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Eric M. Schauber
Southern Illinois University Carbondale

Dave Kelly
University of Canterbury

Peter Turchin
University of Connecticut

Chris Simon
University of Connecticut

William G. Lee
Landcare Research

See next page for additional authors

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Authors
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MASTING BY EIGHTEEN NEW ZEALAND PLANT SPECIES: THE ROLE OF TEMPERATURE AS A SYNCHRONIZING CUE

Eric M. Schauber,[1,2,8] Dave Kelly,[3] Peter Turchin,[1] Chris Simon,[1] William G. Lee,[4] Robert B. Allen,[5] Ian J. Payton,[5] Peter R. Wilson,[5] Phil E. Cowan,[6] and R. E. Brockie[7]

[1]*Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, Connecticut 06269 USA*
[2]*Institute of Ecosystem Studies, Millbrook, New York 12545 USA*
[3]*Plant and Microbial Sciences, University of Canterbury, Christchurch 1, New Zealand*
[4]*Landcare Research, Private Bag 1930, Dunedin, New Zealand*
[5]*Landcare Research, P.O. Box 69, Lincoln, New Zealand*
[6]*Landcare Research, Private Bag 11052, Palmerston North, New Zealand*
[7]*Biological Sciences, Victoria University, P.O. Box 600, Wellington, New Zealand*

Abstract. Masting, the intermittent production of large flower or seed crops by a population of perennial plants, can enhance the reproductive success of participating plants and drive fluctuations in seed-consumer populations and other ecosystem components over large geographic areas. The spatial and taxonomic extent over which masting is synchronized can determine its success in enhancing individual plant fitness as well as its ecosystem-level effects, and it can indicate the types of proximal cues that enable reproductive synchrony. Here, we demonstrate high intra- and intergeneric synchrony in mast seeding by 17 species of New Zealand plants from four families across >150 000 km^2. The synchronous species vary ecologically (pollination and dispersal modes) and are geographically widely separated, so intergeneric synchrony seems unlikely to be adaptive per se. Synchronous fruiting by these species was associated with anomalously high temperatures the summer before seedfall, a cue linked with the La Niña phase of El Niño–Southern Oscillation. The lone asynchronous species appears to respond to summer temperatures, but with a 2-yr rather than 1-yr time lag. The importance of temperature anomalies as cues for synchronized masting suggests that the timing and intensity of masting may be sensitive to global climate change, with widespread effects on taxonomically disparate plant and animal communities.

Key words: abiotic factors; Chionochloa; *cross-correlation;* Dacrydium; *El Niño–Southern Oscillation;* Elaeocarpus; *masting; New Zealand;* Nothofagus; Phormium; *synchrony; temperature.*

Introduction

Masting, also known as mast seeding or mass flowering, is the intermittent production of large crops of flowers or seeds by a population of perennial plants (Janzen 1971, Kelly 1994). Masting results from synchronized variations in reproductive output of individual plants, and such synchrony may benefit the fitness of individual plants, e.g., through increased pollination efficiency or satiation of seed consumers (Janzen 1971, Silvertown 1980, Nilsson and Wästljung 1987, Smith et al. 1990). In addition, masting has powerful direct and indirect effects on populations of seed consumers, as well as other species and ecosystem processes (King 1983, Jedrzejewska and Jedrzejewski 1998, Jones et al. 1998, Curran and Leighton 2000, Ostfeld and Keesing 2000).

The fitness benefits accrued by plants and the effects of masting on other ecosystem components are mediated by the spatial and taxonomic extent of masting synchrony (Curran and Leighton 2000). Masting can be synchronous over distances measured in hundreds or thousands of kilometers (Koenig and Knops 1998, 2000, Kelly et al. 2000). Synchronous masting over large spatial scales prevents consumers from aggregating to and eliminating local patches of seed production. Instead, consumers are effectively starved during intermast intervals and swamped during mast events, driving large fluctuations in consumer abundance and increasing the potential fitness benefit of masting (Curran and Leighton 2000). Similarly, synchronous masting by sympatric taxa that share seed predators can increase the predator-swamping benefits of masting and increase the amplitude of fluctuations in consumer abundance (Shibata et al. 1998, Kelly et al. 2000). In addition, if seed consumers strongly prefer particular fruits or seeds, then less preferred species may escape seed predation by masting in synchrony with a preferred species (Curran and Leighton 2000).

If individual plants do not communicate directly with one another, then masting synchrony must result from responses to external factors, or cues. Synchronizing cues must be spatially consistent, to enable synchrony of entire populations, and be easily detected by plants through strong physiological effects. Weather conditions, especially temperature, are likely candidates be-

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[8] Address correspondence to: Institute of Ecosystem Studies, Box AB, Millbrook, NY 12545 USA.
E-mail: SchauberE@ecostudies.org

PLATE 1. The 1998–1999 season was a high-flowering season throughout New Zealand for most species, including *Phormium tenax*, shown here in fruit in January 1999 near Dunedin. This long-lived herbaceous monocot has straplike leaves 2–3 m long and compound inflorescences 3–4 m tall with bird-pollinated flowers. Photograph by Dave Kelly.

cause they strongly affect photosynthesis and growth and are spatially autocorrelated (Norton and Kelly 1988, Koenig et al. 1999, Koenig and Knops 2000). Temperatures during flower or cone initiation appear to control subsequent seed or flower production in a variety of taxa (e.g., Matthews 1955, Maguire 1956, Connor 1966, Lester 1967, Forcella 1981, Brockie 1986, Norton and Kelly 1988, Allen and Platt 1990, Cowan and Waddington 1990, Pucek et al. 1993, Kelly et al. 2000). Mark (1965) and Greer (1979) demonstrated experimentally that relocating alpine plants in the genus *Chionochloa* to a lower elevation (and higher temperature) can cause a sustained run of high seed production. Ashton et al. (1988) found that mass flowering by a suite of dipterocarp species was cued by a series of cool nights associated with El Niño. Consequently, large-scale climatic processes such as El Niño–Southern Oscillation (ENSO) and global warming may alter the frequency and intensity of masting, substantially altering geographically and taxonomically distant plant and animal communities (McKone et al. 1998).

Masting in New Zealand

Masting is a worldwide phenomenon (Kelly 1994, Herrera et al. 1998) but appears to be especially prevalent in the New Zealand flora (Webb and Kelly 1993; see Plate 1). The ultimate reasons for high masting prevalence in New Zealand are mysterious, but New Zealand's long history before humans and mammalian herbivores arrived may have enabled even herbs and grasses to evolve long life spans, which are necessary for masting to be a viable strategy. Alternatively, data on masting in other parts of the world may simply be incomplete.

Several New Zealand plant taxa are reputed to mast in synchrony with one another (Connor 1966, Brockie 1986), although such synchrony has rarely been quantified (Burrows and Allen 1991, Kelly et al. 2000). Our first objective was to quantify the degree of masting synchrony over space and across taxa for 18 New Zealand species in five genera of five families. Our second objective was to evaluate temperature as a putative synchronizing environmental cue, by testing whether masting and temperatures are consistently correlated in time and space. Our final objective was to determine to what extent any temperature cues found are linked to large-scale weather cycles such as ENSO.

The plants we studied have all attracted empirical research by virtue of high variance in flower or seed production. Two genera are herbaceous monocots (*Chionochloa*, Poaceae; and *Phormium*, Phormiaceae), two are dicot trees (*Elaeocarpus*, Elaeocarpaceae; and *Nothofagus*, Fagaceae), and one is a gymnosperm tree (*Dacrydium*, Podocarpaceae). The genera are ecologically diverse in several respects. *Chionochloa* (snow tussocks) are perennial tussock-forming grasses common in alpine and subalpine meadows (Wardle 1991) with wind-pollinated flowers and gravity-dispersed seeds. *Chionochloa* exhibit extremely high variation in flowering intensity, with coefficients of variation (CV) exceeding 3.0 (Kelly 1994, Kelly et al. 2000). Several *Chionochloa* suffer severe predispersal predation on seeds and florets by specialist insects, and masting appears to benefit the plants by satiating these predators

TABLE 1. Summary statistics for raw and standardized masting data sets.

Genus and species	Reference†	Fig. 1 Panel	Fig. 1 Symbol	Site	*N* (yr)	Method
Chionochloa						
crassiuscula (Kirk) Zotov	1	A	A	Takahe Valley	28	visual count, 100–200 plants
rubra Zotov	1	A	B	Takahe Valley	28	visual count, 100–200 plants
teretifolia (Petrie) Zotov	1	A	C	Takahe Valley	28	visual count, 100–200 plants
rigida (Raoul) Zotov	1	A	D	Takahe Valley	28	visual count, 100–200 plants
pallens Zotov	1	A	E	Takahe Valley	28	visual count, 100–200 plants
pallens	1	A	H	Mt. Misery	24	visual count, 200 1 m^2 plots
australis (Buchanan) Zotov	1	A	I	Mt. Misery	24	visual count, 200 1 m^2 plots
pallens	1	A	F	Mt. Hutt	15	visual count, 80 plants
macra Zotov	1	A	G	Mt. Hutt	11	visual count, 17–34 plants
pallens	1	A	J	Camp Creek	19	visual count, 50 plants
conspicua (Forst. f.) Zotov	1	A	K	Camp Creek	19	visual count, 50 plants
flavescens Zotov	1	A	L	Camp Creek	20	visual count, 50 plants
crassiuscula	1	A	M	Camp Creek	19	visual count, 50 plants
oreophila (Petrie) Zotov	1	A	N	Camp Creek	19	visual count, 50 plants
rubra	1	A	O	Camp Creek	19	visual count, 50 plants
Dacrydium						
cupressinum	2	D	A	Wanganui S. F.	33	eight 0.86-m^2 trays, 20 m apart
cupressinum	3	D	B	Ianthe Forest	11	35 0.28-m^2 seed trays, 20 m apart
Elaeocarpus						
dentatus	4	C	D	Orongorongo	33	0.28-m^2 trays under 21 trees
Nothofagus						
solandri (Hook. f.) Oerst.	5	B	A	Craigieburn A	35	eight 0.28-m^2 trays 40 m apart
solandri	5	B	B	Craigieburn B	35	eight 0.28-m^2 trays 40 m apart
solandri	5	B	C	Craigieburn C	35	eight 0.28-m^2 trays 40 m apart
solandri	6	B	D	Takahe Valley	20	eight 0.28-m^2 trays 40 m apart
solandri	5	B	E	Mt. Thomas	34	eight 0.28-m^2 trays 40 m apart
menziesii (Hook. f.) Oerst.	7	B	F	Rowallan	19	eight 0.28-m^2 trays 40 m apart
menziesii	8	B	G	Takitimu	29	2 to 8 0.28-m^2 trays 40 m apart
fusca (Hook. f.) Oerst.	7	B	H	Rahu	16	eight 0.28-m^2 trays 40 m apart
fusca	6	B	I	Eglinton	11	eight 0.28-m^2 trays
solandri	9	B	J	Mt. Misery	24	10 0.28-m^2 trays
fusca	9	B	K	Mt. Misery	24	17 0.28-m^2 trays
menziesii	9	B	L	Mt. Misery	24	17 0.28-m^2 trays
truncata (Col.) Ckn.	10	B	M	Orongorongo	32	2 to 21 0.28-m^2 trays
Phormium						
tenax J. R. et G. Forst.	11	C	A	Ngauranga	18	visual count, 250 plants
tenax	11	C	B	Thorndon	18	visual count, 260 plants
cookianum Le Jolis	11	C	C	Thorndon	18	visual count, 45 plants

Notes: Data sets are annual measurements of inflorescence or seed production, as described in *Methods*. Data are shown in Fig. 1 with the panels and symbols indicated. For site locations, see Fig. 2.

† Key to references: 1, Kelley et al. (2000); 2, Norton and Kelly (1988); 3, James and Franklin (1978); 4, Cowan and Waddington (1990) (in part; some data previously unpublished); 5, Allen and Platt (1990) (in part; some data previously unpublished); 6, W. G. Lee, *unpublished data*; 7, Wardle (1984); 8, Burrows and Allen (1991); 9, Wilson et al. (1998) (in part; some data previously unpublished); 10, P. Cowan and J. Alley, *unpublished data*; 11, Brockie (1986).

‡ Significantly nonnormal, Shapiro-Wilks *W* test, $P < 0.01$.

(Kelly et al. 1992, Kelly and Sullivan 1997, Kelly et al. 2000). *Phormium* (New Zealand flaxes) are lowland strap-leaved herbs, which produce large floral displays attractive to nectar-feeding birds (Brockie 1986) (see Plate 1); the seeds are wind dispersed. *Elaeocarpus dentatus* J. R. et G. Forst. (hinau) is a tree that occurs primarily at lower elevations on the North Island, and the insect-pollinated flowers produce seeds in fleshy drupes that are dispersed by native birds (Brockie 1986). *Nothofagus* (southern beeches) are trees of lowland and montane habitats noted for producing highly variable seed crops over large spatial scales (Wardle 1984, Allen and Platt 1990, Burrows and Allen 1991). *Nothofagus* have wind-pollinated flowers and wind-dispersed seeds; the latter are important foods for a variety of native birds (Wardle 1984, Wilson et al. 1998), as well as introduced birds and rodents (King 1983, O'Donnell and Phillipson 1996). *Dacrydium cupressinum* Lamb. (rimu), also inhabits lowland and lower montane habitats. Rimu cones are wind pollinated, while the seeds are carried on fleshy podocarps, which are dispersed by several native birds (Norton and Kelly 1988, O'Donnell and Dilks 1994).

METHODS

Data sets

We analyzed 34 published and unpublished time series of yearly flower or seed production (Table 1, Fig.

TABLE 1. Extended.

	Raw data		Standardized	
CV	Skew	Kurtosis	Skew	Kurtosis
2.73	3.93	16.98‡	0.90	−0.54‡
1.76	2.15	4.11‡	0.24	−1.73‡
2.28	2.56	5.52‡	0.67	−1.24‡
2.23	2.99	8.69‡	0.38	−1.42‡
1.67	1.88	2.64‡	0.14	−1.54‡
1.49	1.50	1.09‡	0.01	−1.38
1.91	3.03	10.54‡	0.10	−1.44
1.69	1.80	1.83‡	−0.06	−1.37
1.44	1.49	0.91‡	0.11	−1.57
1.85	2.19	4.32‡	0.60	−1.43‡
1.62	1.61	1.79‡	0.76	−1.26‡
1.77	1.85	2.41‡	0.69	−1.39‡
1.86	1.94	2.77‡	0.97	−0.80‡
1.57	2.30	5.99‡	0.45	−1.21‡
1.96	2.05	3.26‡	1.12	−0.53‡
1.41	1.80	2.68‡	−0.61	−0.34
1.18	0.71	−1.52‡	−0.06	−1.77
0.77	1.26	1.16‡	−0.78	0.76
1.78	2.84	9.60‡	−0.02	−1.50‡
1.63	2.47	7.39‡	−0.23	−1.32
1.47	1.62	2.10‡	−0.24	−1.33
1.26	1.51	1.53‡	−0.51	−0.61
1.82	2.31	5.14‡	0.18	−1.16
1.32	1.34	0.73‡	−0.08	−1.47
1.59	1.95	3.92‡	−0.01	−1.36
1.53	1.29	−0.10‡	0.15	−1.60
1.48	1.23	−0.50‡	−0.55	0.28
1.95	2.60	6.26‡	0.88	−0.41‡
1.84	3.14	11.27‡	0.27	−1.32‡
1.89	3.70	15.68‡	−0.17	−1.65‡
2.06	2.04	2.77‡	−0.19	−0.43
1.11	1.42	1.43‡	−0.15	−1.30
0.95	0.86	−0.55‡	−0.11	−1.41
0.74	0.61	−0.38	−0.77	0.21

1). These data cover 780 site-years (Table 1) from 15 sites throughout the South Island and southern North Island (Fig. 2), an area of >150 000 km^2. Sites ranged in elevation from 15 to 1430 m, and in mean rainfall from 1000 to >6400 mm/yr. Table 1 briefly summarizes measurement methods for previously published data sets, but we urge the reader to consult the primary sources for details. *Chionochloa* flowering intensity was measured by censusing inflorescences per tussock, usually on permanently tagged plants in unmodified alpine and subalpine meadows (Kelly et al. 2000). *Phormium* flowering intensity was measured by censusing flowering stems per plant. Seed production by *Dacrydium*, *Elaeocarpus*, and *Nothofagus* was measured as seeds/m^2 of ground, using seed trays. At the Orongorongo Valley research site, 18 km from Wellington, *Nothofagus truncata* seeds were collected in lowland sites from 0.28-m^2 seed trays under individual trees. Trays were added over time, from two in 1968, three from 1971, 15 from 1974, 18 from 1978, 20 from 1979, and 21 thereafter (Fitzgerald et al. 1996, Alley et al. 1998).

Sampling methods, mean, and variance differed among data sets and data were not normally distributed. All raw masting data sets had strong positive skew (median = 1.91) and most had positive kurtosis (median = 2.72), indicating asymmetric long-tailed (leptokurtic) distributions. All data sets but one failed the Shapiro-Wilks *W* test for normality (StatSoft 1994) at the 99% level (Table 1). To account for methodological differences and reduce deviations from normality, all masting data were transformed by natural log and standardized to mean = 0 and standard deviation (SD) = 1 before analysis (Herrera et al. 1998). If a raw data set contained zeroes, then the smallest positive value in that data set was added to all values before they were transformed. Standardized data sets were consistently much less skewed (median = 0.08) and kurtotic (median = −1.33) than raw data, although they tended to be short tailed (kurtosis < 0; platykurtic) and 15 of 34

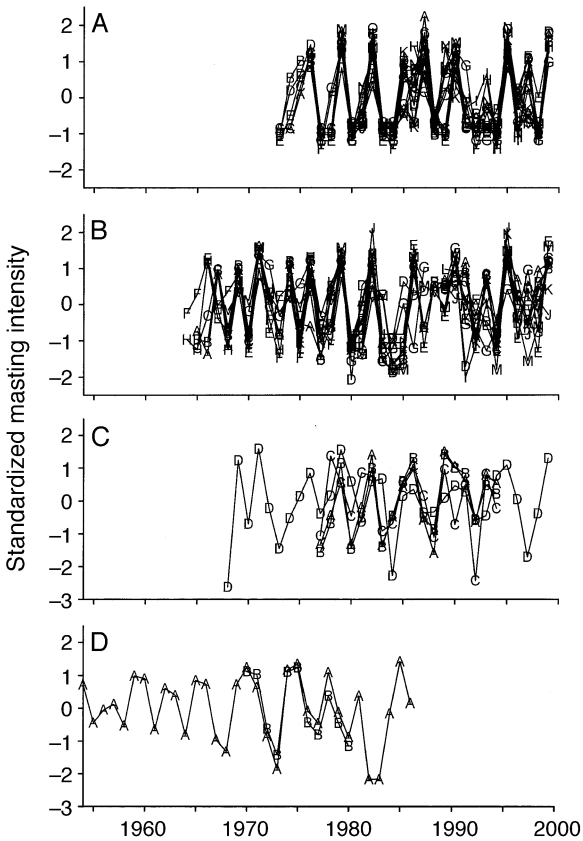

FIG. 1. Standardized time series of masting by (A) *Chionochloa* spp., (B) *Nothofagus* spp., (C) *Phormium* spp. and *Elaeocarpus dentatus*, and (D) *Dacrydium cupressinum* at various sites in New Zealand. Raw data were natural log-transformed and standardized to mean = 0 and SD = 1 (see *Methods* for details). Each time series in a panel is indicated by a different letter symbol. Species names, symbols, and sources are in Table 1.

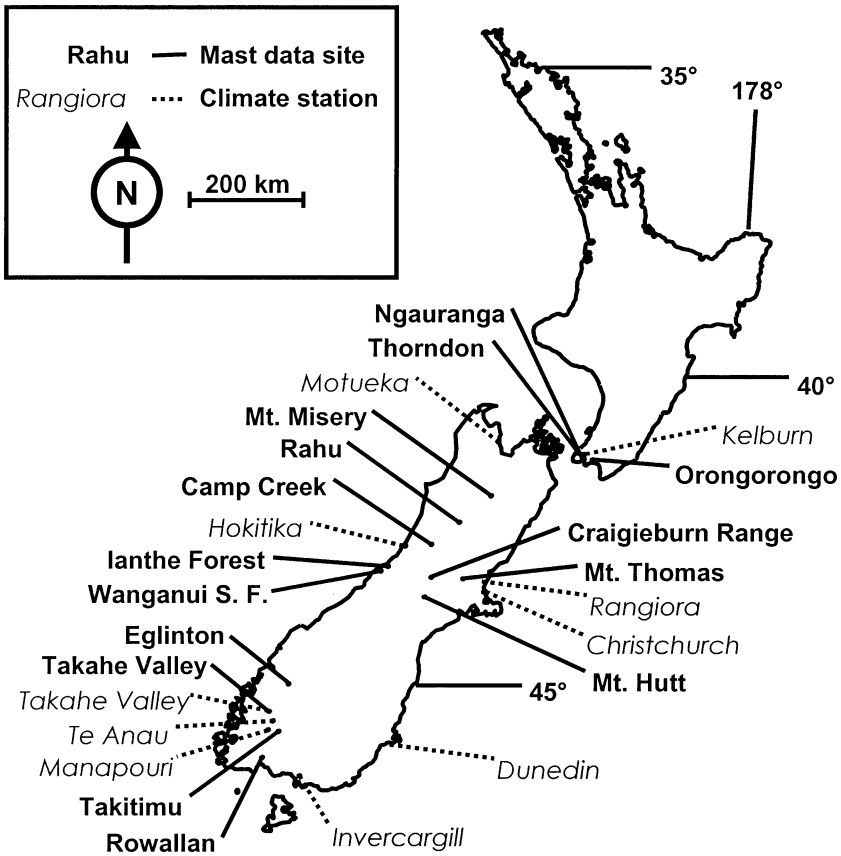

FIG. 2. Sites of masting and weather data collection in New Zealand.

standardized data sets remained significantly nonnormal at the 99% level (Table 1).

Testing for synchrony within and among genera

Masting synchrony among species and sites was quantified by pairwise cross correlation (Hanski and Woiwod 1993, Bjørnstad et al. 1999, Koenig 1999), i.e., the Pearson correlation (r) between concurrent values of each pair of standardized masting time series with $n > 10$ yr of overlap. Our decision to measure synchrony by cross-correlation is based on the assumption of normal masting (Kelly 1994). That is, high and low seed production are not dichotomous, but represent opposing tails of a continuous distribution. For that reason, our question of interest was not whether seed production peaks and troughs occur in the same years for different data sets, but rather whether relative deviations from the long-term mean seed production are correlated among data sets.

The standardized data sets were somewhat platykurtic, but r is robust to all but extreme deviations from normality for reasonable sample sizes ($n > 10$; Edgell and Noon 1984). However, r is not robust to temporal autocorrelation, which can increase the type I error rate (Abraham and Ledolter 1983), and seed production tends to be temporally autocorrelated (Norton and Kelly 1988, Sork et al. 1993, Crawley and Long 1995, Koenig and Knops 2000). Therefore, the statistical significance of each cross-correlation was evaluated after calculating the adjusted degrees of freedom (n_{adj}) according to Sciremammano (1979). Because $n_{adj} < 30$ in nearly all cases, we applied Hotelling's modified z transformation (Sokal and Rohlf 1981), which has an approximately normal distribution with standard deviation (SD) $\sigma_{z^*} = (n_{adj} - 1)^{-0.5}$, to each r. P values were two-tailed and based on a normal distribution with mean = 0 and SD = σ_{z^*}. Cross-correlations with $n_{adj} \geq 10$ were considered valid for significance testing (Sciremammano 1979), and the significance of each comparison was evaluated after sequential Bonferroni correction (Rice 1989).

Testing for influence of temperature and ENSO

Based on previous studies, we hypothesized a priori that standardized seed production would be correlated with temperature during floral initiation for all species and sites. To test this hypothesis, we cross-correlated each masting time series with the seasonal (3-mo) mean temperature (National Institute of Water and Atmospheric Research, Auckland, New Zealand) recorded at

the nearest of 10 climate stations (Fig. 2) during the period of floral initiation (summer 2 yr before seedfall for *Dacrydium*, summer 1 yr before seedfall for all others). However, temperatures during other time periods could also conceivably affect seed production. Therefore, as an exploratory analysis, we tested for cross-correlations between masting time series and seasonal mean temperatures for all seasons between floral initiation and seedfall. Weather variables other than temperature were not included in these analyses, because previous empirical studies have consistently pointed to temperature as an important predictor of masting in New Zealand. Excluding alternative cues may reduce our ability to explain masting synchrony, but also greatly reduces the number of potential explanatory variables and, consequently, the risk of type I errors (Crawley and Long 1995). Significance of correlations between masting and temperature variables was assessed in the same manner as for tests of masting synchrony. Sequential Bonferroni corrections were applied for exploratory analyses but not for a priori analyses.

Across New Zealand, yearly variations in temperature and, to a lesser degree, precipitation are associated with ENSO (Gordon 1986, Salinger et al. 1995). Relatively high New Zealand temperatures are associated with high values of the Southern Oscillation Index (SOI), which accompany the La Niña phase of ENSO. Because New Zealand temperatures vary with ENSO, we also tested whether masting was correlated with 3-mo mean SOI (downloaded from the Commonwealth of Australia Bureau of Meteorology website)[9] between floral initiation and seedfall. Statistical testing for significant correlations between masting and ENSO was performed in the same manner as tests for masting synchrony.

Separating associations with weather and distance

To more rigorously evaluate the hypothesis that temperature cues are responsible for the masting synchrony we observed, we compared the spatial pattern of masting with that of summer temperature. If temperatures cue masting behavior, then the degree of masting synchrony between two sites should be positively associated with the degree of similarity in temperature variations at those sites (Koenig et al. 1999). This analysis is confounded by spatial autocorrelation, because both masting and weather conditions are likely to be more similar between nearby sites than distant sites. Therefore, partial correlations (Sokal and Rohlf 1981) were used to separate the potential effects of weather and distance. Each pair of masting data sets was characterized by (1) the degree of masting synchrony, expressed as z^*; (2) the degree of temperature similarity, expressed as the correlation (r) between mean summer temperatures at the two sites; and (3) the geographic distance (km) between sites. Across all pairs of masting data sets, we calculated the simple and partial Pearson correlations between masting synchrony, temperature similarity, and geographic distance. The statistical significance of these correlations was evaluated by Mantel randomization tests (Manly 1997), in which the matrices of masting synchrony and temperature similarity were randomly and independently permuted 10 000 times. We report the proportion of permutations (P) resulting in correlations of equal or greater absolute value than the observed correlation. Partial-correlation analysis was conducted separately for within-genus comparisons among *Nothofagus* spp., *Chionochloa* spp., and between-genus comparisons excluding *Dacrydium* (correlations including *Dacrydium* were too weak to analyze further).

[9] URL: ⟨http://www.bom.gov.au/climate/current/soihtm1.shtml⟩

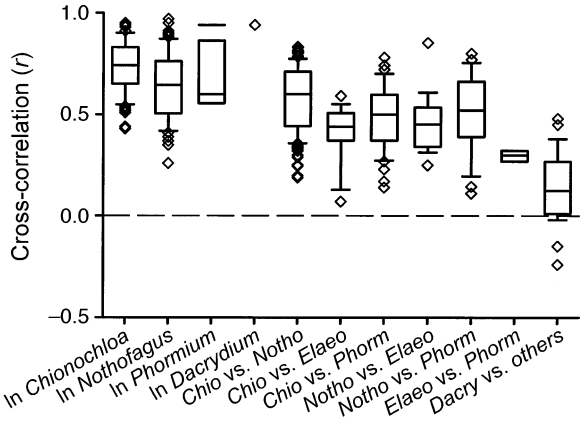

FIG. 3. Box-and-whisker plots summarizing cross-correlations between masting time series within and among genera. Each box spans the 25th and 75th percentiles, with the median indicated by a cross line. Whiskers indicate the 10th and 90th percentiles, and diamonds indicate outlying observations. ''Dacry vs. Others'' indicates masting cross-correlations between *Dacrydium* and other genera.

RESULTS

Synchrony within and among genera

Masting was highly synchronous within genera (Fig. 3), as all 171 within-genus comparisons with $n \geq 10$ yr of overlap yielded $r > 0.26$ (median $r = 0.71$). Out of 160 within-genus cross-correlations valid for significance testing ($n_{adj} \geq 10$), 140 (88%) were individually significant at $\alpha = 0.05$, and 58 (36%) were significant after sequential Bonferroni correction. Masting also tended to be synchronous between genera other than *Dacrydium* (265 comparisons, all $r > 0.07$, median $r = 0.54$; Fig. 3). Out of 248 valid cross-correlations between genera, excluding *Dacrydium*, 160 (65%) were significantly positive individually, but only nine comparisons (all between *Nothofagus* and *Chionochloa*) were significant after sequential Bonferroni correction. However, out of 295 total cross-correlations between

all genera, only seven (all comparisons between *Dacrydium* and *Nothofagus*) yielded a negative *r*. Such a result would be extremely unlikely if these tests were independent and each had a 50% chance of being negative. In this case, the individual cross-correlations are not fully independent of one another: if *A* is positively correlated with *B*, and *B* is positively correlated with *C*, then *A* and *C* will also tend to be positively correlated. Based on a two-tailed binomial test assuming 50% probability of positive or negative correlations, the result of seven or fewer negative correlations would only be likely ($P > 0.05$) if the effective number of independent correlations was ≤24 (<10% of the raw number). Because such an extreme reduction in effective sample size seems unlikely, we conclude that the preponderance of positive cross-correlations among genera other than *Dacrydium* is not due to random chance.

None of the 24 correlations between *Dacrydium* and other genera with $n_{adj} \geq 10$ was significant individually, and the median *r* was only 0.12. *D. cupressinum* seeds fall 2 yr after floral initiation (Norton and Kelly 1988), whereas seedfall is 1 yr after flowering in the other species we studied (Mark 1970, Brockie 1986, Allen and Platt 1990). If the same environmental cue controls masting in all species by acting during floral initiation, then the response of *D. cupressinum* should lag a year behind that of other species. However, masting by *D. cupressinum* was negatively correlated ($-0.69 \leq r \leq -0.13$, median $r = -0.41$) with that of all other species the year before and positively correlated ($0.06 \leq r \leq 0.76$, median $r = 0.53$) with that of all other species the year after.

Weather and masting synchrony

Out of 33 valid ($n_{adj} \geq 10$) cross-correlations identified a priori between seed production and temperature during floral initiation, 20 had $P < 0.05$ and another four correlations had $0.05 \leq P \leq 0.10$. Masting by *Phormium* was not evidently correlated with floral initiation temperature ($0.06 \leq r \leq 0.25$, all $P \geq 0.41$). *Dacrydium* seed production at Wanganui was negatively correlated with floral initiation temperatures ($r = -0.59$, $P = 0.0065$) as reported by Norton and Kelly (1988), whereas seed production and temperature were positively correlated for *Chionochloa* ($0.13 \leq r \leq 0.59$, 12 of 15 $P < 0.05$), *Elaeocarpus* ($r = 0.40$, $P = 0.038$), and *Nothofagus* ($0.28 \leq r \leq 0.63$, 6 of 13 $P < 0.05$).

In exploratory analyses, no correlation between masting and temperature and only two correlations with SOI (June–August lag 1 vs. *N. menziesii* from Takitimu and *C. rigida* from Takahe Valley) were statistically significant after sequential Bonferroni correction. However, certain apparent generalities should be noted. Among *Chionochloa*, *Elaeocarpus*, and *Nothofagus* species, seed production tended to be positively correlated with temperatures during the summer of seedfall, the previous autumn, and the summer of floral initiation (Fig. 4). For *D. cupressinum*, seed production was positively correlated with temperatures during the summer of seedfall and negatively correlated with temperatures during floral initiation (two summers before seedfall; Fig. 4). For all taxa other than *D. cupressinum*, masting was positively correlated with SOI the previous winter, and 12 of 32 valid cross-correlations were individually significant at $P < 0.05$. However, correlations with SOI were generally weaker than those with temperature (Fig. 4).

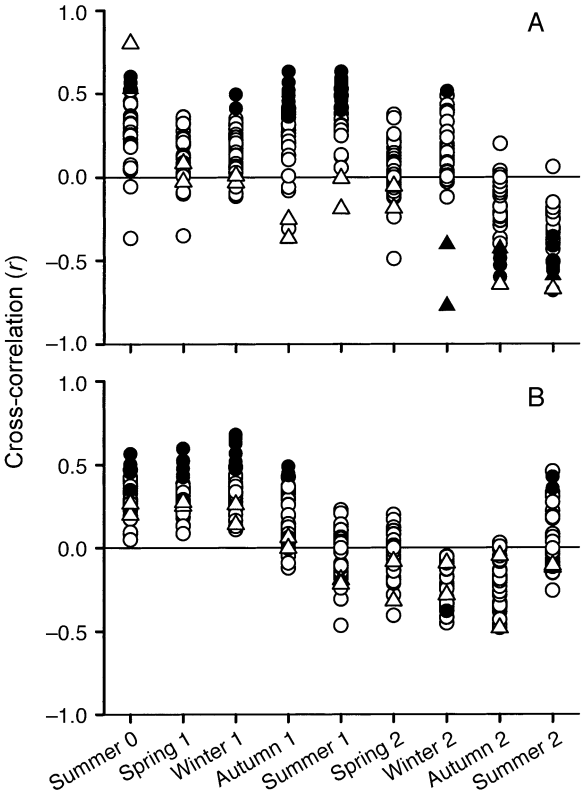

FIG. 4. Links between climate and masting time series in 17 New Zealand species (circles) and New Zealand *Dacrydium cupressinum* (triangles). Each circle or triangle represents a single cross-correlation between masting and 3-mo means of (A) daily temperature or (B) Southern Oscillation Index, working backward in time from the summer of seedfall (Summer 0). Filled symbols denote individually significant ($P < 0.05$) correlations, but note that only one was significant after Bonferroni correction (see *Results*).

Masting synchrony within and between genera decreased with geographic distance (Fig. 5), although within-genus synchrony remained strong ($r \sim 0.5$) between even the most distant sites. Masting synchrony was positively correlated with temperature similarity (Fig. 5), and significant partial correlations with temperature similarity remained after controlling for geographic distance. Partial correlations between masting synchrony and distance, controlling for temperature similarity, were also highly significant (Fig. 5).

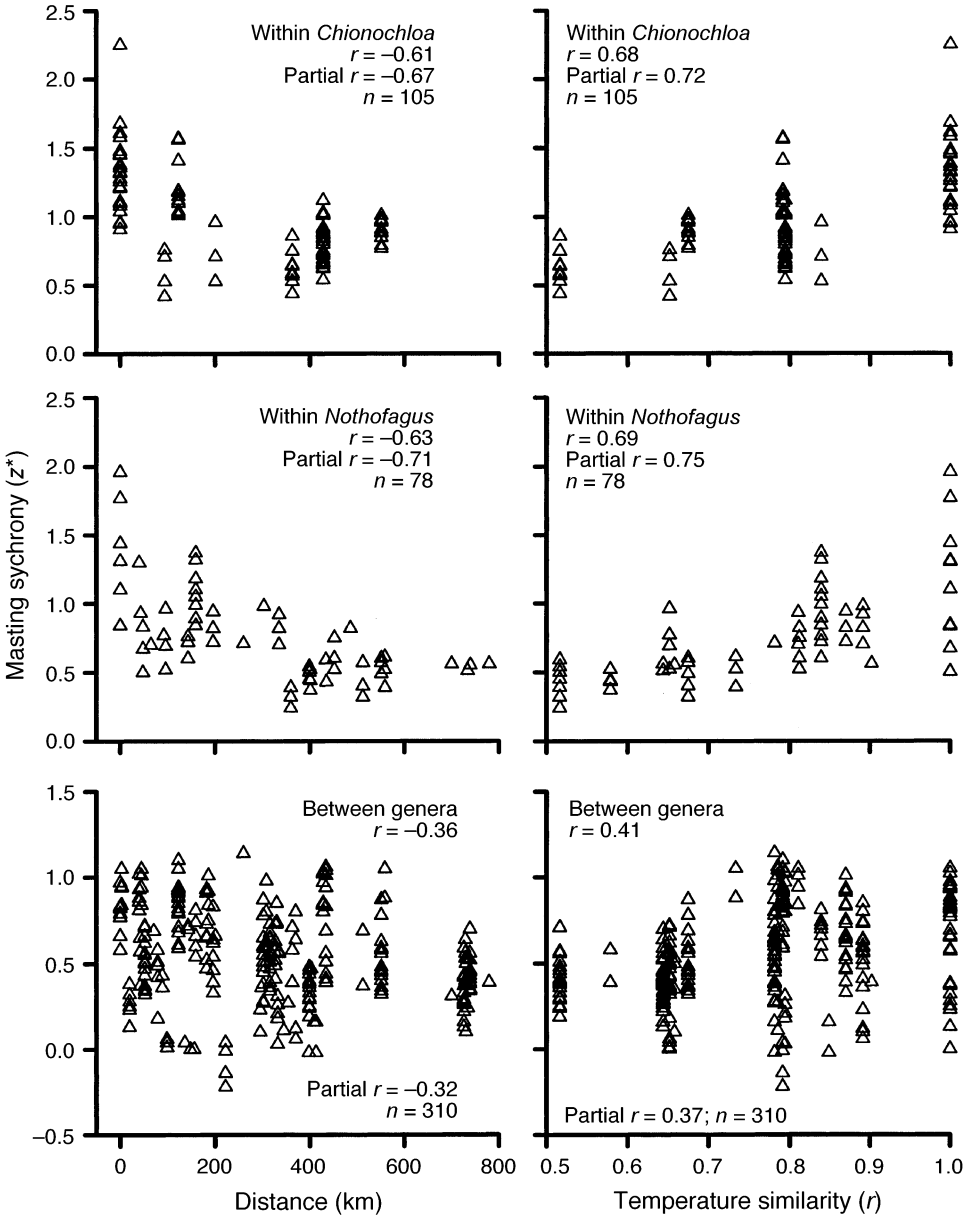

FIG. 5. Association of masting synchrony with geographic distance and similarity of summer temperature variations. Associations are graphed separately for synchrony within *Chionochloa*, within *Nothofagus*, and between genera except *Dacrydium*. All simple and partial Pearson correlations (r) are significant at $P \leq 0.0001$ based on Mantel randomization tests, and all are significant after sequential Bonferroni correction.

DISCUSSION

Fluctuations in seed production by New Zealand plants are synchronized among closely and distantly related taxa over great distances. We wish to emphasize two points: (1) although synchrony among sympatric species that share a seed predator could be favored by natural selection, there is no evidence to support the hypothesis that the synchrony across taxonomic families of New Zealand plants that we observed is itself adaptive, and (2) multitaxon masting synchrony appears to result from unrelated plants responding to shared or highly correlated environmental cues (temperatures during floral initiation), which act in a consistent manner across distance and habitats.

Synchrony among congenerics was strong, even between sites separated by >700 km, and within-genus synchrony may be adaptive. *Chionochloa* spp. were especially synchronous, with interspecific and intraspecific correlations of similar magnitude (Fig. 3). Synchrony among *Chionochloa* spp. probably serves to swamp seed predators that are generalists among *Chionochloa* spp. but rarely attack other genera (Kelly

et al. 2000, McKone et al. 2001), although this hypothesis has not been empirically tested. *Nothofagus* spp. may benefit from masting primarily through improved pollination success (Wardle 1984, Burrows and Allen 1991, Kelly et al. 2001) rather than predator satiation. The evolutionary significance of masting in *E. dentatus* and *Phormium* spp. is unclear, but in *Phormium* may derive from high accessory costs of reproduction (Kelly 1994).

We found a surprising level of masting synchrony among these ecologically disparate genera (Figs. 1 and 3). Seed and flower production by alpine grasses, montane nut-producing trees, lowland fleshy-fruited trees, and lowland herbaceous plants were substantially intercorrelated. Synchronous masting by such disparate species could be adaptive if they share seed predators (Shibata et al. 1998, Curran and Leighton 2000), but there is no evidence that any of the genera we studied share important seed predators. New Zealand lacks native generalist mammalian granivores (Webb and Kelly 1993) that may promote multitaxon masting synchrony in other terrestrial systems.

Dacrydium and *Phormium* are exceptions to our general pattern of results. *D. cupressinum* masting was not correlated with that of other taxa, although it was strongly synchronized between Ianthe and Wanganui State Forest sites 15 km apart (Fig. 3), and also between Wanganui and Pureora (Beveridge 1973), which is 650 km away in the central North Island ($n = 7$, $r = 0.93$, $P = 0.003$). As Norton and Kelly (1988) reported, *D. cupressinum* seed production is negatively correlated with temperatures during floral initiation (two summers before seedfall) and positively correlated with temperatures during seedfall. Norton and Kelly (1988) also showed that within-plant competition for resources between ripening seeds and new cone buds produces a negative correlation between seed production in a particular year and seed production two years before. Our reanalysis of these data suggests that masting by *D. cupressinum* is more strongly driven by temperature cues than by internal competition for resources. Standardized *D. cupressinum* seed production at Wanganui in year t was more strongly correlated with summer temperatures in year $t - 2$ ($r = -0.59$) than with seed production in year $t - 2$ ($r = -0.47$) or with summer temperatures in year t ($r = 0.53$). In addition, there was a strong partial correlation ($r = -0.46$) between seed production in year t and summer temperatures in year $t - 2$, after accounting for seed production in year $t - 2$. However, the partial correlation between seed production in years t and $t - 2$, after accounting for temperatures in year $t - 2$, was weak ($r = -0.23$). Thus, *D. cupressinum* appears to respond to the same cue (summer temperatures) as other taxa but in different directions and with different lags, resulting in lack of synchrony in concurrent masting.

Brockie (1986) reported that *Phormium* flowering was correlated with prior autumn temperatures based on a 10-yr time series. However, we found no statistically significant correlation with temperatures during the prior summer ($0.06 \leq r \leq 0.25$) or autumn ($-0.06 \leq r \leq 0.22$) in our analysis of further data from the same sites (18-yr time series), despite strong correlations with other genera (except *Dacrydium*). *Phormium* flowering was most strongly correlated with concurrent summer temperatures ($0.44 \leq r \leq 0.60$). However, *Phormium* spp. flower quite early in summer (early December) and floral buds elongate even earlier, so the link with concurrent summer temperatures is probably spurious. *Phormium* masting may respond to temperature cues missed by our coarse averaging over seasons.

Although masting was not strongly correlated with SOI in our analyses, New Zealand temperatures are affected by ENSO (Gordon 1986, Mullan 1998). However, a great deal of variance in New Zealand temperature anomalies is not explained by ENSO (Francis and Renwick 1998), and El Niño events may have greater and more predictable effects than La Niñas (Mullan 1996). Consequently, low SOI values (El Niño) may be better predictors of mast failures in New Zealand than high SOI values (La Niña) are of mast peaks. An ENSO-related weather cue is also linked to intergeneric masting synchrony in Malaysia and Borneo (Ashton et al. 1988, Curran et al. 1999, but cf. Wich and van Schaik 2000), and a similar link to climatic cues could explain the large-scale multitaxon masting synchrony in North American coniferous trees (Koenig and Knops 1998). Combined with our results, these studies suggest that weather-related cues contribute to synchronous reproduction over large spatial scales in widespread and taxonomically diverse floras.

Implications

Our results add to an extensive list of taxonomically disparate plants for which seed production is tightly associated with temperatures during critical periods of floral bud formation and differentiation. This shared cue appears to be responsible for the observed masting synchrony within and among genera of New Zealand plants. We note, as did Tapper (1996) for fruiting by ash (*Fraxinus excelsior*), that the cue seems to be deviation from local expected temperature, not absolute temperature. Thus, plants may mast in synchrony at different elevations, with greatly different mean temperatures, if temperature anomalies are spatially consistent. Local adaptation may enable fine-tuning of plants to particular sites across generations (Mark 1965), or plants might physiologically acclimate to their environment (but cf. Sullivan and Kelly 2000). However, if acclimatization is weak, then climatic changes could substantially alter the masting pattern (McKone et al. 1998). The commonness of floral-initiation temperatures as a masting cue suggests that the process of bud differentiation may involve a temperature-sensitive process shared by many masting taxa. Floral initiation and differentiation are affected by gib-

berellins, production of which may be affected by temperature (Pharis and King 1985). The existence of such a ready triggering mechanism may have contributed to the commonness of masting worldwide.

The importance of seasonal weather conditions, especially temperature during floral initiation, as cues for many plants to invest in reproduction implies that the frequency and intensity of masting are sensitive to global climate change (McKone et al. 1998), both directly through mean temperatures and indirectly through effects on phenomena like ENSO (Trenberth and Hoar 1996, Hunt 1999) and the North Atlantic Oscillation. Climatic change could therefore alter the temporal pattern of masting, with potential repercussions for plant communities and entire food webs. Production of a large seed crop typically entails reduced investment in growth that year (Koenig and Knops 1998). The masting response to temperature appears to be the result of local adaptation (Mark 1965, Greer 1979), implying that the growth–reproduction trade-off is subject to selection for optimum, rather than maximum, seed production. Consequently, if global warming causes masting plants to produce large seed crops more frequently, their growth and survival may be reduced, potentially altering plant community composition.

In addition, changes to the temporal pattern of masting are likely to affect consumer populations, with potentially widespread indirect effects. Strong numerical responses of granivores to regionally synchronized masting events can propagate a chain of indirect effects on other trophic levels at regional scales (Ostfeld and Keesing 2000). For example, high acorn production in eastern North America may suppress gypsy moth outbreaks (Elkinton et al. 1996, Ostfeld et al. 1996) but increase Lyme disease risk (Ostfeld et al. 2001), and *Nothofagus* mast seed events indirectly elevate the abundance of stoats, increasing predation on New Zealand native birds (O'Donnell and Phillipson 1996, Wilson et al. 1998). Consequently, an altered masting regime in response to changing climate could have repercussions for plant and animal populations on spatial scales measured in hundreds of kilometers.

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