

Testing the resource-matching hypothesis in the mast seeding tree *Nothofagus truncata* (Fagaceae)

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Abstract: The genus *Nothofagus* in New Zealand and Australia exhibits strong mast seeding (i.e. highly variable seed crops between years). Seed crop variation is synchronized within and between species over large spatial scales, and results in greatly increased wind pollination efficiency which could provide a selective benefit favouring the maintenance of mast seeding. However, the null hypothesis (that plants simply match their reproductive effort to the variable resources available each year) has not been tested in *Nothofagus*. Here we use a 33-year dataset on seedfall and wood ring increments for 19 individual *Nothofagus truncata* trees at Orongorongo, New Zealand, to test for the presence of switching (exaggeration of seedfall variability by diverting resources into, then out of, reproduction). A generalized least squares model explained 40.7% of the variance in standardized ring widths, using six weather variables (absolute minimum temperatures in March (lag 0) April (lag 0 and lag 1), May (lag 0) and rainfall in November and February (lag 0)) and seedfall. Seedfall had a negative relationship with the current year's ring widths even after controlling for all significant weather variables. This shows that switching is occurring in *N. truncata* within individuals among years, and therefore that masting in this species is the result of selective forces such as increased wind pollination efficiency. As this result has been demonstrated for very few masting species, we call for this test to be applied more widely.

Key words: annual ring growth, climate, economies of scale, switching, wind pollination.

INTRODUCTION

Mast seeding, the intermittent production of large seed crops by a population of perennial plants (Kelly 1994; Koenig & Knops 2000), is important for two reasons. First, the variable supply of resources has downstream effects on the whole community (Ostfeld & Keesing 2000). Second, masting should be selected against because of inescapable costs (e.g. higher density-dependent mortality, lost opportunities for reproduction and lower population reproductive rates: Rees *et al.* 2002) unless there are counterbalancing benefits such as economies of scale (Norton & Kelly 1988; Kelly 1994). To demonstrate that masting in a particular plant population is the result of selection for variable seed production, rather than simply a response to climate, requires one of several types of information (Kelly & Sork 2002), the most important of which is data indicating the presence of switching (diversion of resources towards reproduction in some years, and away from reproduction in other years: Norton & Kelly 1988). In this paper, we test for the presence of switching in *Nothofagus truncata* (Col.) Cockayne (Fagaceae) (hard beech), a strongly masting forest tree from New Zealand.

The term 'mast seeding' or 'masting' is used in three different, but related, ways in the ecological literature. Most informally, the term is used as shorthand for the study of interannual variation in seed crops in perennial plants. Different species of plant range on a continuum from extremely variable seed production among years, to highly constant (Kelly 1994; Herrera *et al.* 1998; Koenig & Knops 2000; Kelly & Sork 2002). Both extremes (variable and constant) are of interest (Kelly 1994), but only the variable end will include species that can properly be called masting. Herrera (1998) therefore argued against using the term 'masting' in this informal sense. (Herrera actually argued against using it in any sense, but the core of his argument was against this general usage).

Masting is also used to refer to perennial plants that vary 'greatly' among years in their seed crops, hence the definition cited above of 'intermittent production of large seed crops by a population of perennial plants'. This usage does avoid the drawback mentioned by Herrera (1998) of including all possible seeding schedules, but still faces two problems. The first is that 'greatly' is undefined, and because there is continuous variation among plants in levels of variation in reproductive output, the choice of any cut-off would be somewhat arbitrary (Kelly 1994). The second problem is that masting defined in this way does not necessarily imply anything of evolutionary signifi-

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cance. Plants could simply be matching their reproductive output each year to the variable resources available to them (resource matching), which in a highly variable environment could result in highly variable seeding with no underlying selective pressures for exaggerated variation. This is what Kelly (1994) called 'putative' masting, where it is assumed because seed crops vary greatly that selection is operating to increase variation in seed crops, but there is no actual evidence to disprove the null hypothesis of resource matching.

The third and most precise meaning of masting is applied to cases where some evolutionary force is operating to exaggerate variation in seed crops. This is what Kelly (1994) called 'normal' and 'strict' masting (or 'true' masting: Koenig & Knops 2000). There are different kinds of evidence that can falsify the resource-matching hypothesis and prove the presence of selective factors (reviewed by Kelly & Sork 2002). The most decisive is showing the presence of switching, that is, a negative relationship within a plant among years between resources devoted to reproduction, *versus* resources devoted to growth. If resource matching was occurring, plants should do more of everything (growth and reproduction) in good years, and less of everything in poor years, leading to a positive correlation between growth and reproduction. When the opposite is found, resource matching is falsified, masting *sensu stricto* is present, and the question becomes why the plant has traits that divert resources into reproduction in some years, and away from reproduction in other years. This shifts the conceptual focus from statistically describing supra-annual variability in seed production into discriminating between ultimate and proximate explanations for seedfall variation.

Switching may also result in negative autocorrelations in reproduction time series and bimodality (high and low years) in reproduction (Kelly 1994; Kelly & Sork 2002). However, these latter two tests, while useful, may not be universally reliable; spurious autocorrelations that are apparently unrelated to the reproductive cycle can occur (e.g. *Pinus*; Koenig & Knops 2000) and variability in seed production is often not bimodally distributed (Kelly 1994; Koenig & Knops 2000).

We know of only one well-documented case of resource matching. Growth and reproduction are positively correlated within plants among years in the strongly serotinous *Pinus banksiana* (Despland & Houle 1997). There may be more, as yet undocumented, examples from extreme environments such as deserts where reproduction and growth are only possible in good years (e.g. following rain; Kelly & Sork 2002). However, in contrast, there are a number of proven cases of switching in trees, where high reproduction is associated with low growth (measured as

radial wood increment). Such negative correlations have been shown in the Northern Hemisphere genera *Abies*, *Acer*, *Betula*, *Fagus*, *Picea*, *Pinus* and *Pseudotsuga* (Kelly & Sork 2002). However, the number of species with published demonstrations of switching (10) is far smaller than the number of species with published highly variable seedfall datasets (of 175 species in Kelly & Sork 2002; 66 species have coefficients of variation of 1.5 or greater). There are very few published examples of resource switching in Southern Hemisphere species. Norton and Kelly (1988) report a negative trend in *Dacrydium cupressinum* (rimu) using population means, rather than data for individual trees. Alley *et al.* (1998) showed that annual litter production in *N. truncata* was significantly lower in a high-seedfall year relative to low-seedfall years, but this could be equally explained by longer leaf retention rather than lower leaf production.

In this study we test for resource matching in *N. truncata*. This species is a particularly suitable case to study, for four reasons. First, annual variation in seedfall in *Nothofagus* has received considerable attention (e.g. Poole 1955; Wardle 1984; Allen & Platt 1990; Burrows & Allen 1991; Hickey & Wilkinson 1999; Schaubert *et al.* 2002), because the level of variation among years is especially high (Kelly 1994; Kelly & Sork 2002), with Tasmanian and New Zealand species of *Nothofagus* filling four of the global top 20 places in one compilation of 210 seedfall datasets (Kelly *et al.* 2000). Second, *Nothofagus* is a classic Gondwanan genus and is quantitatively important in many southern forested landscapes. Third, variation in beech seedfall is a significant driver of rodent population cycles (King 1983; O'Donnell & Phillipson 1996; Choquenot & Ruscoe 2000) and affects predation of, and breeding by, some New Zealand endemic bird species (Elliott *et al.* 1996; Wilson *et al.* 1998). Fourth, in two *Nothofagus* species (*N. solandri* and *N. menziesii*) masting has been shown to provide strong economies of scale from more successful wind pollination (Kelly *et al.* 2001).

However, despite all of the above, there has been no test of the resource-matching hypothesis in *Nothofagus*. It is thought that flowering in *Nothofagus* is triggered by warm dry summers during the previous year (Wardle 1984; Allen & Platt 1990; Schaubert *et al.* 2002) with *Nothofagus* populations showing considerable within- and between-species synchrony over spatial scales in excess of several hundred kilometres (Schaubert *et al.* 2002). Notwithstanding the initial results of Alley *et al.* (1998) on variation in litter production, resource matching remains a strong null hypothesis given the climatic cues postulated to synchronize seed production in beech. In this paper we evaluate the resource-matching hypothesis for variation in seed production in *N. truncata* using an outstanding long-term 33-year fruiting record, compared

with radial wood growth increments as a measure of vegetative growth.

METHODS

Study area

The study site was located in the Orongorongo Valley Research Area on the eastern flanks of the Rimutuka Range, Wellington, New Zealand (41°21'S; 174°58'E). The valley carries old-growth forest with some minor impacts by introduced browsing ungulates (Brockie 1992). Within this valley, *N. truncata* is locally dominant on gently sloping, well-drained remnants of older alluvial fans and ridges below 300 m a.s.l. (Campbell 1984) and it was within these sites at approximately 100–140 m that the data were collected. Scattered regeneration of *N. truncata* was present throughout the sites (Brockie 1992), although all *Nothofagus* species regenerate predominantly after large-scale canopy opening (Wardle 1984), so abundant saplings would not be expected under the intact canopies where the seed traps were situated.

The climate on the valley floor is relatively mild. The mean annual temperature is 13°C (Brockie 1992) and there are few heavy frosts (Campbell 1984). Between 1966 and 2000 the average annual rainfall in the study area was 2340 mm. In that period the driest months (January and February) averaged 123 mm rainfall per month. This was less than half the mean monthly rainfall (276 mm per month) during the wettest months (June and July).

Seed collection

The first *N. truncata* seeds begin to fall in January, and numbers peak in March. Seedfall is essentially complete by the end of June (Alley *et al.* 1998). Seed collection in the *N. truncata* stands was initiated by M. J. Daniel and the first two seed-traps were in place by 1968 (Alley *et al.* 2001). By 1971 there were three traps, 15 traps from 1974, 18 from 1978, 20 from 1979 and 21 from 1980. Traps were placed in *N. truncata* forest but not sited specifically under isolated individual trees. The seed collecting traps were circular, sampling an area of 0.28 m², and were mounted 1.2 m above the ground. The traps were cleared monthly and the seeds from each trap counted. This is one of the most extensive masting datasets, both for number of years and for number of individual seed traps (Schauber *et al.* 2002; Koenig *et al.* 2003). Although the total trap area (~6 m²) was relatively small, the high seed densities (up to 6000 m⁻²) meant that large numbers of seeds were caught. There was a

high level of synchrony among individual seed traps across years, with a mean pairwise correlation coefficient of 0.87 (Koenig *et al.* 2003).

Most of the traps were at least 18–20 m from any other trap. Seedfall declines rapidly with distance in *Nothofagus*, as seeds fall under gravity with no structural modifications to extend their travel (Wardle 1984). *Nothofagus truncata* nuts are the heaviest of the New Zealand *Nothofagus* (7.7 mg; Ledgard & Cath 1983). Eighty-five percent of *N. menziesii* seeds (less than half the weight of *N. truncata* seeds) have been recorded as falling less than 20 m from the forest edge (Wardle 1984). Furthermore, by catching seeds at 1.2 m height these traps prevent secondary dispersal after seeds hit the ground, reducing dispersal distances. Hence, each of these traps was treated as being independent. Two groups of two traps, however, were located 13 m or less from one another. An analysis of the data with one trap from each of these two trap pairs randomly excluded from the dataset did not alter our conclusions, therefore we chose to include data from these traps in the analysis we present in this paper.

Tree core samples

At each seed trap, the nearest mature *N. truncata* individual to the trap was selected for coring. Two cores were taken from each tree using a 5-mm increment borer. Ring widths were measured to the nearest 0.001 mm using a Velmex tree ring measuring system (Velmex Inc. Bloomfield, NY, USA). The cores were cross-dated (Fritts 1976) with the aid of the computer program COFECHA (Holmes 1999). COFECHA indicates regions and rings that are poorly correlated with a master series that has been obtained by averaging the ring widths over all of the other tree ring series. These regions were then re-examined under the microscope to ensure that all rings (including narrow rings) were identified and measured correctly and that the proposed dating of each ring series was correct. Hence, any correlation among trees in ring widths represents synchronized growth, rather than an artefact created by the cross-dating process. Once cross-dated, mean annual ring widths were calculated for each tree. Where only one core from each tree was suitable for measurement, the values from this core were used. For one tree, neither core could be reliably cross-dated and so these data were excluded from the analysis, and one tree was omitted because the seedfall record was missing in 1 year, giving a total of 19 useable trees. All ring chronologies were completed 'blind' without reference to the seedfall data (which was collected previously by other workers), before comparing the two datasets.

Herrera (1998) has pointed out that one potential problem with using seedfall traps placed within stands of trees is that they may contain information (i.e. seeds) from more than one individual. The seedfall recorded in the trap is a weighted mean of the seedfall from each tree near the trap, where the weighting function is dependent on the distance from the trap. To estimate the expected growth response of this population in relation to the observed seedfall we would then have to obtain a weighted mean of the growth responses of each of the trees contributing seed. We cored only the tree closest to each trap, therefore our measurements are biased estimators of the annual mean growth response corresponding to each trap. We believe, however, that this bias was small, for two reasons. First, the tree closest to the trap will have provided most of the seedfall in the trap. The distribution of seedfall with distance from source is strongly leptokurtic with most seeds falling relatively close to the tree, both generally (Howe & Westley 1986), and especially in *Nothofagus* (see *Seed collection*). Second, annual ring growth in any one individual tree from the sample used to fit the model was a reasonable predictor of the average growth response of the remaining trees (mean correlation \pm SE; $r = 0.63 \pm 0.04$). So information on growth from the nearest tree to each trap will also be representative of the nearby trees contributing lesser quantities of seedfall to the trap. Hence, we expected any relationship between seedfall and radial growth from these trees to be a reasonable reflection of resource allocation within individual trees.

Analysis

Ring width standardization

Examination of the rings revealed tree-specific cycles of growth suppression and release, manifest as differences in the long term trends of the annual ring increments. As we wished to examine short-term (i.e. high frequency) changes in ring increment, we removed these low frequency trends by standardizing each ring series. Standardized ring indices were obtained by dividing each ring series by the fitted values of polynomial curves modelling each tree ring series (Fritts 1976; Woollons & Norton 1990). The polynomial order was restricted to less than six to preserve as much high-frequency variation in each tree ring series as possible, fitting the polynomial to up to 51 years of ring width data, depending on the tree. The polynomial of best fit was chosen using the minimum Akaike Information Criterion (Sakamoto *et al.* 1986; hereafter referred to as AIC) to find the simplest models that best described the trends in the data. Where the dif-

ference in AIC between the best model and another model with fewer parameters was less than 1, the simpler model was accepted if a likelihood ratio test (Pinheiro & Bates 2000) indicated no significant difference (at $\alpha = 0.05$) in the fit of the two models. The resulting indices were log transformed prior to further analysis.

Climatic variables

Twelve climatic variables were chosen *a priori* as being likely predictors of radial growth in *N. truncata*. These variables included monthly rainfall data from November through to February (four variables), total degree-days over the growing season (one variable), monthly absolute minimum temperatures from March through May for the year prior to, and of, seedfall (lags 1 and 0, respectively; six variables), and bimonthly absolute minimum temperature for June through July lag 1 (one variable).

Monthly rainfall data for November through February were obtained from the Orongorongo Valley weather station immediately beside the study site. We assessed water availability during this period as likely to be important for radial growth because peak bud burst in *N. truncata* occurs during November and December during low-seedfall years (Alley *et al.* 1998) and water demands by the canopy are likely to be high during this period due to leaf expansion and shoot elongation. Summer soil moisture is positively correlated with mean annual sapwood cross sectional area in hard beech (Hosking & Hutcheson 1986) and Brockie (1992) noted the death of 40-year-old *N. truncata* during a summer drought in the Orongorongo Valley in early 1987.

All temperature data were obtained from the weather station at Kelburn, Wellington (National Institute of Water and Atmospheric Research, New Zealand), as these data were not available from the Orongorongo weather station for the period covered by the study. The Kelburn weather station is located only 18 km from the study area, is at a similar altitude, and temperature data obtained from this site are strongly correlated with measured values in the Orongorongo Valley (A. Tokeley, Victoria University of Wellington, Wellington, New Zealand, unpubl. report 1992). Temperature is a key determinant of radial growth in trees (Fritts 1976). Two measures of temperature were used in this study: total degree-days over the growing season (assumed to be November to April of each year) and monthly absolute minimum temperature. Degree-days (Thornley & Johnson 1990) were used to integrate temperature effects over the main growing season assuming a threshold temperature of 8°C. The mean daily temperatures used in the degree-day calculations were obtained by averag-

ing the daily minimum and daily maximum free air temperatures over the period as measured at Kelburn. The absolute minimum temperature during autumn is often correlated with ring width (Fritts 1976). In addition, chilling prior to the year of growth may also be a necessary precursor to initiate plant developmental processes (Leathwick 1995). On this basis we chose to include monthly absolute minimum temperature at Kelburn for March–May in the year prior to growth (lag 1), in the year of growth (lag 0) and the bimonthly absolute minimum temperature for the early winter months June–July (lag 1) as the other temperature variables.

Model-fitting procedure

Initial attempts at model fitting used linear mixed effects models (Pinheiro & Bates 2000) with the ring data grouped by tree. However, there was no evidence that modelling climate as random effects associated with individual trees was justified and because the ring series were standardized to a common mean, a random intercept term was unnecessary. We therefore chose to model these data using the generalized least squares framework. Generalized least squares models may be considered as simplified, linear mixed effects models in which there is no random effects component (Pinheiro & Bates 2000). This framework allows the user to model the serial dependence between observations that is common with time series data such as tree rings (e.g. Fritts 1976; Woollons & Norton 1990).

We used a forward/backward model-fitting procedure to produce a highly parameterized initial model that incorporated non-linear transformations of the terms where appropriate. The minimum AIC was used as the criterion by which single terms were added or deleted at each step.

Dependence between observations within each tree ring time series was modelled using autoregressive (AR) processes up to lag 6. The minimum AIC value was again used to select the best model but subject to the additional constraint that the model was also significantly different (using likelihood ratio tests) from the model with the next lowest AIC that had fewer parameters. Having arrived at a suitable autocorrelation structure for the model, single term deletions (utilizing likelihood ratio tests on the reduced and parent models) of the fixed effects terms were then used to arrive at the final model. Hypothesis testing for each of the variables in the final model used Wald F -tests (Pinheiro & Bates 2000).

The final model was cross-validated using a form of K -fold cross validation (Davison & Hinkley 1997). The data were divided into K (19) groups corresponding to the trees that the ring measurements were made on. For each j th group, the model was

fitted to all groups $k \neq j$ and the resulting parameter values used to predict the responses for the j th group. The mean squared error of prediction was then computed and averaged over the K parts. This allowed us to assess the effect of the sample of trees on the model fit.

RESULTS

Total annual seedfall per square metre was highly variable (Fig. 1). The coefficient of variation over the 33 years was 2.10 (see also Schaubert *et al.* 2002). High-seedfall years were observed in 1971, 1979, 1986, 1990, 1995 and 1999, and those 6 years (19% of the years) produced 94% of all seeds collected throughout the study. Sharp declines in the mean annual ring index were observed during each of the four highest seedfall years (arrowed in Fig. 1).

Details of the fitted model are shown in Table 1. The overall model explained 40.7% of the observed variance in the ring indices for the 19 trees (Fig. 2). The cross-validated mean squared error of prediction (0.0337) was only 2.8% larger than the observed error (0.0329) demonstrating that the tree-specific effect on the model fit was small. We can be confident therefore that the analysis was robust to the inclusion or omission of particular trees. The model showed that annual ring increment can be predicted by a combination of the absolute minimum temperature ('Amin') during April (lags 1 and 0), March (lag 0) and May (lag 0), annual seedfall, and rainfall during November and February. The model included an AR5 correlation structure to the residuals to account for the large autocorrelation at lag 5 (Table 1). Annual seedfall, next to absolute minimum tempera-

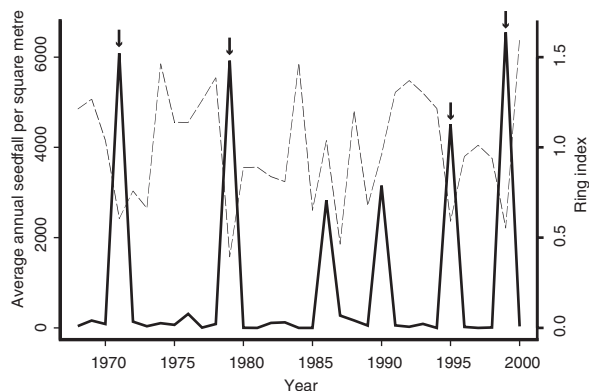


Fig. 1. Mean annual seedfall (seeds per square metre, solid line) and mean annual ring growth index (dashed line) for *Nothofagus truncata* trees, Orongorongo Valley, Wellington, New Zealand. Arrows indicate high-seedfall years in which the mean annual ring growth was depressed relative to the previous year.

Table 1. Generalized least squares fit of predictors of the log-transformed ring indices obtained from *Nothofagus truncata*

Source	Coefficient value	d.f.	F-value	Pr > F	Effect size
Intercept	0.207	1	4.02	0.0456	
Amin(April, lag 1)	-1.78				
Amin(April, lag 1) ²	-0.566				
Amin(April, lag 1) + Amin(April, lag 1) ²		2	41.95	<0.0001	0.094
Seedfall	-0.0000353	1	84.17	<0.0001	0.092
log(November rainfall)	0.0776	1	27.931	<0.0001	0.029
log(February rainfall)	0.0469	1	9.65	0.0020	0.013
Amin(April, lag 0)	-0.0356	1	26.08	<0.0001	0.038
Amin(Mar, lag 0)	0.0217	1	11.90	0.0006	0.023
Amin(May, lag 0)	-0.0155	1	5.26	0.0222	0.008
Error		491			
Autocorrelation					
Lag	Autocorrelation	Pr > T			
1	0.161	<0.01			
2	0.101	NS			
3	-0.136	NS			
4	-0.036	NS			
5	-0.255	<0.001			

Hypothesis tests use the marginal sums of squares obtained by deleting one term from the model at a time. The coefficients of absolute minimum temperature during April at lag 1 (Amin (April, lag 1)) and the second order polynomial term (Amin (April, lag 1)²) are jointly tested to be zero. The overall variance explained by the model is 40.7%. Effect size is the additional variation explained by the term given the other variables are already in the model. The autocorrelations for the model in the absence of modelling the correlation structure of the residuals are also shown with the *P*-values Bonferroni adjusted.

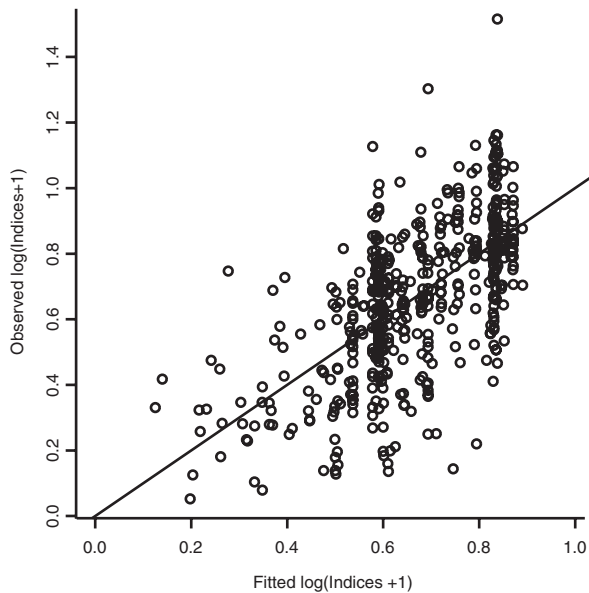


Fig. 2. Values from the fitted model in *Nothofagus truncata* plotted against the log transformed ring index observations used to construct the model. The solid line has slope 1 and corresponds to an exact match between the predicted values and the observations.

ture in April in the previous year, had by far the largest effect on ring increment with an effect size of 9.2%.

The highly significant negative relationship between seedfall and radial growth (Fig. 3; $F_{1,491} = 84.17$, $P < 0.0001$) demonstrated that available resources are switched away from radial growth in high-seedfall years, even after allowing for weather. While there was still considerable unexplained variance in the data after fitting the model, this is not unexpected. Climatic signals from single trees are notoriously variable due to the slightly different histories and environmental conditions experienced by individuals within a site (Fritts 1976), and the model is unable to account for tree-specific events such as branch loss in storms.

DISCUSSION

Resource matching in *N. truncata*

We found a highly significant negative correlation between seedfall and radial growth increment in *N. truncata*. Large seed crops were associated with narrower growth rings in the year of seedfall. The width of radial growth rings reflects the allocation of resources to vegetative growth throughout the plant.

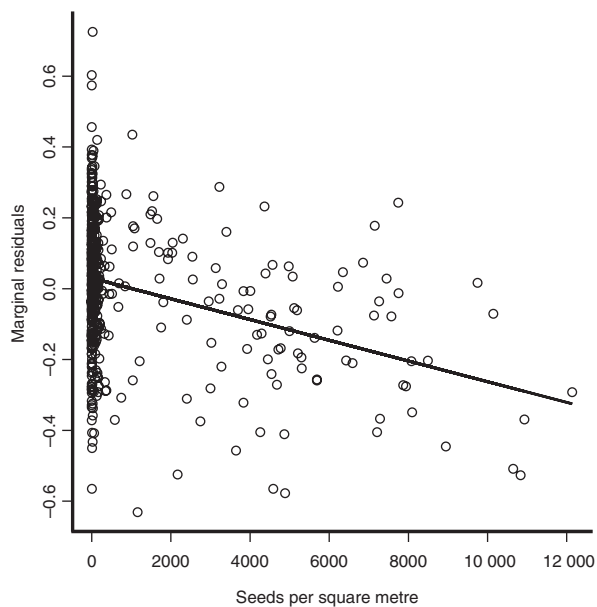


Fig. 3. The relationship between seedfall (seeds per square metre) in *Nothofagus truncata* and the residuals of annual ring widths from the marginal model allowing for the weather variables (see Table 1), based on 19 trees over 33 years. The line of best fit shown is highly significant ($F_{1,491} = 84.17$, $P < 0.0001$).

Conversely, any allocation of resources away from resource-capturing structures will decrease radial growth. The finding of Alley *et al.* (1998), that leaf-fall was greatly reduced during a high-seedfall year compared with low-seedfall years in *N. truncata*, parallels the negative seedfall relationship with the ring increments that we found. This is consistent with the interpretation that radial growth is a general index of vegetative growth. Consequently, our tree ring data give us confidence that we can reject resource matching as a sufficient explanation for mast seeding in *N. truncata*.

Weather and resources will always be involved in mast seeding, in several ways (Kelly & Sork 2002). First, plants can only allocate to reproduction resources that they have already accumulated, so overall net assimilation rates (affected by climate) will have an effect on the frequency and intensity of reproductive episodes. Second, masting as a selective response to factors like wind pollination or predator satiation always requires a synchronizing cue, which is nearly always a climatic variable such as temperature or drought (Norton & Kelly 1988; Kelly & Sork 2002). Third, unfavourable weather can prevent reproduction, such as frost damaging flowers or wet weather preventing wind pollination (see examples in Kelly & Sork 2002). All these factors mean that resource dynamics driven by weather can be crucial to the dynamic behaviour of masting, and to which specific

years turn out to be high-seed years (Rees *et al.* 2002). None of this alters the overall conclusion, however, that masting in *N. truncata* is not simply a non-adaptive matching of reproductive effort to the varying weather environment. Some selective factor must be invoked.

Selective benefits of masting in *Nothofagus*

Having shown that *N. truncata* is not merely displaying resource matching, we can consider what selective benefits could favour such highly variable reproduction in a forest tree species, where the strategy carries costs of lost opportunities for reproduction, lower population growth rates, and more intense density-dependent seedling competition (Kelly 1994). Enhanced pollination success is probably the strongest contender to explain the evolution of mast seeding in beech. *Nothofagus* flowers are wind pollinated and seed viability is considerably lower in low-seedfall years relative to high-seedfall years (Wardle 1984; Allen & Platt 1990; Burrows & Allen 1991; Alley *et al.* 1998). Recent work on *Nothofagus solandri* and *N. menziesii* has shown quantitatively that both species gain very large pollination benefits from masting, by increasing the percentage of seeds which are viable from <10% in low-seed years to >60% in mast years (Kelly *et al.* 2001). Although successful establishment in *Nothofagus* is also dependent on disturbance (Wardle 1984), the large increase in seed viability provides a strong selective benefit to masting individuals. *Nothofagus truncata* also has low seed viability in low-seedfall years (Alley *et al.* 1998; Fitzgerald *et al.* 2004), so it seems highly likely that wind pollination also provides a selective benefit to individuals of this species that mast in synchrony with the rest of the population.

Another possible, albeit less well documented, factor contributing to mast seeding in beech is predator satiation. *Nothofagus* trees are probably highly apparent to their predators due to their dominance within the forest communities in which they occur. Beech nuts are eaten by a range of native and introduced birds, and during high-seed years, appear to be a significant part of the diet (Elliott *et al.* 1996; Wilson *et al.* 1998). Unfortunately, avian seed predation may prove difficult to test in the current New Zealand environment, as the avifauna has been severely depleted in the years following human settlement. Of course, there may be several independent factors that contribute to favouring mast seeding in any particular species, with some being stronger than others (Kelly 1994; Kelly & Sullivan 1997; Kelly *et al.* 2001), so evidence in support of predator-satiation benefits is not necessarily evidence against wind-pollination benefits.

Overall importance of testing the resource-matching hypothesis

In some ways the conclusion of this paper (that intermittent heavy seeding in *N. truncata* comes at a cost in reduced radial wood growth during the same year) may seem unsurprising. The idea of trade-offs is a familiar paradigm in ecology. However, we argue firstly, that this finding is non-trivial and, secondly, that more such data on other species would be very valuable.

The reason this finding is non-trivial is that the existence of switching is the key to demonstrating that a masting plant species is not simply responding to the variable environment, but is under selection to exaggerate reproductive variation. In other words, evidence of switching is needed to prove the presence of masting *sensu stricto*, rather than ‘putative’ masting. Moreover, the relationship between plant growth and reproduction within a year is not necessarily negative. The question is not one of the ultimate trade-off between growth and reproduction in the long term, but simply one of how plants arrange the relative allocation of resources to growth and reproduction across years. The example of *P. banksiana* (Despland & Houle 1997) shows that it is possible for plants to allocate excess resources equally to growth and reproduction in favourable years. And finally the result is important because *N. truncata* is one of the best-documented cases of switching, in terms of number of years of data, number of individuals, and degree of correction for weather factors.

We call for more such data on other mast seeding species because there are surprisingly few well-documented cases where reproduction and growth in the same year are compared statistically in the same individuals. The review by Kelly and Sork (2002) listed evidence for switching in only 10 species, from the 60 or more trees known to mast seed, let alone the

hundreds of other species that probably mast but do not have published seedfall datasets. There are four main types of evidence from the literature (Table 2). The first type is what could be considered the iconic graph proving switching: tree wood growth plotted against size of the same year’s seed crop over many years (e.g. Fig. 3), but we only know of two previously published examples (Table 2), and neither presented formal statistical tests of the relationship. Both studies compared annual means of growth and reproduction, rather than individual values. In fact for *Pseudotsuga menziesii* it is not even clear whether growth and reproduction were measured on the same trees.

A second group of shorter-term studies show convincingly that shoot extension, height growth, leaf size, and/or wood radial increment are reduced in high-seed years or high-seeding plants (Table 2). Of interest is that wood radial increment seems to be less sensitive to size of the seed crop than are shoot growth and leaf length in the same species (Morris 1951; Gross 1972; Tappeiner 1969). This raises the interesting question of whether reductions in length of the current season’s leaves have much effect on the overall growth rate of a tree carrying many age-classes of leaves. In some species, it has been shown that leaf size is reduced only on branches bearing fruit (Miyazaki *et al.* 2002).

The third and fourth types of study claim that ring widths are depressed in high-seed years, but provide no statistical proof. Again, some of these studies use annual means, and may be comparing growth and seed-crop series from different trees. Koenig and Knops (1998) looked for trade-offs between seeding and growth across 298 datasets, but used population means from wide geographical areas, sometimes with seedfall and growth data from different populations, rather than data from the same individuals.

The overall conclusion is that reproduction is often assumed to impact negatively on current growth, but rigorous demonstrations of a negative effect *within*

Table 2. Published evidence for switching of resources between growth and reproduction within individual plants

Type of evidence	Examples	Problems
Graph of tree-ring widths <i>vs.</i> size of seed crop	<i>Dacrydium cupressinum</i> (Norton & Kelly 1988); <i>Pseudotsuga menziesii</i> (Eis <i>et al.</i> 1965)	No statistics; use annual means of growth <i>vs.</i> annual means of seedfall
Show current shoot growth, leaf length, etc. reduced in high-seed years	<i>Abies balsamea</i> (Morris 1951; Silvertown & Dodd 1999); <i>Betula papyrifera</i> and <i>Betula alleghaniensis</i> (Gross 1972); <i>Pseudotsuga menziesii</i> (Tappeiner 1969)	Often short-term (2–6 years) and few trees (14–20); sometimes confounded with site differences
Juxtapose time series of annual ring width and annual seed crops	<i>A. balsamea</i> (Morris 1951); <i>Abies grandis</i> (Eis <i>et al.</i> 1965); <i>Fagus sylvatica</i> (Harper 1977)	Data not analysed; use annual means
State that ring widths are depressed in high-seed years	<i>Pinus monticola</i> (Eis <i>et al.</i> 1965)	Data not presented

individuals, as presented here, are exceedingly scarce. This is probably a widespread phenomenon, but very few studies have tested for it in a way which can unambiguously disprove resource matching. This may be because the negative effect of reproduction on growth is thought to have already been well documented.

We predict that few plant species will show resource matching (Kelly & Sork 2002), and that it will be concentrated in two situations. The first is in strongly serotinous species (i.e. species where seeds are held in woody infructescences which only release the seeds after fire) that do not have significant levels of seed predation from the unopened infructescences. In such species, like *P. banksiana*, seeds are accumulated across years in the infructescences and the exact year of production of seeds is immaterial, so the species are free to use resources in reproduction as soon as they become available. The second situation is in highly variable, unfavourable environments (e.g. semi-deserts) where reproduction and growth are both only possible in good years (e.g. after rain). Apart from plants in these two specialized ecological situations, we predict that most plants will be under some selective pressure concerning exactly when they reproduce, and therefore that resource matching will be rare. These predictions cannot, however, be fully evaluated until the tests presented in this paper are applied to more plant species.

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