Reproductive ecology of some members of the Amaryllidaceae

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University of Cape Town

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Pollinator limitation and evolution of the inflorescence of *Amaryllis belladonna* (Amaryllidaceae)

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SUMMARY

Pollinators rather than resources, determined the capsule seed set of individuals of *Amaryllis belladonna* in a population on the Cape Peninsula, South Africa. Increased number of seeds per capsule was however, associated with a decline in seed mass. This indicates that resources determine seed quality, but not quantity in this species.

Total seed production per plant was positively correlated with inflorescence height as well as the number of flowers per inflorescence. Height and flower number together explained only 23% of the variance in total seed set. There was no significant relationship between inflorescence size and the seed set per flower. The difficulty of interpreting results where the heritability of a trait is unknown and where resource levels vary among plants is emphasised.

INTRODUCTION

The presentation of flowers in a manner attractive to pollinators is often an important function of the inflorescence (Wyatt, 1980). The number of flowers per inflorescence and the height of an inflorescence are two key traits which potentially influence the rate of pollinator visitation and thus the seed set of a plant, given that pollinator visits determine seed set (Willson and Price, 1977; Wyatt, 1980; Udovic, 1981; Pyke, 1981). Studies which investigate the adaptive nature of an inflorescence go hand in hand with experiments to determine if resources or pollinators determine seed set (Udovic, 1981; Bierzychudek, 1981; Pyke, 1987).

Normally it is assumed that if hand-pollinated flowers set more seed than naturally-pollinated controls, then the plant is pollinator limited (Bierzychudek, 1981; Campbell, 1987; Pyke, 1987; Spears, 1987). Alternatively if hand pollinated plants set the same amount of seed as controls, then resource limitation is assumed (Pyke, 1982; Udovic, 1981; Horvitz and Schemske, 1988).

Recently Haig and Westoby (1988) suggested that natural selection favours plants which allocate resources to both pollen attraction and seed production with an optimum where female fitness is co-limited by both pollinators and resources. The relative balance between pollinator and resource limitation would, however, fluctuate on an ecological timescale.

The traditional dichotomy between pollinator and resource limitation is associated with a number of uncertainties. Male fitness, defined as the number of offspring sired in other plants, is distinct from female fitness which is roughly equivalent to seed set. The male component of fitness complicates the pollinator/resource limitation framework which considers only female fitness (Pyke, 1987; Campbell, 1989). At present, paternity analysis is the only reliable method for estimating male fitness (but see Campbell, 1989).

Increases in seed set in hand-pollinated plants do not translate into proportional increases in fitness if seed quality is compromised. Recent evidence suggests that a trade-off often exists between seed number and size (Andersson, 1988; Lalonde and Roitberg, 1989). Perhaps the most serious problem with the pollinator/resource limitation dichotomy is that it does not take lifetime cost of reproduction into account (Schemske, 1980; Zimmerman and Mitchell Aide, 1989). Increased seed production may prejudice flowering and seed production the following year as demonstrated by Montalvo and Ackerman (1987) for the orchid *Ionopsis utriculariodes*. Despite these caveats the pollinator/resource limitation dichotomy provides a useful starting point from which to examine the adaptive nature of inflorescence design.

The primary aims of this study were to ascertain whether individuals in a population of *Amaryllis belladonna* were pollinator limited and to investigate the relationships between inflorescence size and seed set. I also aimed to test the hypothesis that a trade-off exists between nunber of seeds set and individual seed mass.

MATERIALS AND METHODS

Amaryllis belladonna (Amaryllidaceae) is a large bulbous geophyte. Flowering usually occurs following fire or bush clearing. A single inflorescence consisting of 2-12 flowers emerges during February or March. The pinkish-white flowers are large (ca 10cm length), bell-shaped and strongly scented. There is no foliage at the time of flowering; straplike leaves emerge after the flowers have senesced, and die back during the following summer. Species with this phenological pattern are said to have hysteranthous foliage (Dafni et al, 1981).

According to the only available information (Marloth, 1915), the species is pollinated by Hawkmoths (Sphingidae), but I have never verified this despite nocturnal observations. I found that carpenter bees (*Xylocopa sp*) visited the flowers of *A belladonna* mainly during the morning when they foraged for nectar.

Pollinator/resource limitation

A large population of *A belladonna* near Millers Point on the Cape Peninsula, South Africa, flowered en masse early in 1989 following a large fire the year before (2 May, 1988). Field work at this site commenced in February, 1989 and continued until May when flowering was over. Approximately 200 flowers, each on a separate inflorescence, were bagged while in bud in order to exclude pollinators; following anthesis these were hand-pollinated using pollen from plants either: 0 (selfed) 1, 15, 400 or 5000 metres away. The effects of pollination distance on seed set will be described elsewhere (Johnson, ms in prep.). When seed, if any, had set the capsules were harvested and seeds counted. Of the 200 flowers bagged initially only 65 remained undamaged at the time of harvest. Of these undamaged plants, only those that received outcross pollen (51 plants) were used in the calculations. Damage to inflorescences was due mainly to the Amaryllis moth *Brithys pancratii*. Caterpillars of this species bore out inflorescence stalks with the result that the inflorescence inevitably keels over and snaps in the wind.

Naturally pollinated controls were harvested in three 5 X 5 metre plots within the same sub-populations as the hand-pollinated plants. A total of 102 inflorescences were harvested of which 51 were randomly selected for comparison with hand pollinated plants. Since only one flower per inflorescence was used for the hand-pollinations, it was necessary to select one flower randomly from each inflorescence of the control plants.

Inflorescence size and seed set

The 102 inflorescences harvested in the 5 X 5 metre plots described above formed the basis for an investigation into the effects of inflorescence structure on seed set. I regressed height and number of flowers per inflorescence against total seed set per plant as well as mean seed set per flower. Multiple regression techniques (Zar, 19~~80~~74) were used to determine the combined effects of height and flower number on seed set. The data from the 5 X 5 metre plots were also used to construct frequency distributions of inflorescence height and flower number size classes. I used one way ANOVA to compare levels of seed set between the three subpopulations.

The investigation into effects of capsule seed set on seed mass involved throwing a short line transect into one the subpopulations and harvesting the first eight inflorescences which contained fully mature seed. These were taken to the laboratory where all seed was weighed. All statistical analysis was performed using the "Statgraphics" package.

RESULTS

Pollinator/resource limitation

Seed set of *Amaryllis belladonna* was clearly limited by pollinators since hand pollinated flowers set more than twice the seed per capsule of naturally pollinated controls (Table 1). This difference in seed set between pollination treatments was highly significant. A significant negative relationship was found between seed set per capsule and seed mass (Fig 1). This relationship is based on pooled data from all plants harvested since no significant relationship existed between flower number per inflorescence and seed mass.

Inflorescence size and seed set

Levels of seed set due to natural pollination did not vary significantly between the subpopulations (df=2, F=1.924, P=.1515). Hence correlation between inflorescence size and seed set was tested using pooled data. Although total seed set was correlated significantly with both inflorescence height and number of flowers per inflorescence, these relationships explained little of the variance in seed set (Fig 2). No significant relationship existed between seed set per flower and flower number per inflorescence (Fig 2). Taller inflorescences tended to have significantly more flowers (Fig 2). Multiple regression analysis showed that inflorescence height and flower number could together explain 23% of the variance in total seed set (seed set = 0.93(height) + 3.40(flower no) - 21.41, df=99, R^2 =0.236, P<0.001). The frequency distributions of inflorescence sizes were normal, with intermediate sizes most frequent (Fig 3).

Table 1 Seed set and percentage of flowers setting fruit for hand pollinated flowers and naturally pollinated controls. The significance of the difference in seed set between the two treatments was tested using the Mann-Whitney U test for large samples (Zar, 1974). Values in parenthesis indicate the standard deviation. Sample size is 51 for both treatments and indicates number of plants since one flower was used per plant.

	Controls	Hand pollinated	Z	P
Seed set per capsule	7.1 (10.5)	18.8 (14.1)	4.70	<0.001
Percentage fruit set	66.6	82.0		

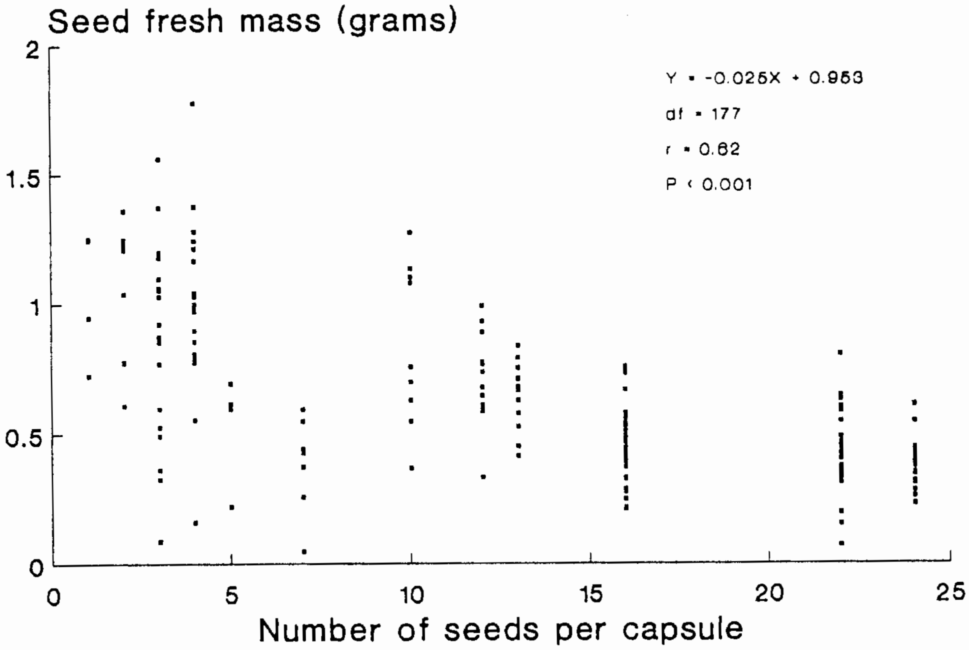
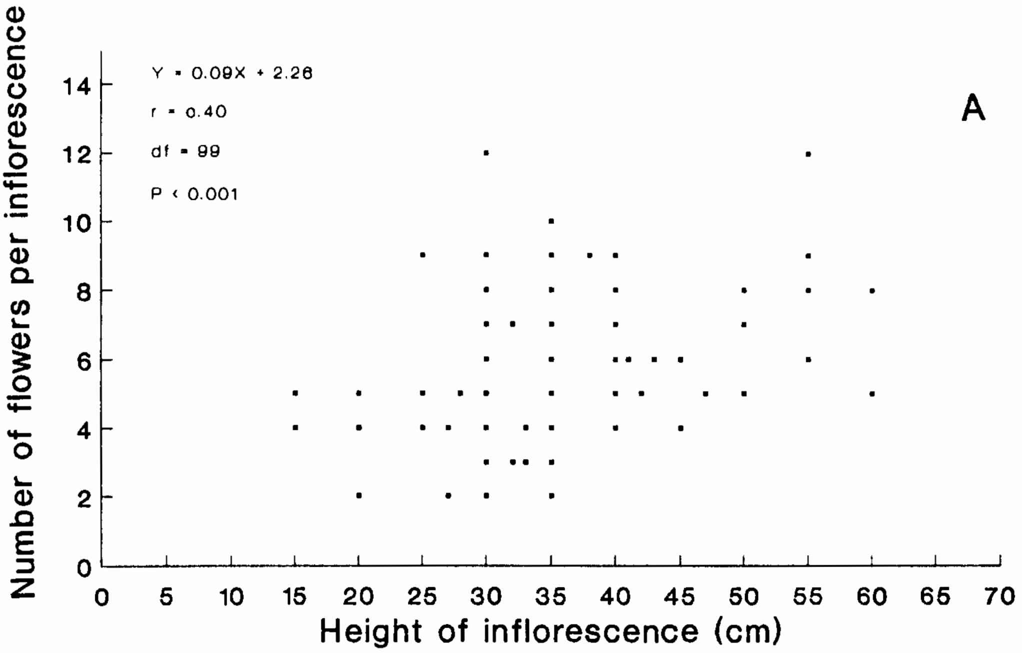
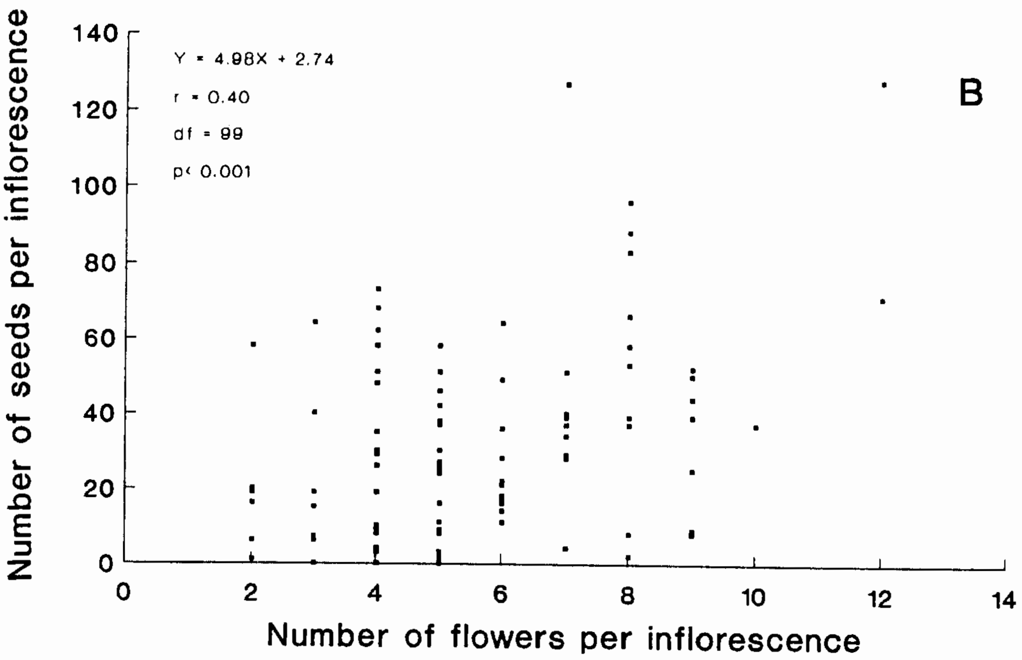
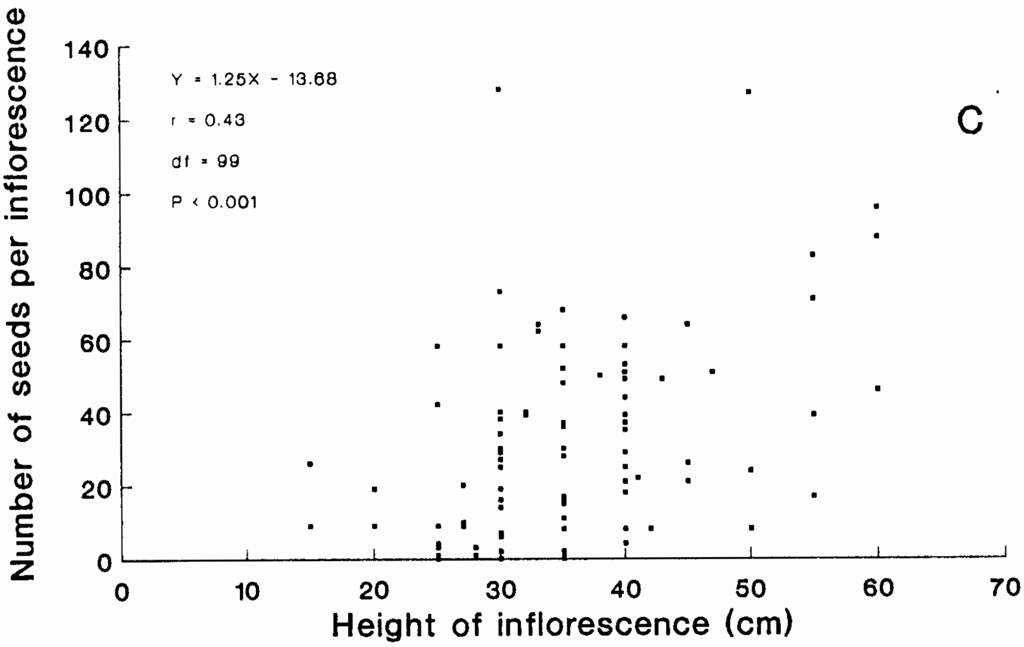


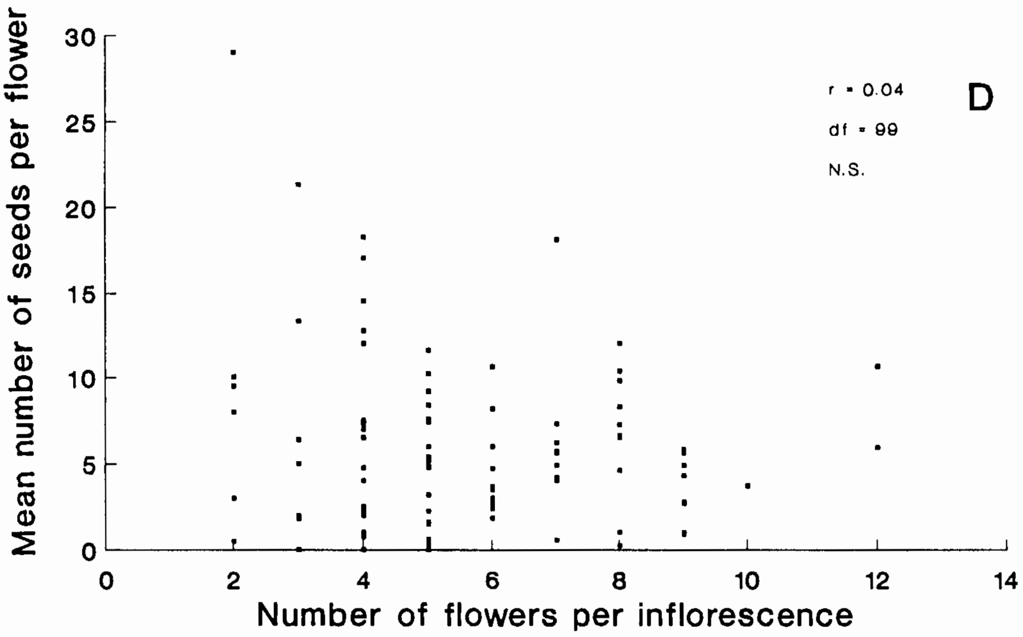
Fig 1 The relationship between number of seeds per capsule and seed mass. Each data point represents a single seed. Data from eight inflorescences were combined.

Fig 2 Relationships between inflorescence height and flower number (A); Flower number and total seeds (B); Inflorescence height and total seeds (C); Flower number and mean number of seeds per flower (D).


Y = 0.09X + 2.26
r = 0.40
df = 99
P < 0.001
A
Number of flowers per inflorescence
0
2
4
6
8
10
12
14
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
Height of inflorescence (cm)


Y = 4.98X + 2.74
r = 0.40
df = 99
p< 0.001
B
Number of seeds per inflorescence
0
20
40
60
80
100
120
140
0
2
4
6
8
10
12
14
Number of flowers per inflorescence


Number of seeds per inflorescence
140
120
100
80
60
40
20
0
Y = 1.25X - 13.68
r = 0.43
df = 99
P < 0.001
C
0
10
20
30
40
50
60
70
Height of inflorescence (cm)


Mean number of seeds per flower
30
25
20
15
10
5
0
r = 0.04
df = 99
N.S.
D
0
2
4
6
8
10
12
14
Number of flowers per inflorescence

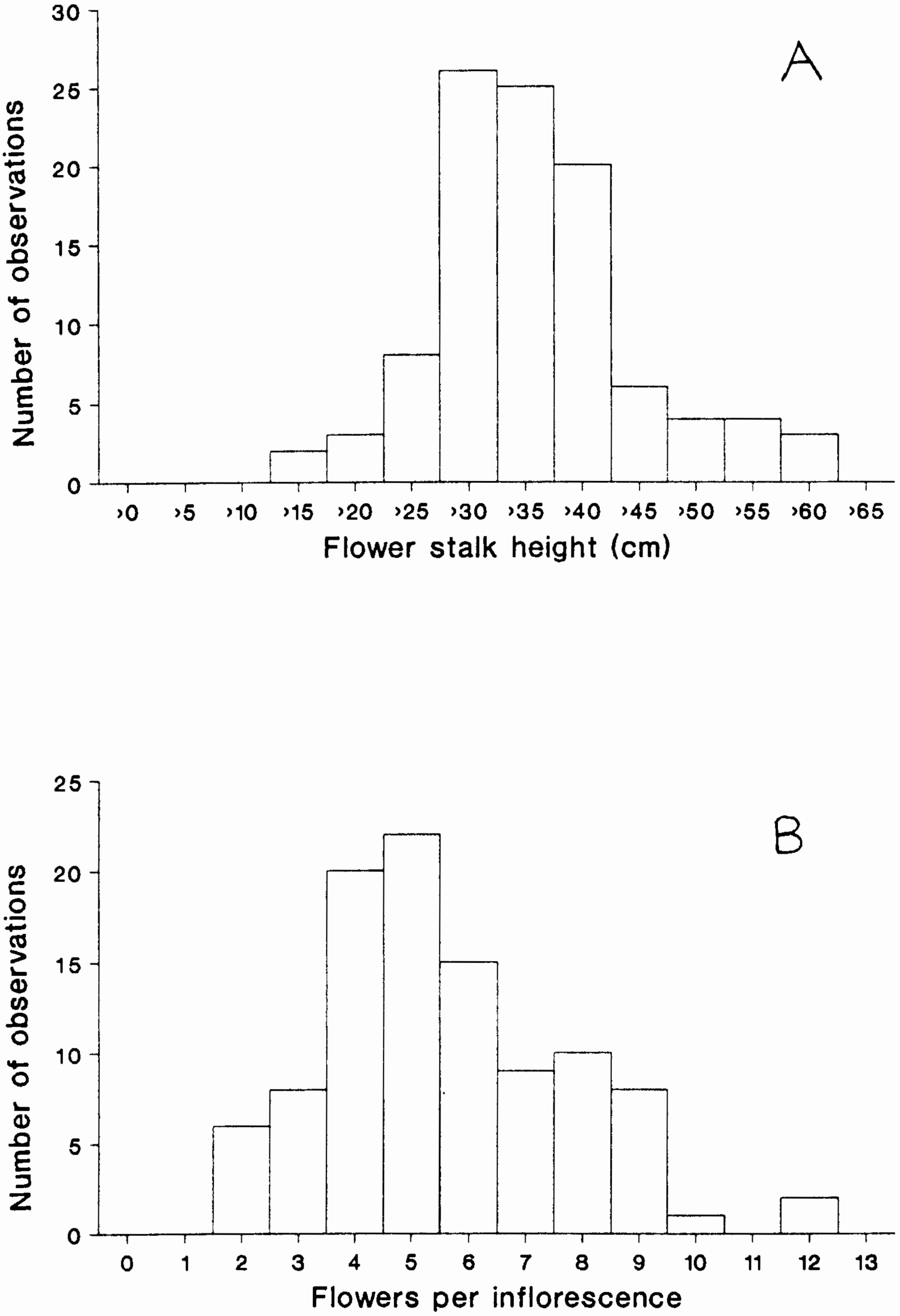


Fig 3 Frequency distributions of inflorescence height (A) and Flower number (B).

DISCUSSION

Pollinator limitation

The results show that seed set of *Amaryllis belladonna* was strongly limited by pollinators. Good reasons exist for assuming that insect pollinators are generally limited in the Cape flora. The bulk of the vegetation known as mountain fynbos occurs on extremely nutrient poor soils. According to Cottrell (1985) the relative unpalatability of these fynbos species has resulted in the absence of a distinct local butterfly fauna. Few data exist for other insect groups but R. Marloth, an early naturalist at the Cape, noted that insects were often conspicuously absent though "the fields may be aglow with flowers" (Marloth, 1908). Fynbos geophytes ,including *A belladonna* which flower mainly after fire are notable for their large showy inflorescences. This phenomenon could be attributed to a scarcity of insects following fire which would lead to strong selection for attractive floral displays. Carpenter bees which pollinate *A belladonna* make nests in branches (Watmough, 1974) and are thus "homeless" following a fire. Competition for the few insects following a fire would be intense and result in strong selection on floral characters and inflorescence structure.

A general scarcity of insects in the fynbos, especially following fire, is not the only explanation for pollinator limitation of *A belladonna*. Inclement weather, including periods of cold and rain as well as high wind velocities on the Cape Peninsula would reduce the number of days on which pollinators would be active. It would be interesting to know if the ±30% of flowers of *A belladonna* which did not set fruit (see Table 1) were open during unfavourable weather. One adaptive means of coping with this uncertainty is to stagger flowering over a period of weeks, as occurs in *A belladonna*.

No studies dealing with pollinator limitation, with which this study can be compared, exist for the Cape Flora. Studies in Australia indicate that plants in comparable ecosystems to the fynbos tend to be resource limited (Collins and Rebelo, 1987; Pyke, 1987). These studies have, however, mostly dealt with Proteaceae and are thus not directly comparable with the present study for two reasons. Firstly, Proteaceae tend to be shrubs, a very different growth form from geophytes. Secondly Proteaceae which have been studied are pollinated by mammals and birds, not insects. This latter difference is important since it mat be that shortages of insects led to the success of nectarivorous birds in Australia and South africa (see Ford, 1985)

In order to avoid statistical problems I chose to hand-pollinate only one flower per inflorescence. This may have resulted in an overestimate of the extent of pollinator limitation if resources from flowers which were not hand-pollinated were diverted into the hand-pollinated flower (see Campbell, 1987; Horvitz and Schemske, 1988).

Gain in seed number per capsule of *A belladonna* occurs at the expense of seed mass, implying resource limitation of seed quality. This result provides indirect support for the hypothesis of Haig and Westoby (1988) that plants should be co-limited by pollinators and resources for female fitness. My reasons for using fresh seed mass and not dry mass were as follows: firstly, water is probably a limiting resource for summer-flowering species in Mediterranean ecosystems and might therefore be partitioned among seeds. Dry seed mass would not reflect this partitioning. Secondly, Markotter (1936) showed that germination of seeds of *A belladonna* occurs soon after release often during the harsh summer drought. Thus fresh seed mass probably more accurately reflects seed fitness than does dry mass.

The negative relationship between seed number and seed mass implies that gain in seed set following hand-pollination overestimated the extent of pollinator limitation of actual female fitness, since increased quantity of seed resulted in decreased quality. Increased seed set may further overestimate female fitness if gains in seed number prejudice growth, flowering and/ or seed production the following year (Schemske, 1980; Zimmerman and Mitchell Aide, 1989).

Inflorescence size and seed set

Increased inflorescence size of *A belladonna* was associated with increased total seed set (Fig 2). The low variance in total seed set explained by both these variables (23%) is probably typical for pollinator limited plants. In contrast, Udovic (1981) found that inflorescence size explained 54% of the variance in seed set of resource limited *Yucca whipplei* plants.

Interpretation of the relationship between inflorescence size and seed set is difficult in the light of the myriad of suggested selective factors operating on inflorescence design (see Wyatt, 1980). It is often argued that selection through male fitness imposes selective forces as strong or stronger than through female fitness (Willson and Price, 1977; Collins and Rebelo, 1987; Pyke, 1987; Horvitz and Schemske, 1988). The problem here is that paternity analysis is the only reliable means of determining male fitness and is a time-consuming technique. Recently Campbell (1989) reported experiments where she used dye analogues as an approximation of pollen dispersal and therefore male fitness. Her results do not support the male fitness hypothesis for individuals of *Ipomopsis aggregata*. Increases in flower number resulted in disproportionate increases in female fitness but only linear increases in male fitness.

Male fitness has been used as an explanation for the generally low levels of fruit set in hermaphrodite plants (Sutherland and Delph, 1984). Fruit set in *A belladonna* averaged about 66% (Table 1) which is probably higher than average for an hermaphrodite species. Production of flowers which set no fruit but act as pollen donors translates into functional andromonoecy (see Collins and Rebelo, 1987). Because seed set of *A belladonna* is pollinator limited, it is unlikely that selection acts through male function. Selection through male function is probably stronger in resource-limited plants where strong competition exists for access to ovules.

The relationship between flower number and total seed set of *A belladonna* was proportional: twice as many flowers set twice as many seeds. Thus there was no decline in the efficiency of the inflorescence (number of seeds per flower) with increased flower number. In contrast, Andersson (1988) found that increased number of flowers per plant of *Anchusa officinalis* resulted in a significant decline in the percentage of flowers which set fruit, although the total number of fruits per plant increased. Plant fitness depends on the total number and quality of seeds produced and not the number of seeds per flower or percentage fruit set.

Flower number and inflorescence height in *A belladonna* may simply reflect bulb size (ie resource levels). The heritability of inflorescence characters of *A belladonna* is unknown. This problem of interpreting results applies to most evolutionary studies which compare fitness of plants possessing a variable trait without information on the heritability of that trait. The correlation between inflorescence size and seed set found in this study may not indicate cause and effect. For instance, higher levels of resources may allow a plant to produce both more flowers and more seeds. Thus although seed set per capsule may be pollinator limited, production of flowers and total seed set per plant could be determined by resources. This problem of interpretation may prove to be the achilles heel of most studies dealing with evolution of inflorescence architecture. Campbell (1987) suggests that controlling for resource levels by removal of flowers from inflorescences of a fixed size may be a better technique than using inflorescences that vary in size naturally. However removal of flowers involves the risk of physiological stress to plants.

The results of this study indicate that inflorescence height explained more of the variance in total seed set than flower number (Fig 2). At the time of the study, a year after the site was burnt, an understorey had developed which in some cases obscured the inflorescences of *A belladonna*. It does not seem unreasonable therefore to suggest that taller inflorescences were more visible to the carpenter bees and thus achieved higher seed set. Furthermore, taller inflorescences were capable of dispersing seeds further from the parent (SD Johnson, unpublished data) Efficient dispersal may increase offspring fitness in two ways. Firstly, seeds further from the parent are less likely to be shaded when the leaves emerge shortly after seed dispersal. Secondly, inbreeding depression of fitness due to matings with either the mother or siblings is less likely. Alternatively inflorescences of low stature might be favoured if short distance dispersal results in favourable conditions for seedling establishment beneath the foliage. This issue deserves further consideration in studies that deal with adaptive inflorescence design.

Limits to inflorescence size

Frequency distributions of inflorescence size revealed a disparity between the size most frequent in the population (Fig 3) and the size which resulted in greatest seed set. The size most frequent in the population should be the size that has been selected for over evolutionary time (Wyatt, 1980).

Optimum inflorescence configuration results in greater lifetime fitness, even though total seed set may be lower for that inflorescence in a particular year. Resources may limit an iteroparous species such as *A belladonna* over a lifetime (Schemske, 1980; Motten, 1983)). Lifetime resource limitation is probably the primary factor which limits inflorescence size in geophytes and would apply to both pollinator and resource limited plants . Geophytes with hysteranthous foliage only flower if sufficient carbohydrate is accumulated during the leafing season (Burtt, 1970; Dafni et al, 1981). In a concurrent study I censused the number of flowering individuals in March and again in August when the plants were leafing. I found that only about 7% of the adult plants had actually flowered (unpublished data). It may be that mass flowering the year before had prevented most of the plants from flowering again. Production of a moderate sized inflorescence may allow the plant to flower again the following year. Recently Zimmerman and Mitchell Aide (1989) demonstrated that flowering individuals of the orchid *Aspasia principisa* which set seed had lower shoot and flower production the following year relative to flowers which had set no seed.

Selection may occur for smaller inflorescences if stigma clogging by self-pollen resulting from within-inflorescence moves by pollinators decreases success probabilities of outcross pollen (Wyatt, 1980). One adaptive solution to this problem (stigma clogging), that does not involve reducing inflorescence size, could be staggered flowering in an inflorescence with few flowers open at any one time.

A within-season study such as present will never be able to answer all the questions surrounding optimal inflorescence structure. Ecological time differs from evolutionary time. Conditions differ between each fire and between each year following a fire. The answer to the question "what is the optimal inflorescence architecture of *A belladonna* within the architectural constraints the species inherited from its predecessors?" is given in the frequency distributions in Fig 3. The answer to the question "why?" will only be answered fully when all ecological, genetic and life history parameters can be taken into account.

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Pollination distance and seed set in the March lily *Amaryllis belladonna* (Amaryllidaceae)

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SUMMARY

Crosses were performed between individuals of *Amaryllis belladonna* separated by various distances. Seed counts suggested an effect of pollination distance on seed set with an "optimal outcrossing distance" lying within the population.

Plants that received self-pollen only did not set seed indicating that *A belladonna* is self-incompatible. Seed dispersal is extremely limited and no seeds were found more than two metres from the parent. Discussion centres around the mixed evidence for optimal outcrossing distances and the problems of relating such optimum distances (if any) to classic parameters of plant population genetic structure such as neighbourhood area.

INTRODUCTION

A decade has passed since Price and Waser (1979) first reported an "optimal outcrossing distance" for populations of *Delphinium nelsonii*. Although subsequent studies show distance to be a strong factor determining fecundity following mating in some species, evidence for an optimal outcrossing distance within populations remains slim. Crosses are expected to be most successful where the effects of inbreeding depression and outbreeding depression are least pronounced (Waddington, 1983; Waser and Price, 1983). Optimal matings in populations of *Delphinium nelsonii* and *Ipomopsis aggregata* occurred between plants separated by less than a hundred metres (Price and Waser, 1979; Waser and Price 1983).

Both inbreeding and outbreeding depression of fitness following close and far matings respectively are poorly understood processes. Inbreeding depression of seed set has frequently been demonstrated (Price and Waser, 1979; Waser and Price, 1983; Levin, 1984; Harder et al, 1985; Sobrevila, 1988; Redmond et al., 1989). Other studies do not reveal inbreeding depression in the F1 generation (Motten, 1983; Galen et al, 1985). Selfers which do not have a high genetic load are usually less susceptible to inbreeding depression (Levin, 1984). Obligate outcrossers on the other hand may suffer inbreeding depression following near neighbour pollinations as a result of sharing of incompatibility alleles by closely related plants (Levin, 1984; 1989) and/or expression of deleterious alleles early in seed development (Price and Waser, 1979; Levin, 1984; Charlesworth, 1989).

Limited gene flow among plants results in isolation by distance and allows differentiation to occur on a micro-geographical scale. At the species level co-adaptation of the plant genome, rather than gene flow is probably responsible for species integrity. Large populations of species with limited dispersal of pollen and seed are not panmictic, but comprise several neighbourhoods which may display genetic heterogeneity. It is this fine scale of differentiation which is of interest here and could be revealed by effects of pollination distance on reproductive success.

Matings between distant plants may result in outbreeding depression of fitness (Price and Waser, 1979). Genomes which are locally adapted may prove incongruent when combined in matings (Price and Waser, 1979). Also, mating between distant partners may break up co-adapted gene complexes (Campbell and Waser, 1987). It is still unclear whether plants have the ability to discriminate between pollen grains in a graded fashion. If so they possses a profound adaptation since seed lands in the immediate female enviroment. Crossing with plants adapted to that enviroment and yet not too genetically similar should maximise offspring survival (Waser and Price, 1989).

Hand-pollinations between plants separated by various distances provide a qualitative means of investigating the scale of intra and inter-population genetic differentiation. Loveless and Hamrick (1985) have provided a synopsis of the effect of ecological factors on the genetic structure. However it is still premature to assess the affect that ecological factors, plant life history traits and plant breeding systems have on optimal outcrossing distances (if any). There is strong theoretical evidence and some experimental evidence that limited gene flow in a population of self-incompatible plants would result in short optimal outcrossing distances (Waser and Price, 1983; Waddington, 1983; Campbell and Waser, 1987). The Cape Flora is exceptionally species rich (Bond and Goldblatt, 1985) suggesting that ecological factors in the region have promoted speciation (Linder, 1985). As yet we know very little about inter and intra-population differentiation of species in the Cape Flora. Studies such as the present dealing with the fecundity of crosses between plants separated by various distances provide a unique qualitative way of investigating the spatial scale of genetic differentiation in species.

The aims of this paper were to investigate pollination distance effects on seed set of Amaryllis belladonna and to measure propagule dispersal in nature.

MATERIALS AND METHODS

Field work for this study took place between February and May of 1989 at a site located about 3km south of Millers point on the Cape Peninsula. A fire the year previously had resulted in a mass display of the March lily *Amaryllis belladonna* (Amaryllidaceae). A large population with a diameter of about 500 metres was chosen for field experiments. This population was not uniform in density but consisted of smaller dense patches (metapopulations).

Amaryllis belladonna is a bulbous geophyte with hysteranthous foliage (cf Dafni et al. 1981). The species flowers mainly in response to fire and bush clearing, but some flowering occurs between fires as well. The single inflorescence, a pseudo-umbel consists of 2-12 large (ca 10 cm length) bell shaped flowers which range in colour from white to dark pink. Flowers are hermaphrodite and very weakly protandrous. Vegetative reproduction may occur by the production of daughter bulbs. Strap-like leaves emerge after seed has been released. Although the species is popular as a garden subject, nothing (to my knowledge) was known of its reproductive biology except for remarks in the Flora of South Africa (Marloth, 1915). I carried out about 40 hours of observation at the site in order to determine the pollen vectors of the species.

Effects of pollination distance on seed set

About 200 flower buds, each on a separate plant were bagged with sections of nylon stocking. Following anthesis each bagged flower was assigned to receive pollen from a distance of either 0 (selfed), 1, 15, 400 or 5000 metres. The 5000 metre crosses were between plants from different populations. One metre was considered a sufficient distance to avoid matings between sister ramets. Hand pollination consisted of removing a ripe stamen from the pollen donor and gently brushing it across the receptive stigma. Receptivity is easily identified when the stigma opens out and becomes furry. I standardised the time between breaking off a stamen and pollination and also attempted to do all pollinations around midday to control for possible daily changes in stigma receptivity. Some bagged flowers were not pollinated but left intact to check that the nylon stockings were in fact pollinator-proof (assuming that the species is not cleistogamous).

I used a single flower per plant to avoid pseudoreplication; a population of flowers on an inflorescence is interdependent in terms of resource allocation.

Following pollination the plants were left for seed to mature. During this time it became apparent that the Lily borer *Brithys pancratii* (Lepidoptera) had destroyed a high percentage of the inflorescences. In order to avoid further damage I harvested the flowers before the seed was fully mature, but still easy to count. The final count showed that only 75 of the original 200 bagged flowers were not damaged. Capsule seed set was determined and statistically analysed using one way analysis of variance and polynomial regression to determine whether pollination distance had an effect on seed set. The use of polynomial regression follows Newport (1989) who described it as a "rigorous statistical approach." I used a variety of linear and polynomial regressions on both untransformed and log-transformed data (x axis only). All statistical analyses were performed with the 0 metre distance (selfed) excluded. I used the "statgraphics" package for data analysis.

Dispersal

The extent of gene flow will affect population differentiation and possibly the optimal outcrossing distance (Waddington, 1983). Gene flow normally occurs via seed and pollen dispersal in plants.

I attempted to measure dispersal of fluorescent dyes as an approximation of pollen flow (Stockhouse, 1976). However this section of the study failed despite two attempts of 24 hours duration each. It appears that the method is unsuitable for plants where the rate of visitation is low.

Seed dispersal on the other hand, could be easily estimated. Seed of *A belladonna* is large (up to two grams) and easily found in the field. I chose 14 plants which were isolated from other plants by a few metres and counted all seed around the plant noting the distance of dispersal.

RESULTS

Observations at the site indicated that carpenter bees (*Xylocopa sp*) were the primary diurnal visitors to the flowers of *Amaryllis belladonna*. The bees worked mainly in the morning when they gathered nectar, becoming dusted with a thick layer of pollen in the process. Other visits by small bees and flies were occasional and probably not effective in pollination. Nocturnal observations failed to verify the statement by Marloth (1915) that hawk moths (Sphingidae) are responsible for pollination. Possibly I was not present at the site on nights which were warm and still enough for sphingids to be active.

Effects of pollination distance on seed set

Flowers which were bagged but not hand pollinated set no seed indicating that the bags effectively excluded insects. Self-pollination resulted in practically no seed production in *A belladonna* indicating that the species is self-incompatible.

The hypothesis that pollination distance affects seed set was supported by the data although the results were not qiute significant at the 5% level.(Fig 1; ANOVA P=0.07; Regression P=0.055).

Log transformed distances were found to best predict seed set in a variety of regression models. The predicted optimal outcrossing distance from the fitted curve was 73 metres, well within the population.

Dispersal

Seed dispersal is extremely limited in *A belladonna* (Fig 2). Seed dispersal occurs by a shake and toss method where the inflorescence acts as a catapult operated by the wind. I found no evidence of animal dispersal or predation on the seeds.

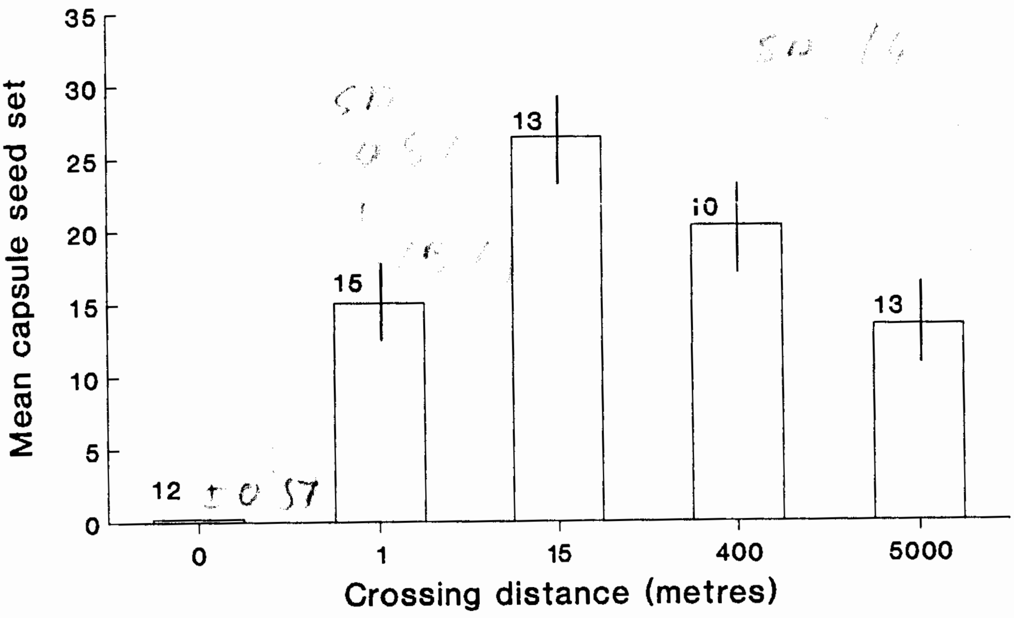

Fig 1 Effects of crossing distance on seed set per capsule for a population of *A belladonna*. Histograms represent means ± s.e with sample sizes (number of plants) shown. Two statistical tests were used: ANOVA F=2.447, P=0.07; Quadratic regression df=49, R^2 =0.076, P=0.055, $Y = 12.21 + 14.26(\text{Log } X) - 3.81(\text{Log } X)^2$. Predicted optimal outcrossing distance from this curve is 73 metres.

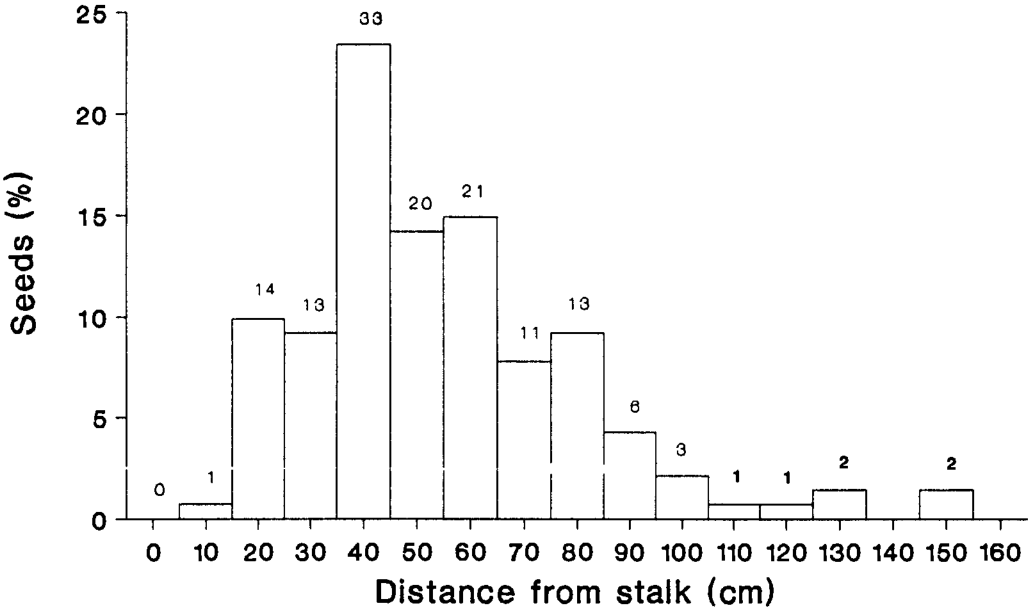

Fig 2 Seed dispersal of *A belladonna* (n=14). Values above each histogram represents the number of seeds recovered per class interval (0-10, 10-20 cm etc).

DISCUSSION

Optimal outcrossing distances have only rarely been reported (Price and Waser, 1979; Waser and Price, 1983; Levin, 1984; Schemske and Pautler, 1984; see also Sobrevila, 1988). An optimum within a population has only been reported for *Delphinium nelsonii* and *Ipomopsis aggregata* (Price and Waser, 1979; Waser and Price, 1983). My data suggest an effect of pollination distance on seed set, but is not quite significant at the 5% level. Nevertheless if we are to proceed to an understanding of the ecological and life history parameters which affect population genetic structure and thus optimal outcrossing distances then studies such as the present have a role to play. Quantitative analysis in pollination ecology is confounded by "the vagaries of nature" which tend to whittle away at sample sizes during an experiment (Price and Waser, 1989). Newport (1989) found that variance between reciprocally crossed pairs was substantial and probably reflects the mosaic of resource levels and genetic variation in a plant population.

Inbreeding depression

Seed set resulting from one metre crosses was about half that resulting from 15 metre crosses. There are two possible explanations for this effect. In a self incompatible species such as *A belladonna* reduced seed set following pollination with near neighbours may result from self-incompatibility alleles shared by closely related plants (Levin, 1989). On the other hand genetic load is usually higher in outcros~~s~~sers relative to selfers and may explain inbreeding depression of fitness in the F1 generation. Deleterious alleles are usually expressed during seed development (Levin, 1984).

Harder et al (1985) and Sobrevila (1988) found that variation in seed set was greater following near crosses than following far crosses. I found no difference in variance of seed set between any of the crossing distances. If self incompatibilty alleles are shared between neighbours then seed should either be present or absent resulting in a high variance in seed set. On the other hand inbreeding depression due to high genetic load should be characterised by a consistent depression of seed set with a low variance. A tentative conclusion therefore might be that genetic load rather than self incompatibility alleles explain the reduced seed set following hand pollinations between neighbouring individuals of *A belladonna*.

Levin (1989) showed that pollen-pistil compatibility increases with distance in populations of *Phlox drummondii* which is practically self incompatible. This phenomenon if common in nature has tremendous implications for population genetic structure. If near pollen is rejected outright, far pollen will have greater success and inbreeding will be reduced (Levin, 1989). Greater success of far pollen at the expense of near pollen will have the effect of opening up the genetic structure of a population (Levin, 1989). Self compatible species may behave somewhat differently: Fenster and Sork (1988) found no effect of crossing distance on pollen germination and pollen tube growth for *Chamaechrista fasciculata*., despite an effect of pollination distance on progeny fitness in this species.

Outbreeding depression

The fitted quadratic regression predicted that seed set follwinf crosses between parents separated by 73 metres would be optimal and that more distant crosses would reduce seed set. This should not be taken too literally. The nature of a fitted curve would vary depending on which discrete distance intervals I decided to use.

The study population is situated on the interface of two soil types. Nutrient poor soil derived from Table mountain sandstone occurs on the upper slopes and is juxtaposed with soil derived partially from granite nearer the coast. Thus selective gradients may have resulted in micro-adaptation within sub-units of the population.

Outbreeding depression of fitness results from incongruency of genomes or the breakdown of co-adapted gene complexes (Price and Waser, 1989). It is impossible at this stage to know the relative contributions of genetic drift and micro-adaptation to the apparent differentiation within and between the populations of *A belladonna*.

Dispersal

Limited gene flow clearly increases the potential for divergence between populations, whether divergence occurs through genetic drift or adaptation (Levin, 1982). I found it impossible to estimate pollen flow using dye powder, but observation of carpenter bee flights indicated that most movement was on a neighbour to neighbour basis. Occasional long distance escape flights were further (up to 20 metres). This pattern of flights results in a leptokurtic distribution (Levin, 1981).

Seed dispersal of *A belladonna* is clearly very limited (Fig 2). This is especially significant for gene flow since seeds carry twice the allelic content of pollen.

Waser and Price (1983) discussed the apparent paradox that limited pollen dispersal in *Ipomopsis aggregata* and *Delphinium nelsonii* indicated that these species might not in fact achieve optimal matings. If the optimal outcrossing distance for my study population was around 73 metres as suggested by the polynomial regression, then *A belladonna* might also not achieve optimal matings. I saw no carpenter bee flights approaching 73 metres, but then effective pollen flow may be higher due to pollen carryover (Schaal, 1980). Waddington (1983) has argued that optimal matings cannot be achieved through selection on plant traits that encourage longer distance pollen dispersal. Increased gene flow will increase the optimal outcrossing distance resulting in runaway selection, a situation akin to chasing a shadow. An allele for greater pollen dispersal might initially benefit an individual but would become gradually less effective as it spread through the population as it would push the zones of inbreeding and outbreeding depression further away and therefore the optimal outcrossing distance as well.

The issue is unresolved; recently Campbell and Waser (1987) carried out multilocus simulations of selection at "dispersal loci". The results showed that plants converged for intermediate dispersal alleles. Exactly how floral traits affect dispersal remains unclear (Waser and Price, 1983; Waddington, ,1983) Changes to the inflorescence structure and changes in nectar composition may result in a pollinator shift. Variation in pollen grain sculpturing may affect pollen carryover.

Changes to inflorescence and seed characters resulting in increased seed dispersal distances were left out of the model of Campbell and Waser (1987). Waddington (1983) did not consider seed dispersal. Long distance seed dispersal via wind-dispersed inflorescences in some Amaryllids scatters siblings over a wide geographic area (pers obs). In this way the problem of inbreeding depression following matings between closely related neighbours may be circumvented.

[illegible]

Does seed set equal fitness?

Plants have a fixed amount of resources which are allocated to seed production. A high seed set will not translate into increased fitness for a plant if few seeds germinate or if seedling survivorship is low. In a concurrent study I found a negative relationship between seed mass and number of seeds per capsule (S D Johnson, ms in prep). On the other hand a long term study on *Ipomopsis aggregata* showed that crosses at 10 metres resulted in highest seed set and also highest survivorship and lifetime fitness of offspring (Price and Waser, 1989). The use of seed set as a rough measure of success can be defended on the grounds that by far the most viability depression in plants is expressed during seed development (Levin, 1984).

The subject of optimal outcrossing distances is at present loosely defined and does not seem to fit into either the field of genetics proper, nor traditional ecology and is not natural history. The Cape Flora provides an ideal testing ground for some of the theoretical concepts that have emerged over the last 10 years. It is commonly assumed that a combination of limited gene flow, enviromental heterogeneity and fire disturbance have promoted speciation in the Cape flora (Linder, 1985). Most of these assumptions have been made with little evidence. In this paper I have presented evidence that micro-diffferentiation may occur within a population of *A belladonna*. Ample scope exists for this type of research in the Cape Flora. It would be interesting for instance to compare the effects of pollination distance on seed set in species of Proteaceae which have wind dispersed seeds to those which have ant-dispersed seeds (myrmecochory). When enough studies have accumulated it may be possible to develop equations which predict optimal outcrossing distances from classical genetic parameters such as neighbourhood area, life history characteristics and breeding system? A direct conservation implication of this study is that small nature reserves resulting from fragmentation of the natural landscape might contain non-viable plant populations if the perimeter of the reserve falls within the zone of inbreeding depression. Reserves should be large enough to contain individuals capable of optimal matings.

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THE DIVERSITY OF POLLINATION AND SEED DISPERSAL IN FYNBOS AMARYLLIDS

STEVEN JOHNSON

Aeropetes tulbaghia is that large brown, fast flying butterfly, common in the Western Cape during summer. The species is better known as the Table Mountain Butterfly or simply "Meneris", after its old Generic name. The butterfly pollinates *Disa uniflora* and a host of other summer flowering species. If you climb high on the sides of one of the kloofs around Bettys Bay during May, you will find the Guernsey lily (*Nerine sarniensis*) in full bloom. The Guernsey Lily is pollinated by the Table Mountain butterfly which moves rapidly between flowers, pausing only occasionally to forage on nectar.

The Guernsey lily was one of four species I chose to study for an ecology project that formed part of the Botany honours course at UCT. Natural history (like watching butterflies) formed only a part of that project, the rest was tedious stuff that involved long hours of "number crunching" at a computer. It may be argued that watching butterflies is not science. Maybe but the reality of the situation is that we know a minimal amount about pollination in the fynbos. Certainly many walkers must know "what pollinates what" but unless this information is recorded on paper no-one else benefits.

My four study species were the Guernsey lily (*Nerine sarniensis*), March lily (*Amaryllis belladonna*), Blood flower (*Haemanthus coccineus*) and Candelabra flower (*Brunsvigia orientalis*). All these species belong to the family Amaryllidaceae and have large showy flower heads which appear in late Summer or Autumn. Another thing they have in common is hysteranthous foliage. This simply means that the leaves emerge after the flowers and die down again the following Summer. Hysteranthous foliage is particularly common in the fynbos and seems to be associated with the Mediterranean climate.

Amaryllis belladonna

A large population of *A belladonna* flowered near Millers point during February, 1989 following the Simonstown fire a year before. According to Marloth, author of The Flora of South Africa (1915) , *A belladonna* is pollinated by hawk moths (Sphingoidea). Despite observing at night I never saw Hawk moths at the Millers point population. What I did observe were carpenter bees (*Xylocopa* sp) which foraged for nectar mainly in the mornings. Their bodies were grey with Amaryllis pollen. Carpenter bees are better known as the pollinators of legumes such as the Keurboom (*Virgilia oroboides*).

The seed of the March lily is large and fleshy. I found that seed was dispersed by gravity and fell within a metre of the parent plant where it tends to germinate almost immediately. I saw no evidence of seed dispersal by animals.

Brunsvigia orientalis

There is a small population of the candelabra flower (*Brunsvigia orientalis*) near Milnerton. I visited the site a few times during March and noticed that lesser double collared sunbirds (*Nectarinia chalybea*) visited the flowers. According to Marloth (1915) the Table Mountain butterfly also visits this species. The dried inflorescences (flower heads) scatter seeds when they are dislodged and blown about by the wind. Since I was interested to know how far they were dispersed I labelled a few inflorescences with coloured plastic, marked the site and returned a few weeks later. Most had not moved far at all ,only a few metres but others moved up to 300 metres before becoming lodged in an *Acacia* or other bush. I labelled 18 plants and recovered 15 flower heads. The missing three may have dispersed further or otherwise been "stolen" by a crafty thief for aesthetic purposes.

Haemanthus coccineus

While staying at Bettys Bay in May, I was directed to a small population of *H coccineus*, flowering on a small peninsula on the Sea Farm Shareblock Private Nature Reserve. Here I found Carpenter bees foraging for nectar, becoming dusted with bright yellow pollen (Fig 1). I have also seen the Table Mountain butterfly visting *H coccineus* on the Constantiaberg. This butterfly has an infatuation with red flowers and will even visit red hats! Marloth (1915) noted that "birds" (presumably sunbirds) visit the flowers. *Haemanthus* has berry like fruits suggesting animal dispersal, although I have never observed animals dispersing the fruits. Usually the flower stalk keels over dispersing seed in the immediate vicinity of the plant.

Nerine sarniensis

During the same stay at Bettys Bay I studied a large population of *N sarniensis* on the steep slopes above Luiperds Kloof in the Harold Porter Botanical garden (Fig 2). Here two splendid days were spent watching the Table Mountain Butterfly engaged in what appeared to be mating behaviour with occasional nectar breaks. It struck me that the butterfly seldom landed to take nectar. If one considers the flower structure of *N sarniensis* it is immediately obvious that the stamens project far above the base of the petals, clearly pollen is deposited on the butterfly not when it forages for nectar which it does while hanging beneath the flowers, but rather while it makes "a pass" brushing the stamens in the process. It seemed that the Table Mountain Butterflies were engaged in mating behaviour, butterflies would meet at a flower then twist off together in flight, sometimes settling in the vegetation. At this stage I do not know if this was not simply aggressive behaviour between males or mating or both. The population of *N sarniensis* may be a mating rendezvous, certainly the number of butterflies was staggering. The flowering season of *N sarniensis* corresponds to the end of the adult phase of the Table Mountain butterfly. Conspicuous among the Table Mountain butterflies were another less common butterfly later identified as *Catopsilia florella* (Pieridae). This butterfly was quite deliberate in its task of obtaining nectar. Apparently *C florella* often migrates to the South Western Cape from the Kalahari. But the pollination story of *N sarniensis* is not complete! While visting the Vogelgat nature reserve I was surprised to see a female sunbird (too far away to identify) visiting the Nerines flowering in the area. Like Amaryllis, the seed of *N sarniensis* is simply dumped in the near vicinity of the plant.

Nectar

Nectar is the sole food source of most pollinators. It is the reward that entices animals to visit flowers thus effecting pollination. The energy value of nectar depends mainly on the amount of sugar contained in nectar, this is usually expressed as a concentration (g/100g). The volume of nectar is a critical variable: no matter how concentrated the sugar content of nectar, too small a volume of nectar will not entice pollinators. It has been found, not suprisingly, that bird pollinated flowers secrete large quantities of nectar. Bee pollinated flowers often secrete small quantities of highly concentrated nectar.

The nectar of the four study species differs in volume and concentration. I measured nectar volume in small capillary tubes and sugar concentration using a "refractometer". The results are shown in table 1. Samples of nectar were collected at random from separate flowers at different times of the day. Nectar secretion often occurs at the time a pollinator is most active. The most concentrated nectar was that of *N sarniensis*, while that of *A belladonna* was nearly half as dilute. Nectar availibilty varies throughout the day, *A belladonna* secretes nectar mainly in the morning and *B orientalis* mainly in the afternoon (Table 1).

Concluding notes

Petaloid monocots in the fynbos are outstanding for their bold floral displays. Why the fynbos ?. Years of walking in both the fynbos, Eastern Cape and Transvaal have convinced me that the fynbos is relatively depauperate in terms of insect pollinators, especially following fires when many petaloid monocots tend to flower. Marloth whom we have seen was a keen "pollination biologist" noted in a paper that "Local botanists as well as entomologists have repeatedly noticed that often there seems to be an entire absence of insect life although the fields or the hillsides may be aglow with flowers (Marloth, 1908).Have you ever seen a Fynbos *Gladiolus* visited by insects?. There are a number of exceptions to the general abscence of insects. Protea beetles are common and bees are often abundant, however bees often originate from beekeepers and cannot be considered "natural"!

Butterflies are uncommon in the fynbos with the great exception of *Aeropetes tulbaghia*. The unpalatibilty of fynbos to caterpillars has been suggested as an explanation for the abcence of a fynbos butterfly fauna. A great many summer flowering petaloid monocotyledons including *N sarniensis*, *Haemanthus coccineus* and *Disa uniflora* have capitalised on the seeming abundance of the Table Mountain Butterfly. In general fynbos geophytes have large showy flowers to attract the occasional insect. One way of coping with the insect shortage is to appeal to birds. Many fynbos plants including geophytes are pollinated by sunbirds (*Nectarinia*) or sugarbirds (*Promerops*). However bird pollination is expensive, note the large volumes of nectar secreted at high concentrations by *B orientalis* (Table 1).

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Table 1 Volume (Vol)and concentration (Conc) of nectar from flowers of the four study species. Values are means with standard deviation in parentheses and sample size (No of flowers) below. Units are ul (volume) and g/100g (concentration).

	***Amaryllis belladonna* ***		***Brunsvigia orientalis* ***		***Haemanthus coccineus* ****		***Nerine sarniensis* ****	
Time	Vol	Conc	Vol	Conc	Vol	Conc	Vol	Conc
6 AM	1.3(1.2)	21	17.3(6.0)	37.3(1.5)				
	5	1	4	4				
12 AM	7.3(1.2)	23.3(2.3)	13.2(2.2)	34.7(6.1)	2.0(1.9)	33(1.7)	4.3(1.8)	36.1(4.5)
	3	3	3	3	23	7	10	8
6 PM	3.9(3.0)	17.5(9.2)	46.3(34)	34.3(6.1)			1.6(1.4)	38.8(2.9)
	5	2	3	3			16	5
12 PM	1.4(1.5)	18	20.7(8.6)	34(1.5)	2.7(1.9)	33.3(2.0)		
	5	1	3	3	13	3		

* Samples taken from cut inflorescences in water.

** Samples from intact inflorescences in the field.