SHORT COMMUNICATION

Large-tree growth and mortality rates in forests of the central North Island, New Zealand

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Abstract: Large trees are a significant structural component of old-growth forests and are important as habitat for epiphytic biodiversity; as substantial stores of biomass, carbon and nutrient; as seed trees; and as engineers of large gap sites for regeneration. Their low density across the landscape is an impediment to accurately measuring growth and mortality, especially as infrequent tree deaths are rarely captured without long periods of monitoring. Here we present large-tree ($\geq$ 30 cm in diameter at breast height) growth and mortality rates for six common New Zealand tree species over a 42-year period from 28 large permanent plots (0.4–0.8 ha) in the central North Island. Our goal was to examine how rates of growth and mortality varied with tree size and species. In total we sampled 1933 large trees across 11.6 ha, corresponding to a large-tree density of 167 trees ha^{-1}, of which we used 1542 as our six study species. Mean annual mortality rates varied more than 10-fold among species being least in *Dacrydium cupressinum* (0.16%) and greatest in *Weinmannia racemosa* (2.21%). Diameter growth rates were less variable among species and ranged from 1.8 mm yr^{-1} in *Ixerba brexioides* to 3.3 mm yr^{-1} in *D. cupressinum*. Tree size influenced the rate of mortality in *Beilschmiedia tawa*, *I. brexioides* and *W. racemosa* but there was no support for including tree size in models of the remaining three species. Likewise, tree size influenced growth rates in *I. brexioides* and *Nothofagus menziesii* but not the remaining four species. These data provide robust size- and species-specific estimates of large-tree demographic rates that can be used as baselines for monitoring the impacts of management and global change in old-growth forests.

Keywords: demographic rates; permanent plots; scaling theory

Introduction

Large trees are a significant structural component of old-growth forests worldwide. In New Zealand forests, trees $\geq$ 30 cm in diameter at breast height (dbh) are only c. 5% of live tree stems yet they store >50% of forest biomass, carbon and nutrients (Coomes et al. 2002; Hart et al. 2003), provide essential habitat for epiphytic plant species (Hofstede et al. 2001; Burns & Dawson 2005) and nesting or roosting animal species (e.g. Sedgeley & O'Donnell 1999), and produce a disproportionately large amount of forest seedfall (West 1995). After death, they support diverse deadwood communities (e.g. Allen et al. 2000) and, finally, fall to produce the large canopy gaps that initiate regeneration and, in so doing, control the structure and function of forest ecosystems (Enright et al. 1993). Low stem density, long lifespans and slow growth rates of New Zealand canopy tree species (Wardle 1991; Lusk & Smith 1998) are impediments to gathering statistically robust estimates of demographic rates, as many individuals are needed over a relatively long time period in order to capture measurable growth and to census sufficient mortality events to estimate rates (Ogden 1985; Clark & Clark 1996; Peltzer et al. 2005). As a consequence, estimates of large-tree growth and mortality rates for New Zealand tree species are limited to national-scale analyses that pool across species (Coomes et al. 2003) or to compositionally simple *Nothofagus*-dominated forests (Wardle 1984; Coomes & Allen 2007a). This situation is not unique to New Zealand; worldwide, there are relatively few estimates of large-tree mortality rates for individual species.

Diameter growth and the probability of mortality both vary with tree size (e.g. Harcombe 1987; Busing 2005), but the nature of those size-dependent relationships remains unclear. Enquist et al. (1999) and Brown et al. (2004) used a series of scaling rules to predict that tree growth and mortality should scale with tree size, with size being a proxy for resource availability. They predicted that the rate of growth should increase with tree size and the probability of mortality should decrease. These universal scaling rules have been challenged by analyses of large permanent-plot datasets from natural forests that demonstrated that scaling rules were poor predictors of growth and mortality (Coomes et al. 2003; Muller-Landau et al. 2006) and that large trees frequently had slower growth rates and higher mortality rates than predicted by scaling rules alone. These departures from scaling rules are thought to reflect exogenous disturbance, senescence, and size-dependent allocation to reproduction.

Here we examine how demographic rates of large trees scale with tree size and how they vary among six widespread tree species of widely differing lifespans, including two long-lived podocarp species. Data were collected at a regional scale from conifer–broadleaved and broadleaved forests across the central North Island of New Zealand over a c. 40-year period. This information responds to a wider need for more knowledge of large-tree demographic rates in old-growth forests and contributes to the development of mechanistic models of forest dynamics in New Zealand that require such size- and species-specific rates of mortality and growth (Ogden 1985).

Materials and methods

Study region and location of permanent plots

Data on tree mortality and growth were collected from 27 0.4-ha (20 × 210 m) permanent plots and a single 0.8-ha (20 × 420 m) plot that were established during 1958–1962 in unlogged indigenous forests across the central North Island including the Urewera Ranges (McKelvey & Cameron 1958). Plots were subjectively located a priori, using aerial photographs, to sample the range of forest types present in the region, which range from those dominated by *Beilschmiedia tawa* (Lauraceae)[1], *Weinmannia racemosa* (Cunoniaceae), *Dacrydium cupressinum* (Podocarpaceae) and *Prumnopitys ferruginea* (Podocarpaceae) at low to moderate elevations to those dominated by *Nothofagus menziesii* (Nothofagaceae) at higher elevations (McKelvey 1963, 1973). Less widespread but locally common species include *Ixerba brexioides* (Grossulariaceae), *Phyllocladus trichomanoides* (Podocarpaceae) and *Prumnopitys taxifolia* (Podocarpaceae). On each plot, all trees with a diameter ≥ 30 cm at 1.4 m (dbh) were identified to species and permanently tagged at 1.4 m. Diameter at breast

height was measured at the time of plot establishment and remeasured between 1998 and 2007. Soils are almost entirely of volcanic origin (McKelvey 1963, 1973); mean soil total nitrogen in the upper 100 mm of mineral soil was 0.32% and mean soil total phosphorus was 277 mg kg^{-1}. Plots range in elevation from 260 to 1115 m but largely sample forests between 400 and 800 m; the few high-elevation plots predominantly sample *N. menziesii*. Modelled mean annual temperature ranges from 8.1 to 12.5ºC and mean annual precipitation from 1379 to 2657 mm (climate modelled for each plot; Leathwick 2001; Leathwick et al. 2002).

Individual-tree mortality

We selected the six tree species with at least 90 trees across all plots (Table 1) and used the logistic model of Yao et al. (2001) to model the probability of individual-tree survival. This model uses a logit link function and the census interval as an exponent to allow trees of a species to be modelled together, despite being censused over varying time periods. Size-specific individual-tree survival was modelled for each species as:

$$\text{Probability of survival} = [1 / (1 + \{\exp[-(a + b*D)]\})]^{L} \quad (1)$$

where a is an intercept estimated by the model, b is a coefficient estimated by the model to describe the effect of dbh (*D*) on the probability of survival and *L* is the number of years over which each individual tree was censused. The probability of survival for each tree was converted to the probability of mortality by subtracting values from 1. These values were used to estimate a mortality rate for the sample using the standard mortality rate formula of Sheil & May (1996). For each species we also conducted a null model with no effect of dbh to evaluate whether there was support for including a size effect in the model. The advantage of our modelling approach is that it allows us to concurrently model trees with differing census intervals – a consequence of each plot being established and remeasured over varying time intervals. However, the penalty of such an approach is that we cannot incorporate a random effect of plot into our analysis. We consider that capturing the varying census intervals is more important than trying to capture a random-plot effect, especially as there are insufficient data (*N* = 28 plots) to fit random effects with statistical confidence. Further, their inclusion does not influence model coefficients, only the estimates of variance around those coefficients (Uriarte et al. 2004), which we do not present here. Models were performed using the *gnlr* function from the *gnlm* and *rmulti* libraries in R v. 2.2.0 (R Development Core Team 2008). For each species we present the overall mortality rate of the measured population and the modelled mortality rate for an individual with a tree size corresponding to the 95th

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[1] Plant names follow Allan Herbarium (2002-2006)

Table 1. Mean annual mortality and median annual growth rates for large trees (≥30 cm dbh) of six widespread species in the central North Island, New Zealand. The mortality dataset includes all trees alive when plots were established; the growth dataset only includes those trees that survived during the census interval. Overall mortality and overall median diameter growth rates are the true values from the population of trees censused. Modelled rates are for a tree size corresponding to the 95th percentile tree diameter for that species nationally (D_{95th}); this standardises rates among species to a common functional size/age.

	Beilschmiedia tawa	*Ixerba brexioides*	*Nothofagus menziesii*	*Weinmannia racemosa*	*Dacrydium cupressinum*	*Prumnopitys ferruginea*
Lifespan (years)	450[1,2]	250[3]	600[4]	450[5]	600–1200[6]	650–770[7,8]
D_{95th} (cm)	46.2	41.3	48.8	31.1	81.3	57.3
MORTALITY						
Overall mortality rate (% yr^{-1})	0.60	0.69	0.38	2.21	0.16	0.42
Modelled mortality rate at D_{95th} (% yr^{-1})	0.62	0.67	0.39	1.68	0.17	0.36
N trees	635	261	160	229	165	92
GROWTH						
Overall median diameter growth rate (mm yr^{-1})	2.0	1.8	3.0	2.1	3.3	2.7
Modelled median diameter growth rate at D_{95th} (cm yr^{-1})	1.9	1.8	3.0	2.3	3.1	2.7
N trees	485	195	131	92	154	77

[1]Knowles & Beveridge (1982); [2]West (1995); [3]Smale et al. unpubl. data; [4]Herbert (1973); [5]Wardle (1966); [6]Norton et al. (1988); [7]Enright & Ogden (1995); [8]Lusk & Ogden (1992).

percentile for that species nationally. This was calculated from the New Zealand Carbon Monitoring System plot network, administered by the Ministry for the Environment and archived in the National Vegetation Survey (NVS) Databank (http://nvs.landcareresearch.co.nz). This approach assumes that tree size and age are correlated within a species and allows us to compare across species at a common upper tree-size/age (Table 1).

Individual-tree growth

Mean annual diameter growth for all surviving trees was calculated by subtracting the initial diameter of each stem from the final diameter and then dividing this growth by the census interval in years. Estimating diameter growth rates of large trees using diameter tapes is problematic because of measurement errors introduced by buttresses, sloughing bark, vines and epiphytes – which cause overestimation, and decay and loss of form – which cause underestimates (Sheil 1995). The estimates of diameter growth presented here include these errors. Diameter growth was modelled in relation to tree diameter using non-linear quantile regression with a power function (after Muller-Landau et al. 2006) in the *nlqr* function from the *quantreg* library in R v. 2.6.2 (R Development Core Team 2008). Non-linear quantile regression allows the relationship between median growth rates and size

to be modelled alongside the relationships between any specified quantile of individuals within a population; for example, the 0.95 quantile delineates the fastest 5% of individuals in a sample (Coomes & Allen 2007b). Models of median (0.50 quantile) growth rates using quantile regression accommodate the non-normal distribution of growth data and are generally robust to outlier values (Lieberman et al. 1985; Laurance et al. 2004). Here we present the overall median growth rate of each species from the measured population and the modelled median growth rate for an individual with a tree size corresponding to the 95th percentile for that species nationally, as for mortality rates. For each species we compared our model against a null model with no size effect, as for the mortality models.

Results

Mortality rates

The overall annual mortality rate for all large trees across all species was 0.70%. The mean annual mortality rate for the two conifer species was 0.25% and for the four angiosperm species was 0.80%. Annual mortality rates varied more than 10-fold among species from <0.2% for *Dacrydium cupressinum* and >2.0% for *Weinmannia*
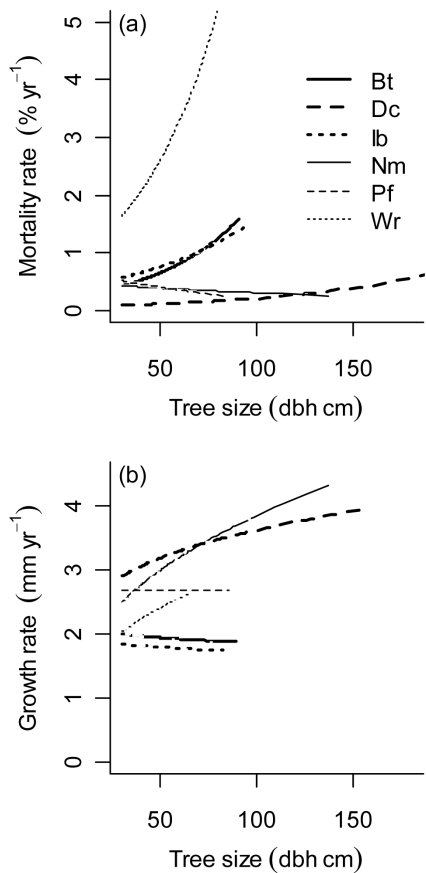
Figure 1. Modelled size-specific (a) mean mortality rates and (b) median diameter growth rates for six widespread tree species in the central North Island, New Zealand. Lines are fitted using model coefficients (see Materials and methods). Bt = *Beilschmiedia tawa*; Dc = *Dacrydium cupressinum*; Ib = *Ixerba brexioides*; Nm = *Nothofagus menziesii*; Pf = *Prumnopitys ferruginea*; Wr = *Weinmannia racemosa*.

Figure 2. Relationships between estimated lifespan and (a) mean mortality and (b) median growth rates for an individual with a tree size corresponding to the 95th percentile for that species in six widespread tree species in the central North Island, New Zealand (see Table 1). Bt = *Beilschmiedia tawa*; Dc = *Dacrydium cupressinum*; Ib = *Ixerba brexioides*; Nm = *Nothofagus menziesii*; Pf = *Prumnopitys ferruginea*; Wr = *Weinmannia racemosa*.

racemosa (Fig. 1a; Table 1). Mortality rates were generally negatively related to estimated lifespan in the order *Ixerba brexioides* > *Beilschmiedia tawa* > *Nothofagus menziesii* > *Prumnopitys ferruginea* > *D. cupressinum*, although mortality rates for *W. racemosa* were substantially higher than would be expected for a lifespan of 450 years (Fig. 2a). Mortality models incorporating a size effect had substantially more support than null models for three species, *B. tawa*, *I. brexioides* and *W. racemosa*. For the remaining species inclusion of a size effect had a negligible effect on the models (model selection results not shown; Fig. 1a). The effect of size on mortality was particularly pronounced for *W. racemosa* (Fig. 1a); of the
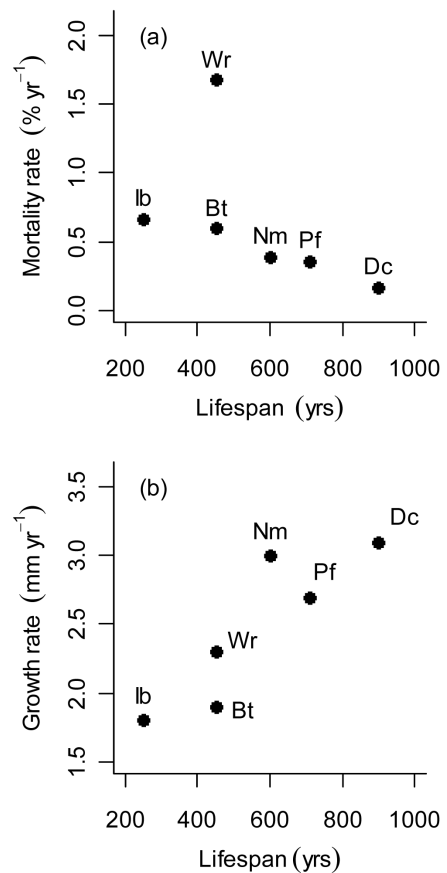
44 *W. racemosa* individuals with an initial diameter ≥ 50 cm dbh only 12 survived and all eight trees with an initial diameter ≥ 70 cm died.

Growth rates

The overall median growth rate across all species was 2.3 mm yr^{-1}. The median growth rate for the two conifer species was 3.0 mm yr^{-1} and for the four angiosperm species was 2.1 mm yr^{-1}. Growth rates varied less among species than did mortality rates (Table 1; Fig. 1). Median growth rate was lowest for *Ixerba brexioides*, the shortest-lived species, and greatest for *Dacrydium cupressinum* (Table 1; Fig. 2b). Growth models incorporating a size

effect had substantially more support than null models for two species, *I. brexioides* and *Nothofagus menziesii*, and the effect of size on growth was negative for the first species and positive for the second. For the remaining species inclusion of a size effect had a negligible effect on the models (model selection results not shown; Fig. 1b).

Discussion

Mortality rates of large trees

The mean annual mortality rates presented here, largely below 1%, conform to estimates from temperate forests in North America (Busing 2005; van Mantgem et al. 2009) and tropical forests (Clark & Clark 1996; Muller-Landau et al. 2006), although our value of 0.16% for *Dacrydium cupressinum* is conspicuously lower than in most studies that have had sufficient statistical power to report on low mortality rates within species (Peltzer et al. 2005). This low rate contrasts with much higher rates (c. 1.8–3.8%) reported for *Nothofagus solandri* var. *cliffortioides* ($\geq$30 dbh) in South Island montane forest (Coomes & Allen 2007a). Mortality rates in this study varied substantially among species with some indication that longer-lived species had lower mortality rates, which has been reported in tropical forests (Korning & Balslev 1994; Laurance et al. 2004).

A notable outlier to the relationship between lifespan and mortality was *Weinmannia racemosa*, for which high mortality rates have also been reported by Bellingham et al. (1999) for the central North Island. In part, these high mortality rates reflect the likely age of this species at $\geq$30 cm dbh, relative to the other species reported here. However, even when standardised to a common size/age (Table 1) the rates remain high. Beveridge (1973) considered that *W. racemosa* was a moderately long-lived successional species that develops after disturbances such as vulcanism or Polynesian fires (McGlone et al. 1988) remove the canopy of emergent podocarps. If forests in the central North Island are currently recovering from a period of disturbance then *W. racemosa* should be in a state of decline as forests progress towards late-successional forests dominated by shade-tolerant tree species, such as *Beilschmiedia tawa*. However, this successional hypothesis cannot satisfactorily account for all *W. racemosa* mortality as this species commonly occurs in admixtures as much as in even-aged cohorts formed by disturbance. The interpretation of mortality rates in *W. racemosa* is further complicated by the recent influence of canopy browsing by introduced brushtail possums *Trichosurus vulpecula* (Nugent et al. 2001), which may exacerbate natural mortality (Batcheler 1983; Bellingham & Lee 2006).

The probability of mortality increased substantially with tree size for three of our six species. Increasing mortality with tree size supports the hypothesis that

senescence and disturbance augment mortality among the largest trees (Zimmerman et al. 1994; Coomes et al. 2003; Muller-Landau et al. 2006). For the remaining species inclusion of a size effect in the mortality models had little support, suggesting that large-tree mortality is stochastic and size-independent. None of the species tested here supported the hypothesis that mortality rate should scale negatively with tree size (Enquist et al. 1999; Brown et al. 2004). The size–mortality relationships presented here reflect the census period over which they were collected and will strongly reflect the disturbance events captured by that period, albeit averaged over many years. However, the 40-year period of measurement in this study, substantial in research terms, captures only a small portion of a tree lifespan: 15% for *Ixerba brexioides* and only 4–5% for the two conifers (*Prumnopitys ferruginea* and *Dacrydium cupressinum*). Applying these 'short-term' glimpses of tree mortality to predictive models of forest dynamics remains a significant challenge.

Growth rates of large trees

Average growth rates between 1 and 3 mm yr^{-1} are typical for large trees in temperate rainforests elsewhere (Kohyama 1987; Lusk 1999) and are unsurprisingly less than those in tropical rainforests (Clark & Clark 1992; Muller-Landau et al. 2006). Diameter growth rates of large *Beilschmiedia tawa* range from 0.7 mm yr^{-1} to 2.2 mm yr^{-1} (Smale et al. 1985; West 1995), which encompasses our overall median growth rate of 2.0 mm yr^{-1}. Likewise, our reported value for *Weinmannia racemosa* (2.1 mm yr^{-1}) aligns well with the rate of 2.2 mm yr^{-1} reported by Lusk & Ogden (1992). The ecology of *Ixerba brexioides* is poorly known; Smale et al. (1997) reported growth rates of 1.6–2.4 mm yr^{-1} from 14 individuals and our overall median growth rate of 1.8 mm yr^{-1} aligns well with this estimate. Large-tree growth rates of *Nothofagus menziesii* in Fiordland ranged from 0.8 mm yr^{-1} at high elevations to 3.2 mm yr^{-1} on terrace sites (Herbert 1973) and our overall median growth rate of 3.0 mm yr^{-1} therefore represents relatively fast growth for this species. Although our samples for this species come from high-elevation sites we suggest that the relatively fast growth rates reported here reflect superior tree growth on free-draining volcanic soils.

Diameter growth rates of the two conifer species, *Dacrydium cupressinum* and *Prumnopitys ferruginea*, were unexpectedly high relative to other data from those species around New Zealand. Annual diameter growth rates of large, mature *D. cupressinum* range from 0.5 mm yr^{-1} to 2.8 mm yr^{-1} (Norton et al. 1988; Franklin 1973; Herbert 1980; Smale et al. 1985, 1987; Lusk & Ogden 1992) although semi-mature stems on fertile pumice soils can achieve 10 mm yr^{-1} (Franklin 1968). Fewer published values are available for diameter growth of *P. ferruginea* but range from <0.1 mm yr^{-1} to 1.6 mm yr^{-1} (Katz 1980; Smale et al. 1985; Lusk & Ogden 1992). The overall median growth rates presented here

for *D. cupressinum* (3.3 mm yr^{-1}) represent relatively fast growth for this species and the growth rate for *P. ferruginea* (2.7 mm yr^{-1}) appears substantially higher than other published values, although with so few studies available that present size-specific growth rates of large stems it is difficult to determine this with confidence. A consequence of the unexpectedly high conifer growth rates was that long-lived species had fast growth rates, which is contrary to theory (Silvertown & Charlesworth 2001) and empirical data from tropical forests (Lieberman et al. 1985; Laurance et al. 2004). Clearly, further investigation of large-tree growth rates of New Zealand species would be profitable to clarify the growth potential of long-lived species. In particular, studies that employ both diameter tape measurements and increment core data would be useful for reconciling differences in growth rate related to measurement method.

There was support for including a size effect in the growth models of two species, one of which had positive relationships between size and growth and one which was negative. Published studies generally suggest that growth rate should increase with tree size, typically reaching an asymptote among the larger individuals. Weak negative relationships between tree size and growth rate do not support the hypothesis that growth should scale positively with tree size (Enquist et al. 1999; Brown et al. 2004) and may reflect senescence among the larger, older individuals (Muller-Landau et al. 2006).

Management applications

Future changes in large-tree population dynamics will reflect endogenous change within natural populations alongside anthropogenic change. The latter will be expressed both directly through fragmentation and management practices, and indirectly through the pervasive impacts of climate change and elevated atmospheric carbon dioxide. Our capacity to manage old-growth forests for any given set of goals (e.g. minimising impacts of introduced browsers on tree mortality, timber production) relies on adequate monitoring so that we can detect and respond appropriately to changes in tree population dynamics. Detecting low mortality rates and changes in low mortality rates requires a combination of many trees and long census intervals (Peltzer et al. 2005). Clearly, for widely spaced large individuals, this would require either an impracticable monitoring effort to capture sufficient individuals over a short time frame, or long-term monitoring programmes that include sufficient time to capture mortality among a smaller number of individuals. This underscores the value of maintaining long-term permanent plot networks to achieve effective monitoring of management and global change impacts on large trees. With increasing focus on multiple management goals for old-growth forests that maximise biodiversity gains alongside long-term carbon storage, refined knowledge and management of large trees should be an imperative.

Acknowledgements

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