

## CLIMATE AND NET CARBON AVAILABILITY DETERMINE TEMPORAL PATTERNS OF SEED PRODUCTION BY *NOTHOFAGUS*

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**Abstract.** We analyzed seed production of mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest along an elevational gradient in New Zealand from 1020 to 1370 m (treeline) for the years 1973–2002. We used seed production data from nine elevations and a site- and species-specific net carbon (C) availability model from two elevations (1050 m and 1340 m) to examine how three variables (temperature, soil moisture, and net C availability) during three key periods (resource priming, flowering primordia development, and flowering) influence seed production. These three strongly interrelated variables have all been considered determinants of seed production but have not previously been tested together in a single analysis. Seed production increased over the 30-year period, with the greatest increases at high elevations; this increase was driven by a greater frequency of intermediate-sized seeding years. We then determined how temperature, soil moisture, and net C availability determined seeding, and examined whether temporal trends in the seeding data could be linked to similar temporal trends in temperature, soil moisture, or net C availability. High seed production was related to cool summers with high soil moisture during resource priming, warm summers during flower primordia development, and low net C availability during flowering. Positive temporal trends in temperatures during the period of flower primordia development accounted for the increase in seed production, suggesting that increasing temperatures are promoting more frequent seed production at high elevations.

**Key words:** carbon dioxide; evergreen; global change; masting; montane; mountain beech; New Zealand; reproduction; respiration; soil moisture; temperature; warming.

### INTRODUCTION

Irregular seed production among years is a widespread characteristic of many long-lived plant species populations (Harper 1977, Kelly and Sork 2002). Many studies have identified that previous summer temperature is strongly correlated with mean seed production within a population (e.g., Koenig and Knops 1998, Schaubert et al. 2002). Warm temperatures may be related to seed production because they act as a synchronizing cue (e.g., Schaubert et al. 2002), but it is also possible that temperature is a proxy for other interrelated factors that ultimately determine seed production, such as soil moisture (Abrahamson and Layne 2003) or the effect of warm temperatures on net C availability (Allen and Platt 1990). Furthermore, a recent meta-analysis of seed production by northern hemisphere beech (*Fagus sylvatica*) revealed that irregular seed production is driven not only by warm temperatures during the previous summer, but additionally by cool, moist summers two years previously (Piovesan and Adams 2001). This relationship between

cool, moist summers and high seed production could be related to favorable conditions for net C accumulation, which primes the tree to respond to warm summer temperatures one year later, during flowering primordia development (Piovesan and Adams 2001). A similar influence of resource priming has been modeled by Rees et al. (2002) for a long-lived grass species (*Chionochloa*). Given that resource availability (i.e., net C availability) is likely to be strongly related to variation in temperature and soil moisture, there is a need to evaluate how all three interrelated factors operate together during different periods leading to seed development to determine irregular seed production. We hypothesize that the strong relationships between seed production and warm summer temperatures are underpinned by the interrelated effects of warm temperatures on soil moisture and net C availability, and that heavy seed production two years following a cool, moist summer is related to high net C availability.

Decadal-level warming (e.g., Salinger 1995) could increase mean seed production in instances where seed production is related to a temperature cue (e.g., Schaubert et al. 2002). Alternatively, if mean seed production is positively correlated with summer net C availability, potential increases in net C availability, through rising atmospheric CO<sub>2</sub> partial pressures (C<sub>a</sub>), will affect de-

Manuscript received 25 May 2004; revised 7 September 2004; accepted 8 September 2004. Corresponding Editor: F. C. Meinzer.

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decadal-level variation in seed production (LaDeau and Clark 2001). However, the positive effect of rising  $C_a$  on net C availability will be strongly moderated if concurrent warming and reduced soil moisture increase respiration (Clark et al. 2003; but see Körner 1996). This raises the possibility that warming may decrease net C availability and thus reduce seed production. The effects of warming, and related net C availability, are also thought to be more pronounced at species' distributional limits where climatic and resource constraints operate more strongly (Graglia et al. 1997). We hypothesize that any decadal-level response of seed production to warming, changes in soil moisture, and rising  $C_a$  should be greater at high elevations, relative to low elevations, in a montane tree species.

We explore these hypotheses by testing for relationships between net C availability, temperature, soil moisture, and seed production using 30 years of data from an elevational gradient in mountain beech (*Nothofagus solandri* var. *cliffortioides* (Hook.f.) Poole: Fagaceae) forest (see Appendix). Few studies have investigated how long-term seed production varies within a species over its distributional range or for periods sufficiently long to detect decadal-level shifts in seed production (but see Holm 1994, Kullman 2002). To address our hypotheses, we determined whether (1) there were long-term increases in seed production and whether these increases varied with elevation; (2) decadal-level changes in summer temperature, soil moisture, and  $C_a$  have affected summer net C availability; and (3) seed production is related to either summer net C availability or summer soil moisture, in addition to summer temperatures. Having established if there were relationships between seed production and net C availability, soil moisture, or temperature, we then evaluate whether any decadal-level changes in summer temperature, soil moisture, and  $C_a$  have independently affected summer net C availability and seed production.

## METHODS

### *Study site*

Data were collected from the Craigieburn Range, South Island, New Zealand (43°13' S, 171°69' E). Two climate stations were available within 3 km of the study site: one at 914 m elevation in forest and one at 1550 m in alpine tussock grassland (McCracken 1980). Mean annual temperature was 8.4°C at 914 m (1973–2002) and 3.6°C at 1550 m (1972–1982). Daily temperatures (mean, minimum, and maximum air temperatures) at two elevations between the two climate stations were estimated by calculating and applying adiabatic lapse rates to the daily measurements. Mean annual precipitation was 1559 mm at 914 m (1973–2002). Daily precipitation was taken from the climate station at 914 m and was not scaled with elevation because the mean difference in annual precipitation between the two climate stations was only 100 mm. Mean annual solar

irradiance was 4458 MJ/m<sup>2</sup> at 914 m (1973–2002), and daily totals from this climate station were used for both elevations.

Mountain beech is a long-lived (250–350 years), monoecious tree species that dominates montane and subalpine forests in eastern parts of New Zealand through to treeline, ~1370–1390 m (Wardle 1984). In the Craigieburn Range, mountain beech forms monospecific stands between the valley bottoms at 800 m and treeline (1380 m). Stand structure changes with increasing elevation: biomass, net productivity, stand height, and mortality all decline with increasing elevation, whereas stem density and basal area both increase (Harcombe et al. 1998).

We refer to three periods either hypothesized to be of significance to mountain beech reproduction or known to be of significance: (resource) priming, which we hypothesize occurs during the summer growing season (December–March; Wardle 1984) two years before seed production; primordia development, which occurs over the period January–April the year before seed production (Allen and Platt 1990); and flowering, which occurs over the period December–February immediately before seed production (Allen and Platt 1990). Each ovule produces a seed that is shed between March and September (Wardle 1984).

### *Seed production*

Seeds were collected into circular traps (area 0.28 m<sup>2</sup>) elevated ~1.3 m above the ground (Wardle 1984, Allen and Platt 1990). Canisters beneath traps were emptied at intervals between March and September during seedfall. From 1965 to 1972, there were three lines of eight traps, aligned at 1050, 1190, and 1340 m up a uniform slope (~25°). Traps were ~40 m apart in lines perpendicular to the slope. In 1973, a further six lines of traps were added at 1020, 1095, 1145, 1240, 1295, and 1370 m elevation, each line of which contained only two traps. In this analysis we used data from the nine lines of traps between 1973 and 2002, and standardized the trap lines by including only two of the eight traps at 1050, 1190, and 1340 m (see Burrows and Allen 1991). These two traps were selected randomly from the lines of eight. To substantiate any long-term trends in seed production from the period 1973–2002, we also tested for trends using the series from 1965–2002 for three elevations.

### *Modeling net C availability*

Daily net C availability was estimated for the period 1973–2002 using net canopy C uptake from the model of Whitehead et al. (2002), and subtracting estimates of root, stem, and branch respiration. We estimated net C availability at two contrasting seed trap line elevations (1050 m and 1340 m near to treeline) where parameters were available or obtainable. Net canopy C uptake was calculated from estimates of photosynthesis and respiration (Farquhar et al. 1980) coupled with

TABLE 1. List of parameters used in the net C availability model to estimate daily net canopy C uptake for mountain beech forest at the elevations of two seed trap lines.

Parameter	Definition	Reference†	1050 m	1340 m	Units
$V_{\text{cmax}}$	maximum rate of carboxylation at top of canopy	1,2,3	75.1	74.0	$\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
$J_{\text{max}}$	maximum rate of electron transport at top of canopy	1,2,3	141.6	121.2	$\mu\text{mol (quanta)}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
$R_{\text{d}}$	light-independent rate of respiration	4	0.42	0.62	$\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
$\alpha$	quantum yield of electron transport	2	0.11	0.10	mol/mol (quanta)
$\tau$	convexity of the light response curve	1	0.66	0.66	
$a$	parameter related to intercellular $\text{CO}_2$ concentration	1	6.3	6.3	$\mu\text{mol/mol}$
$g_{\text{sc0}}$	residual stomatal conductance to $\text{CO}_2$ transfer	1	2.5	2.5	$\text{mmol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$
$D_{\text{s0}}$	sensitivity of stomatal conductance to $D$	1	817.6	817.6	Pa
$D_{\text{smin}}$	minimum value of $D$ for decreasing $g_{\text{sc}}$	1	250	250	Pa
LAI	canopy annual maximum leaf area index	3,5	7.2	6.0	$\text{m}^2/\text{m}^2$
$W_{\text{max}}$	soil water storage capacity	6	80	60	mm

Notes: Values for the photosynthetic parameters are estimated from measurements made at 20°C.  $D$  indicates air saturation deficit.

† References: 1, D. Whitehead and M. G. Ryan (*unpublished data*); 2, F. E. Carswell and S. J. Richardson (*unpublished data*); 3, Hollinger (1989); 4, Benecke and Nordmeyer (1982); 5, Hollinger et al. (1994); 6, T. W. Webb and I. H. Lynn (*unpublished data*).

stomatal conductance (Leuning 1995). The dependence of photosynthesis on temperature followed Bernacchi et al. (2001), with parameter values from Dungan et al. (2003). The model used our daily estimates of solar irradiance, minimum and maximum air temperatures, and precipitation. Parameters required to calculate net canopy C uptake (Whitehead et al. 2002) were derived from measurements made at or near the Craigieburn Range or from other published values for *Nothofagus* (Table 1).

Models were run using  $C_a$  that increased from 329.7 ppm ( $\mu\text{mol/mol}$ ) in 1973 to 371.9 ppm in 2002.  $C_a$  data were from Mauna Loa, Hawaii (Keeling and Whorf 2004). Data were not available for the full period from New Zealand, but for those years in common, the regression between Hawaii and New Zealand was Hawaii = 1.04 (New Zealand) - 9.96;  $r = 0.99$ ;  $P < 0.0001$ ; the mean annual difference between the two sites corresponded to <0.7%. To estimate the effect of increasing  $C_a$  on net canopy C uptake, an additional model was run at each elevation using stable  $C_a$  (329.7 ppm throughout). The net effect of rising  $C_a$  on net canopy C uptake was calculated as the difference between these two models (expressed as a percentage relative to stable  $C_a$ ). Furthermore, to assess whether long-term trends in climate (i.e., solar irradiance, minimum and maximum air temperatures, and precipitation) had moderated the effect of rising  $C_a$  on net C availability, models were run at each elevation that used either stable or rising  $C_a$ , with stable climate conditions. Stable climate conditions were the mean daily values of solar irradiance, minimum and maximum air temperatures, and precipitation for the first five years of climate data (1973–1977). The effect of rising  $C_a$  on net C canopy uptake under stable climate conditions was calculated

as the difference between these two models (expressed as a percentage relative to stable  $C_a$ ).

Soil moisture in the root zone (soil moisture, hereafter) was generated as an output from the canopy net C uptake model using measurements of root zone depth (Table 1) and soil texture (Anonymous 1968). Daily calculations included components of transpiration from the tree canopy and evaporation from the wet tree canopy and soil. Mean soil moisture (percentage of full saturation capacity) was calculated for the periods of resource priming, flowering primordia development, and flowering.

The wood respiration values subtracted from the estimates of net canopy C uptake to calculate net C availability for the stand of trees at each trap line were based upon the area of tissue and the respiration rate per unit area. The relative amounts of woody tissue area as roots, stems, and branches were calculated using stem diameter at breast height and allometric relationships (Benecke and Nordmeyer 1982, Hart et al. 2003; P. W. Clinton, *unpublished data*). Stem diameters of all individuals within an 8 m radius of each seed trap were measured in January 1995. Wood respiration was modeled using parameters in Benecke and Nordmeyer (1982) and Benecke (1985). Daily estimates of net C availability were totaled for the summer, i.e., the mountain beech growing season between December and March (Wardle 1984). Annual totals and the ratios of gross photosynthesis to woody respiration were also calculated so as to compare model performance with other estimates of mountain beech annual net C availability.

#### Statistical analyses

Seed production data were transformed using  $\log_{10} + 1$  for all analyses. A generalized least-squares (GLS)

model with an autoregressive correlation structure (Fox 2002, Crawley 2003) was used to test whether there was an effect of year (i.e., a linear temporal trend in seed production), elevation, and an interaction between year and elevation on the mean number of seeds from the two traps at each elevation. Slopes describing the relationship between the number of seeds and year were additionally calculated for each of the nine elevations in order to assess how the rate of change (i.e., the slope) varied with elevation. To additionally confirm the presence of any linear temporal trends in seed production, the longest time series (1965–2002) from three elevations was tested using the same GLS model: with only three elevations, this model has comparatively less statistical power to detect elevational effects.

The relationships between summer mean daily temperature, mean soil moisture, and total net C availability were estimated at the two elevations (1050 m and 1340 m; see *Modeling net C availability*). Although daily minimum and maximum temperatures were used to model net C availability, we related total net C availability to the mean daily temperature using quadratic regressions (Cunningham and Read 2002) in order to compare our analysis with other studies that have determined the relationship between temperature and net C availability. The relationships between mean summer soil moisture and net C availability and between mean daily temperature and mean summer soil moisture were not described using regression because there was no a priori mechanistic relationship. Long-term trends in summer total net C availability, mean summer soil moisture, and summer mean daily mean, maximum, and minimum temperatures were calculated using linear regression.

To establish whether net C availability and soil moisture affected seed production in addition to temperature, we also used data from just two elevations (1050 m and 1340 m; see *Modeling net C availability*). To model the relationship between seed production, temperature, soil moisture, and net C availability, we focused on three periods during which temperature, soil moisture and net C availability are known to strongly influence seed production: resource priming, flowering primordia development, and flowering. To test whether resource availability, i.e., net C availability, “primes” mountain beech to subsequently respond to temperature cues, we totaled daily net C availability over the summer in each year and tested whether this was related to seed production two years later. To determine whether the relationship between seed production and net C availability during the period of priming was independent of a temperature or soil moisture effect during priming, we additionally calculated priming mean soil moisture and priming mean daily maximum and minimum temperatures. These temperatures were both correlated with seed production, and the temperature with the highest correlation  $r$  was included as an effect in the model. For consistency with the net C canopy up-

take model, we calculated mean daily minimum and maximum temperatures in each year for primordia development and flowering and correlated these with seed production. The temperature with the highest correlation  $r$  for each of these two periods was included as an effect in the model. To determine whether the relationships between warm temperatures during primordia development and flowering were related to low net C availability, we totaled net C availability in each year for those two periods. Mean soil moisture for the periods of primordia development and flowering were also calculated. In total, this gave nine variables (net C availability, temperature, and soil moisture, each for three periods).

A GLS model with an autoregressive correlation structure was used to evaluate which of these nine variables, plus year (i.e., time), as fixed effects determined seed production. Elevation was included as a categorical variable and each of the fixed effects was tested individually and as an interaction with elevation. Effects were removed using a backward selection procedure until only significant ( $P < 0.10$ ) terms remained. ANOVA with marginal sums of squares was conducted to estimate  $F$  and  $P$ . To establish whether effects significant at  $P < 0.10$  should be retained in the model, an alternative model was run without those effects, and AIC statistics and maximum likelihood ratios were used to assess whether inclusion of those effects significantly improved the model fit (Crawley 2003). Year was included as a fixed effect to accommodate any linear change in seed production over time. If year  $\times$  elevation or year remained as fixed effects, it was assumed that any change in seed production over time was independent of the other fixed effects tested. However, if year was eliminated during the backward selection procedure, then it was assumed that the other fixed effects in the model had subsumed any linear change in seed production over time. If year became significant when another fixed effect was removed, it was assumed that the removed effect had subsumed variation previously accounted for by year. All analyses were completed using R Version 1.7.1. (Fox 2002).

## RESULTS

### *Seed production in relation to elevation and time*

Mean seed production increased at high elevations over the 30-year period (Figs. 1 and 2; model term for elevation by year:  $F_{1,266} = 6.08$ ,  $P = 0.014$ ). Regression coefficients were greater at high elevations, indicating that seed production had increased more rapidly at high elevations relative to low elevations (Fig. 2). Increased seed production at high elevations was largely driven by the declining frequency of very small seeding years ( $<100$  seeds·m<sup>-2</sup>·yr<sup>-1</sup>) and increasing frequency of intermediate seeding years ( $>1000$  seeds·m<sup>-2</sup>·yr<sup>-1</sup>; Fig. 1), during the second half of the time series. The maximum number of seeds produced did not change (Fig.

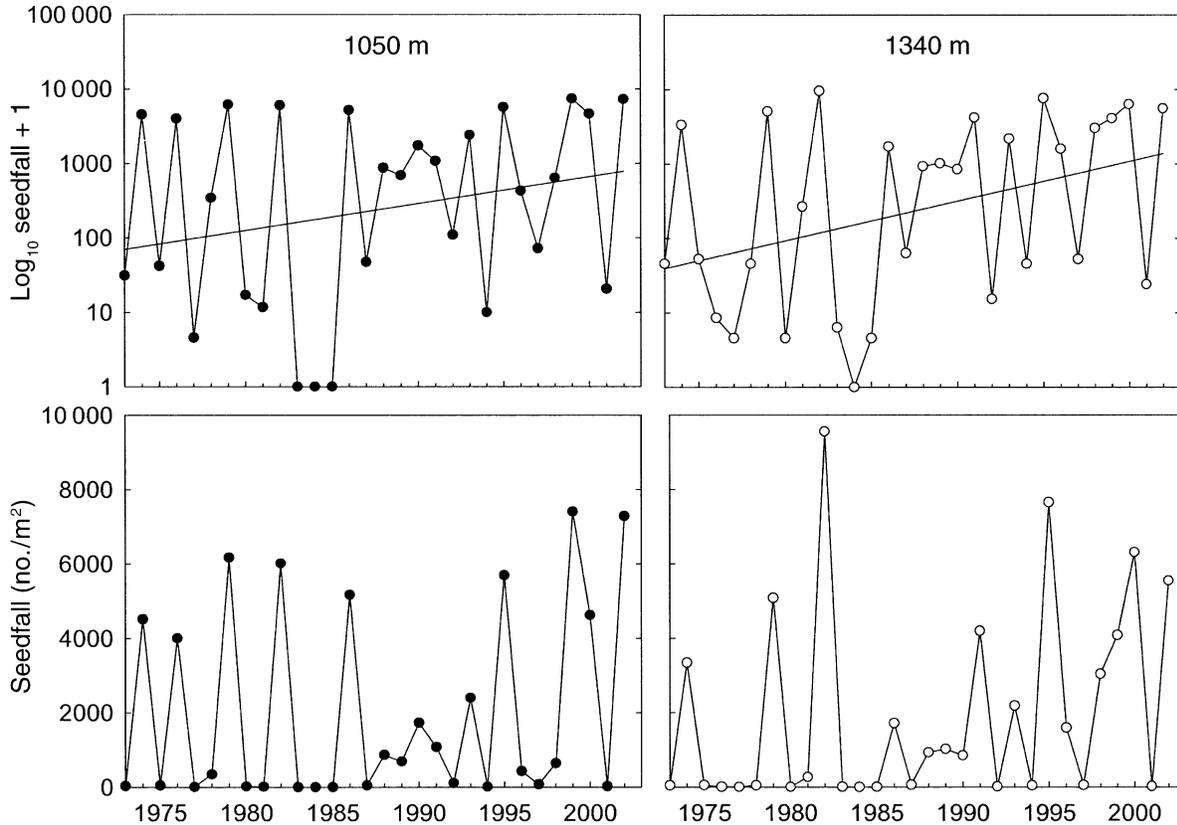


FIG. 1. Mean annual seed production by mountain beech at two elevations over a 30-yr period. Both raw and log-transformed data are presented, and linear regression relationships between time and log-transformed data are illustrated. Regression lines: for 1050 m,  $\log \text{ seedfall} + 1 = 1.81 + 0.04(\text{year})$ ,  $F_{1,28} = 1.81$ ,  $P = 0.19$ ; for 1340 m,  $\log \text{ seedfall} + 1 = 1.54 + 0.05(\text{year})$ ,  $F_{1,28} = 4.81$ ,  $P = 0.04$ .

1). Mean seed production also increased over the longer time period (1965–2002; model term for year:  $F_{1,112} = 5.83$ ,  $P = 0.017$ ), although there was no interaction term between year and elevation. However, slopes describing the relationship between year and mean annual

seed production increased with elevation (0.016, 0.019, 0.028 for 1050, 1190, and 1340 m, respectively).

*Net C availability in relation to elevation, time, temperature, soil moisture, and  $C_a$*

Mean annual net C availability was  $1.42 \pm 0.02$  and  $0.89 \pm 0.01 \text{ kg}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$  (mean  $\pm 1 \text{ SE}$ ) at elevations of 1050 m and 1340 m, respectively. The difference in net C availability between the two elevations was greatest during summer (up to  $3 \text{ g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ) and least during winter ( $<1 \text{ g}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$ ), when net C availability at 1340 m was frequently close to zero or even slightly negative. The mean ratio of gross canopy net C uptake to wood respiration (including roots) was  $3.31 \pm 0.34$  and  $1.90 \pm 0.19$  at elevations of 1050 m and 1340 m, respectively.

Summer net C availability varied among years and was greater in cool, moist summers than in warm, dry summers, at both elevations (Fig. 3). Maximum summer net C availability occurred at summer mean daily temperatures of  $10.4^\circ\text{C}$  at 1050 m and at  $8.5^\circ\text{C}$  at 1340 m (second-order polynomial curves; for 1050 m,  $y = -0.78 + 0.29(\text{temp}) - 0.01(\text{temp}^2)$ ,  $R^2 = 0.49$ ,  $P < 0.001$ ; for 1340 m,  $y = -0.44 + 0.22(\text{temp}) -$

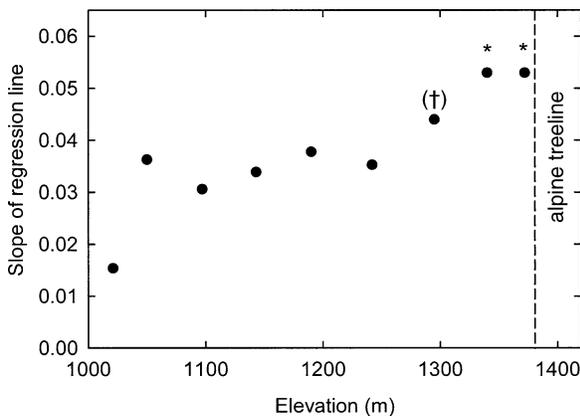


FIG. 2. Slopes describing the linear regression between year and annual seed production by mountain beech at nine elevations over a 30-yr period. Significance of individual slopes is indicated thus: (†),  $P < 0.10$ ; \*  $P < 0.05$ .

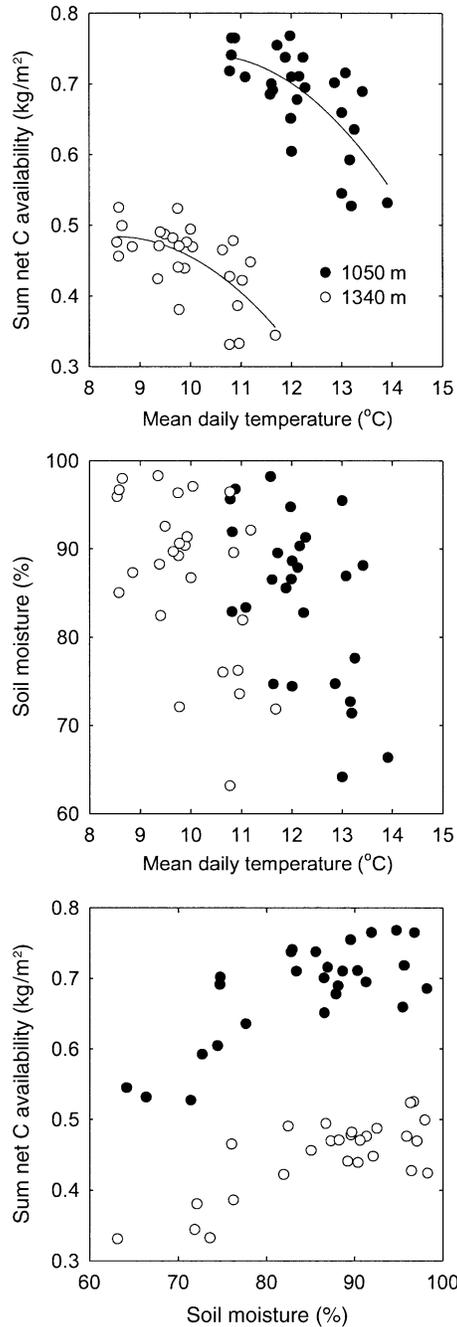


FIG. 3. Relationships between summer mean daily temperature, mean soil moisture, and sum net C availability for mountain beech forest at two elevations over a 30-yr period. Regressions between mean daily temperature and net C availability are shown using second-order polynomials (see *Statistical analyses*).

0.01(temp<sup>2</sup>),  $R^2 = 0.42$ ,  $P < 0.001$ ; see Fig. 3). Although net C availability among years declined with increasing summer temperatures, during other parts of the year, low net C availability was typically associated with low temperatures. Variation in summer net C

availability among years was also positively related to soil moisture (Fig. 3), reaching a plateau when soil moisture was greater than ~90% (Fig. 3).

There were no long-term trends in summer (i.e., priming period) total net C availability, mean, minimum, or maximum daily temperature, or soil moisture. However, mean daily maximum temperatures for both primordia and flowering periods increased over the study period. For 1050 m, primordia max. temp =  $16.5 + 0.06(\text{year})$ ; for 1340 m, primordia max. temp =  $13.3 + 0.06(\text{year})$ ; both  $R^2 = 0.20$ , both  $P = 0.017$ . For 1050 m, flowering max. temp =  $17.7 + 0.07(\text{year})$ ; for 1340 m, flowering max. temp =  $14.4 + 0.07(\text{year})$ ; both  $R^2 = 0.17$ , both  $P = 0.029$ . Neither net C availability nor soil moisture during primordia development or flowering exhibited long-term trends. Rising  $C_a$  only had a small (~5%) positive effect on summer total net C availability, under both ambient and stable climate conditions. Under ambient climate conditions (i.e., real climate data), summer total net C availability was 5.4% (at 1050 m) and 5.8% (at 1340 m) greater with increasing  $C_a$  relative to stable  $C_a$ . Under stable climate conditions (i.e., using the mean daily climate for 1973–1977), summer total net C availability was 4.9% and 4.2% greater with increasing  $C_a$  relative to stable  $C_a$  at 1050 and 1340 m, respectively.

*Temperature, soil moisture, net C availability, and seed production*

Net C availability during priming was positively correlated with seed production, and this correlation was stronger at 1340 m than at 1050 m (Fig. 4). Mean daily minimum temperature during priming was more strongly correlated with seed production than was mean daily maximum temperature during priming (−0.38 vs. −0.30, at both elevations). Mean daily minimum temperature during priming was negatively correlated with seed production, an effect that was the same at both elevations (Fig. 4). Soil moisture during priming was positively correlated with seed production, and this effect was stronger at 1340 m than at 1050 m (Fig. 4). Mean daily maximum temperature during primordia development was more strongly correlated with seed production than was mean daily minimum temperature during primordia development (0.74 vs. 0.37 and 0.71 vs. 0.22, at 1050 and 1340 m, respectively). Temperature during this period was strongly and positively correlated with seed production at both elevations (Fig. 4). Furthermore, net C availability during primordia development was negatively correlated with seed production at 1050 m (Fig. 4). Soil moisture during primordia development was negatively correlated with seed production at both elevations (Fig. 4). Mean daily maximum temperature during flowering was more strongly correlated with seed production than was mean daily minimum temperature during flowering (0.34 vs. 0.22 and 0.51 vs. 0.38, at 1050 and 1340 m, respectively). Neither temperature nor net C availability dur-

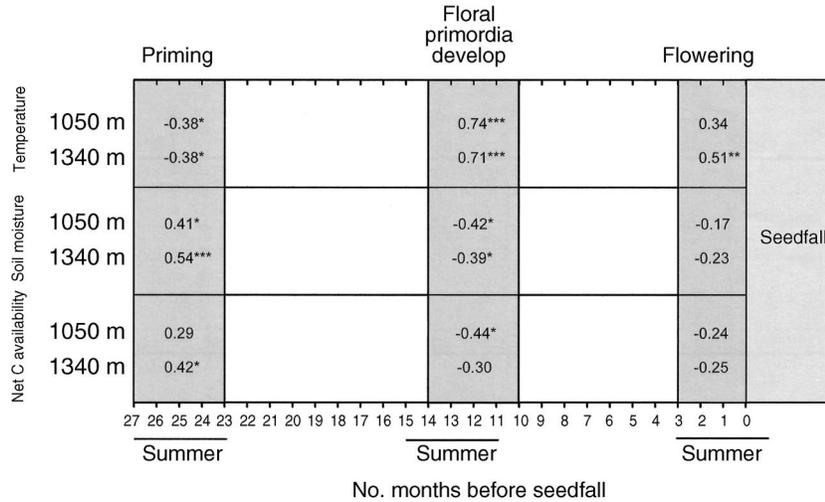


FIG. 4. Correlations between seed production and temperature, soil moisture, and total net C availability during three periods: priming, floral primordia development, and flowering. Both the mean daily minimum and maximum temperatures were tested for correlations with seed production; the correlation with the highest *r* is illustrated: mean daily minimum temperature for priming, and mean daily maximum temperature for floral primordia development and flowering. Correlations are presented for two elevations, *N* = 28. \* *P* < 0.05; \*\* *P* < 0.01; \*\*\* *P* < 0.005.

ing flowering was significantly correlated with seed production at 1050 m, but at 1340 m, there was a positive correlation between temperature and seed production (Fig. 4). Soil moisture during flowering was not correlated with seed production at either elevation (Fig. 4).

Temperature, soil moisture, and net C availability were all retained in the GLS model, indicating that all three accounted for variation in seed production (Table 2). High seed production was determined by low temperatures and high soil moisture during priming, warm temperatures during primordia development, and low net C availability during flowering (an alternative model excluding net C availability during flowering was a significantly inferior model (maximum likelihood ratio = 4.27, *P* = 0.039) thus this effect was retained in the model at *P* = 0.056 (Table 2). The year effect was not significant, indicating that at least one of the significant temperature, soil moisture, or net C availability effects had subsumed the linear increase in seed production

through time. Year became highly significant if temperature during primordia development was excluded from the model; no other fixed effect subsumed the linear increase in seed production. Mean daily maximum temperature during primordia development has increased over the 30-year period and these analyses strongly suggest that this warming has driven the increase in seed production at high elevations.

DISCUSSION

*Seed production in relation to elevation and time*

Seed production increased at high elevations near treeline over the 30-year study period (Figs. 1 and 2). In general, this provides support for our hypothesis that any long-term changes in seed production would be more pronounced at the elevational limit of the species, where climatic and resource constraints are greater relative to other parts of a species' range (Graglia et al. 1997, Woodward 1998). Increased seed production was

TABLE 2. Generalized least-squares (GLS) model of mountain beech annual seed production (1973–2002) as a function of elevation, temperature, soil moisture, and net C availability from three periods: priming, floral primordia development, and flowering.

Fixed effect	Coefficient	<i>F</i>	<i>P</i>
Priming mean daily minimum temperature	-0.402	13.26	0.0006
Priming soil moisture	0.028	7.77	0.0075
Primordia development maximum temperature	0.742	76.53	<0.0001
Flowering net C availability	-0.348	3.83	0.0560
Elevation	0.004	8.14	0.0063
Model <i>R</i> <sup>2</sup>			0.72

Notes: All single and interaction terms were entered and removed using a backward selection procedure, until only significant variables remained. ANOVA *F* and *P* statistics are presented. Numerator and denominator degrees of freedom were 1 and 50, respectively.

driven by a lower frequency of low seeding years and a higher frequency of intermediate-sized seeding years (Fig. 1). These changes support the hypothesis of Kelly and Sork (2002) that greater resource availability, i.e., increasing temperatures, should promote seed production in the lowest production years, rather than an increase in the maximum number of seeds produced (Fig. 1). Greater seed rain may underpin the recent *Nothofagus* treeline advances quantified in New Zealand (Wardle and Coleman 1992, but see Wardle 1984).

*Net C availability in relation to elevation, time, temperature, soil moisture, and C<sub>a</sub>*

One way to evaluate our net C availability model is to compare our estimates of mean annual net C availability with those calculated from measurements of annual biomass increment. Benecke and Nordmeyer (1982) estimated mountain beech net C availability from annual biomass increment, and their values of 1.7 and 0.9 kg·m<sup>-2</sup>·yr<sup>-1</sup> at 1000 m and 1320 m, respectively, compare well with our modeled values of net C availability (1.4 and 0.9 kg·m<sup>-2</sup>·yr<sup>-1</sup> at 1050 and 1340 m, respectively). Likewise, using physiological measurements, Benecke and Nordmeyer (1982) estimated the ratio of gross canopy net C uptake to wood respiration to be 2.8 at 1000 m, which corresponds reasonably well with our modeled value of 3.3 at 1050 m. Also, our modeled optimum temperatures for maximum summer net C availability at two elevations (8.5–10.4°C) are supported by measurements of other cool-temperate, evergreen tree species (Cunningham and Read 2002). Summer net C availability neither increased nor decreased over the 30-year period. Rising C<sub>a</sub> produced only modest (~+5% in 2002) positive effects on net C availability, and there was no indication that this positive effect had been moderated by increased respiration from concurrent increasing maximum temperatures.

*Temperature, soil moisture, net C availability, and seed production*

Our analyses demonstrate that the influence of temperature on seed production is associated with inter-related influences of soil moisture and net C availability (Table 2). Allen and Platt (1990) suggested that the strong positive relationships between summer temperatures and seed production were related to high net C availability. Warm temperatures during primordia development and flowering were both correlated with high seed production. Temperatures during these warm summers exceeded the optimum temperature for maximizing total summer net C availability (Fig. 3). Therefore, the positive relationships between temperature and seed production were accompanied by negative relationships between net C availability and seed production (Fig. 4). This negative relationship between net C availability and seed production was retained in the model for the period of flowering (Table 2), but not for

the period of primordia development. This strongly suggests that warm temperatures during the period of primordia development act either as a synchronizing cue (Schauber et al. 2002), or via an alternative resource to net C availability (e.g., nitrogen; Davis et al. 2004). The significance of low net C availability during flowering suggests that warm temperatures prior to high seed production (e.g., Sork et al. 1993, Tapper 1996) may be associated with short-term resource depression and suboptimal conditions (Phillipson 1990). Selås et al. (2002) similarly observed that the photosynthetic optimum temperature must be exceeded during the warm summers when floral primordia develop in *Picea abies*. The contribution of short-term resource depression for seeding has been somewhat overlooked in the ecological literature (but see Forcella 1981, Piovesan and Adams 2001, Selås et al. 2002), yet suboptimal conditions are frequently employed in silvicultural systems to induce or enhance tree seed production (Phillipson 1990).

Piovesan and Adams (2001) suggested that the correlation between cool, moist summers and seed production two years later by northern hemisphere beech (*Fagus*), was likely to be underpinned by high net C availability. Our study similarly identified a strong positive relationship between cool summers with high soil moisture and high seed production two years later in a southern hemisphere beech species (*Nothofagus*) (Table 2). Although these cool, moist summers were favorable for high net C availability (Fig. 3), there was no evidence from the model that net C availability during priming explained more variation in seed production than did the climate variables alone (Table 2). Further support for this conclusion was obtained using a maximum likelihood comparison between two alternative models, one using temperature and soil moisture during priming (Table 2) and a second using net C availability during priming instead of temperature and soil moisture: the original model using temperature and moisture was a significantly better model (maximum likelihood ratio = 11.39,  $P < 0.0001$ ). Cool, moist summers may indirectly affect seed production two years later through their influence on endogenous plant processes, such as resource allocation. The influence of climate and/or resources in the year before primordia development is rarely considered in seed production, yet is clearly deserving of wider study.

The decadal-level increase in seed production at high elevations (Figs. 1 and 2) was driven by increasing mean daily maximum temperatures during primordia development. Overall, there were no significant long-term trends in modeled net C availability as a result of rising C<sub>a</sub>. Therefore, in spite of evidence from short-term enrichment experiments that tree seed production is enhanced at higher C<sub>a</sub> (LaDeau and Clark 2001), we found no supporting evidence for this in long-term observations from a natural forest.

We would advocate two areas of research to develop the conclusions from this study. First, there is a need for long-term demographic studies that explore the consequences of increased seed production for seedling dynamics, especially at high elevations close to the current distributional limit of the species. Further, there is a need to examine whether seed predator population dynamics will modify the influence of increased seedfall on seedling recruitment. Second, it is important to understand how long-term increases in summer temperatures (i.e., more frequent cues to flower) bring about increased seed production. We hypothesize that tree species are able to respond to increasing temperatures and the cue to flower more frequently because warmer summer temperatures enhance rates of soil nitrogen mineralization and, therefore, resource availability. Studies of seed production along soil resource gradients would be one approach at addressing the important interactive effects of climate and soil resources on seed production (Kelly and Sork 2002, Davis et al. 2004).

#### ACKNOWLEDGMENTS

We thank J. A. Wardle for establishing the seed traps and M. E. Brignall-Thayer and the many other individuals who collected and sorted seeds. R. J. Dungan kindly loaned canopy access equipment, P. W. Clinton modeled tree surface areas, I. H. Lynn and T. W. Webb provided unpublished data on soils, C. Bezar provided editorial review, and R. P. Duncan and A. S. Walcroft assisted with modeling. P. J. Bellingham, L. E. Burrows, J. E. Hunt, D. Kelly, W. G. Lee, M. S. McGlone, A. Monks, D. A. Peltzer, S. K. Wiser, and an anonymous referee provided useful comments on components of the study. The work was financially supported by the former New Zealand Forest Service, the former Ministry of Forestry, and the Foundation for Research, Science and Technology (contract number CO9X0206). S. J. Richardson was funded from Landcare Research's retained earnings.

#### LITERATURE CITED

- Abrahamson, W. G., and J. N. Layne. 2003. Long-term patterns of acorn production for five oak species in xeric Florida uplands. *Ecology* **84**:2476–2492.
- Allen, R. B., and K. H. Platt. 1990. Annual seedfall variation in *Nothofagus solandri* (Fagaceae), Canterbury, New Zealand. *Oikos* **57**:199–206.
- Anonymous. 1968. Soils of New Zealand. New Zealand Soil Bureau Bulletin 26. (3 volumes.) Department of Scientific and Industrial Research, Wellington, New Zealand.
- Benecke, U. 1985. Tree respiration in steep-land stands of *Nothofagus truncata* and *Pinus radiata*, Nelson, New Zealand. Pages 61–70 in H. Turner and W. Tranquillini, editors. Establishment and tending of subalpine forests: research and management. Swiss Federal Institute of Forestry Research Report 270, Birmensdorf, Switzerland.
- Benecke, U., and A. H. Nordmeyer. 1982. Carbon uptake and allocation by *Nothofagus solandri* var. *cliffortioides* (Hook.f.) Poole and *Pinus contorta* Douglas ex Loudon ssp. *contorta* at montane and subalpine altitudes. Pages 9–21 in R. H. Waring, editor. Carbon uptake and allocation in subalpine ecosystems as a key to management. Forest Research Laboratory, Oregon State University, Corvallis, Oregon, USA.
- Bernacchi, C. J., E. L. Singsass, C. Pimental, A. R. Portis, Jr., and S. P. Long. 2001. Improved temperature response functions for models of Rubisco-limited photosynthesis. *Plant Cell and Environment* **24**:253–259.
- Burrows, L. E., and R. B. Allen. 1991. Silver beech (*Nothofagus menziesii* (Hook.f.) Oesrt.) seedfall patterns in the Takitimu Range, South Island, New Zealand. *New Zealand Journal of Botany* **29**:361–365.
- Clark, D. A., S. C. Piper, C. D. Keeling, and D. B. Clark. 2003. Tropical rain forest tree growth and atmospheric carbon dynamics linked to interannual temperature variation during 1984–2000. *Proceedings of the National Academy of Sciences (USA)* **100**:5852–5857.
- Crawley, M. J. 2003. Statistical computing. An introduction to data analysis using S-Plus. John Wiley, Chichester, UK.
- Cunningham, S. C., and J. Read. 2002. Comparison of temperate and tropical rainforest tree species: photosynthetic responses to growth temperature. *Oecologia* **133**:112–119.
- Davis, M. R., R. B. Allen, and P. W. Clinton. 2004. The influence of N addition on nutrient content, leaf carbon isotope ratio, and productivity in a *Nothofagus* forest during stand development. *Canadian Journal of Forest Research* **34**:2037–2048.
- Dungan, R. J., D. Whitehead, and R. P. Duncan. 2003. Seasonal and temperature dependence of photosynthesis and respiration for two co-occurring broad-leaved tree species with contrasting leaf phenology. *Tree Physiology* **23**:561–568.
- Farquhar, G. D., S. von Caemmerer, and J. A. Berry. 1980. A biochemical model of photosynthetic CO<sub>2</sub> assimilation in leaves of C<sub>3</sub> species. *Planta* **149**:78–90.
- Forcella, F. 1981. Ovulate cone production in pinyon: negative exponential relationship with late summer temperature. *Ecology* **62**:488–491.
- Fox, J. 2002. An R and S-PLUS companion to applied regression. Sage Publications, Thousand Oaks, California, USA.
- Graglia, E., S. Jonasson, A. Michelsen, and I. K. Schmidt. 1997. Effects of shading, nutrient application and warming on leaf growth and shoot densities of dwarf shrubs in two Arctic-alpine communities. *Écoscience* **4**:191–198.
- Harcombe, P. A., R. B. Allen, J. A. Wardle, and K. H. Platt. 1998. Spatial and temporal patterns in stand structure, biomass, growth, and mortality in a monospecific *Nothofagus solandri* var. *cliffortioides* (Hook.f.) Poole Forest in New Zealand. *Journal of Sustainable Forestry* **6**:313–345.
- Harper, J. L. 1977. Population biology of plants. Academic Press, London, UK.
- Hart, P. B. S., P. W. Clinton, R. B. Allen, A. H. Nordmeyer, and G. Evans. 2003. Biomass and macro-nutrients (above- and below-ground) in a New Zealand beech (*Nothofagus*) forest ecosystem: implications for carbon storage and sustainable forest management. *Forest Ecology and Management* **174**:281–294.
- Hollinger, D. Y. 1989. Canopy organization and foliage photosynthetic capacity in a broad-leaved evergreen montane forest. *Functional Ecology* **3**:53–62.
- Hollinger, D. Y., F. M. Kelliher, J. N. Byers, J. E. Hunt, T. M. McSeveny, and P. L. Weir. 1994. Carbon dioxide exchange between an undisturbed old-growth temperate forest and the atmosphere. *Ecology* **75**:134–150.
- Holm, S.-O. 1994. Reproductive patterns of *Betula pendula* and *B. pubescens* coll. along a regional altitudinal gradient in northern Sweden. *Ecography* **17**:60–72.
- Keeling, C. D., and T. P. Whorf. 2004. Atmospheric CO<sub>2</sub> records from sites in the SIO air sampling network. In Trends: a compendium of data on global change. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, USA. (<http://cdiac.esd.ornl.gov/trends/co2/sio-mlo.htm>)
- Kelly, D., and V. L. Sork. 2002. Mast seeding in perennial plants: why, how, where? *Annual Review of Ecology and Systematics* **33**:427–447.

- Koenig, W. D., and J. M. H. Knops. 1998. Scale of mast-seeding and tree-ring growth. *Nature* **396**:225–226.
- Körner, Ch. 1996. The response of complex multispecies systems to elevated CO<sub>2</sub>. Pages 20–42 in B. Walker and W. Steffen, editors. *Global change and terrestrial ecosystems*. Cambridge University Press, Cambridge, UK.
- Kullman, L. 2002. Rapid recent range-margin rise of tree and shrub species in the Swedish Scandes. *Journal of Ecology* **90**:68–77.
- LaDeau, S., and J. S. Clark. 2001. Rising CO<sub>2</sub> levels and the fecundity of forest trees. *Science* **292**:95–98.
- Leuning, R. 1995. A critical appraisal of a combined stomatal-photosynthesis model for C<sub>3</sub> plants. *Plant Cell and Environment* **18**:339–357.
- McCracken, I. J. 1980. Mountain climate in the Craigieburn Range, New Zealand. Pages 41–59 in U. Benecke and M. R. Davis, editors. *Mountain environments and subalpine tree growth*. New Zealand Forest Service, Forest Research Institute Technical Paper Number 70, Christchurch, New Zealand.
- Phillipson, J. J. 1990. Prospects for enhancing flowering of conifers and broadleaves of potential silvicultural importance in Britain. *Forestry* **63**:223–240.
- Piovesan, G., and J. M. Adams. 2001. Masting behaviour in beech: linking reproduction and climatic variation. *Canadian Journal of Botany* **79**:1039–1047.
- Rees, M., D. Kelly, and O. N. Bjørnstad. 2002. Snow tussocks, chaos, and the evolution of mast seeding. *American Naturalist* **160**:44–59.
- Salinger, M. J. 1995. Southwest Pacific temperatures: trends in maximum and minimum temperatures. *Atmospheric Research* **37**:87–99.
- Schauber, E. M., D. Kelly, P. Turchin, C. Simon, W. G. Lee, R. B. Allen, I. J. Payton, P. R. Wilson, P. E. Cowan, and R. E. Brockie. 2002. Masting by eighteen New Zealand plant species: the role of temperature as a synchronizing cue. *Ecology* **83**:1214–1225.
- Selås, V., G. Piovesan, J. M. Adams, and M. Bernabei. 2002. Climatic factors controlling reproduction and growth of Norway spruce in southern Norway. *Canadian Journal of Forest Research* **32**:217–225.
- Sork, V. L., J. Bramble, and O. Sexton. 1993. Ecology of mast-fruiting in Missouri oaks. *Ecology* **74**:528–541.
- Tapper, P.-G. 1996. Long-term patterns of mast fruiting in *Fraxinus excelsior*. *Ecology* **77**:2567–2572.
- Wardle, J. A. 1984. *The New Zealand beeches*. New Zealand Forest Service, Christchurch, New Zealand.
- Wardle, P., and M. C. Coleman. 1992. Evidence for rising upper limits of four native New Zealand forest trees. *New Zealand Journal of Botany* **30**:303–314.
- Whitehead, D., et al. 2002. Analysis of the growth of rimu (*Dacrydium cupressinum*) in south Westland, New Zealand, using process-based simulation models. *International Journal of Biometeorology* **46**:66–75.
- Woodward, F. I. 1998. *Climate and plant distribution*. Cambridge University Press, Cambridge, UK.

#### APPENDIX

A table of descriptive statistics for seed production data from mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest at nine elevations for the period 1973–2002 is available in ESA's Electronic Data Archive: *Ecological Archives* E086-052-A1.