

Predator satiation and recruitment in a mast fruiting monocarpic forest herb

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- **Background and Aims** Cross-pollination and satiation of seed predators are often invoked to explain synchronous mast reproduction in long-lived plants. However, explanations for the synchronous death of parent plants are elusive. The roles of synchronous seeding and post-reproductive mortality were investigated in a perennial monocarpic herb (*Isoglossa woodii*) in coastal dune forest in South Africa.
- **Methods** Pre-dispersal seed predation and seed production were assessed by measuring fruit and seed set of inflorescences sprayed with insecticide or water and with no spray treatments. Seed predation was measured at different densities of *I. woodii* plants by monitoring removal rates of seed from the forest floor. The influence of adult plants on establishment of *I. woodii* seedlings was assessed by monitoring growth and survivorship of seedlings in caged and uncaged 1 × 1 m plots in understorey gaps and thickets.
- **Key Results** Fruit and seed set were similar between spray treatments. An *I. woodii* stem produced 767.8 ± 160.8 seeds (mean \pm s.e.) on dune crests and 1359.0 ± 234.4 seeds on the foredune. Seed rain was greater on the foredune than in other topographic locations. Seed predation rates were 32 and 54 % on dune crests and in dune slacks, respectively, and decreased with seed abundance, number of inflorescences per stem and plant height. Seedling recruitment was greater beneath synchronously dying adult plants than in natural understorey gaps (no *I. woodii*). However, seedling growth rate beneath *I. woodii* mid-way through its life-cycle was less than in gaps, although survivorship was similar.
- **Conclusions** The selective advantage of masting in *I. woodii* derives from satiation of both pre- and post-dispersal seed predators. In addition, post-seeding mortality of adult plants facilitates seedling establishment. Satiation of seed predators and the benefits of seedling establishment are strong drivers of the evolution of synchronous monocarpy in *I. woodii*.

Key words: Synchronous flowering, understorey gaps, *Isoglossa woodii*, seed predation, seedling establishment, monocarpy.

INTRODUCTION

The best known evolutionary advantages of synchronous reproduction or masting in plants are pollination efficiency for wind-pollinated species and satiation of seed predators (Silvertown, 1980; Ims, 1990; Smith *et al.*, 1990; Kelly, 1994; Kelly and Sork, 2002; Schaubert *et al.*, 2002). In many perennial plants exhibiting synchronous reproduction, reproduction is supra-annual, with intervening periods ranging from 3 to >100 years (Janzen, 1976; Keeley and Bond, 1999; Sharma *et al.*, 2008). Masting supra-annually gains an evolutionary advantage if longer reproductive cycles result in higher fitness compared with annually reproducing plants. In masting monocarpic species of Acanthaceae, satiation of seed predators and facilitation of seedling establishment by the synchronous death of parent plants have been proposed as the ultimate causes of synchronous reproduction (Janzen, 1976; Struhsaker, 1997). We examine these propositions by investigating the effect of the density and the synchronicity of mortality of adult plants on rates of seed predation and seedling establishment, respectively, of a dominant monocarpic herb (*Isoglossa woodii*) in sub-tropical forests of eastern South Africa.

Isoglossa woodii is a widespread herbaceous to semi-woody broad-leaved plant that dominates the understorey of sub-tropical coastal dune forests of eastern South Africa and south-eastern Mozambique (Griffiths *et al.*, 2007; Tsvuura *et al.*, 2007). Isolated patches of *I. woodii* can be found up to 10 km or more from the coast, varying in extent from a few stems covering a few square metres to thickets extending over several hundred hectares (Fig. 1) covering at least 65 % of the forest floor (Griffiths *et al.*, 2007). The species exhibits synchronous reproduction and mortality events on a 4–7 year cycle (Griffiths *et al.*, 2010). Following flowering and seed dispersal, *I. woodii* dies back and the population regenerates from seed. Such synchronous monocarpy is a feature of many species of the Acanthaceae (Tweedie, 1965, 1976; Janzen, 1976; Struhsaker, 1997; Sharma *et al.*, 2008).

The outcrossing hypothesis (Janzen, 1976; Augspurger, 1980; Stephenson, 1982) suggests that a large visual display associated with synchronous flowering increases the chances of cross-pollination and benefits the parent plant by producing high quality seed. In self-compatible species, synchronous flowering may also lead to geitonogamous self-pollination, which provides reproductive assurance but conflicts with the

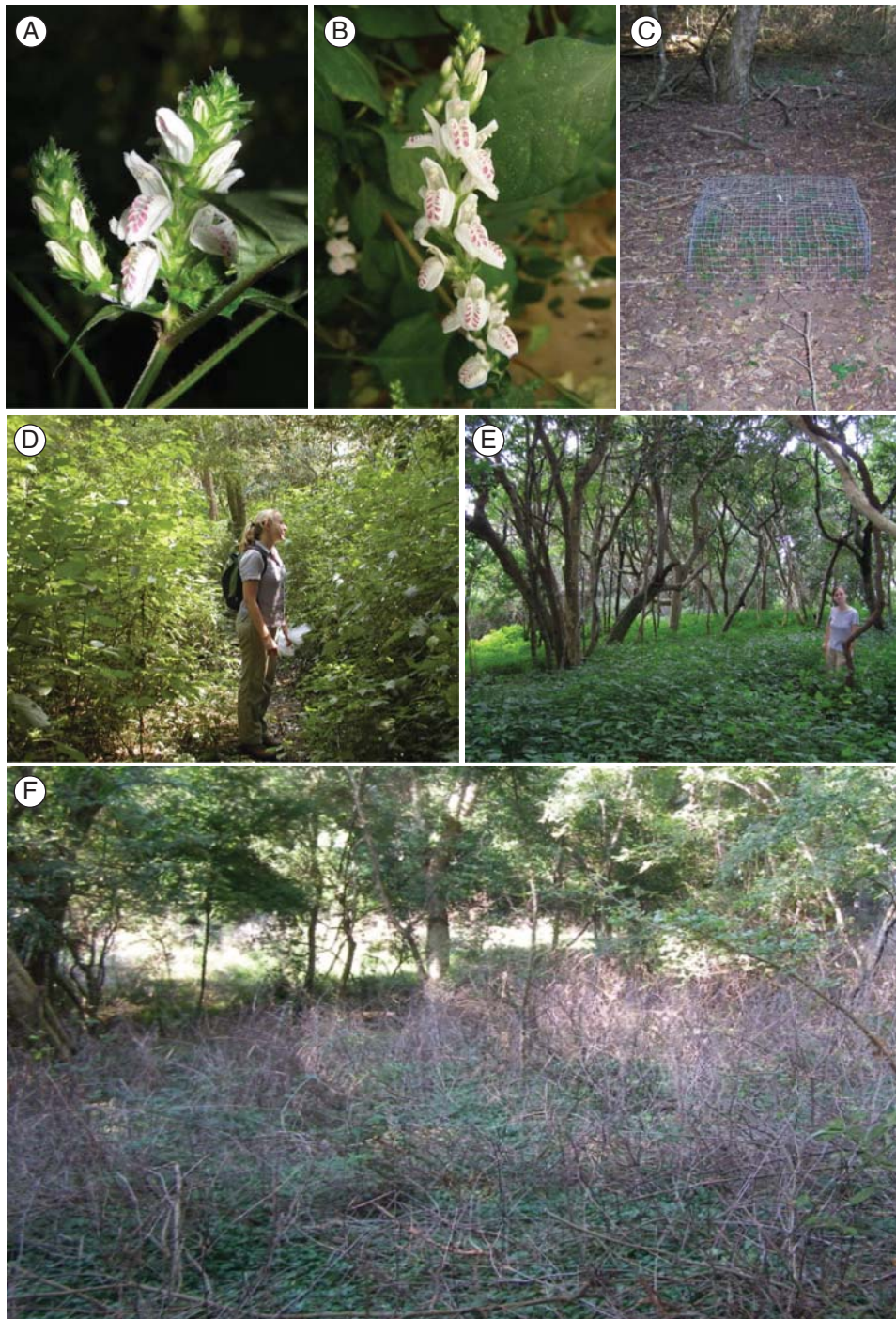


FIG. 1. *Isoglossa woodii* growth form, habitat and cover. (A, B) Developing inflorescences of *I. woodii*; (C) example of experimental 1 × 1 m cage in a natural gap in *I. woodii* cover; (D) 4-year-old *I. woodii* on a foredune was typically tall (cf. with height of Megan Griffiths), while (E) 5-year-old stands on dune crests were short (cf. with height of Charmaine Meyer). (F) *Isoglossa woodii* die-back in April 2008 with regeneration beneath dead stems.

benefits of outcrossing. As *I. woodii* is both self-compatible and animal pollinated (Griffiths *et al.*, 2010), the out-crossing hypothesis is not a compelling explanation for synchronous monocarpy and is not examined here.

The predator satiation hypothesis (Janzen, 1976; Silvertown, 1980; Augspurger, 1981) proposes that synchronous reproduction in long-lived species produces more seed than can be

consumed by seed predators in most years, and starves the seed predators in non-seeding years. Where predation pressure is high, a fitness advantage is predicted for individual plants that flower synchronously with the rest of the population. If predation rates are high then asynchronous lineages will eventually be eliminated from the population. By removing asynchronously flowering individuals from the tails of the

time-of-seeding distribution, predation pressure, through stabilizing selection, effectively selects for synchronous reproduction.

A third hypothesis is that interspecific competition, particularly regarding the timing of establishment of seedlings, may have driven the evolution of reproductive synchrony in monocarpic species (Struhsaker, 1997). The dominance of monocarpic species in the community is maintained by synchronized mass reproduction and seedling establishment, which excludes seedlings of other species beneath the parent plants. As the parent plants die, their seedlings are released from competition. Individuals that release their seedlings from competition in this way gain a fitness advantage leading to synchronized seedling establishment and ultimately synchronized reproduction, which in turn outcompetes other species, thereby maintaining herb dominance. The evolution of facilitation of seedling establishment through post-reproductive mortality of adult plants requires that seeds, and eventually seedlings, of an individual plant fall directly below the parent (Janzen, 1976), which is feasible and potentially adaptive in species that passively disperse their seed (Foster, 1977; Gadgil and Prasad, 1984). In *I. woodii*, fruits dehisce explosively on drying so that seeds are actively dispersed, but for relatively short distances in comparison with other vectors.

In this study two hypotheses of the evolution of synchronous flowering in *I. woodii* were experimentally examined, and mechanisms that determine its ubiquitous cover in sub-tropical coastal forest were explored. To explore the efficacy of the predator satiation hypothesis, we determined whether insect consumers limit seed production by feeding on flowers and developing seed and fruit. Seed production was measured and the predator satiation hypothesis was tested at a local scale by monitoring removal of *I. woodii* seed from seed stations located in areas of different *I. woodii* densities. For seed predation to be a driver of synchronous monocarpy we predicted that seed predation would be greater at sites where the number of seed in the soil seed bank was lower. We also tested the hypothesis that the mortality of parent plants facilitates seedling establishment ('seedling facilitation hypothesis', *sensu* Foster, 1977; Struhsaker, 1997) using a seedling transplant experiment situated at two locations where the *I. woodii* population was in vegetative or post-reproductive phases. We predicted that seedling establishment post-reproduction would be greater in areas with *I. woodii* cover than in areas with no *I. woodii* cover.

MATERIALS AND METHODS

Study species populations

Several populations of *Isoglossa woodii* (C.B. Clarke, Acanthaceae) occur in the iSimangaliso Wetland Park in KwaZulu-Natal Province, South Africa. Two of these, at Cape Vidal (28°16'S, 32°29'E) and Mapelane Nature Reserve (28°24'32"S, 32°25'17"E), cover hundreds of hectares of the understorey in the coastal dune forest. The Cape Vidal population flowered from March to October 2007, and seedling establishment after flowering was measured at this site. The Mapelane population last had a mass flowering event in 2003, was in mid-cycle at the time of this study and in this

population seedling establishment was measured under established *I. woodii* stands.

Seed set, pre-dispersal flower and seed predation

Pre-dispersal flower and seed predation were measured using a modification of the design of Louda and Potvin (1995). Thirty *I. woodii* plants at least 5 m apart were tagged on the foredune, dune crest, backdune and in dune slacks. Density, height and basal diameters of the plants were measured, and on six inflorescences on each plant three treatments were applied randomly: insecticide spray [Chlorpirifos, Agro-Serve (Pty) Ltd, Silverton, South Africa]; water spray (as a control for the physical effects of spraying); and no spray. Treatments were initiated when inflorescences were still developing before any flower buds were evident. Spraying was carried out once per fortnight, during which the number of insect-damaged flowers and fruits was also recorded. After the main flowering event and before the dispersal of seed, all inflorescences were harvested and each was kept separately in paper envelopes. In the laboratory, the numbers of flowers and fruits developed on each inflorescence was counted. Eight fruits were dissected from each inflorescence and the number of seeds in each was counted. Fruit set (number of fruits/number of flowers) was calculated for each inflorescence as well as seed set (number of seeds/number of ovules) for each fruit.

Seed production

Seed production was measured before dispersal when fruits were maturing. Thirty *I. woodii* plants of different sizes were randomly selected for measurement, ten each from the foredune, dune crest and dune slack. For each plant, its size (number of stems, stem diameter and height) was measured and the number of inflorescences was counted. Ten inflorescences representing the range of sizes (i.e. number of flowers per inflorescence) present on the plant were selectively harvested from each plant. The number of flowers and fruits developed on each inflorescence was counted. For five inflorescences from each plant five fruits were dissected and the number of seeds in each was counted. The mean fruit and seed set for each plant was calculated. The number of seeds produced by each plant was estimated as the product of the number of inflorescences and the mean fruit set and mean seed set per inflorescence.

Seed predation

Post-dispersal seed predation was investigated using the modified method of Wurm (1998) of placing seeds in Petri dishes at sites and monitoring their removal rate. Seeds were collected during the *I. woodii* flowering event and the experiment was conducted towards the end of *I. woodii* seed fall in July–August 2007. Seed removal rates were compared in areas with different stem and inflorescence densities, including *I. woodii* gaps. Each sampling unit consisted of a 1 m² quadrat where stems were counted, their heights and numbers of inflorescences were measured and the level of browsing damage was estimated. Then seed densities were measured in the top 1 cm

of soil by sieving four Petri dish (circle with diameter = 9 cm) samples covering 0.25 m². In the centre of the quadrat two Petri dishes were placed 20 cm apart, filled with seed-free sand. One of the two Petri dishes was randomly selected for placing seed for measurement of removal rates. The other dish was retained as a control with no seed to allow estimation of seed fall into the treatment dish. Eight seeds were placed at known positions on the soil surface of the dish. Seed stations were marked, and the dishes were checked for removal or addition of seed three times at 10–13 d intervals between July and August 2007. Removed seeds were replaced while surplus seeds were removed.

There were 28–46 seed stations in use at each sampling interval. Stations were spaced at least 10 m apart at two sites on the foredunes, two on dune crests and two in dune slacks. Each site had 4–21 stations. The site with four stations was established in the second and third sampling intervals to increase sample size and to increase area coverage of the experiment.

Establishment of I. woodii seedlings in gaps during die-back

At Cape Vidal, the understorey consists of large areas of *I. woodii* cover and some patches that are naturally free of such cover (Griffiths *et al.*, 2007). To investigate the factors limiting *I. woodii* recruitment at favourable locations, four 1 × 1 m plots of *I. woodii* seedlings were planted in each of 15 sites located around natural gaps between 9 September and 29 November 2007. Two plots were in the gap, at least 5 m from the edge, and two were in the nearby *I. woodii* thicket and 10 m from the edge of the gap. Each plot contained 16 seedlings in a grid layout. One plot in the gap and one in the thicket was covered by a cage to prevent large mammalian herbivores from disturbing the seedlings (Fig. 1). Seedlings that died within 10 d after transplanting were assumed to have died of transplant shock and were replaced. Seedling survival was recorded at 3 month intervals and evidence of browsing (apex of shoot removed) and severe herbivory ($\geq 50\%$ of leaf eaten) was also recorded. Final measurements were carried out in early November 2008.

Establishment of I. woodii seedlings beneath adult conspecific plants

To test the hypothesis that synchronous reproduction and the associated synchronous mortality of adult plants facilitates recruitment, we examined whether *I. woodii* seedlings were capable of establishing beneath mature plants. In late March 2008 *I. woodii* seedlings from Cape Vidal were transplanted to ten sites 40 km south at Mapelane Nature Reserve. Each site consisted of three 1 × 1 m plots whose centres formed the corners of a 5 m-sided equilateral triangle. One sub-plot was always located in a natural gap in the *I. woodii* thicket, another in the centre of an artificial 2 × 2 m gap created by removing the *I. woodii* to ground level and a third located under stands of mature *I. woodii*. The number of stems removed in the artificial gap and the size of the natural gap were recorded. In each plot, 16 *I. woodii* seedlings from Cape Vidal, with heights of 80–120 mm (but choosing similarly sized seedlings in any one sub-plot), were planted in a

grid layout. Seedlings that died of transplant shock were replaced after 10 d. *Isoglossa woodii* stems re-growing into artificial gaps were removed regularly. Eight months after transplanting, survivorship and height growth of seedlings were measured.

Data analysis

Flower, fruit set and seed set data from pre-dispersal flower and seed predation were analysed using a general linear model with the spray treatment as a fixed factor, topographic location a random factor and *I. woodii* stem density, height and basal diameter as covariates. For seed production data, Pearson correlation coefficients were calculated to explore the nature of relationships between plant size (stem diameter and height) and each of seed set, fruit set and number of inflorescences per stem.

The proportion of seed lost to predation was arcsine square-root transformed to fit a normal distribution of residuals before analysis (Kéry and Hatfield, 2003). The data were analysed using a general linear model with site as a random factor nested in topographic location. *Isoglossa woodii* stem density and height, number of inflorescences per *I. woodii* stem, soil seed bank density and mean date of sampling were additional predictor variables (covariates). Because there was collinearity among the density predictor variables, a separate analysis was run for each. In case density effects on predation occur at coarser scales, neighbourhood-scale densities were also calculated by averaging the size of the soil seed bank, stem density and number of inflorescences for a station and its two nearest stations, and these variables were tried as alternatives to the fine-scale density variables.

In both transplant experiments, seedling growth was calculated as (final height – initial height)/initial height, while survivorship was the proportion of the 16 seedlings that survived in each sub-plot. Growth data were square-root transformed while survivorship data were arcsine square-root transformed to obtain normality of residuals.

At Cape Vidal, seedling growth and survivorship were analysed among the 15 sites using a split-plot analysis, with sites as blocks each containing two plots: gap and thicket. Each of these was split into a caged and uncaged plot. At Mapelane, growth and survivorship of seedlings beneath adult conspecific plants were compared among three *I. woodii* habitats: thickets, artificial clearings and natural gaps, using analysis of covariance with gap size, stem density and stem height of cleared *I. woodii* plants as covariates. All analyses were carried out in SPSS v. 15 (SPSS, 2007).

RESULTS

Seed set, pre-dispersal flower and seed predation

Flower production per inflorescence was similar between the natural condition (no spray) and the insecticide and water spray treatments ($F_{2,153} = 1.45$, $P = 0.24$). On both sprayed and non-sprayed inflorescences, only occasional (<3%) flowers or fruits were insect damaged (petals or corolla tube browsed; petals, corolla tube or fruit with insect holes) so that fruit set was similarly high among treatments ($F_{2,153} =$

TABLE 1. Mean (\pm s.e., %) fruit and seed set of inflorescences of *I. woodii* treated with insecticide spray, water spray and no spray

Treatment	Fruit set	n	Seed set
Insecticide	61.13 \pm 2.44	434	39.24 \pm 1.60
Water spray	61.37 \pm 2.34	427	42.33 \pm 1.57
No spray	61.14 \pm 3.11	386	46.68 \pm 1.37

0.32, $P = 0.73$, Table 1) but varied among topographic locations ($F_{3,153} = 3.09$, $P = 0.03$). Fruit set was greater on the foredune and backdune than in the dune slack, while the density, height and basal diameter of *I. woodii* stems did not influence fruit set (data not shown). Seed set was also similar between the spray treatments ($F_{2,163} = 0.53$, $P = 0.59$, Table 1) and none of the covariates was significant ($P > 0.05$ in all cases). Of the 1247 fruits examined, 74.3 % contained only one seed, 4.5 % had two seeds and the rest were selectively aborted, which was also the case with the remaining two ovules that did not set seed.

Seed production

Both fruit set and seed set were not correlated with plant height and stem diameter ($-0.035 < r < 0.235$, $P > 0.05$, $n = 30$ in all cases). However, the number of inflorescences on an individual plant was positively correlated with both plant height and stem diameter (Fig. 2).

Individual *I. woodii* stems produced 767.8 ± 160.8 seeds on dune crests and 1359.0 ± 234.4 seeds on the foredunes (overall mean across topographic locations = 1083.4 ± 144.4 , $n = 30$). Considering that stem densities are only slightly greater on the dune crests than on the foredunes (10.4 vs. 8.0 stems m^{-2}), a square metre of ground surface on the foredunes receives more seed than other topographic locations.

Seed predation

The main predator of *I. woodii* seeds that dispersed to the forest floor was an ant species, *Pheidole* spp. (Formicidae), with occasional sightings of *Meranoplus* spp. (Formicidae) at seed stations. The losses of post-dispersal seed to predation ranged from 32 % on dune crests to 54 % in dune slacks, but were statistically similar across these topographical locations ($P > 0.1$ in all cases, data not shown). Seed predation decreased with the size of the soil seed bank, stem density and height of *I. woodii* (Table 2). A decrease in seed predation with an increase in the mean number of inflorescences among a station and its two nearest neighbours was also found. This indicates that there were spatial density effects on predation at a broader scale (significant covariate inflorescence3, Table 2). However, in terms of the soil seed bank and stem density, there were no spatial density effects on predation ($P > 0.05$). There were significant interactions between topographic location and both seed bank size and stem density (Table 2), which reflects the lower stem density and soil seed bank size in the dune slacks (Fig. 3).

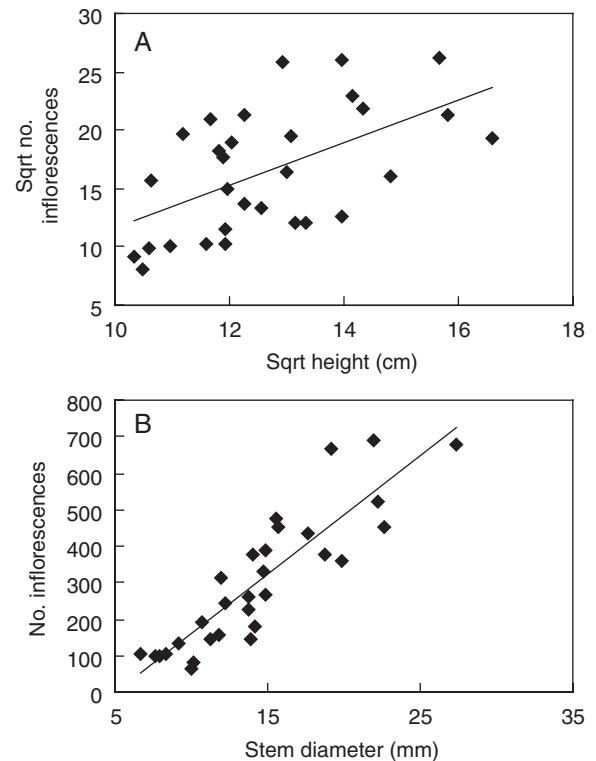


FIG. 2. Number of inflorescences on various sizes of *I. woodii* plants. In (A) the relationship is $y = 1.84x - 6.87$ ($F_{1,28} = 14.72$, $P = 0.001$, $r^2 = 0.32$), and in (B) $y = 32.49x - 167.9$ ($F_{1,28} = 99.18$, $P < 0.0005$, $r^2 = 0.78$).

TABLE 2. Analysis of covariance for predation of *I. woodii* seed at Cape Vidal

Source	d.f.	MS	F	P
Seed bank	1	1.799	8.66	0.004
Seed bank \times topography	2	0.862	4.15	0.018
Residual	108	0.208		
Seed bank3	1	0.409	1.78	0.184
Residual	110	0.229		
Stem density	1	1.163	5.63	0.019
Stem density \times topography	2	1.398	6.77	0.002
Residual	108	0.206		
Stem density3	1	0.716	3.16	0.078
Inflorescence	1	0.803	3.56	0.062
Residual	110	0.226		
Inflorescence3	1	1.729	7.95	0.006
Residual	110	0.217		
Stem height	1	2.415	11.44	0.001
Residual	110	0.211		

Seed bank, stem density, stem height and number of inflorescences per stem are covariates. Density3, seed bank3 and inflorescence3 were derived by averaging their values at each station and the nearest two stations. The proportion of seed predated was arcsine square-root transformed before analysis.

Establishment of *I. woodii* seedlings in gaps during die-back

After 11 months, seedling growth was greater in the *I. woodii* thicket than in the gaps ($F_{1,14} = 7.18$, $P = 0.02$) and in the caged plots than in the open ($F_{1,668} = 13.42$, $P < 0.001$, Table 3a). These trends were evident only 8

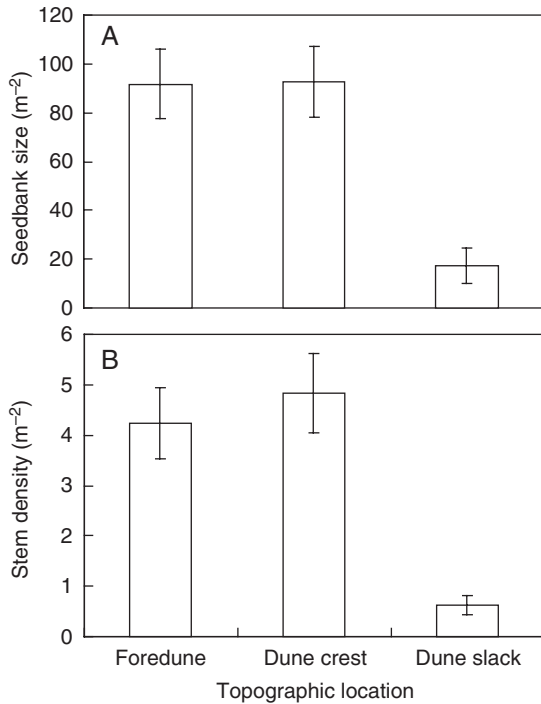


FIG. 3. Influence of topographic location on the soil seedbank and stem density of *I. woodii* at Cape Vidal.

TABLE 3. Growth (a) and survivorship (b) of *I. woodii* seedlings grown in caged and uncaged sub-plots in *I. woodii* die-back thicket and *I. woodii* gap habitats at Cape Vidal

Source of variation	d.f.	MS	F	P
(a) Growth				
Site	14	0.474	2.06	0.09
Residual	14	0.230		
Habitat	1	1.566	7.18	0.02
Residual	14	0.218		
Site × habitat	14	0.230	7.27	<0.001
Cage	1	0.424	13.42	<0.001
Habitat × cage	1	0.011	0.36	0.55
Residual	668	0.032		
Overall residual	699	0.049		
(b) Survivorship				
Site	14	0.050	0.69	0.75
Residual	14	0.072		
Habitat	1	0.292	4.05	0.06
Residual	14	0.072		
Site × habitat	14	0.072	4.25	0.001
Cage	1	0.227	13.35	0.001
Habitat × cage	1	0.011	0.65	0.43
Residual	28	0.017		
Overall residual	59	0.046		

months after the experiment was initiated (Fig. 4). Similarly, caging and the thicket habitat had higher seedling survivorship than uncaged and gap habitats (Table 3b, Fig. 5). These patterns show that accounting for herbivory, the *I. woodii* habitat appears to facilitate the establishment of *I. woodii* seedlings.

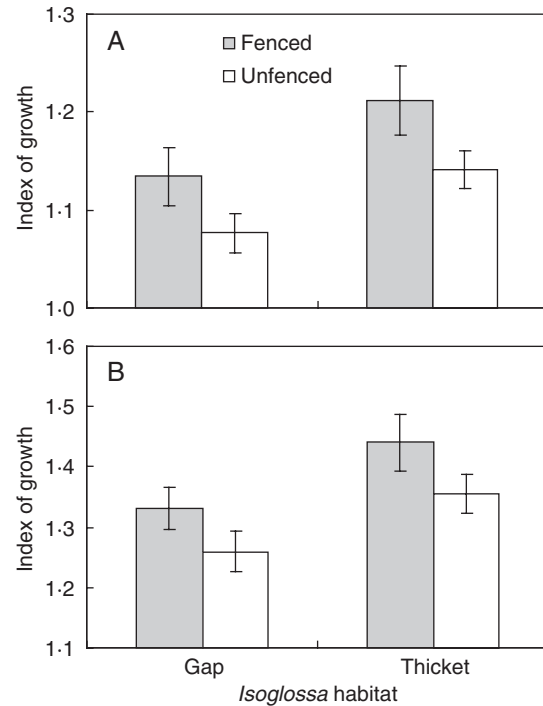


FIG. 4. Mean (\pm s.e.) growth of *I. woodii* seedlings transplanted into caged and uncaged plots in *I. woodii* gaps and thickets at Cape Vidal after (A) 8 months and (B) 11 months. Index of growth is based on the square-root transformation $\sqrt{(\text{growth} + 1)}$.

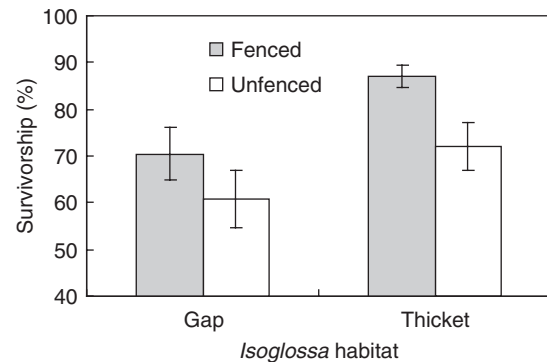


FIG. 5. Mean (\pm s.e.) survivorship of seedlings in caged and uncaged plots under habitats where *Isoglossa woodii* is present (thicket) and absent (gap) at Cape Vidal.

Establishment of *I. woodii* seedlings beneath adult conspecific plants

Eight months after the experiment was initiated at Mapelane, seedling growth was more suppressed in the thicket than in the gaps ($F_{2,432} = 25.92$, $P < 0.001$, Table 4), and was highest in the artificial gaps (artificial gap > natural gap > thicket, Fig. 6). Survival was greater in the natural gaps than in the thicket and artificial gaps (Fig. 6) but differences in survivorship among the gap habitats were not significant (Table 4b). Although gap size and stem density of cleared *I. woodii* plants influenced growth and survivorship of the *I. woodii* seedlings (Table 4), they were not important

TABLE 4. Growth (a) and survivorship (b) of *I. woodii* seedlings grown in natural and artificial gaps of *I. woodii*, and thicket, at Mapelane

Source	d.f.	MS	F	P
(a) Growth				
Habitat	2	0.798	21.55	<0.001
Stem density	1	0.009	0.23	0.63
Stem height	1	0.008	0.23	0.64
Gap size	1	0.398	10.76	0.001
Habitat × gap size	1	0.016	0.44	0.51
Residual	431	0.037		
Total	438			
(b) Survivorship				
Habitat	2	0.051	1.38	0.27
Stem density	1	0.183	4.96	0.037
Stem height	1	0.013	0.36	0.56
Gap size	1	0.015	0.41	0.53
Habitat × stem density	2	0.012	0.32	0.73
Residual	22	0.037		
Total	30			

predictors of growth and survivorship (insignificant habitat × gap size and habitat × stem density interaction terms, Table 4).

DISCUSSION

Seed predation

Little evidence was found for pre-dispersal flower and seed predation in a synchronously reproducing *I. woodii* population. Values of fruit set from this study (61 %) did not differ from the 60 % of Griffiths *et al.* (2010). As reproduction in the species is not pollen limited, fruit set did not differ between treatments and was similar to that found in natural conditions. At 39–47 %, seed set is similar to the 48 % reported in Griffiths *et al.* (2010).

Silvertown (1980) reported an increase in pre-dispersal seed survival with an increase in seed crop size for 24 of 59 data sets and concluded that these data sets supported the predator satiation hypothesis. Our high value (>97 %) of pre-dispersal seed survival during a synchronous reproductive event may be similarly associated with predator satiation (see below). Attempts to obtain seed from isolated plants flowering out of synchrony with the rest of the population in 2005 at St. Lucia, approx. 35 km south of Cape Vidal, and in 2006 at Cape Vidal, were largely unsuccessful because of high levels of pre-dispersal seed predation (Z. Tsvuura, pers. obs.). The latter strengthens the case for mast reproduction events satiating seed predators. At St Lucia, post-seed dispersal plants were visited several times until they senesced but no seedlings germinated beneath the dying canopies. However, during masting of the Cape Vidal and St Lucia populations in 2007 and 2008, respectively, seed could readily be obtained and a carpet of seedlings emerged within 2 months of seed fall. The low levels of pre-dispersal seed predation may therefore be an effect of masting, which satiates seed predators.

Silvertown (1980) identified three interdependent elements to the predator satiation hypothesis. The first is that there should be enough seed produced for predators to consume and spare some. The second is that the interval between

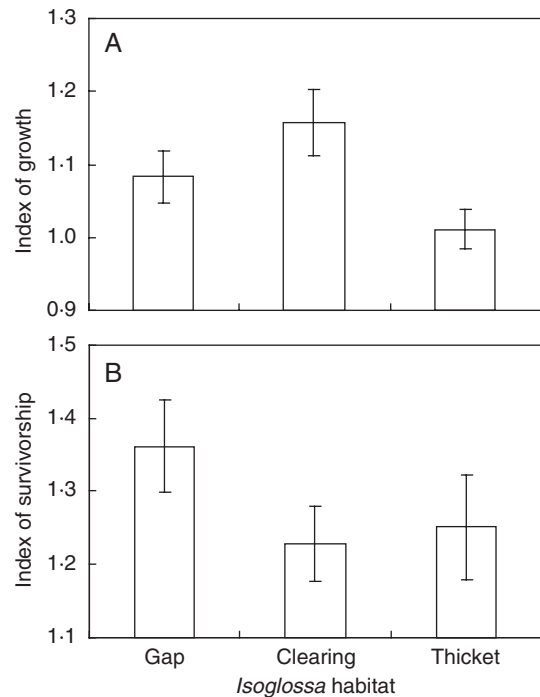


FIG. 6. Mean (\pm s.e.) growth (A) and survivorship (B) of *I. woodii* seedlings from Cape Vidal grown at three *I. woodii* habitats at Mapelane. The index of survivorship is based on arcsine square-root transformed values.

masting events should be sufficiently long to result in marked declines of the predator population (or at least prevent sustaining a large predator population), and finally that reproduction should be synchronized within the population and between sympatric species sharing the same seed predators. In our study system the first condition is realized: the 3 month long seed fall period could result in up to 14 100 seeds m^{-2} depending on plant size, topographic location and/or stem density, and there was abundant recruitment of seedlings. The period between the last observed masting event for the *I. woodii* population at Cape Vidal was 7 years, which is sufficiently long to prevent the maintenance of large populations of invertebrate seed predators that specialize on *I. woodii* seed. The main post-dispersal predator of *I. woodii* seed, *Pheidole* spp., is a generalist seed-eating ant species, and as such is unlikely to manifest a numerical response to the stages of the reproductive cycle of *I. woodii*.

Reproductive synchrony was evident in May 2007, when >90 % of the Cape Vidal *I. woodii* population flowered synchronously (Griffiths *et al.*, 2010). We observed no other species of either monocarpic (e.g. *Isoglossa cooperi* C.B. Clarke) or iteroparous Acanthaceae in flower at the same time as *I. woodii*. A similar finding of non-synchronized flowering of sympatric monocarps was reported in India, where it was associated with predator satiation (Janzen, 1976), but a similar association was not detected at Kibale Forest in Uganda (Struhsaker, 1997). Synchronized mast fruiting among many species of the Dipterocarpaceae has also been explained in terms of predator satiation (Janzen, 1974; Ashton *et al.*, 1988).

Post-dispersal predation of *I. woodii* seed decreased with an increase in the abundance of seed on the ground, the number of

inflorescences on stems nearest to the seed station and with height and density of *I. woodii* stems at the seed station. Thus, levels of seed loss demonstrate fine-scale predation effects. However, we found similar levels of predation from site to site, which indicates the absence of coarse-scale (site) predation effects. At both scales of measurement of predation, seed availability surpassed seed loss, which is consistent with the expectations of the predator satiation hypothesis.

Post-reproductive senescence and seedling establishment

The facilitation of establishment of *I. woodii* seedlings by the death of adult *I. woodii* plants may occur through increased light levels (Read *et al.*, 2006), through improved aeration and penetrability of the soil as a result of dying and decomposing roots, through improved water penetration and availability, or through the release of nutrients by the decomposing adult skeleton (see Vitousek and Denslow, 1986). Death of adult plants may also eliminate the transfer of allelopathic compounds and species-specific pests and diseases to establishing seedlings (Clark and Clark, 1984; Smith, 1984; Kitajima and Augspurger, 1989). Seedling establishment was greater under dying plants than in gaps, which suggests that the monocarpic strategy facilitates recruitment of seedlings. Gap sites may be unsuitable for recruitment of *I. woodii* in general (*sensu* Griffiths *et al.*, 2007). However, at $6.3 \pm 0.5 \mu\text{mol m}^{-2} \text{s}^{-1}$ the leaf-level light compensation point of the species is lower than background levels of light in understorey gaps (Tsvuura *et al.*, 2010), which should not preclude *I. woodii* establishment. Nevertheless, our finding of greater *I. woodii* establishment beneath dying conspecific plants concurs with Foster (1977), who suggested that post-reproductive death of *Tachigalia versicolor* trees at Barro Colorado Island in Panama facilitates establishment of its seedlings. In fact, Kitajima and Augspurger (1989) found enhanced growth and survivorship of *T. versicolor* seedlings growing beneath dying conspecific adult trees compared with under the canopies of living conspecific and non-conspecific trees. Light gaps created by the death of a monocarpic plant may be open for colonization by seedlings of pioneer species, but for a species exhibiting prolific reproduction the vacant sites are rapidly taken over by emerging seedlings of the species. The absence of seed dormancy in these monocarps (Young, 1982; Taylor and Inouye, 1985) increases the probability that regeneration sites will be occupied by conspecific seedlings.

Struhsaker (1997) suggested that the death of parent plants of monocarpic Acanthaceae allows seedlings of the species to swamp seedlings of other species competitively, thereby maintaining the dominance of the monocarp. The death of mature *I. woodii* plants may also facilitate seedling establishment through competitive release. However, facilitative effects of understorey plant mortality may be accompanied by suppressive effects. For example, Paul *et al.* (2004) have shown that collapsing dead stems of a dominant undercanopy shrub, *Acanthus pubescens*, smother and suppress tree seedlings in logging gaps. This is in sharp contrast to the death and eventual collapse of an *I. woodii* plant. After seed dispersal, the *I. woodii* plant starts to die, beginning with the inflorescences and inflorescence stalks, followed by the small thin branches that support inflorescences, then proceeds gradually

to the larger branches and main stem. In addition, over the flowering period, leaves undergo translocation of nutrients and drop off (Porizias and Balkwill, 2008). By the time the larger stem dies, the inflorescences and inflorescence-bearing stalks have fallen off so that at any one time very little biomass falls off an *I. woodii* plant. This mortality pattern is unlikely to smother *I. woodii* seedlings but could enhance their chances of establishment, as suggested for the mortality pattern of the monocarpic tree *T. versicolor* (Foster, 1977).

Greater establishment of *I. woodii* seedlings was found in the artificial and natural gaps than beneath adult plants at Mapelane. This lends further support to the notion that the mortality of post-reproductive plants enhances establishment of their seedlings. Patterns of survivorship showed that the natural gaps were associated with higher seedling survivorship than the artificial gaps and *I. woodii* thicket, which had similar survivorship. This suggests mortality due to below-ground competition, perhaps for water as most mortality occurred in the dry season after winter rainfall.

As *I. woodii* reproduces synchronously within and among plants and produces large numbers of seed at supra-annual intervals, the selective advantage of masting in the species probably derives from its ability to satiate predators. Seedling establishment in the species is facilitated by synchronous mortality of post-seeding plants. We conclude that satiation of seed predators and the benefits of seedling establishment have driven the evolution of synchronous monocarpy in *I. woodii*.

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