) and diameter (D; μm) for New Zealand angiosperm tree species. Black points are observed values. Planes are fitted surfaces based on a parameter estimate from the statistical model in eqn 3. Relationships are plotted on natural log scales. Note the change in orientation of the two horizontal axes.

MAXIMUM HEIGHT AS AN AXIS OF DIFFERENTIATION AMONG SPECIES

Maximum height was positively correlated with wood traits associated with hydraulic conductance, but there was no relationship with wood density (Fig. 5, Fig. S7). Analyses across species and using PICs were consistent, except for the relationship of maximum height with conduit frequency (Fig. 5a). The difference was largely due to podocarps with tall maximum heights, but narrow, frequent tracheids. Across angiosperm species alone, the relationship between conduit frequency and maximum height was stronger ($r = -0{\cdot}31$, $P = 0{\cdot}072$, $N = 34$) and more consistent with the result

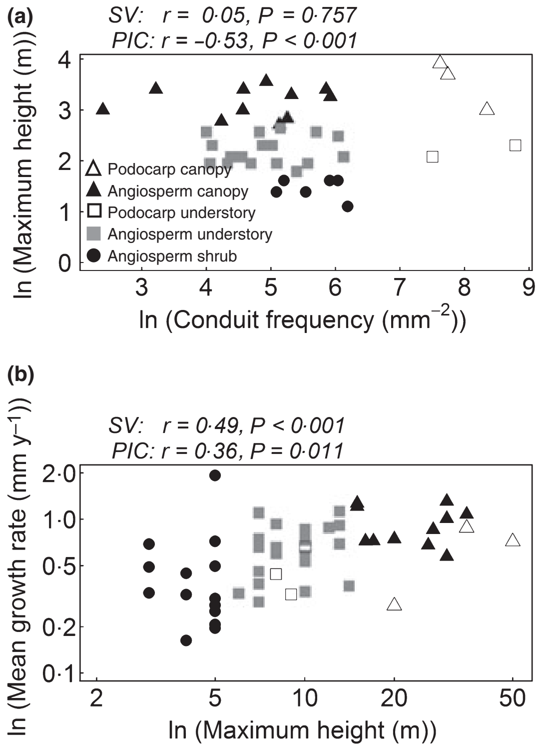

Fig. 5. Statistically significant relationships, after correction for multiple comparisons, of maximum tree height with the five wood properties examined in this study and juvenile growth and mortality rates of New Zealand tree species: (a) maximum height and conduit frequency and (b) juvenile observed mean growth rate and maximum height. See *Demographic data and analytical methods* for details. Symbols: triangles, canopy trees; squares, understory trees; circles, shrubs; filled symbols, angiosperms; open symbols, conifers. Correlation statistics for species' values (SV) and phylogenetically independent contrasts (PICs) are above each panel. Relationships are plotted on natural log scales. Note that in (b), the mean correlation coefficient and maximum probability for PICs are based on 1000 random resolutions of the phylogeny (Appendix S2, Fig. S2). See also Fig. S7.

based on PICs. Based on analyses across species and PICs, tree species reaching taller maximum heights had faster juvenile observed growth rates and lower adult observed mortality rates (Fig. 5b; Table S3). Across angiosperm species alone, the tallest species had the largest hydraulic capacities ($r = 0{\cdot}55$, $P < 0{\cdot}001$, $N = 34$).

Discussion

RELATIONSHIPS BETWEEN WOOD DENSITY AND VASCULAR PROPERTIES

It is widely accepted that trade-offs must exist among wood properties related to mechanical support and hydraulic efficiency and safety, particularly involving wood density (Meinzer 2003; Chave *et al.* 2009). Nevertheless, although several xylem traits were significantly correlated with each other in our sample of New Zealand woody species, none was significantly correlated with wood density. Wood density was negatively correlated with lumen fraction across species, consistent with other studies (Denne, Cahalan & Aebischer 1999; Preston, Cornwell & DeNoyer 2006), but the correlation was weak and non-significant because podocarps maintained high lumen fractions across a range of wood densities due to their high tracheid frequencies. Among angiosperms, the relationship between lumen fraction and wood density was stronger and appeared to be constrained at an upper boundary: at a given wood density, there appeared to be a maximum attainable lumen fraction. *Leptospermum scoparium* was the one angiosperm outlier: this small, early successional species had the highest wood density in our data set, but also a high lumen fraction, presumably due to the dense matrix of fibres in which the xylem elements are embedded (Patel 1994). Indeed, it was a large, influential contrast involving this species that caused the relationship based on PICs to be so weak (Fig. S8).

These results suggest that wood density is only partly determined by lumen fraction: the frequency and size of vessel fibres in angiosperms and the thickness of cell walls in conifers may enable wood density to vary somewhat independently of lumen fraction (Hacke *et al.* 2001; Preston, Cornwell & DeNoyer 2006). Because wood density (D_w) is related to lumen fraction, F, as $D_w = D_m(1 - F)$ (Preston, Cornwell & DeNoyer 2006), variation in the density of the matrix outside of the lumens (D_m) may play an important role in allowing woody species to escape some putative trade-offs involving wood density and conductivity. Furthermore, as vessel diameter is the chief determinant of hydraulic conductivity in angiosperm wood, wood density may be partially decoupled from conductivity.

The diameter of vessels was inversely related to vessel frequency, and this trade-off partly constrained variation in wood density and growth rate among the angiosperm tree species in our sample, as was also found by Preston, Cornwell & DeNoyer (2006) for wood density. In other words, a limited range of wood densities and growth rates arose from these vessel diameters and frequencies, relative to what was possible given the ranges of each, had they not been negatively related. The New Zealand species covered *c.* 58% of the global range in wood densities (wood density range in the 39 New Zealand species: 0·4–1·1 g cm^{-3}; global range: *c.* 0·1–1·5 g cm^{-3}; Chave *et al.* 2006). Neither the lightest woods, which would result from frequent conduits with wide diameters, nor the heaviest woods, which would result from infrequent, narrow conduits, were represented among the New Zealand species. The trade-off between diameter and frequency is linked to several interacting mechanisms (Carlquist 1975): there is both a lower limit to the density of wood required to support a tree crown without buckling (Greenhill 1881; McMahon 1973; McMahon & Kronauer 1976), which would be approached if conduits are too wide or too frequent, and an upper limit to the density of wood due to a threshold of hydraulic resistance before inhibition of leaf expansion and photosynthesis occurs in the canopy (Brodribb *et al.* 2003; Koch *et al.* 2004; Niklas & Spatz 2004). Aside from end-wall resistance, hydraulic conductivity of wood can be increased with longer conduits, conduits of larger diameter or with greater numbers of conduits per unit area (Carlquist 1975). All alternatives have costs:

longer and wider conduits have greater risk of cavitation, whereas increasing conduit frequency requires more biomass in wood be used to supply the same leaf area (Castro-Diez *et al*. 1998; Tyree & Ewers 1991).

RELATIONSHIPS BETWEEN WOOD PROPERTIES AND DEMOGRAPHIC RATES

Wood density was not significantly correlated with demographic rates in our data. This finding contradicts the idea that wood density is a good proxy for a tree species' position along a slow–fast rate-of-living continuum. Although strong relationships between wood density and growth and mortality rates have been observed (Smith & Tumey 1982; Putz *et al.* 1983; King 1986; Chave *et al*. 2006; King *et al*. 2006b; Osunkoya *et al*. 2007), studies analysing variation across larger numbers of species have found that when these correlations are statistically significant, they are often weak (Poorter *et al.* 2008; Chave *et al*. 2009). Instead, growth rate was more strongly related to xylem traits linked directly to hydraulic conductance, consistent with previous studies (Castro-Diez *et al*. 1998; Denne, Cahalan & Aebischer 1999; Brodribb & Feild 2000). The lack of a significant relationship between the demographic rates and wood densities of the New Zealand species may arise because the same wood density can be achieved by different combinations of conduit frequency, conduit diameter and wood fibre traits, and these three xylem properties each have different functional consequences for growth and mortality. Wood traits, maximum height and growth capacity are presumably functionally optimized (Niklas & Spatz 2006). Nevertheless, we would expect those traits most closely linked to the particular functions that are under the greatest selection pressure in an environment to have the strongest relationships with demographic rates.

Our finding that mortality rates are not significantly correlated with wood traits suggests that causes of death that are independent of wood vascular properties, such as landslips and herbivory (e.g. Allen, Bellingham & Wiser 1999; Bee, Kunstler & Coomes 2007; Wardle 1991; Wardle & Allen 1983; Wardle, Hayward & Herbert 1971; Wells, Stewart & Duncan 1998), may play a key role in New Zealand's forests. Our findings are inconsistent with the idea that denser woods, which should minimize of the hazards of falling debris, storms, wood-boring insects or pathogens (Bultman & Southwell 1976; Putz *et al*. 1983; King 1986; Poorter *et al*. 2008), enhance tree survival in New Zealand. Similarly, our results do not support a relationship between shade tolerance and wood density (cf. King *et al*. 2006b), and we found no relationship between mortality rate and conduit diameter, as might be expected if species with wider vessels were at greater risk of cavitation.

MAXIMUM HEIGHT AS AN AXIS OF DIFFERENTIATION AMONG SPECIES

Maximum height was an important axis of differentiation among tree species in New Zealand, as in Malaysian, Australian and neotropical rain forests (Thomas 1995; Kohyama *et al*. 2003; King, Davies & Supardi 2006a; Poorter *et al.* 2008). In contrast to Malaysian tree species (Thomas 1995), we found little evidence suggesting that taller tree species had lower density woods. We also found little evidence that the correlation between wood density and maximum height was mediated by a relationship between wood density and growth rate (Preston, Cornwell & DeNoyer 2006).

In our data, the most conductive woods were those with fewer, wider vessels and tended to be of species reaching the tallest maximum heights, at least among angiosperms. These results suggest that tree species achieving greater heights require greater hydraulic capacity (cf. Koch *et al*. 2004). For angiosperms hydraulic efficiency is primarily accomplished through wider conduits, whereas for conifers it is achieved partly through increases in tracheid frequency (Sperry, Meinzer & McCulloh 2008). Podocarps may be able to achieve such heights due to the structure of their tracheids, which are longer and have lower end-wall resistance provided by torus-margo pits, relative to angiosperms (Sperry, Hacke & Pittermann 2006).

PHYLOGENETIC PATTERNS

Our analyses with and without incorporation of evolutionary relationships were often consistent with each other. When they were not, it was frequently due to particular outlying species or related to fundamental differences in the wood anatomy of angiosperms vs. conifers, which are accounted for by including phylogenetic information in the analyses. Taxon sampling (i.e. the number or type of taxa included) can affect inferences made about correlated trait evolution among species, particularly when communities are assembled as a result of non-random processes, including dispersal (Ackerly 2000; Clark 2009). We sampled most of the common woody species in New Zealand. Nevertheless, with a few exceptions (e.g. *Coprosma*; Rubiaceae), they derive from diverse lineages, likely a result of the strong influence of dispersal on the New Zealand flora (McGlone 2005). Indeed, 20 families are represented among the 59 woody species in our data set. Thus, the effects of taxon sampling may be an additional factor explaining why we failed to find some trait correlations that have been documented in other studies (Putz *et al*. 1983; Lawton 1984; Enquist *et al*. 1999; King *et al*. 2006b; Preston, Cornwell & DeNoyer 2006; Osunkoya *et al*. 2007).

Conclusion

Our analyses of interspecific variation in wood density, xylem traits and demographic rates among tree species in New Zealand found little support for the idea that wood density is a good proxy for a tree species' position along a fast–slow rate-of-living continuum. Wood density was largely decoupled from the traits' most influencing hydraulic function: vessel diameter, lumen fraction and conductivity index. Instead, the strong, negative relationship between vessel diameter and frequency that we found may limit variation in wood density and growth, but not mortality, rates of tree species in New Zealand, and thereby constrain the realized diversity of demographic niches (*sensu* Condit *et al.* 2006). Trade-offs in function can therefore be important determinants of individual performance and have the potential to shape functional diversity and ecology of forest communities by linking selection on structure and function to population-level dynamics.

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Supporting information

Additional Supporting information may be found in the online version of this article.

Fig. S1. The phylogenetic hypothesis for woody plant species of New Zealand used in phylogenetic comparative analyses, drawn with unitary branch lengths and polytomies.

Fig. S2. Distributions of the Pearson correlation coefficient and probability value for the relationship between phylogenetic independent contrasts calculated from juvenile observed growth (a and b) and mortality (c and d) rates with maximum height of New Zealand's tree species, based on 1000 random resolutions of polytomies in the phylogenetic tree (Fig. S1; Appendix S2).

Fig. S3. The relationships between five wood properties of New Zealand tree species: wood density (g cm^{-3}), number of conduits per mm^2, mean diameter of conduits (μm), conductivity index (μm^2) and lumen fraction (mm^2 mm^{-2}), plotted on log–log scales.

Fig. S4. Relationships between observed growth and mortality rates and those predicted by a neighbourhood crowding model.

Fig. S5. The relationships of five wood properties with juvenile growth rates of tree species of New Zealand.

Fig. S6. The relationships of five wood properties with juvenile mortality rates of New Zealand tree species.

Fig. S7. The relationships of maximum tree height (m) with five wood properties (a–e) and juvenile growth and mortality rates (f–i) of New Zealand tree species.

Fig. S8. The influence of *Leptospermum scoparium* (Myrtaceae) on inferred relationships between lumen fraction and wood density.

Table S1. Wood traits and growth and mortality rates of woody species of New Zealand.

Table S2. Values of Akaike's information criterion (AIC) for ordinary least squares (OLS) and phylogenetic generalized least squares (PGLS) fits to the model, $\log(R) = a \log(N) + b \log(D) + c$, where R is the dependent variable (either species' wood density or observed mean growth or mortality rate), N is the vessel frequency, D is the vessel diameter and a, b and c are fitted parameters.

Table S3. Relationships between wood properties and adult growth and mortality rates of New Zealand woody species.

Appendix S1. Details of our approach to modelling tree growth and mortality.

Appendix S2. Details of phylogenetic independent contrast analyses for cases with polytomies.

Appendix S3. Details of the phylogenetic generalized least squares analyses.