

## Masting in *Buxus balearica*: assessing fruiting patterns and processes at a large spatial scale

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Masting consists of the synchronous highly variable seed production among years by a plant population. We studied spatiotemporal variation in fruit production in ten populations of *Buxus balearica* (six in the Balearic Islands and four in the Iberian Peninsula) from 2001 to 2004 in the light of masting. In some of them we assessed, by means of both observational and experimental data, the relationship between fruit production and some abiotic variables, the role of previous reproduction, the “pollination efficiency” and the “predator satiation” hypotheses, as well as the consequences for seedling density and survival. Fruit production in *B. balearica* showed substantial between-year variation, especially in island compared to mainland populations. Correlative evidence indicated that this variation and its geographic pattern were related to differences between regions in rainfall variability, cost of reproduction and the degree of ambophily. We found no indication of predator satiation. However, experimental tests failed to support many of our results, namely a negative effect of previous reproduction on future flowering in island populations and lower pollen limitation with increasing flower production. We therefore warn against exclusive reliance on correlations when testing hypotheses related to masting. In addition, seedling recruitment increased after some episodes of high fruit production but probably additional factors had a role in recruitment, suggesting that mast events not always translate into increased reproductive success. Although a limited time series only allows considering *B. balearica* as showing ‘putative’ masting, weather and pollination-related processes are good candidates for further exploration of fruiting patterns and processes at a large spatial scale.

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Mast seeding (masting hereafter) consists of the synchronous highly variable seed production among years by a plant population (Kelly 1994). A continuum exists from annual reproduction through unsynchronized supra-annual reproduction to strict masting (Kelly 1994, Herrera et al. 1998), depending on the degree of synchrony achieved in the originally chaotic fluctuation in fruit production by individual trees (Koenig et al.

2003). Patterns of annual variation in seed production have been mainly investigated at the plant population level, and only rarely at the individual level (but see Herrera 1998, Rees et al. 2002, Koenig et al. 2003).

The ecological and evolutionary significance of masting (Kelly 1994, Kelly and Sork 2002) revolves around the following two groups of hypotheses: (1) the “resource matching” hypothesis, which proposes that plants

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allocate more resources to reproduction only under more favourable conditions, i.e. reproductive output passively adjusts to fluctuations in available resources driven by climate, and (2) the “economy of scale” argument, which states that larger, occasional reproductive effort is more successful than smaller, regular effort. This second category includes the ‘pollination efficiency’ (Nilsson and Wästljung 1987, Norton and Kelly 1988, Smith et al. 1990), the “predator satiation” (Janzen 1971, Silvertown 1980) and the “attraction of seed dispersers” (for those biotically dispersed plants; Ims 1990) hypotheses. The name of each hypothesis refers to the factor considered as responsible for the fitness benefit of mast seeding.

The abovementioned hypotheses are supported to a different extent by empirical data (Kelly and Sork 2002). Two findings are usually considered to support the “resource matching” hypothesis: (1) correlations between mast years and previous climatic conditions (Norton and Kelly 1988, Houle 1999, Piovesan and Adams 2001) and (2) negative lag 1 or 2 temporal autocorrelations in seed production, usually interpreted as resource depletion after reproduction (Norton and Kelly 1988, Piovesan and Adams 2001, Kobro et al. 2003). However, both kinds of evidence face problems: the first is also compatible with the role of climate as a synchronizing cue (as required by the “economy of scale” hypotheses; see however, Abrahamson and Layne 2003); the second cannot produce by itself synchronization at a population level (Norton and Kelly 1988, Rees et al. 2002).

The “economy of scale” arguments are generally accepted to adequately explain mast seeding and have received most empirical and experimental attention. Pollen limitation (Allison 1990), predator satiation (Nilsson 1985, Sork 1993, Tapper 1996, Kobro et al. 2003), or both (Nilsson and Wästljung 1987, Koenig et al. 1994, Shibata et al. 1998, 2002) have been shown to be involved in masting. The “attraction of seed dispersers” hypothesis, in contrast, has not received so much attention. Although Herrera et al. (1998) and Kelly and Sork (2002) concluded that masting was comparatively less frequent in species with fleshy fruits, improved dispersal in masting species with scatter hoarded fruits has been demonstrated (Vander Wall 2002).

A possibility not often considered (but see Sullivan and Kelly 2000) is that the underlying causes of masting may differ among populations depending on their ecological context (Kelly et al. 2001). Indeed, both pollen limitation (Burd 1994) and seed predation (Hulme and Benkman 2002) have been shown to vary among populations in several species. Therefore, the strength of the selective advantage of mast seeding could differ among sites, generating differences in masting patterns (Sullivan and Kelly 2000). In fact, differences in masting patterns have been found among sites for several species,

e.g. larger inter-annual variability at higher altitudes (Webb and Kelly 1993, Kelly et al. 2000, 2001, Sullivan and Kelly 2000), or latitudinal differences in the amplitude of the reproductive cycle (Koenig and Knops 2000, Kelly and Sork 2002, Satake et al. 2004). Detection of these differences requires studies at a large spatial scale in which not only patterns, but also processes, are studied. For instance, as pollen limitation is considered to be the main force driving masting behaviour in anemophilous species (reviewed by Koenig and Ashley 2003), spatial differences in the masting patterns in wind-pollinated masting species, could be predicted if there are spatial differences in the extent of pollen limitation, or if alternative and effective reproductive modes, such as ambophily (i.e. pollination by both wind and insects), are acting in some regions.

Moreover, masting literature generally lacks experimental evidence to support the observational data and most studies rely exclusively on correlations to proof some hypotheses (especially pollination efficiency) as the cause of selective advantage of such behaviour (Kelly and Sullivan 1997, Shibata et al. 1998, Houle 1999; but see Augspurger 1981). As far as we know, no study has used before pollen limitation indexes after hand-pollination experiments to support the correlative evidence.

*Buxus balearica* is a Mediterranean ambophilous shrub, currently distributed along fragmented and isolated populations. We assessed the occurrence of masting in this species over a large spatial scale, using six populations from the Balearic Islands and four from the Iberian Peninsula. First, we investigated the variability in fruit production both at individual and population levels, and related the latter to abiotic factors (elevation, mean rainfall and variability in the rainfall). Second, we studied the role of previous reproduction as a proximate cue for flowering and fruiting. Third, we tested the “pollination efficiency” and “predator satiation” hypotheses in this ballistically dispersed species. And fourth, we evaluated the consequences of mast seeding on seedling density and survival. As long as possible, we added experimental tests of masting processes to the observational evidence and extended the discussion to differences found at a large scale both in patterns and processes underlying masting.

## Material and methods

### Study species

*Buxus balearica* Lam. (Buxaceae) is an evergreen monoecious shrub (*Buxus* hereafter) endemic to the Mediterranean Basin that occurs in limestone lands, often on rocks, under subhumid conditions, between sea level and 1000 m (Benedí 1997). It flowers from late February to May, depending on the population. The species is ambophilous and it is also capable of selfing

(Lázaro and Traveset 2005). It is monoecious and a single individual can produce over 30 000 inflorescences. Each inflorescence contains one female flower surrounded by a variable number (one to six, mainly four) of male flowers; a variable number of male inflorescences can also be found in some individuals (Lázaro 2005). The dehiscent fruits disperse seeds ballistically from June to July and dispersed seeds are removed in a high (mean ca 80%) percentage mainly by generalist rodents and ants (Lázaro 2005). Almost none of them are efficient seed dispersers (Lázaro 2005); therefore, although eventual secondary dispersal is possible, estimates of seed removal can be in fact considered as estimates of seed predation. Seeds germinate in March, usually in low densities and under *Buxus* plants; most seedlings die during the hot, dry summer (Lázaro 2005). There is no permanent soil seed bank in this species (Lázaro 2005).

### Study areas

The four Iberian Peninsula populations (Fig. 1) were Cerro Gordo, a coastal population close to a creek (Granada province), Frigiliana, located at a wash in Aljara mountains (Málaga province), and two subpopulations (I and II) located at different elevations of Rágol, in a canyon in Gádor mountains (Almería province). In the Balearic Islands, three of the six populations studied in Mallorca, the largest island, are located on the coast: in a hollow (Andratx), in a limestone cliff (Sant Vicenç I), and in a rocky plateau

(Sant Vicenç II), while the other three are found at high elevations within the Serra de Tramuntana, a mountain range extending from northwest to southwest: Lluc occurs in an Aleppo pine forest, while Cúber and Galatzó are found in mountain limestone cliffs. At Sant Vicenç, the two subpopulations considered differed in exposure to seawind (Sant Vicenç I being more protected than Sant Vicenç II). At all ten sites, vegetation was dominated by Mediterranean shrubs. Traits of each population are given in Table 1. Rainfall data (Table 1) were taken from the nearest meteorological stations to the study areas. For the Balearic Islands populations a five-year data series was available, while for the Iberian Peninsula populations a ten-year data series was available.

### Spatio-temporal variation in fruit production and seed set

Fruit production was estimated by counting the number of fruits in a portion (usually 1/4) of the canopy and extrapolating to the whole canopy. We estimated fruit production in all populations from a total of 15–45 (depending upon population size) haphazardly chosen individuals. Fruit production was monitored from 2001 to 2004 in Rágol I, Rágol II, Cúber and Galatzó, from 2002 to 2004 in Cerro Gordo, Frigiliana, Andratx, Sant Vicenç I, and Lluc, and from 2003 to 2004 in Sant Vicenç II. All monitored individuals reproduced at least once during the four-year period.

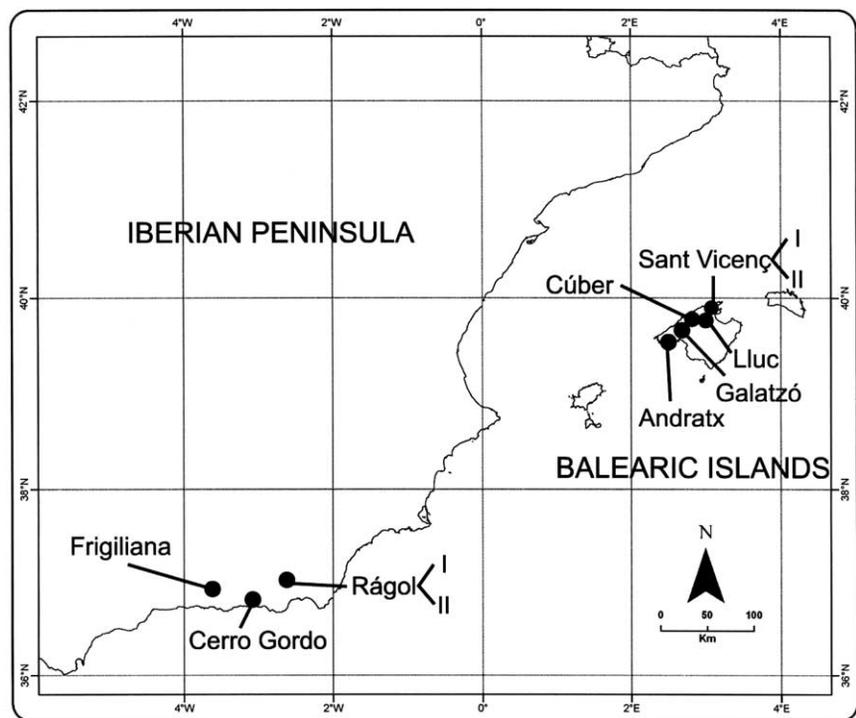


Fig. 1. Map of the western Mediterranean basin where the study populations are located.

Table 1. Environmental characteristics and UTM coordinates of the studied sites (M: mainland; I: island). Rainfall is showed as annual averages (mm) from ten-year (Iberian Peninsula) or five-year data series (Balearic Islands) (meteorological station data).  $CV_{rainfall}$ : coefficient of variation of annual rainfall. Variables measured and experiments performed in each population are indicated in the last column: F: fecundity; BR: bud removal; PL: pollen limitation; SP: seed predation; D: seedling density, and S: seedling survival.

Site	Region	UTM	Elevation (m)	Rainfall	$CV_{rainfall}$	Sampling type
Cerro Gordo	Iberian Peninsula (M)	30SVF3068	0	460.52	0.341	F-PL-D-S
Frigiliana	Iberian Peninsula (M)	30SVF2170	300	462.35	0.242	F-D-S
Rágol I	Iberian Peninsula (M)	30SWF2792	440	258.24	0.351	F- PL-SP-D-S
Rágol II	Iberian Peninsula (M)	30SWF2793	720	328.71	0.371	F-SP-D-S
Andratx	Balearic Island (I)	31SDD4875	5	489.65	0.448	F-D-S
Sant Vicenç I	Balearic Island (I)	31SEE0420	40	318.13	0.357	F-BR-PL-D-S
Sant Vicenç II	Balearic Island (I)	31SEE0420	60	318.13	0.357	F-BR-D-S
Lluc	Balearic Island (I)	31SDE9106	320	1253.65	0.454	F-PL-SP-D-S
Cúber	Balearic Island (I)	31SDE8202	660	1079.00	0.502	F-BR-SP-D-S
Galatzó	Balearic Island (I)	31SDD5687	900	746.05	0.359	F-PL-SP-D-S

A population-level coefficient of variation ( $CV_p$  hereafter) was computed from the mean and standard deviation (SD/mean) of the overall fruit production obtained for each population and year by adding fruit crops of all monitored plants (only those individuals monitored all study years were included, following Herrera 1998). For each individual plant, we also calculated a coefficient of variation ( $CV_i$  hereafter) in fruit production across all study years, and obtained afterwards a population mean  $\overline{CV}_i$ . Mean pairwise correlation coefficients were used to assess the degree of supra-annual synchrony among individuals (Buonaccorsi et al. 2003).

Seed set (seeds/ovules per fruit) was estimated in 2001–2003 in six populations (Rágol I, Rágol II, Sant Vicenç I, Lluc, Cúber and Galatzó) and in 2002–2003 in three additional populations (Cerro Gordo, Frigiliana, and Andratx). We randomly collected 15–30 fruits from each of 10–15 randomly chosen individuals per population, and counted the number of ovules and mature seeds after dissecting them.

### Relationship between abiotic conditions and variability in fruit production

We examined the relationship between our three estimates of variability in fruit production, i.e.  $CV_p$ ,  $\overline{CV}_i$  and synchrony, and the following abiotic variables: elevation, mean rainfall and the variability (CV) in the rainfall.

### Previous reproduction as a proximate cue for flower and fruit production

We assessed the effect of previous reproduction on subsequent fruit production in two ways. First, we related fecundity (flower and fruit production) in 2004 to fecundity in 2003 and to plant size, using path analysis. Flower production was estimated following the same procedure than for fruit production. We

estimated individual size as:  $volume = \frac{2}{3} \pi (h \times D/2 \times d/2)$ , where  $h$  is plant height,  $D$  is the longest canopy diameter and  $d$  is the shortest canopy diameter, all measured to the nearest cm. Second, to indirectly estimate the cost of reproduction at a branch level we carried out a flower bud removal experiment during 2003 and 2004 in three of the Mallorcan populations: Sant Vicenç I, Sant Vicenç II and Cúber. In 2003, two branches bearing similar numbers of flower buds were labelled on 15 individuals per population. All buds from one branch were removed whereas the other intact branch served as control. In spring 2004, we recorded the number of inflorescences and fruits in both control and treated branches.

### Testing the “pollination efficiency” and the “predator satiation” hypotheses

We tested the “pollination efficiency” hypothesis in two ways. First, we analyzed the correlation between mean flower production and fruit production, fruit set (estimated as fruits/flowers per plant), seed set and seed production (fruit production  $\times$  seed set). Second, we studied the relationship between mean flower production and mean pollen limitation at the population level, assessed in an experimental way. Flower production and pollen limitation were estimated during the spring of 2002 and 2003 in five populations: Cerro Gordo and Rágol I in the mainland, and Sant Vicenç I, Lluc and Galatzó in the island. A pollen limitation index was obtained using the formula:  $PL = 1 - C/XI$ , where  $C$  and  $XI$  are percentage of initiated fruits after open pollinations and hand-pollinations, respectively (Lázaro and Traveset, in press).

The “predator satiation” hypothesis was tested by quantifying post-dispersal seed removal (an estimate of seed predation) from 2001 to 2003 in five populations (Rágol I, Rágol II, Lluc, Cúber, and Galatzó). In 2002, seed removal could only be studied in Rágol I and Cúber due to the low fruit production in the other populations.

We placed a total of 20 trays in each population and year (except when very few or no seeds were produced). Trays consisted of 15 × 15 cm plastic net with 10 seeds each. The experiment was set in June, July and/or August (depending on the phenology of each population), and trays were monitored weekly until all seeds had disappeared or until six weeks went on without seed removal.

### Variation in seedling density and survival

We recorded the number of seedlings emerging in spring after each reproductive event (2002, 2003 and 2004) in all ten populations. Due to low seedling emergence, we counted every seedling found and divided it by the total area examined in each population to obtain seedling density. In 2004, however, seedling density in Lluc was quite high and thus this year we counted the number of seedlings in a total of 240 plots of 25 × 30 cm. An overall seedling density was obtained by pooling all plots. Seedling survival data for each year and population, taken from Lázaro (2005), were utilised to test the relationship between seed production and seedling survival.

### Statistical analysis

We used t tests to compare  $\overline{CV}_i$ ,  $CV_p$  and synchrony between mainland and island populations. We also compared  $\overline{CV}_i$  among populations by means of one-way ANOVA. All comparisons were performed for our 2002–2004 (nine populations) time series only, because sample size for our 2001–2004 time series (four populations), which clearly overlap with the former, precluded conclusive statistical results.

We used Pearson correlations to determine the relationships between: (1)  $\overline{CV}_i$ ,  $CV_p$  and synchrony; (2) mean flower production and several estimates of reproductive success: fruit and seed production and fruit and seed set (all populations and years pooled); (3) flower production and the index of pollen limitation; (4) seed predation (seed removal) and fruit production; (5) seedling density and previous seed production, and (6) seedling survival and previous seed production. We examined the relationship between  $CV_p$ ,  $\overline{CV}_i$  and synchrony and elevation, mean rainfall and CV of rainfall using Sperman's correlations.

Separate path analyses for mainland and island populations were performed to study the influence of plant size and number of flowers and fruits in 2003 on the number of flowers and fruits in 2004 (see model in Fig. 3; CALIS proc., SAS). Data were previously normalized with the log transformation.

We used generalized linear models and repeated measures analyses (GLIM; GENMOD Proc., in SAS)

to test for differences in the probability of flowering and fruiting and the intensity of flowering depending on previous reproduction (debudding experiment). For these analyses all populations were pooled as the interaction population × treatment was not significant. Individual was included as a random factor (subject), and year (within-subject) and debudding treatment were fixed factors in the models. Probability of flowering and fruiting were analyzed using binomial distributions with logit as link functions, whereas a gamma distribution with log as a link function was the best fitting the observed data on the intensity of flowering (whole-model deviance = 1.135).

All contrasts obtained in SAS were corrected with the sequential Bonferroni test (Rice 1989). Except otherwise indicated, mean values ± standard errors are presented.

## Results

### Spatio-temporal variation in fruit production

Fruit production and seed set showed a broad variation among years in *Buxus*, although the extent of that variation differed among populations (Fig. 2). The year 2003 was a high fruiting year in most populations, and at least in island populations the same was true for 2001 (Fig. 2). On the contrary, 2002 and 2004 were low fruiting years in most populations (Fig. 2).

$CV_p$ ,  $\overline{CV}_i$  and synchrony for each population are shown in Table 2. The relationships between  $CV_p$  and  $\overline{CV}_i$  and between  $\overline{CV}_i$  and synchrony were positive and significant ( $n=9$ ,  $r=0.914$ ,  $P=0.00006$  and  $n=9$ ,  $r=0.827$ ,  $P=0.006$ , respectively). We did not find a significant relationship between  $CV_p$  and synchrony ( $n=9$ ,  $r=0.539$ ,  $P=0.134$ ).

$CV_p$  was greater in island than in mainland populations ( $1.715 \pm 0.054$  vs  $1.115 \pm 0.115$ ;  $t_7 = -5.079$ ,  $P=0.0014$ ; Table 2).  $\overline{CV}_i$  was statistically similar for mainland and island ( $t_7 = -1.494$ ,  $P=0.179$ ), although it differed among populations ( $F_{8,134} = 5.48$ ,  $P < 0.0001$ ).  $\overline{CV}_i$  showed basically the same pattern as  $CV_p$ , except for Galatzó where a huge crop in 2001 was followed by small crops in 2002–2004 (Table 2, Fig. 2). Mainland populations tended to be less synchronous than island ones ( $0.574 \pm 0.081$  vs  $0.805 \pm 0.087$ ), although such differences were only marginally significant ( $t_7 = -1.905$ ,  $P=0.09$ ). Andratx and Lluc showed the highest levels of synchrony and Frigiliana the lowest (Table 2).

### Relationship between abiotic conditions and variability in fruit production

$CV_p$ ,  $\overline{CV}_i$  or synchrony were not correlated with elevation ( $n=9$ ,  $r_s=0.433$ ,  $P=0.244$ ,  $n=9$ ,  $r_s=0.033$ ,

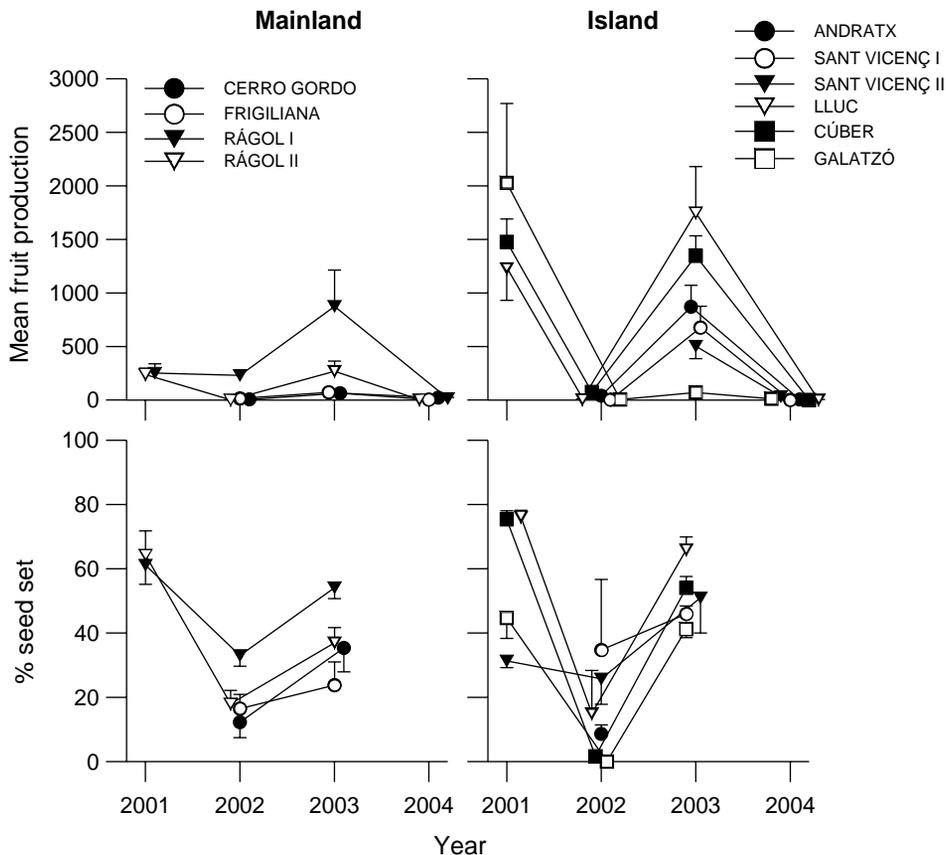


Fig. 2. Mean fruit production and mean seed set (seeds/ovules per fruit)  $\pm$ SE for each year in each population (all individuals pooled per population;  $n=7-30$ ). To improve clarity, some symbols have been slightly shifted.

$P=0.932$ , and  $n=9$ ,  $r_s=0.183$ ,  $P=0.636$  respectively) or mean rainfall ( $n=9$ ,  $r_s=0.583$ ,  $P=0.099$ ,  $n=9$ ,  $r_s=0.433$ ,  $P=0.244$  and  $n=9$ ,  $r_s=0.433$ ,  $P=0.244$  respectively). However, there was a marginally significant relationship between  $CV_p$  and the variability in the

rainfall ( $n=9$ ,  $r_s=0.600$ ,  $P=0.088$ ), and significantly positive relationships between the variability in the rainfall and  $\overline{CV}_i$  ( $n=9$ ,  $r_s=0.733$ ,  $P=0.025$ ) and between the variability in the rainfall and synchrony ( $n=9$ ,  $r_s=0.867$ ,  $P=0.002$ ).

Table 2. Annual variability in fruit production in the studied populations. (A) 2002-2004 time series; (B) 2001-2004 time series.  $n$ : number of individuals.  $CV_p$ : coefficient of variation at population level.  $\overline{CV}_i$ : average coefficient of variation at individual level ( $\pm$  SE). Means with different letters indicate significant differences among populations. Synchrony: mean ( $\pm$  SE) pairwise correlation coefficients ( $r$ ), used to measure among individuals synchrony in fruit production over years.

Site	$n$	$CV_p$	$\overline{CV}_i$	Synchrony
<b>(A)</b>				
Cerro Gordo (M)	8	0.854	$1.095 \pm 0.164$ a	$0.426 \pm 0.179$
Frigiliana (M)	21	1.201	$1.326 \pm 0.084$ a	$0.460 \pm 0.141$
Rágol I (M)	30	1.019	$1.282 \pm 0.052$ a	$0.639 \pm 0.090$
Rágol II (M)	12	1.387	$1.453 \pm 0.112$ a	$0.771 \pm 0.103$
Andratx (I)	22	1.614	$1.504 \pm 0.060$ bc	$0.942 \pm 0.026$
Sant Vicenç I (I)	10	1.704	$1.520 \pm 0.117$ abc	$0.624 \pm 0.217$
Lluc (I)	10	1.727	$1.682 \pm 0.041$ c	$0.998 \pm 0.002$
Cúber (I)	23	1.623	$1.657 \pm 0.029$ c	$0.890 \pm 0.073$
Galatzó (I)	11	1.911	$1.098 \pm 0.104$ ab	$0.571 \pm 0.128$
<b>(B)</b>				
Rágol I (M)	16	1.029	$1.205 \pm 0.082$	$0.588 \pm 0.106$
Rágol II (M)	12	1.317	$1.345 \pm 0.070$	$0.897 \pm 0.028$
Cúber (I)	22	1.107	$1.342 \pm 0.065$	$0.679 \pm 0.072$
Galatzó (I)	11	1.912	$1.729 \pm 0.138$	$0.676 \pm 0.166$

## Previous reproduction as a proximate cue for flower and fruit production

Goodness of fit of the path analysis model was high both for island and mainland populations (GFI: 0.913, NFI: 0.876;  $\chi^2 = 29.04$ ,  $df = 3$ ,  $P < 0.0001$ ; and GFI: 0.873, NFI: 0.849;  $\chi^2 = 47.04$ ,  $df = 3$ ,  $P < 0.0001$ , respectively). Partial coefficients and their significance are shown in Fig. 3. In both regions, a positive path joined plant size, flower and fruit production in 2003 (high-fruited year). In 2004 (low-fruited year), however, plant size did not influence flower production, although flower and fruit production were positively influenced by flower and fruit production in the previous year. In addition, two negative paths appeared in the island populations, one joining fruit production in 2003 with flower production the following year and the other joining flower and fruit production in 2004.

Regarding the flower bud removal experiment, only 32% of control and 41% of debudded branches produced at least one inflorescence in the following year. Although the percentage of flowering branches differed among populations (Sant Vicenç II: 50%, Sant Vicenç I: 13%, Cúber: 36%; Table 3A), bud removal did not affect the percentage of flowering branches in any of them (Table 3A). The number of inflorescences per branch did not vary between treatments or among populations and there was no interaction between the two factors (Table 3B).

Fruit production in the marked branches was large enough (29% of branches) to test the effect of previous reproduction on the percentage of fruiting branches only at Sant Vicenç II. The percentage of fruiting branches was not affected by bud removal in the previous year (Table 3C).

## Testing the “pollination efficiency” and the “predator satiation” hypotheses

As expected from the pollination efficiency hypothesis, higher flower production was positively associated to several estimates of reproductive success, such as fruit production (all populations and years pooled:  $n = 20$ ,  $r = 0.678$ ,  $P < 0.00001$ ), fruit set ( $n = 20$ ,  $r = 0.780$ ,  $P < 0.0001$ ; Fig. 4A), seed set ( $n = 10$ ,  $r = 0.700$ ,  $P = 0.024$ ; Fig. 4A), and seed production ( $n = 10$ ,  $r = 0.784$ ,  $P = 0.007$ ). However we found no relationship between mean flower production and the pollen limitation index ( $n = 9$ ,  $r = -0.02$ ,  $P = 0.958$ ). Pollen limitation did not differ between regions (ANCOVA: results not shown).

Mean fruit production was not associated to seed removal (all populations and years pooled:  $n = 12$ ,  $r = 0.374$ ,  $P = 0.231$ ; Fig. 4B). We did not find differences in seed removal between regions (ANCOVA: results not shown).

## Variation in seedling density and survival

Correlation between total seed production and seedling density was positive and significant when pooling all populations and years ( $n = 25$ ,  $r = 0.449$ ,  $P = 0.024$ ), and when considering only the data from 2004 ( $n = 9$ ,  $r = 0.748$ ,  $P = 0.020$ ). However, the correlation was not significant for the 2002 or 2003 data ( $P \gg 0.05$ ; Table 4).

There was no relationship between total seed production and seedling survival after the first summer either pooling all populations and years ( $n = 21$ ,  $r = -0.189$ ,  $P = 0.410$ ), or considering years separately (all  $P \gg 0.05$ ; Table 4).

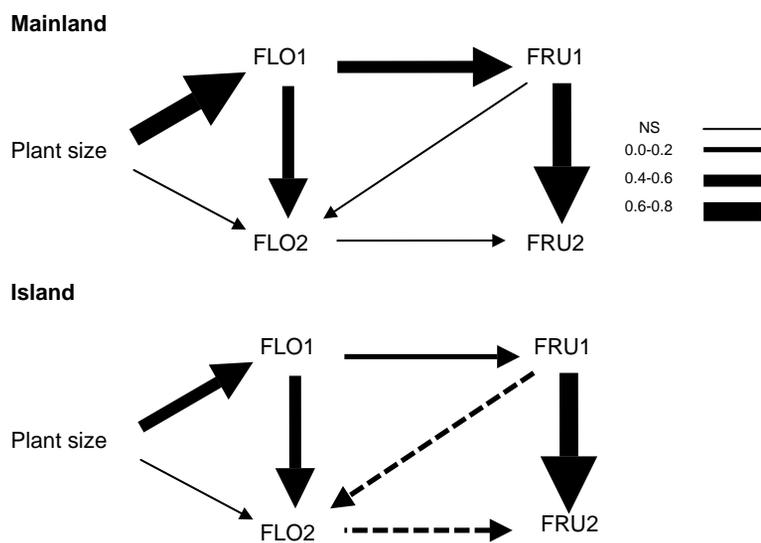


Fig. 3. Results of the path analysis showing the relationships between flower and fruit production in 2003 and 2004. Continuous and discontinuous lines represent positive and negative coefficients, respectively. Line thickness indicates the strength of the correlation between variables. Plant size: individual plant size; FLO: number of inflorescences (1-in 2003; 2-in 2004); FRU: number of fruits (1-in 2003; 2-in 2004).

Table 3. Results of the Generalized Linear Models for the bud removal experiment.

Variable/effect	Coefficient	SE	Z	P	Deviance $\chi^2$	change P
<b>(A) Percentage of flowering branches</b>						
Treatment					0.68	0.410
control	-0.486	0.840	-0.58	0.563		
bud removal	0					
Population					8.06	0.018
Cüber	-1.584	0.932	-1.70	0.089		
Sant Vicenç II	-2.788	0.963	-2.90	0.004		
Sant Vicenç I	0					
Treatment x population					1.61	0.447
<b>(B) Intensity of flowering</b>						
Treatment					0.61	0.435
control	-0.072	1.507	0.00	0.962		
bud removal	0					
Population					1.49	0.475
Cüber	-1.602	1.230	1.70	0.193		
Sant Vicenç II	-0.862	1.151	0.56	0.454		
Sant Vicenç I	0					
Treatment x population					1.21	0.545
<b>(C) Percentage of fruiting branches</b>						
Treatment					0.66	0.418
control	-0.693	0.874	-0.79	0.428		
bud removal	0					

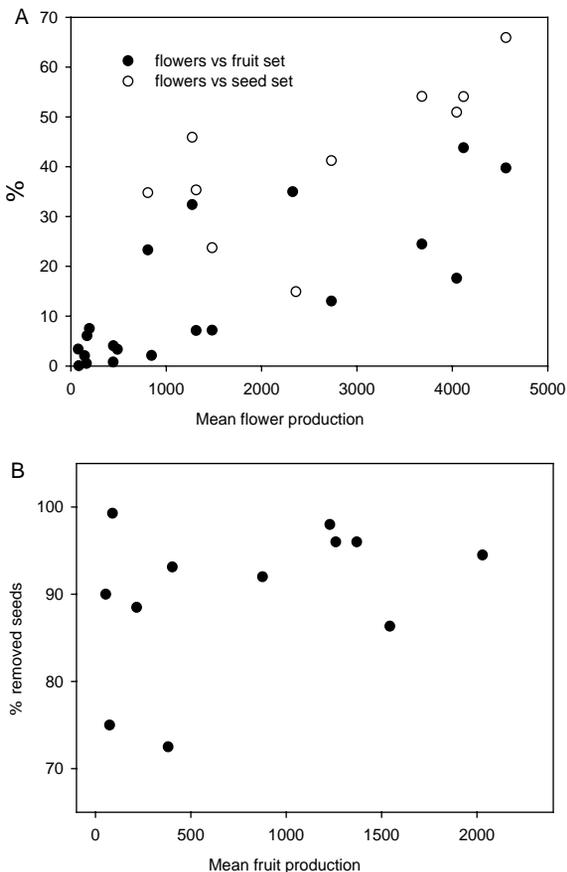


Fig. 4. Tests of the “scale economy” hypotheses. (A) ‘Pollination efficiency’ hypothesis: relationship between flower production and fruit set and between flower production and seed set (all populations and years pooled). (B) ‘Predator satiation’ hypothesis: relationship between fruit production and mean seed removal (all populations and years pooled).

## Discussion

### Spatio-temporal variation in fruit production

Both fruit production and seed set in *Buxus* were variable across years and spatially synchronized. Population variability in fruit production was more strongly correlated with individual variability than with synchrony, as also has been reported for other species (Herrera 1998, Koenig et al. 2003). In addition, individuals in the populations with larger inter-annual variability in fruit production tended to be more synchronized than those in populations with low inter-annual variability. Such relationship was also found by Koenig et al. (2003), but not by Herrera (1998). These mixed results are not surprising because selection can act separately on each variable (e.g. a more efficient wind-pollination may select for synchrony but not necessarily for greater variability), and because the combination of both variables (i.e.  $CV_i$  and synchrony) may affect population variability (Koenig et al. 2003).

Island populations of *Buxus* tended to be more synchronous and showed greater variation in fecundity across years than mainland populations, as reflected by  $CV_p$  (Table 2).  $CV_p$  for the island fell within the tail of the CV frequency distribution of annual seed output for the 144 species reviewed in Herrera et al. (1998). However, although the ranges of  $CV_p$ ,  $CV_i$  and synchrony fitted well within the ones reported for “normal” masting species (Herrera et al. 1998, Koenig et al. 2003), our short time series only allows to rate *Buxus* as showing “putative” masting. According to Kelly (1994) reproduction is variable in ‘putative’ masting species, but resource matching cannot be ruled out and evidence for a selective advantage of masting is lacking. In the

Table 4. Seedling density (D; seedlings m<sup>-2</sup>) and seedling survival (S; percentage of surviving seedlings after the first summer) after high-fruited years (2001 and 2003) and a low-fruited year (2002), in the four mainland (M) and six island (I) populations.

Population	2002		2003		2004	
	D	S	D	S	D	S
Cerro Gordo (M)	2.083	28.2	0.042	0.0	2.767	44.5
Frigiliana (M)	0.002	0.0	0.000		0.000	
Rágol I (M)	0.073	56.0	0.059	100	0.257	13.7
Rágol II (M)	0.127	34.6	0.035	0.0	0.200	39.2
Andratx (I)	0.013	50.0	0.000		0.006	0.0
Sant Vicenç I (I)	7.267	26.2	0.267	25.0	1.667	2.0
Sant Vicenç II (I)	0.852	25.7	0.002	0.0	0.086	2.6
Lluc (I)	0.889	18.8	0.048	0.0	57.83	23.0
Cúber (I)	0.258	5.4	0.000		0.168	0.0
Galatzó (I)	0.900	13.3	0.030	0.0	0.040	100

following, we discuss several of the factors that could contribute to partially synchronic interannual variation in fruit production in *Buxus*. We also discuss to which extent they could be responsible for the differences between regions in the patterns of fruit production.

### Relationship between abiotic conditions and variability in fruit production

The relationship between variability in fruit production and environmental variables was limited. In contrast to the prediction and findings by Kelly et al. (2001), the variability in fruit production or synchrony was not correlated to altitude in *Buxus*. However, we found a significant relationship between variability in the rainfall (but not mean rainfall) and variability in both individual fruit production and synchrony. Koenig and Knops (2000) reported a decrease in fruit production variability with latitude, related to a decrease in both rainfall and CV<sub>rainfall</sub>. This relationship could explain, at least partly, the differences in fruit production variability and synchrony between the island and the mainland populations, as rainfall was somewhat less variable in the mainland (CV<sub>rainfall</sub>=0.326) than in the island (CV<sub>rainfall</sub>=0.413) ( $t_8 = -2.192$ ,  $P = 0.060$ ).

### Previous reproduction as a proximate cue for flower and fruit production

A path analysis showed a negative influence of reproduction in year  $t$  on reproduction in year  $t + 1$ , although only for the island populations. This was consistent with the greater variability in reproduction in the island compared to mainland populations. These differences between mainland and island could be related to the prevalence of male-biased gender expression in mainland populations (Lázaro and Méndez, unpubl.), because maleness usually entails lower reproductive costs and annual flowering (Delph 1999).

However, although correlations between year  $t$  and year  $t + 1$  are commonly used as support for the

“resource matching” hypothesis, we urge caution with this kind of evidence because (1) correlative evidence is not strong support for resource depletion-related costs of reproduction (Reznick 1985) and (2) differences between regions in the path analysis output could merely reflect differences in the strength of the masting pattern.

Our flower bud removal experiment did not show any effect on subsequent reproduction. This might be related to the assumption in the experimental design that different branches would act as independent physiological units (Watson and Casper 1984). Resource sharing between branches could have diluted the differences between treatments. Another caveat is that subsequent vegetative growth, not flowering, is a more appropriate variable to test for resource matching (Kelly and Sork 2002, Monks and Kelly 2006).

### Pollen limitation and predator satiation

#### “Pollination efficiency” hypothesis

Koenig and Ashley (2003) suggested that pollen limitation could be a crucial driving force behind the highly variable and widely synchronous seed crops characteristic of wind-pollinated masting species. Not only fruit and seed production, but also fruit and seed set were positively correlated with number of flowers, i.e. greater flower crops translate into greater probabilities of setting fruits and seeds, probably as a result of lower levels of pollen limitation (Augspurger 1981, Shibata et al. 1998, but see Sork 1993). In our case, longer data series will be necessary to test adequately such relationship. However, once more we have to be cautious with the interpretation of this kind of correlative evidence. Lower fruit and seed production or fruit and seed set could equally result from low resource availability, which probably sets a limit both to flower production and to fruit and seed maturation (Muñoz et al. 2005). Indeed, experimental hand-pollinations in two mainland and three island populations (Lázaro and Traveset, in press) showed that pollen limitation was not related to flower production at a population level. However, individuals of *Buxus* with larger flower crops tended to be less-pollen limited

than those with small flower crops (Lázaro and Traveset, in press), indicating that pollination efficiency increases with flower production at the individual level. Unfortunately, although an experimental test of the “pollination efficiency” hypothesis is more robust than correlative evidence, it can be difficult to implement in many individuals and populations due to the lack of fruit production in low-fruited years.

Mast flowering is more likely to evolve in wind-pollinated species because increased pollen availability enhances pollination success, while in animal-pollinated species increased flowering may saturate the pollinators (Nilsson and Wästljung 1987, Norton and Kelly 1988, Smith et al. 1990). In mainland populations of *Buxus*, insects contribute to pollination, whereas it does not occur in the island (Lázaro and Traveset 2005). We suggest that differences in the interannual variability between mainland and island could be also related to higher reliance on wind pollination in the island (Lázaro and Traveset 2005). Different strength of ambophily between mainland and island populations could have decreased the differences between both regions in pollen limitation.

#### “Predator satiation” hypothesis

The percentage of removed seeds in *Buxus* did not depend upon seed production, and thus there was no evidence of predator satiation, a phenomenon that has been reported for several masting species (Kelly and Sullivan 1997, Shibata et al. 1998, Kobro et al. 2003, Satake et al. 2004). Despite a highly variable flowering effort, we found constant relative seed losses, which has also been previously reported for other species (Kelly et al. 2000).

One possible explanation for the lack of a predator satiation effect is that it might be detected in a between-year comparison (testing numerical-response), which we could not carry out with our data (Kelly and Sork 2002). In addition, our experimental design did not allow quantifying seed predation in some populations during low-fruited years, because of a lack of seeds, and this could be hiding a relationship between seed predation and fruit production. Lastly, Vander Wall et al. (2005) asked for caution when using removal data as an estimate of predation, as we did here. In our case, although secondary dispersal cannot be completely ruled out, it was deemed to be negligible based on previous work on this study system (Lázaro 2005).

#### Seedling density and survival

We found a positive relationship between seed production one year and seedling density in the following spring. Large numbers of seedlings the year following masting have been reported for a number of species (Sato

2000, Vilà and Lloret 2000). In *Buxus*, which lacks persistent soil seed bank (Lázaro 2005), seedling density in spring can be taken as initial recruitment.

However, density-, herbivore- or stress-dependent poor survival of the seedlings after their initial recruitment could decrease or negate any benefit of high fruit production (Sato 2000, Henkel et al. 2005, Wright et al. 2005). No seedling density effect was found on seedling survival in *Buxus* (Lázaro 2005), and we have never observed any sign of herbivory on seedlings of this species. However, a heavy (ca 71%) seedling mortality occurs during the first summer of life due to drought and high irradiation (Lázaro 2005). In this study we show that the extent of such mortality is not related to seed production.

Therefore, *Buxus* can have episodes of recruitment after high-fruited years, but other factors such as summer weather or safe sites can also regulate recruitment success (Lázaro 2005). Nevertheless, the relationship between cycles of fruit production and seedling establishment in this species remains unclear and a long-term study would be desirable.

#### Conclusions

Fruit production in *B. balearica* showed substantial between-year variation, especially in island compared to mainland populations. Correlative evidence indicated that this variation and its geographic pattern was related to differences between regions in rainfall variability, cost of reproduction and in the degree of ambophily. We found no indication of predator satiation. However, experimental tests failed to support many of these results, such as a negative effect of previous reproduction on future flowering in island populations or lower pollen limitation with increasing flower production at the population level. This warns against exclusive reliance on correlations to address questions related to masting. In addition, seedling recruitment increased after some episodes of high fruit production but probably additional factors had a role in recruitment, suggesting that mast events not always translate into increased reproductive success. Although a limited time series only allows considering *B. balearica* as showing “putative” masting, weather and pollination-related processes are good candidates for further exploration of fruiting patterns and processes at a large spatial scale.

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## References

- Abrahamson, W. G. and Layne, J. N. 2003. Long-term patterns of acorn production for five oak species in xeric Florida uplands. – *Ecology* 84: 2476–2492.
- Allison, T. D. 1990. Pollen production and plant density affect pollination and seed production in *Taxus canadensis*. – *Ecology* 71: 516–522.
- Augsburger, C. K. 1981. Reproductive synchrony of a tropical shrub: experimental studies on effects of pollinators and seed predators on *Hybanthus prunifolius* (Violaceae). – *Ecology* 63: 775–788.
- Benedí, C. 1997. *Buxus balearica*. – In: Castroviejo, S., Aedo, C., Benedí, C. et al. (eds), Flora Ibérica. Vol. VIII. Real Jardín Botánico, Madrid, pp. 187–189.
- Buonaccorsi, J. P., Elkinton, J., Koenig, W. et al. 2003. Measuring mast seeding behavior: relationships among population variation, individual variation and synchrony. – *J. Theor. Biol.* 224: 107–114.
- Burd, M. 1994. Bateman's principle and plant reproduction: the role of pollen limitation in fruit and seed set. – *Bot. Rev.* 60: 83–139.
- Delph, L. F. 1999. Sexual dimorphism in life history. – In: Geber, M. A., Dawson, T. E. and Delph, L. F. (eds), Gender and sexual dimorphism in flowering plants. Springer-Verlag, pp. 149–173.
- Henkel, T. W., Mayor, J. R. and Woolley, L. P. 2005. Mast fruiting and seedling survival of the ectomycorrhizal, monodominant *Dicymbe corymbosa* (Caesalpinaceae) in Guyana. – *New Phytol.* 167: 543–556.
- Herrera, C. M. 1998. Population-level estimates of interannual variability in seed production: what do they actually tell us? – *Oikos* 82: 612–616.
- Herrera, C. M., Jordano, P., Guitián, J. et al. 1998. Annual variability in seed production by woody plants and the masting concept: reassessment of principles and relationship to pollination and seed dispersal. – *Am. Nat.* 152: 576–594.
- Houle, G. 1999. Mast seeding in *Abies balsamea*, *Acer saccharum* and *Betula alleghaniensis* in an old growth, cold temperate forest of north-eastern North America. – *J. Ecol.* 87: 413–422.
- Hulme, P. E. and Benkman, C. W. 2002. Granivory. – In: Herrera, C. M. and Pellmyr, O. (eds), Plant-animal interactions: an evolutionary approach. Blackwell, pp. 132–153.
- Ims, R. A. 1990. The ecology and evolution of reproductive synchrony. – *Trends Ecol. Evol.* 5: 135–140.
- Janzen, D. H. 1971. Seed predation by animals. – *Annu. Rev. Ecol. Syst.* 2: 465–492.
- Kelly, D. 1994. The evolutionary ecology of mast seeding. – *Trends Ecol. Evol.* 9: 465–470.
- Kelly, D. and Sullivan, J. J. 1997. Quantifying the benefits of mast seeding on predator satiation and wind pollination in *Chionochloa pallens* (Poaceae). – *Oikos* 78: 143–150.
- Kelly, D., Harrison, A. L., Lee, W. G. et al. 2000. Predator satiation and extreme mast seeding in 11 species of *Chionochloa* (Poaceae). – *Oikos* 90: 477–488.
- Kelly, D., Hart, D. E. and Allen, R. B. 2001. Evaluating the wind pollination benefits of mast seeding. – *Ecology* 82: 117–126.
- Kelly, D. and Sork, V. L. 2002. Mast seeding in perennial plants: why, how, where? – *Annu. Rev. Ecol. Syst.* 33: 427–447.
- Kobro, S., Søreide, L., Djonne, E. et al. 2003. Masting of rowan *Sorbus aucuparia* L. and consequences for the apple fruit moth *Argyresthia conjugella* Zeller. – *Popul. Ecol.* 45: 25–30.
- Koenig, W. D., Mumme, R. L., Carmen, W. J. et al. 1994. Acorn production by oaks in central coastal California: variation within and among years. – *Ecology* 75: 99–109.
- Koenig, W. D. and Knops, J. M. H. 2000. Patterns of annual seed production by Northern Hemisphere trees: a global perspective. – *Am. Nat.* 155: 59–69.
- Koenig, W. D. and Ashley, M. V. 2003. Is pollen limited? The answer is blowin' in the wind. – *Trends Ecol. Evol.* 18: 157–159.
- Koenig, W. D., Kelly, D., Sork, V. et al. 2003. Dissecting components of population-level variation in seed production and the evolution of masting behaviour. – *Oikos* 102: 581–591.
- Lázaro, A. 2005. Aspectos ecológicos y filogeográficos del relicto mediterráneo *Buxus balearica* en poblaciones insulares y continentales. – PhD thesis. Univ. de les Illes Balears-Majorca.
- Lázaro, A. and Traveset, A. 2005. Spatio-temporal variation in the pollination mode of *Buxus balearica* (Buxaceae), an ambophilous and selfed species: mainland-island comparison. – *Ecography* 28: 640–652.
- Lázaro, A. and Traveset, A. in press. Reproductive success of the endangered shrub *Buxus balearica* Lam. (Buxaceae): pollen limitation, and inbreeding and outbreeding depression. – *Plant Syst. Evol.*
- Monks, A. and Kelly, D. 2006. Testing the resource-matching hypothesis in the mast seeding tree *Nothofagus truncata* (Fagaceae). – *Aust. Ecol.* 31: 366–375.
- Muñoz, A. A., Celedon-Neghme, C., Cavieres, L. A. et al. 2005. Bottom-up effects of nutrient availability on flower production, pollinator visitation, and seed output in a high-Andean shrub. – *Oecologia* 143: 126–135.
- Nilsson, S. G. 1985. Ecological and evolutionary interactions between reproduction of beech *Fagus sylvatica* and seed eating animals. – *Oikos* 44: 157–164.
- Nilsson, S. G. and Wästljung, U. 1987. Seed predation and cross-pollination in mast-seeding beech (*Fagus sylvatica*) patches. – *Ecology* 68: 260–265.
- Norton, D. A. and Kelly, D. 1988. Mast seeding over 33 years by *Dacrydium cupressinum* Lamb. (rimu) (Podocarpaceae) in New Zealand: the importance of economies of scale. – *Funct. Ecol.* 2: 399–408.
- Piovesan, G. and Adams, J. M. 2001. Masting behaviour in beech: linking reproduction and climatic variation. – *Can. J. Bot.* 79: 1039–1047.
- Rees, M., Kelly, D. and Bjørnstad, O. N. 2002. Snow tussocks, chaos, and the evolution of mast seeding. – *Am. Nat.* 160: 44–59.
- Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. – *Oikos* 44: 257–267.
- Rice, W. R. 1989. Analyzing tables of statistical tests. – *Evolution* 43: 223–225.
- Satake, A., Bjørnstad, O. N. and Kobro, S. 2004. Masting and trophic cascades: interplay between rowan trees, apple fruit moth, and their parasitoid in southern Norway. – *Oikos* 104: 540–550.
- Sato, T. 2000. Effects of rodent gnawing on the survival of current-year seedlings of *Quercus crispula*. – *Ecol. Res.* 15: 335–344.
- Shibata, M., Tanaka, H. and Nakashizuka, T. 1998. Causes and consequences of mast seed production of four co-occurring *Carpinus* species in Japan. – *Ecology* 79: 54–64.
- Shibata, M., Tanaka, H., Iida, S. et al. 2002. Synchronized annual seed production by 16 principal tree species in a temperate deciduous forest, Japan. – *Ecology* 83: 1727–1742.
- Silvertown, J. W. 1980. The evolutionary ecology of mast seeding trees. – *Biol. J. Linn. Soc.* 14: 235–250.
- Smith, C. C., Hamrick, J. L. and Kramer, C. L. 1990. The advantage of mast years for wind pollination. – *Am. Nat.* 136: 154–166.

- Sork, V. L., Bramble, J. and Sexton, O. 1993. Ecology of mast-fruiting in the three species of north American deciduous oaks. – *Ecology* 74: 528–541.
- Sullivan, J. J. and Kelly, D. 2000. Why is mast seeding in *Chionochloa rubra* (Poaceae) most extreme where seed predation is lowest? – *N. Z. J. Bot.* 38: 221–233.
- Tapper, P.-G. 1996. Long-term patterns of mast fruiting in *Fraxinus excelsior*. – *Ecology* 77: 2567–2572.
- Vander Wall, S. B. 2002. Masting in animal-dispersed pines facilitates seed dispersal. – *Ecology* 83: 3508–3516.
- Vander Wall, S. B., Kuhn, K. M. and Beck, M. J. 2005. Seed removal, seed predation, and secondary dispersal. – *Ecology* 86: 801–806.
- Vilà, M. and Lloret, F. 2000. Seed dynamics of the mast seedling tussock grass *Ampelodesmos mauritanica* in Mediterranean shrublands. – *J. Ecol.* 88: 479–491.
- Watson, M. A. and Casper, B. B. 1984. Morphogenetic constraints on patterns of carbon distribution in plants. – *Annu. Rev. Ecol. Syst.* 15: 233–258.
- Webb, C. J. and Kelly, D. 1993. The reproductive biology of the New Zealand flora. – *Trends Ecol. Evol.* 8: 442–447.
- Wright, S.J., Muller-Landau, H. C., Calderon, O. et al. 2005. Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. – *Ecology* 86: 848–860.