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

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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 ecosystemlevel 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 km². 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

⁸Address correspondence to: Institute of Ecosystem Studies, Box AB, Millbrook, NY 12545 USA. E-mail: SchauberE@ecostudies.org 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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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 largescale 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 speciesence†PanelSymbolSiteN (yr)MethodChionochloacrassiuscula (Kirk) Zotov1AATakahe Valley28visual count, 100–200 plantsrubra Zotov1ABTakahe Valley28visual count, 100–200 plantstretifolia (Petrie) Zotov1ACTakahe Valley28visual count, 100–200 plantsrigida (Raoul) Zotov1ADTakahe Valley28visual count, 100–200 plantspallens Zotov1AADTakahe Valley28visual count, 100–200 plantspallens Zotov1AAHMt. Misery24visual count, 100–200 plantspallens1AHMt. Misery24visual count, 100–200 plantspallens1AHMt. Misery24visual count, 100–200 plantspallens1AHMt. Misery24visual count, 200 1 m² plots	
Chionochloacrassiuscula (Kirk) Zotov1AATakahe Valley28visual count, 100–200 plantsrubra Zotov1ABTakahe Valley28visual count, 100–200 plantsteretifolia (Petrie) Zotov1ACTakahe Valley28visual count, 100–200 plantsrigida (Raoul) Zotov1ACTakahe Valley28visual count, 100–200 plantspallens Zotov1AETakahe Valley28visual count, 100–200 plantspallens1AETakahe Valley28visual count, 100–200 plantspallens1AHMt. Misery24visual count, 200 1 m² plotsaustralis (Buchanan) Zotov1AIMt. Misery24visual count, 200 1 m² plots	
crassiuscula (Kirk) Zotov1AATakahe Valley28visual count, 100–200 plantsrubra Zotov1ABTakahe Valley28visual count, 100–200 plantsteretifolia (Petrie) Zotov1ACTakahe Valley28visual count, 100–200 plantsrigida (Raoul) Zotov1ADTakahe Valley28visual count, 100–200 plantspallens Zotov1ADTakahe Valley28visual count, 100–200 plantspallens1AETakahe Valley28visual count, 100–200 plantspallens1AHMt. Misery24visual count, 200 1 m² plotsaustralis (Buchanan) Zotov1AIMt. Misery24visual count, 200 1 m² plots	
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teretifolia (Petrie) Zotov1ACTakahe Valley28visual count, 100–200 plantsrigida (Raoul) Zotov1ADTakahe Valley28visual count, 100–200 plantspallens Zotov1AETakahe Valley28visual count, 100–200 plantspallens1AETakahe Valley28visual count, 100–200 plantspallens1AHMt. Misery24visual count, 200 1 m² plotsaustralis (Buchanan) Zotov1AIMt. Misery24visual count, 200 1 m² plots	0 plants
rigida (Raoul) Zotov1ADTakahe Valley28visual count, 100–200 plantspallens Zotov1AETakahe Valley28visual count, 100–200 plantspallens1AHMt. Misery24visual count, 200 1 m² plotsaustralis (Buchanan) Zotov1AIMt. Misery24visual count, 200 1 m² plots	0 plants
pallensZotov1AETakahe Valley28visual count, 100–200 plantspallens1AHMt. Misery24visual count, 200 1 m² plotsaustralis (Buchanan) Zotov1AIMt. Misery24visual count, 200 1 m² plots	0 plants
pallens1AHMt. Misery24visual count, 200 1 m² plotsaustralis (Buchanan) Zotov1AIMt. Misery24visual count, 200 1 m² plots	0 plants
australis (Buchanan) Zotov 1 A I Mt. Misery 24 visual count, 200 1 m ² plots	n² plots
-	n² plots
pallens 1 A F Mt. Hutt 15 visual count, 80 plants	its
macra Zotov 1 A G Mt. Hutt 11 visual count, 17–34 plants	plants
pallens I A J Camp Creek 19 visual count, 50 plants	its
<i>conspicua</i> (Forst. f.) Zotov 1 A K Camp Creek 19 visual count, 50 plants	its
flavescens Zotov 1 A L Camp Creek 20 visual count, 50 plants	its
crassuscula I A M Camp Creek 19 visual count, 50 plants	its
oreophila (Petrie) Zotov I A N Camp Creek 19 visual count, 50 plants	its
<i>rubra</i> I A O Camp Creek 19 Visual count, 50 plants	its
Dacrydium	
<i>cupressinum</i> 2 D A Wanganui S. F. 33 eight 0.86-m ² trays, 20 m ap	20 m apart
<i>cupressinum</i> 3 D B Ianthe Forest 11 350.28 -m ² seed trays, 20 m a	s, 20 m apart
Elaeocarpus	
dentatus 4 C D Orongorongo 33 0.28-m ² trays under 21 trees	21 trees
Nothofagus	
solandri (Hook, f.) Oerst. 5 B A Craigieburn A 35 eight 0.28-m ² trays 40 m apa	0 m apart
solandri 5 B B Craigieburn B 35 eight 0.28-m ² trays 40 m apa	0 m apart
solandri 5 B C Craigieburn C 35 eight 0.28-m ² trays 40 m apa	0 m apart
solandri 6 B D Takahe Valley 20 eight 0.28-m ² trays 40 m apa	0 m apart
solandri 5 B E Mt. Thomas 34 eight 0.28-m ² trays 40 m apa	0 m apart
menziesii (Hook, f.) Oerst. 7 B F Rowallan 19 eight 0.28-m ² trays 40 m apa	0 m apart
menziesii 8 B G Takitimu 29 2 to 8 0.28-m ² trays 40 m ap	40 m apart
<i>fusca</i> (Hook. f.) Oerst. 7 B H Rahu 16 eight 0.28-m ² trays 40 m apa	0 m apart
<i>fusca</i> 6 B I Eglinton 11 eight 0.28-m ² trays	
solandri 9 B J Mt. Misery 24 10 0.28-m ² trays	
<i>fusca</i> 9 B K Mt. Misery 24 170.28 -m ² trays	
<i>menziesii</i> 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	3
Phormium	
tenax J. R. et G. Forst. 11 C A Ngauranga 18 visual count, 250 plants	unts
tenax 11 C B Thorndon 18 visual count, 260 plants	ints
cookianum Le Jolis 11 C C Thorndon 18 visual count, 45 plants	its

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

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 $>150\,000$ km². 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/m² 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-m² 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 $n_{\rm adj} < 30$ 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 $n_{adj} \ge$ 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 May 2002

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 3mo 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





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.

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 10000 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).

RESULTS

Synchrony within and among genera

Masting was highly synchronous within genera (Fig. 3), as all 171 within-genus comparisons with $n \ge 10$ yr of overlap yielded r > 0.26 (median r = 0.71). Out of 160 within-genus cross-correlations valid for significance testing ($n_{adj} \ge 10$), 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 $n_{\rm adj} \ge 10$ 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 $(-0.69 \le r \le$ -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 ($n_{adj} \ge 10$) cross-correlations identified a priori between seed production and temperature during floral initiation, 20 had P < 0.05 and another four correlations had $0.05 \le P \le 0.10$. 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* ($0.13 \le r \le 0.59$, 12 of 15 P < 0.05), Elaeocarpus (r = 0.40, P = 0.038), and *Nothofagus* $(0.28 \le r \le 0.63, 6 \text{ of } 13 P < 0.05)$.

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

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).

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).

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).



1.0

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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 $P \le 0.0001$ 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 $(0.06 \le r \le 0.25)$ or autumn $(-0.06 \le r \le 0.22)$ 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 $(0.44 \le r \le 0.60)$. 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 gibberellins, 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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LITERATURE CITED

- Abraham, B., and J. Ledolter. 1983. Statistical methods for forecasting. Wiley and Sons, New York, New York, USA.
- Allen, R. B., and K. H. Platt. 1990. Annual seedfall variation in *Nothofagus solandri* (Fagaceae), Canterbury, NZ. Oikos 57:199–206.
- Alley, J. C., B. M. Fitzgerald, P. H. Berben, and S. J. Haslett. 1998. Annual and seasonal patterns of litter-fall of hard beech (*Nothofagus truncata*) and silver beech (*Nothofagus menziesii*) in relation to reproduction. New Zealand Journal of Botany **36**:453–464.
- Ashton, P. S., T. J. Givnish, and S. Appanah. 1988. Staggered flowering in the Dipterocarpaceae: new insights into floral induction and the evolution of mast fruiting in the aseasonal tropics. American Naturalist 132:44–66.
- Beveridge, A. E. 1973. Regeneration of podocarps in a central North Island forest. New Zealand Journal of Forestry 18:23–35.
- Bjørnstad, O. N., R. A. Ims, and X. Lambin. 1999. Spatial population dynamics: analyzing patterns and processes of population synchrony. Trends in Ecology and Evolution 14: 427–432.
- Brockie, R. E. 1986. Periodic heavy flowering of New Zealand flax (*Phormium*, Agavaceae). New Zealand Journal of Botany 24:381–386.
- Burrows, L. E., and R. B. Allen. 1991. Silver beech (*Nothofagus menziesii* (Hook. f.) Oerst.) seedfall patterns in the Takitimu Range, South Island, New Zealand. New Zealand Journal of Botany 29:361–365.
- Connor, H. E. 1966. Breeding systems in New Zealand grasses VII. Periodic flowering of snow tussock *Chionochloa rigida*. New Zealand Journal of Botany 4:392–397.
- Cowan, P. E., and D. C. Waddington. 1990. Suppression of fruit production of the endemic forest tree, *Elaeocarpus dentatus*, by introduced marsupial brushtail possums, *Trichosurus vulpecula*. New Zealand Journal of Botany 28: 217–224.
- Crawley, M. J., and C. R. Long. 1995. Alternate bearing, predator satiation and seedling recruitment in *Quercus robur* L. Journal of Ecology 83:683–696.
- Curran, L. M., I. Caniago, G. D. Paoli, D. Astianti, M. Kusneti, M. Leighton, C. E. Nirarita, and H. Haeruman. 1999. Impact of El Niño and logging on canopy tree recruitment in Borneo. Science 286:2184–2188.
- Curran, L. M, and M. Leighton. 2000. Vertebrate responses to spatiotemporal variation in seed production of mastfruiting Dipterocarpaceae. Ecological Monographs 70:101– 128.
- Edgell, S. E., and S. M. Noon. 1984. Effect of violation of normality on the *t* test of the correlation coefficient. Psychological Bulletin **95**:576–583.
- Elkinton, J. S., W. M. Healy, J. P. Buonaccorsi, G. H. Boettner, A. M. Hazzard, H. R. Smith, and A. M. Liebhold. 1996. Interactions among gypsy moths, white-footed mice, and acorns. Ecology 77:2332–2342.
- Fitzgerald, B. M., M. J. Daniel, A. E. Fitzgerald, B. J. Karl, M. J. Meads, and P. R. Notman. 1996. Factors affecting the numbers of house mice (*Mus musculus*) in hard beech (*Nothofagus truncata*) forest. Journal of the Royal Society of New Zealand 26:237–249.
- Forcella, F. 1981. Ovulate cone production in pinyon: negative exponential relationship with late summer temperature. Ecology 62:488–491.
- Francis, R. I. C. C., and J. A. Renwick. 1998. A regressionbased assessment of the predictability of New Zealand climate anomalies. Theoretical and Applied Climatology 60: 21–36.
- Gordon, N. D. 1986. The Southern Oscillation and New Zealand weather. Monthly Weather Review **114**:371–387.
- Greer, D. H. 1979. Effects of long-term preconditioning on

growth and flowering of some snow tussock (*Chionochloa* spp.) populations in Otago, New Zealand. Australian Journal of Botany **27**:617–630.

- Hanski, I., and I. P. Woiwod. 1993. Spatial synchrony in the dynamics of moth and aphid populations. Journal of Animal Ecology 62:656–668.
- Herrera, C. M., P. Jordano, J. Guitián, and A. Traveset. 1998. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. American Naturalist 152:576–594.
- Hunt, A. G. 1999. Understanding a possible correlation between El Niño occurrence frequency and global warming. Bulletin of the American Meteorological Society 80:297– 300.
- James, I. L., and D. A. Franklin. 1978. Recruitment, growth, and survival of rimu seedlings in selectively logged terrace rimu forest. New Zealand Journal of Forestry Science 8: 207–212.
- Janzen, D. H. 1971. Seed predation by animals. Annual Review of Ecology and Systematics 2:465–492.
- Jedrzejewska, B., and W. Jedrzejewski. 1998. Predation in vertebrate communities: the Bialowieza primeval forest as a case study. Springer-Verlag, Berlin, Germany.
- Jones, C. G., R. S. Ostfeld, M. P. Richard, E. M. Schauber, and J. O. Wolff. 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. Science 279: 1023–1026.
- Kelly, D. 1994. The evolutionary ecology of mast seeding. Trends in Ecology and Evolution **9**:465–470.
- Kelly, D., A. L. Harrison, W. G. Lee, I. J. Payton, P. R. Wilson, and E. M. Schauber. 2000. Predator satiation and extreme mast seeding in 11 species of *Chionochloa* (Poaceae). Oikos 90:477–488.
- Kelly, D., D. E. Hart, and R. B. Allen. 2001. Evaluating the wind-pollination benefits of mast seeding. Ecology 82:117– 126.
- Kelly, D., M. J. McKone, K. J. Batchelor, and J. R. Spence. 1992. Mast seeding of *Chionochloa* (Poaceae) and predispersal seed predation by a specialist fly (*Diplotoxa*, Diptera: Chloropidae). New Zealand Journal of Botany **30**: 125–133.
- Kelly, D., and J. J. Sullivan. 1997. Quantifying the benefits of mast seeding on predator satiation and wind pollination in *Chionochloa pallens* (Poaceae). Oikos 78:143–150.
- King, C. M. 1983. The relationships between beech (*Nothofagus* sp.) seedfall and populations of mice (*Mus musculus*), and the demographic and dietary responses of stoats (*Mustela erminea*), in three New Zealand forests. Journal of Animal Ecology **52**:141–166.
- Koenig, W. D. 1999. Spatial autocorrelation in ecological studies. Trends in Ecology and Evolution 14:22–26.
- Koenig, W. D., and J. M. H. Knops. 1998. Scale of mastseeding and tree-ring growth. Nature 396:225–226.
- Koenig, W. D., and J. M. H. Knops. 2000. Patterns of annual seed production by Northern Hemisphere trees: a global perspective. American Naturalist 155:59–69.
- Koenig, W. D., J. M. H. Knops, W. J. Carmen, and M. T. Stanback. 1999. Spatial dynamics in the absence of dispersal: acorn production by oaks in central coastal California. Ecography 22:499–506.
- Lester, D. T. 1967. Variation in cone production of red pine in relation to weather. Canadian Journal of Botany 45: 1683–1691.
- Maguire, W. P. 1956. Are ponderosa pine cone crops predictable? Journal of Forestry 54:778–779.
- Manly, B. F. J. 1997. Randomization, bootstrap and Monte Carlo methods in biology. Second edition. Chapman and Hall, London, UK.
- Mark, A. F. 1965. Ecotypic differentiation in Otago popu-

lations of narrow-leaved snow tussock, *Chionochloa rigida*. New Zealand Journal of Botany **3**:277–299.

- Mark, A. F. 1970. Floral initiation and development in New Zealand alpine plants. New Zealand Journal of Botany 8: 67–75.
- Matthews, J. D. 1955. The influence of weather on the frequency of beech mast years in England. Forestry 28:107– 116.
- McKone, M. J., D. Kelly, A. L. Harrison, J. J. Sullivan, and A. J. Cone. 2001. Biology of insects that feed in the inflorescences of *Chionochloa pallens* (Poaceae) in New Zealand and their relevance to mast seeding. New Zealand Journal of Zoology 28:89–101.
- McKone, M. J., D. Kelly, and W. G. Lee. 1998. Effect of climate change on mast-seeding species: frequency of mass flowering and escape from specialist insect seed predators. Global Change Biology 4:591–597.
- Mullan, A. B. 1996. Non-linear effects of the Southern Oscillation in the New Zealand region. Australian Meteorological Magazine 45:83–99.
- Mullan, A. B. 1998. Southern hemisphere sea-surface temperatures and their contemporary and lag association with New Zealand temperature and precipitation. International Journal of Climatology 18:817–840.
- Nilsson, S. G., and U. Wästljung. 1987. Seed predation and cross-pollination in mast-seeding beech (*Fagus sylvatica*) patches. Ecology 68:260–265.
- Norton, D. A., and D. Kelly. 1988. Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. Functional Ecology **2**:399–408.
- O'Donnell, C. F. J., and P. J. Dilks. 1994. Foods and foraging of forest birds in temperate rainforest, South Westland, New Zealand. New Zealand Journal of Ecology **18**:87–107.
- O'Donnell, C. F. J., and S. Phillipson. 1996. Predicting the occurrence of mohua predation from the seedfall, mouse and predator fluctuations in beech forest. New Zealand Journal of Zoology 23:287–293.
- Ostfeld, R. S., C. G. Jones, and J. O. Wolff. 1996. Of mice and mast: ecological connections in eastern deciduous forests. BioScience 46:323–330.
- Ostfeld, R. S., and F. Keesing. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. Trends in Ecology and Evolution **15**:232–237.
- Ostfeld, R. S., E. M. Schauber, C. D. Canham, F. Keesing, C. G. Jones, and J. O. Wolff. 2001. Effects of acorn production and mouse abundance on abundance and *Borrelia burgdorferi*-infection prevalence of nymphal *Ixodes scapularis* ticks. Vector Borne and Zoonotic Diseases 1:55– 63.
- Pharis, R. P., and R. W. King. 1985. Gibberellins and reproductive development in seed plants. Annual Review of Plant Physiology 36:517–568.
- Pucek, Z., W. Jedrzejewski, B. Jedrzejewska, and M. Pucek. 1993. Rodent population dynamics in a primeval deciduous forest (Bialowieza National Park) in relation to weather, seed crop, and predation. Acta Theriologica 38:199–232.
- Rice, W. R. 1989. Analyzing tables of statistical tests. Evolution 43:223–225.
- Salinger, M. J., R. E. Basher, B. B. Fitzharris, J. E. Hay, P. D. Jones, J. P. MacVeigh, and I. Schmidley-Lelu. 1995. Climate trends in the south-west Pacific. International Journal of Climatology 15:285–302.
- Sciremammano, F. Jr., 1979. A suggestion for the presentation of correlations and their significance levels. Journal of Physical Oceanography 9:1273–1276.
- Shibata, M., H. Tanaka, and T. Nakashizuka. 1998. Causes and consequences of mast seed production of four co-occurring *Carpinus* species in Japan. Ecology **79**:54–64.
- Silvertown, J. W. 1980. The evolutionary ecology of mast

seeding in trees. Biological Journal of the Linnaean Society 14:235–250.

- Smith, C. C., J. L. Hamrick, and C. L. Kramer. 1990. The advantage of mast years for wind pollination. American Naturalist 136:154–166.
- Sokal, R. R., and F. J. Rohlf. 1981. Biometry: the principles and practice of statistics in biological research. Second edition. W. H. Freeman and Co., New York, New York, USA.
- Sork, V. L., J. Bramble, and O. Sexton. 1993. Ecology of mast-fruiting in three species of North American deciduous oaks. Ecology 77:2567–2572.
- StatSoft. 1994. STATISTICA for Windows (Version 5.1). Volume I. General Conventions and Statistics I. StatSoft, Inc., Tulsa, Oklahoma, USA.
- Sullivan, J. J., and D. Kelly. 2000. Why is mast seeding in *Chionochloa rubra* (Poaceae) most extreme where seed predation is lowest? New Zealand Journal of Botany 38:221– 233.
- Tapper, P. G. 1996. Long-term patterns of mast fruiting in Fraxinus excelsior. Ecology 77:2567–2572.

- Trenberth, K. E., and T. J. Hoar. 1996. The 1990–1995 El Niño-southern oscillation event: longest on record. Geophysical Research Letters 23:57–60.
- Wardle, J. A. 1984. The New Zealand beeches: ecology, utilization and management. New Zealand Forest Service, Christchurch, New Zealand.
- Wardle, J. A. 1991. Vegetation of New Zealand. Cambridge University Press, Cambridge, UK.
- Webb, C. J., and D. Kelly. 1993. The reproductive biology of the New Zealand flora. Trends in Ecology and Evolution 8:442–447.
- Wich, S. A., and C. P. Van Schaik. 2000. The impact of El Niño on mast fruiting in Sumatra and elsewhere in Malesia. Journal of Tropical Ecology 16:563–577.
- Wilson, P. R., B. J. Karl, R. J. Toft, J. R. Beggs, and R. H. Taylor. 1998. The role of introduced predators and competitors in the decline of kaka (*Nestor meridionalis*) populations in New Zealand. Biological Conservation 83:175– 185.