Masting in a temperate tree: Evidence for environmental prediction?

K. C. BURNS
School of Biological Sciences, Victoria University of Wellington, PO Box 600, Wellington 6140, New Zealand (Email: kevin.burns@vuw.ac.nz)

Abstract Many plant species produce large fruit crops in some years and then produce few or no fruits in others. Synchronous, inter-annual variation in plant reproduction is known as ‘masting’ and its adaptive significance has yet to be fully resolved. For 8 consecutive years, I quantified every fruit produced by 22 females of a New Zealand tree species (Dysoxylum spectabile), which has an unusual habit of taking a full calendar year to mature fruits after flowering. Fruit production varied strongly among years and was tightly synchronized among trees. Annual variability in fruit production declined with total reproductive output, indicating trees with lower fecundity exhibited a stronger tendency to mast. Although unrelated to temperature, annual fruit production was positively related to precipitation during annual periods of fruit development, and negatively related to fruit production in the previous year. Seedlings had higher rates of survivorship in a wet, high-seed year than in a dry, low-seed year, suggesting that seedlings might be drought sensitive. Therefore, D. spectabile produced large fruit crops during periods of high rainfall prior to fruit maturation, which may enhance survivorship of drought-intolerant seeds. Results were inconsistent with several hypotheses that are widely believed to be the most likely explanations for masting. Instead, results were consistent with the environmental prediction hypothesis, suggesting that this hypothesis may be more important than previously appreciated.

Key words: Dysoxylum spectabile, fruit, New Zealand, plant reproduction, precipitation.

INTRODUCTION

Many plant species reproduce heavily in some years and forgo reproduction altogether in others. Synchronous, inter-annual variation in reproductive effort is commonly known as ‘masting’ and the phenomenon occurs in perennial plant populations across the globe (Herrera et al. 1998; Koenig & Knops 2000; Koenig et al. 2003; Liebhold et al. 2004; Norden et al. 2007). However, the adaptive significance and evolutionary precursors of mast-fruited have yet to be fully resolved (see Kelly 1994; Kelly & Sork 2002).

The resource-matching hypothesis provides the most parsimonious explanation for masting (Norton & Kelly 1988; Sork et al. 1993; Monks & Kelly 2006). It states that plants allocate a constant fraction of assimilated carbon each year to reproduction. Years with benign climatic conditions that promote high rates of carbon assimilation therefore experience greater seed production. In years with poor climatic conditions, plants fix less carbon and produce fewer seeds. Deterministic processes are unimportant under the resource-matching hypothesis and inter-annual variation in seed set results from climatic variation directly.

Alternatively, annual reproductive variability may be adaptive and three non-exclusive hypotheses have been derived to explain the adaptive significance of masting. For example, if reproductive fitness accelerates with reproductive effort, then annual reproductive variability could arise from an evolutionary economy of scale. One mechanism promoting such an economy of scale is predator satiation (Silvertown 1980; Kelly et al. 2000; Kitzberger et al. 2007; Espelta et al. 2008).

The predator satiation hypothesis argues that inter-annual variation in seed set starves seed predators in low-seed years and then overwhelms seed predators during high-seed years, when too many seeds are produced to be completely harvested. A second mechanism promoting an economy of scale is the pollination efficiency hypothesis, which states that masting would be selected for if the probability of successful pollination increases with synchronized reproductive effort (Nilsson & Wästljung 1987; Smith et al. 1990; Kelly et al. 2001). Explanatory hypotheses based on economies of scale are traditionally the most widely accepted explanations for the evolutionary origins of annual reproductive variability (Kelly 1994; Keeley & Bond 1999). However, deterministic processes other than those based on an economy of scale might also select for annual reproductive variability.

The environmental prediction hypothesis postulates that plants mast to capitalize on benign environmental conditions for seedling establishment during particular years (Janzen 1971; see Silvertown 1980; Smith et al. 1990).
Frosts and snow are uncommon. Naturally occurring fires, however, are most common (rainfall averages 1250 mm. Rainfall occurs year-round; an average daily maximum of 20.6°C in February. Annual and seasonal ranges from an average daily minimum of 6.3°C in July to 10.3°C in July. Mean annual temperatures average 12.8°C. The parent material is greywacke; steeper slopes are composed of greywacke, silty loam. Mean annual temperatures average 12.8°C and range from an average daily minimum of 6.3°C in July to an average daily maximum of 20.6°C in February. Annual rainfall averages 1250 mm. Rainfall occurs year-round; however most (~75%) falls in winter (May–September). Frosts and snow are uncommon. Naturally occurring fires are exceedingly rare and fire plays an insignificant role in the dynamics of conifer-broadleaf forests throughout New Zealand (Dawson 1988; Wardle 2002).

*Dysoxylum spectabile* (Forst. f.) Hook. f. (Meliaceae) is a bird-pollinated and bird-dispersed tree species that grows to 5–10 m tall and is endemic to New Zealand. Flowers are produced in clusters on drooping panicles attached to tree trunks in the Austral winter (July) and are pollinated mostly by two bird species (*tui*, *Prosthemadera novaeseelandiae* and waxeyes, *Zosterops lateralis*) in Otari-Wilton's Bush. Fruits are initially round, green and approximately 3 cm in diameter. At maturity, they dehisce to expose six to eight arillate seeds enclosed in orange, fleshy fruit pulp. It takes an unusually long time for fruits to mature; they are retained on parent trees for a year or more after flowering, leading to temporal overlap between flowers and fruits. In some years fruits can also be aborted just prior to dehiscence. Although the breeding system of *D. spectabile* has yet to be resolved precisely, available data indicate that it is 'leaky dioecious', meaning that most individuals are either male or female, but some males occasionally set very small amounts of fruit (Braggins et al. 1999; Gardner 2007).

Like many isolated islands, New Zealand lacks native mammals (aside from two species of bat). However, since the arrival of humans approximately 700 years ago, many herbivorous mammals have been introduced to New Zealand that have deleterious effects on native plant communities. Arguably the most destructive is the brush-tail possum (*Trichurus vulpecula*), which has a particular preference for the leaves, flowers and fruits of *D. spectabile* (Nugent et al. 2002; Buddenhagen & Ogden 2003). Prior to this study in 1993, a major possum control programme was initiated in Otari-Wilton’s Bush (Otari Native Botanic Garden and Wilton’s Bush Reserve 2007). Between July 1994 and June 1996, 50 poisoned bait stations were established at even spatial intervals across the reserve, which initially destroyed over 1000 possums. Only five possums were eliminated after a second more intensive poisoning programme in November 1998 (see O’Leary 1999). Periodic poisoning has been conducted ever since and possum numbers have been maintained at nearly undetectable levels.

**FIELD OBSERVATIONS**

A stratified, random sampling design was used to select 60 trees along a 3-km trail that traversed the length of the reserve. Five trees were randomly selected from within 12 sampling localities that were evenly distributed across the length of the trail. Each tree was permanently marked with a uniquely numbered metal tag and its diameter at breast height was measured at the end of the observation period. Sampling included a range of tree sizes but avoided reproductive immature individuals (<10 cm diameter at breast height and <5 m tall).

The sex of each tree could not be accurately ascertained when they were initially marked, so all trees were treated identically throughout the observation period. However, total fruit set tallies gave a good indication of the sex of each tree, as only 'female' trees produce significant amounts of fruit. I specifically defined female trees as those that produced 10 or more fruits throughout the study period and only female trees were included in individual-based statistical analyses (questions one and two in the Introduction).

**METHODS**

**STUDY SITE AND SPECIES**

All data were collected in Otari-Wilton's Bush, which is located on the southern tip of the North Island of New Zealand (41°14′S, 174°45′E). Otari-Wilton's Bush is a forest reserve comprised of 75 ha of old-growth and regenerating conifer-broadleaf forest (see Burns & Dawson 2005, Burns & Beaumont 2009 for detailed site descriptions). The parent material is greywacke; steeper slopes are composed of a stony colluvium and valley bottoms are covered in silty loam. Mean annual temperatures average 12.8°C and range from an average daily minimum of 6.3°C in July to an average daily maximum of 20.6°C in February. Annual rainfall averages 1250 mm. Rainfall occurs year-round; however most (~75%) falls in winter (May–September). Frosts and snow are uncommon. Naturally occurring fires are exceedingly rare and fire plays an insignificant role in


Journal compilation © 2011 Ecological Society of Australia
Most studies on the annual reproductive variability of individual trees have documented the fruiting behaviour of approximately 30 trees (mean = 32.5, range 5–120 individuals, Koenig et al. 2003). Because previous work suggests that D. spectabile is dioecious (Braggins et al. 1999; Gardner 2007), I initially marked 60 trees in the hope of including 30 trees of each sex to approximate the average sample size of most studies. However, at the close of observations, 22 trees were ‘female’. Therefore, the sample size of all individual-based statistical analyses was n = 22 because of a male-biased population sex ratio.

Visual searches for ripe fruits were made with binoculars just prior to fruit dehiscence in July–August for eight consecutive fruiting seasons (2002–2009). Exact counts of fruits produced by each marked tree were facilitated by their large size and conspicuous location on tree trunks (i.e. cauliflory). Several trees were rooted to the forest floor by multiple stems. For these trees, diameter and fruit count measurements were made separately for each stem and then summed. All branches produced by multi-stemmed individuals could be unambiguously assigned to a single individual.

Analyses of the climatic correlates of population-level fruit production were conducted using precipitation and temperature data obtained from New Zealand’s National Climate Database (CliFlo 2010). Climatic observations were made daily throughout the study period at a location approximately 6 km northwest of the study site. Because D. spectabile fruits take approximately one calendar year to mature, total daily precipitation was summed from 1 August, when flowering usually terminated, to 31 July of the following year when fruit dehiscence commenced. Maximum daily temperatures were averaged similarly.

Seed germination experiment

To evaluate whether rates of seed germination and seedling survivorship might differ between high and low years of seed production, I conducted a seed germination experiment during the last 2 years of observations. Most female trees set large amounts of fruit in 2007 and failed to set fruit in 2008. Therefore, the first cohort of seeds used in the experiment came from a high-seed year and the second came from a low-seed year. In both years, 100 seeds were collected haphazardly from 10 to 15 trees, from which 60 seeds were randomly selected, cleaned of pulp and stored in moistened blotting paper placed within small plastic containers at 5°C for 3 months. Afterwards they were buried approximately 1 cm below the soil surface at 3-m intervals on alternating sides of the entrance of same trail used in observations. Seeds were sown within segments of 10 cm diameter plastic piping that were hammered into the forest floor so that their lip projected 2 cm above the forest floor, to facilitate relocating seeds and seedlings in subsequent observations. A single seed was sown in each plastic container in the spring of 2007 and an additional 60 containers were placed immediately adjacent to these containers in spring 2008. These containers housed the second cohort of seeds, which were treated identically to the 2007 cohort. After transplantation, all seeds were monitored at 4-month intervals to record seed germination (which was defined by the presence of two completely developed, undamaged cotyledons) and seedling survivorship. Seed mortality was defined by the total disappearance of a seedling that previously germinated successfully.

Statistical analyses

To test whether annual variation in fruit production was synchronized among trees, Spearman rank correlations were used to compare annual fruit production by each female tree to summed fruit production by all other females in the population. A non-parametric test was used because most trees failed to set fruit in many years. This resulted in a large number of zeros in the dataset, which made transforming the annual distribution of fruit production to conform to parametric assumptions impossible. A large number of significant, positive correlations and a high average rank correlation coefficient would indicate synchronous population-level fruit production. Mean annual synchrony ($r_s$) was also calculated as the mean of all pairwise Pearson correlation coefficients between individuals, following Koenig et al. (2003).

Two analytical approaches were used to test whether masting intensity of each female tree was associated with its size or fecundity. First, the coefficient of variation in annual fruit production was calculated for each female tree by dividing the standard deviation of annual fruit production across the observational period by its average annual fruit production (CV). Multiple regression was then used to test whether the CV, for each female was related to its diameter or total fecundity, which was defined as the sum of all fruits that it produced throughout the study period. Data were natural logarithm transformed to conform to assumptions. Second, the scaling relationship between average annual fruit production by each female tree and its standard deviation in annual fruit production was evaluated. Because the standard deviation of any randomly sampled population increases passively with its mean, if annual variation in fruit production varies passively with total fecundity, this relationship will be isometric (i.e. slope = 1, intercept = 0, see Taylor 1961). However, statistical differences in the slope and intercept of this relationship from isometry (one and zero, respectively) would indicate annual variation in fruit production varies disproportionally with total fecundity. I therefore regressed average annual fruit production against the standard deviation of average annual fruit production and obtained estimates of the slope and intercept parameters using maximum likelihood in SPSS (2002), in addition to their 95% confidence intervals (CI).

Finally, I used multiple regression to test whether population-level fruit production could be predicted by temperature and precipitation during fruit maturation, or by total fruit production in the previous year. Total annual fruit production, summed among all 60 individuals in the population, was used as the dependent variable. Total annual precipitation and average maximum daily temperature were used as independent variables, in addition to summed fruit production among all individuals in the previous year of observations. The first year of observations (2002) was omitted from this analysis because fruit production in the previous year was unknown. Therefore, the sample size of this analysis was $n = 7$. 

© 2011 The Author
Journal compilation © 2011 Ecological Society of Australia
RESULTS

Of the 60 randomly selected trees that were marked for observation, 38 produced fewer than 10 fruits throughout the study period, suggesting they were male. Therefore, the population appeared to be male-biased, with approximately one-third of the population (22 trees) being female. Female trees produced an average of 129.3 ± 236.7 SD fruits per year (Fig. 1). Total average annual fruit production across the population ranged from 0.3 fruits per individual in 2008 to 350.0 fruits per individual in 2009. The average coefficient of variation among trees (mean CV) was 139, while the population-level coefficient of variation (CV_p) was 104.

Fruit production was highly synchronized among female trees. Annual fruit production in 77% of female trees (17 out of 22) was positively correlated (P < 0.05) with total annual fruit production by the rest of the female population (average correlation coefficient = 0.770 ± 0.180, range = 0.250–0.980). Out of the total 231 pairwise comparisons among individuals, none was significantly negative and 107 were significantly positive (i.e. P < 0.05). Average individual synchrony (the mean of all pairwise correlation coefficients, r_i) was 0.614 ± 0.269 (range = –0.21, 0.98).

Annual reproductive variability declined with total fruit production. The overall multiple regression model relating CV to tree diameter and total fruit production was significant (r^2 = 0.357, P = 0.006). However, only total fruit production contributed to the model (β = –0.672, P = 0.002), tree diameter was unimportant (β = 0.276, P = 0.148). Total fecundity was also unrelated to tree diameter (β = 0.084, P = 0.180). The relationship between the standard deviation in annual fruit production and average annual fruit production confirmed this result (Fig. 2). The standard deviation increased with the mean (r^2 = 0.947, P < 0.001). However, the intercept was greater than zero (0.933, 95% CI = 0.514–1.352) and the slope was less than one (0.855, 95% CI = 0.763–0.947), indicating less fecund trees exhibit higher annual reproductive variability than more fecund trees.

Annual fruit production was positively related to precipitation during annual periods of fruit development and negatively related to fruit production in the previous year (Fig. 3). The overall multiple regression model relating annual fruit production to annual precipitation, mean maximum air temperature and the previous year’s fruit production was significant (r^2 = 0.822, P = 0.044). Both precipitation (β = 0.677, P = 0.039) and previous reproductive effort (β = –0.650, P = 0.034) contributed to the model. Temperature was unimportant (β = 0.177, P = 0.429).

Fig. 1. Fruit set by 22 *Dysoxylum spectabile* trees from 2002 to 2009. Individual trees are listed as rows, years are listed as columns and symbols are proportional to the total number of fruits produced by each tree each year following Koenig et al. (2003). The far right column lists the coefficient of variation in annual fruit production for each tree across the study period (CV_i) and the bottom row lists the total number of fruits produced by all 22 trees each year. The last value in the last column is the population-level coefficient of variation in annual fruit production (CV_p).

Fig. 2. Standard deviation in annual fruit production versus average annual fruit production in 22 *Dysoxylum spectabile* trees. The slope of the observed relationship is significantly less than one and the intercept is significantly greater than zero, indicating trees with lower total fruit production display stronger masting cycles.
Seed germination and seedling establishment were higher in the high-seed year (2007) than in the low-seed year (2008) (Fig. 4). Over 70% of seeds planted in spring 2007 (43 out of 60 seeds) germinated, while just over 50% of seeds planted in spring 2008 (31 out of 60 seeds) germinated. Assuming an equal probability of germination between cohorts, germination rates did not differ statistically between years ($\chi^2 = 1.9$, $P > 0.100$). Approximately 80% of 2007 seedlings were still alive 1 year after planting and 60% were still alive 2 years after planting, while none of the 2008 cohort survived for longer than 4 months. Seedling survivorship in the first year after planting violated the assumption of equal survivorship between cohorts ($\chi^2 = 34.0$, $P < 0.001$).

**DISCUSSION**

Approximately two-thirds of the study population produced little or no fruit throughout the study period. This suggests that they were functionally male and the remainder of the population was female, which supports previous work indicating that *D. spectabile* is dioecious (Braggins et al. 1999; Gardner 2007). Nevertheless, many apparently ‘male’ trees occasionally produced small numbers of fruit (<10). Every effort was made to insure accurate fruit counts, but *D. spectabile* trees often grow quite close to one another with interspersed canopies, so the observation of fruits on apparently ‘male’ trees could have resulted from small sampling errors. Alternatively, incomplete sexual segregation, whereby some male trees occasionally produce viable female flower parts has been documented experimentally in other plant species (Humeau et al. 1999; Venkatasamy et al. 2007). This phenomenon is known as ‘leaky dioecy’ and appears to be particularly common on isolated islands.
The timing of fruit production was tightly synchronized among female trees. Synchronous fruit production is a hallmark of mast-fruiting plant populations and often occurs over large spatial scales (Koenig & Knops 1998; Schauber et al. 2002; Liebhold et al. 2004; Lamontagne & Boutin 2007; Masaki et al. 2008; Sanguinetti & Kitzberger 2008). On the other hand, the coefficient of variation in annual fruit set declined linearly with total fruit production. Therefore, more fecund trees exhibited less pronounced annual reproductive variability. This result was not biased by the two least fecund trees, which produced 54 and 92 fruits, respectively. With these two trees omitted from analyses, CV, still declined with total fruit production ($r^2 = 0.189, P = 0.032$), and the standard deviation of fruit production in individual trees failed to scale isometrically with total fruit production ($r^2 = 0.947$, $P < 0.00$, intercept $= 0.901$, $0.317–1.484$ 95% CI, slope $= 0.862$, $0.738–0.986$ 95% CI).

Explanations for mast-fruiting based on economies of scale, such as the predator satiation and pollination efficiency hypotheses, predict that reproductive fitness accelerates with synchronized reproductive effort in plant populations. If reproductive fitness in D. spectabile varied according to an economy of scale annual reproductive variability should increase with fecundity. However, the opposite pattern was observed. Annual reproductive variability declined with total reproductive effort, suggesting that other processes are at work.

Several native birds prey upon D. spectabile seeds (e.g. kaka Nestor meridionalis), but I saw no evidence of avian seed predation throughout the observational period. The seeds and fruits of D. spectabile are heavily predated by introduced mammals, particularly the brush-tailed possum (Trichosurus vulpecula). Given the extensive effort to control possum numbers in Otari-Wilton's Bush, it seems unlikely that results are biased by possum predation. It is doubtful that possums have influenced the timing of mast-fruiting in D. spectabile, given the short period the two species have been in contact. I also saw no evidence of seed predation by arthropods in any of the seeds collected for the germination experiment. Native birds such as tui (P. novaeelandiae) and waxeyes (Z. lateralis) interact mutually with D. spectabile as both pollinators and seed dispersers. But given that mass flowering and fruiting is likely to satiate pollinators and frugivores, mutualists are likely to select against annual reproductive variability (Kelly & Sork 2002).

Both total fecundity and annual reproductive variability were unrelated to tree diameter. This is somewhat surprising because larger trees in the forest canopy that are exposed to full sunlight should have higher rates of carbon fixation than smaller trees in the forest understory. One explanation for this result stems from the vertical complexity of broadleaf-Podocarp forests in New Zealand, which are as structurally diverse as tropical rainforests (Dawson 1988). While D. spectabile trees can grow to substantial heights, there are many other tree species that grow much taller. So fully mature D. spectabile trees often occur beneath taller, canopy-emergent species such as Beilschmiedia tawa, Knightia excelsa and Dacrydium cupressinum, which can shade them significantly and presumably lower the rate at which they fix carbon. Trees in New Zealand forests can also harbour high liana loads, which might compete with larger trees for light and subsequently lower energy levels available for reproduction. Alternatively, the weak relationship between fecundity and tree size may result from sampling errors, as measurements of tree diameter are only coarse estimates of overall tree size (see Phillips et al. 2002).

Annual fruit production in female trees was negatively related to fruit production in the previous year, indicating that trees ‘rest’ following high-seed years. This pattern is common in many mast-fruiting species and suggests that trees alternate between growth and reproduction between years (see Koenig & Knops 1998). However, ‘switching’ between growth and reproduction could not be investigated per se because D. spectabile does not produce annual growth rings (K. C. Burns, 2006, pers. obs.), so annual growth rates could not be compared with annual rates of reproduction. Nevertheless, lower fruit production in years following high-seed years falsifies the resource-matching hypothesis, which postulates that inter-annual variation in fruit production results from inter-annual variation in climatic conditions alone (see Monks & Kelly 2006).

High-seed years were correlated with precipitation, indicating that fruits matured immediately following periods of higher rainfall. Most mast-fruiting species in New Zealand set fruit following high summer temperatures (Schauber et al. 2002), which suggests that the trigger for the production of large fruit crops in D. spectabile might be unusual. Studies in other localities have also documented that large fruit crops are associated with precipitation (e.g. Piovesan & Adams 2001). However, in these instances drought triggers large fruit crops. Higher rainfall during the build-up to seed release raises the possibility that D. spectabile might adjust reproductive effort according to the soil conditions that seeds are likely to encounter following dispersal. Forests with closed canopies and deep soil horizons can store large amounts of water after heavy rain, and sustained periods of drought are often necessary to lower soil water potential (see Dungan et al. 2007). Given the time lag between the entry and exit of precipitation in forested ecosystems, tree species with water-demanding seeds and seedlings could be at a selective advantage if they released their seeds immediately after wetter periods. If D. spectabile seeds are sensitive to drought, high-seed years following periods of elevated rainfall could help trees ‘anticipate’ periods that are beneficial for recruitment.
Several lines of evidence suggest that *D. spectabile* seeds are indeed sensitive to drought. First, Burrows (1999) investigated the germination behaviour of *D. spectabile* seeds experimentally and found that they failed to germinate after they were separated from fruit pulp and left to air dry for several days. Therefore, successful germination would seem to require moist conditions immediately following seed dispersal.

Second, results from experimental seed plantings in this study showed that rates of seedling survivorship were higher during the high-seed year, which experienced higher rainfall coincidentally with seed sowing (188.9 mm from September to November in the 2007 vs. 133.6 mm in 2008). Germination rates were statistically similar between years, perhaps indicating that drought is not an important factor determining seed mortality. However, both cohorts of seeds were stored in cool, moist conditions in the laboratory in an effort to break seed dormancy prior to seed sowing. In hindsight, planting seeds immediately would have yielded useful information on the link between germination and precipitation. The experiment was also unreplicated among years. Direct support for a positive effect of precipitation on long-term trends in tree recruitment would require many more years of trials wherein seeds were planted immediately following collection.

Finally, high-seed years typically occurred in alternate years with the exception of 2006, when the whole fruit crop appeared to be aborted. Most trees ‘rested’ in 2005, suggesting they had sufficient energetic resources for high fruit production in 2006. Both sexes flowered profusely and female trees produced large crops of unripe fruits, yet annual precipitation was low. Just prior to fruit maturation most trees appeared to withdraw water and nutrients from fruit capsules, which became unusually brittle and discoloured. When fruits dehisced, they only split-open partially and the fleshy arils within were desiccated and blackened. Other mast-fruiting species are known to abort fruits dehisced, they only split-open partially and the fleshy arils within were desiccated and blackened. When fruits dehisced, they only split-open partially and the fleshy arils within were desiccated and blackened. When fruits dehisced, they only split-open partially and the fleshy arils within were desiccated and blackened.

Results were generally consistent with the environmental prediction hypothesis, which postulates that mast-fruiting has evolved to promote recruitment during years that are favourable for seed and seedling survivorship. Previous support for the environmental prediction hypothesis comes mostly from fire-prone ecosystems. For example, dipterocarps in Southeast Asian rainforests typically set fruit after ENSO events, which often damage or kill adult trees thus providing forest gaps for seedling recruitment (Williamson & Ickes 2002). A similar situation may occur with *D. spectabile*. I saw no evidence that adults were sensitive to drought, but their seeds and seedlings appear to be drought sensitive, suggesting that timing high fruit production to coincide with periods of heavy rainfall may increase the probability of recruitment in the absence of marked adult mortality.

Overall, results were inconsistent with the resource-matching hypothesis and various hypotheses based on economies of scale, but were consistent with the environmental prediction hypothesis. Like most investigations of the evolution of mast-fruiting however, data provide only correlative evidence for the processes responsible for annual reproductive variability (cf. Lazaro et al. 2006). Additional experiments on precipitation-driven recruitment patterns and longer-term observations of fruit abortion are needed to test the environmental prediction hypothesis more thoroughly. Support for this hypothesis also hinges on identifying a physiological mechanism that would enable females to detect periods of drought during the build-up to seed release, which is currently unknown. Nevertheless, results clearly indicate that the environmental prediction hypothesis is a viable explanation for the evolution of elevated annual reproductive variability outside fire-prone ecosystems.

ACKNOWLEDGEMENTS

Thanks to Otari-Wilton’s Bush staff for advice and permission to conduct the study and to two anonymous referees who provided constructive comments on an earlier draft. Funding was provided by Victoria University of Wellington.

REFERENCES


