

# The reproductive biology of a riparian Mediterranean shrub, *Nerium oleander* L. (Apocynaceae)

JAVIER HERRERA

[Go to contents](#)

*Departamento de Biología Vegetal, Universidad de Sevilla, Apartado 1095, 41080 Sevilla, Spain*

Received May 1989, accepted for publication October 1989

HERRERA, J., 1991. **The reproductive biology of a riparian Mediterranean shrub, *Nerium oleander* L. (Apocynaceae).** This study presents data on the reproductive characteristics of *Nerium oleander*, an evergreen, sclerophyllous shrub inhabiting the banks of temporary streams in all countries around the Mediterranean seaboard. Two southern Spanish populations (El Garrobo and Grazelema) were selected to investigate flowering, dispersal and seed germination phenologies, together with morphological and functional traits of flowers, fruits and seeds. Observations on pollinator visitation, fruit set, and seedling survival were also carried out.

Plants produce massive flower displays of showy, tubular flowers void of nectar that rely on insect cheating for pollination. Hand-pollinations and seed germination tests demonstrated full self-compatibility. Automatic selfing is prevented by spatial separation of stigma and anthers, and pollinators are thus necessary for reproduction. Low pollinator visitation rates are the rule, as indicated by the fact that observations spread over 2 years yielded only eight insect records. Percentage fruit set of open-pollinated flowers was found to be extremely low (0.1–4.9%), while hand-pollination increased fruiting levels to 34–500%. Direct and indirect evidence point to consistently pollen-limited reproduction in this species. If a large number of flowers within any inflorescence are pollinated artificially, however, resource limitations operate and pods from ovaries pollinated late in the season are aborted. On average, the maximum of ovaries developing into fruit within any inflorescence is 4. It is suggested that, in this nectarless species, about 80% of total are 'excess' flowers which contribute to increase pollinator attraction.

*Nerium oleander* pollen is aggregated into a sticky substance, which allows the fertilization of many ovules after a single, probably rare, pollination event. Fruits are many seeded follicles (181 seeds per fruit on average), so that individual plants often liberate thousands of seeds in spite of the low percent fruit set. The hairy, water-dispersed seeds are released during the rainiest season in the year, and germination follows rapidly. All seedlings tracked died before completing 1 year of life, mostly because of desiccation during the first summer drought.

Pollination by deceit in this Mediterranean species is discussed in terms of phylogenetic constraints within the mainly tropical family Apocynaceae.

ADDITIONAL KEY WORDS:—Deceit — phenology — pollination — shrublands — Spain — water-dispersal.

## CONTENTS

Introduction.....	148
Study sites.....	149
Methods.....	150
Phenology.....	152

Pollination	154
Flower description	154
Compatibility.....	158
Insect visitation	160
Fruiting.....	161
Fruit description.....	161
Fruit- and seed-set	162
Abortion.....	162
Dispersal and germination.....	163
Discussion.....	164
Acknowledgements	170
References	170

## INTRODUCTION

The Apocynaceae is a moderately large angiosperm family (c. 1500 species) with a mainly pan-tropical distribution (Heywood, 1978). However, it has some temperate and Mediterranean representatives including periwinkles (*Vinca*) and oleanders (*Nerium*). According to Hooker & Jackson (1895) the genus *Nerium* has five species which occur from the Iberian Peninsula to Japan, although Engler (1964) recognized just three species. Owing to its showy flowers, oleanders (*Nerium oleander* L.) are widely cultivated for ornament in temperate and warm areas throughout the world. Up to 11 cultivars with either deep-red, pink, cream or white, sometimes fragrant, flowers are known (Cuisance & Seabrook, 1970), but wild plants always have pink, scantily aromatic flowers.

A wild *N. oleander* plant is usually a collection of stems up to 4 m high rising from a common stump with evergreen, coriaceous leaves. If damaged, or even if completely removed, the crown may be recovered by means of vigorous sprouting from the stump. Plant parts present a variety of toxic compounds that mainly include cardiac glycosides, the chief and most consistent cardenolide being oleandrine. Because of this, oleanders have, from very ancient times, a justifiable reputation of being poisonous (Font-Quer, 1973). Domestic animals seldom eat the foliage, although wild African herbivores such as the hyrax (*Procavia*) and gazelles may do so (Harborne, 1982). Several specific insect herbivores are known to eat *Nerium*; these include a hawkmoth (*Daphnis nerii* L., Sphingidae, Lepidoptera), a bug (*Caenocoris nerii* Ger., Lygaeidae, Hemiptera), and an aphid (*Aphis nerii* Fonscolombe, Aphididae, Hemiptera). By sequestering and storing the toxic compounds of oleanders, these insects become toxic themselves and thus distasteful to predators, which is often accompanied by a warning colouration (Rothschild, 1972).

Greuter, Burdet & Long (1984) reported that *N. oleander* occurs in most countries around the Mediterranean seaboard (Portugal, Spain, Italy, Jugoslavia, Albania, Greece, Turkey, Lebanon, Syria, Israel, Jordan, Libya, Tunisia, Algeria and Morocco) and in all the larger Mediterranean islands, but is absent from the Canaries. Scattered populations may be found through the Sahara at oueds (seasonal watercourses) and other moist points, the species not occurring south from the desert (Ozenda, 1977). Across most, or possibly all, of its range no other congener can be found. In southern Spain, *N. oleander* inhabits ravines and highly seasonal streams where flooding conditions prevail during the cool, rainy season. Because of summer drought such streams most often become dry for several months. Populations usually are below 1000 m in southern Spain (Rivas-Goday & Pinies, 1949) while North African populations may grow at

2000 m and above in the Atlas Mountains (J. A. Mateo & R. C. Soriguer, personal communication).

Throughout its natural range, *N. oleander* shows a marked affinity for sites with a steady supply of soil moisture. Needless to say, such habitats are not particularly common within the area inhabited by Mediterranean-type scrub, and the plant is a quite atypical example of sclerophyllous scrub species. Fossil remains of *N. oleander* are known at least since the Oligocene (Pons & Quezel, 1985) which indicates that it is a very old taxon. It belongs to what Quezel (1985) termed the 'tropical element' of the Mediterranean scrub flora, that is, a set of taxa of tropical origin that probably evolved before the onset of the Mediterranean climate but now coexist with more recent, purely Mediterranean elements. In addition to *N. oleander*, the southern Spanish pre-Mediterranean array includes species of Oleaceae, Anacardiaceae, Santalaceae, Rhamnaceae, Arecaceae, Myrtaceae and Liliaceae (Axelrod, 1975). Reproductively, such species form a quite distinct group characterized by a marked incidence of dioecy, large average seed-size, and dispersal systems often mediated by vertebrates (C. M. Herrera, 1984). Because of its habitat and reproductive traits *N. oleander* is something of an exception within both the 'tropical' and 'Mediterranean' arrays. The purpose of this study was to investigate peculiarities of the reproductive biology of an old, Mediterranean riparian plant, and to examine the extent to which its reproductive features differ from those of most other Mediterranean scrub species.

#### STUDY SITES

Most of this study was in Sierra Morena, the main mountain range bordering the Guadalquivir River valley, in Andalucía, southern Spain. All over the area the climate is of the Mediterranean-type (Lines-Escardo, 1970) with most precipitation falling in winter. Dominant vegetation types are cleared, open woodlands of evergreen oak (*Quercus rotundifolia*) and Mediterranean scrub growing on granite or slate substrates. The main population is at 250 m and occupies the rocky margins of a stream which dries up completely during the summer. However, even in the middle of summer, water is not more than 1.5 m deep, as checked by observation of an old well that happened to be at the site. Dense stands of *N. oleander* grow along both banks, with scattered, usually smaller individuals being found a few metres away, intermingled with shrubby vegetation which surrounds the site. This vegetation includes species very common in Mediterranean scrub formations such as, for example, *Cistus ladanifer*, *Cistus monspeliensis*, *Lavandula stoechas*, and *Thymus mastichina*. At the nearest meteorological station (El Garrobo, 7 km away from the site) precipitation averages 680 mm year<sup>-1</sup>. The mean annual temperature is 16.6°C, January being the coldest month (8.2°C) and August the hottest (26.3°C; weather data supplied by the Spanish Servicio Meteorológico Nacional).

In addition to the main study site (El Garrobo), data were gathered from a second population some 150 km south at 1000 m on limestone mountains (Sierra de Grazalema; Grazalema hereafter). In comparison with El Garrobo, Grazalema has shorter and colder summers (mean temperature for August 25.5°C) and much rainier winters (2123 mm year<sup>-1</sup> on average). While most southern Spanish populations of *Nerium* live under conditions similar to those

occurring at El Garrobo (i.e. moderate elevation, less than 1000 mm of rain per year), the Grazalema population should be considered near or at the upper altitudinal limit of the species in this region. Additional data (mostly on nectar secretion and fruit-set) were occasionally gathered in several populations distributed across southern Spain.

#### METHODS

From April 1987 to October 1988 the main population was visited at approximately weekly intervals, or 2–3 times per month when flowering was over. At the beginning of the study ten plants were individually marked and subsequently used to count the number of open flowers, ripening fruits, seed-dispersing fruits, and to note growth and leaf shedding. Owing to the massive size of most individuals (up to 3 m high and 6 m in diameter), and since there was no sign of intra-plant variability in flowering, fruiting or vegetative phenology, counts and observations were made on one large, tagged branch per plant. The same branches were employed in both 1987 and 1988. The number of other shrub species in flower throughout the study period was also recorded.

Nectar secretion of flowers on plants from El Garrobo and Grazalema was studied by bagging 5–10 inflorescences which, after 24 h, were cut and taken to the laboratory. About 100 flowers from these inflorescences were carefully examined under a dissecting microscope for the presence of nectar. Floral attributes including corolla diameter, tube length, mass of whole flower, number of flowers per inflorescence, and number of inflorescences produced by medium-sized individuals were also determined. The corolla, anthers, and pistil + receptacle + calyx were dissected and weighed separately to the nearest 0.1 mg on an electronic balance. The number of ovules in the ovary was counted, and that of pollen grains estimated, in a sample of flowers. After crushing an anther in 0.5 ml of detergent—safranin solution, the number of grains in ten replicates of 5  $\mu$ l was counted, and total number of grains per flower estimated accordingly. In order to determine flower longevity, a number of flowers in each of four plants at El Garrobo was tagged. After being either hand-pollinated or left untreated, flowers were inspected during subsequent days for corolla abscission.

To hand-pollinate a flower, a fine bristle was inserted into the corolla tube passing between two anthers. After moving it up and down once or twice, the bristle picked up pollen that could be used to pollinate the same or a different flower. This method was first used by Darwin (1861) to pollinate vincas. I estimated the total number of pollen grains adhering to the bristle by cutting it into pieces and shaking them in a detergent—safranin solution of known volume. Total number of grains, computed in the same way as when estimating pollen per flower, ranged between 320 and 1710 ( $x = 793 \pm 206$ ; mean + standard error;  $N = 7$ ).

Growth of pollen tubes in the style following cross- and self-pollinations was studied by taking flowering branches to the laboratory and placing them in jars filled with water. Flowers were either selfed or crossed and marked. Six hours later their styles were cleared, stained with decolourized aniline-blue (Martin, 1959) and observed under UV-light in a Zeiss-Axiophot fluorescence microscope.

In 1987 I selected five plants at El Garrobo in order to investigate self-fertility

by hand-pollinating flowers with pollen from either its own anthers or (as controls) from another flower on a different plant. Developing pods were counted and measured periodically to the nearest mm until they reached final size. Fruits were removed slightly before seed dispersal and the number of seeds counted. The relative quality of progeny resulting from self- and cross-pollinations was investigated for three plants by comparing percent and rate of germination, seed mass and seedling growth. For any plant and treatment, 30 randomly chosen seeds from several fruits were weighed to the nearest 0.1 mg. In germination tests, six groups of 40 seeds (one for each plant x treatment combination) were placed in petri dishes filled with tap water and the number of emerging seedlings noted periodically. A seed was considered germinated when its radicle was 1 mm long. Dishes were near a window in a room where temperature ranged between 12° and 20°C. Germinated seeds were then transferred to numbered vials with tap water and grown for 30 days, after which the total length of seedlings (from the tip of the radicle to the base of cotyledons) was measured to the nearest mm.

During 1987 and 1988 flowering *N. oleander* plants, usually bearing several hundred flowers, were observed to record insect visitors at both El Garrobo and Grazalema. Censuses totalled 27.6 h and were carried out at any moment from the beginning to the end of the flowering season (El Garrobo) or at the population flowering peak (Grazalema). Observations were spread over 20 different dates but, for simplicity, results have been grouped by months. Most observations were made in fine weather, during either morning, afternoon, dusk, or night periods. During observations, visitor behaviour was noted and the insects identified as accurately as possible without disturbing or capturing them. Given the scarcity of insects at flowers, I was frequently able to record the number of plants and flowers that an individual insect visited before losing sight of it. At night, a head-lamp with a red filter was used to scan the plants. Night census time was 6% of the total.

In order to obtain an insight into visitation rates and pollen flow, two plants of intermediate size, bearing approximately 175 flowers as a whole and separated by a distance of 4 m, were selected at El Garrobo. On July 1988 one source flower in each of ten inflorescences per plant was marked and the outside of anthers smeared with fluorescent powder applied with a toothpick. A different colour was used for each plant. Some 72 hours later, at night, a sample of flowers on the plants was scanned with a UV-lamp for traces of dye inside the corolla tube.

To quantify fruit and seed set, branches containing several inflorescences in a number of plants (see [Table 5](#)) were marked at El Garrobo and Grazalema populations in both 1987 and 1988. In each of the plants, 1–3 inflorescences were covered with nylon netting bags to exclude pollinators, while others remained exposed to insect visits. In another set of branches, flowers (4–11 per inflorescence) were both hand-pollinated and exposed to pollinators. Given the complete self-fertility demonstrated in previous experiments, most pollinations were made with self-pollen. The number of fruits reaching final size following each treatment is reported as a percentage of total flower number. Total female reproductive effort of medium-sized plants was estimated by counting the number of fruits in 10–15 plants per population and year. The overall number of propagules produced by a plant was also estimated. While the same individual

plants were used to count fruits at El Garrobo in 1987 and 1988, this was not the case for the Grazalema population.

A hand-pollination experiment at El Garrobo was designed to obtain information on changes in abortion rates according to the date of pollination. On six dates from May to July 1988, flowers in tagged branches were pollinated and marked on their pedicels with a small dot of enamel paint, a different colour being used for each date. Open-pollinated flowers in the same branches were also marked. I checked the number of ovaries which initiated a pod (ovary larger than 5 mm), and noted periodically if they grew, aborted or were damaged by fruit predators.

In addition to fruit traits such as size, mass and seeds per fruit, some dispersal-related characteristics of the achene-like seeds of *N. oleander* were investigated. The rate of descent in still air of 15 seeds was determined by releasing them from a height of 2.75 m and noting the time elapsed until they reached the floor. This also permits one to obtain an estimate of the horizontal distance to which a seed could be transported with a given wind velocity (Augsburger, 1986). The height of release is comparable to that of a medium- to large-sized *N. oleander* plant.

To determine the influence of pappus on the floating ability of the propagules I placed 60 seeds with all of their longest hairs clipped off, and 60 untreated seeds in water. Twenty days later I recorded the number of seeds that had sunk or were still floating. To make observations on seedling behaviour and growth, some germinated floating seeds were transferred to vials filled with tap water and with a 20 mm-thick layer of sand on the bottom. The seedlings were observed for a 5-month period.

The germination of naturally dispersed seeds was studied in the field during 1988 by tracking the number of seedlings in three permanent square plots (30 x 30 cm) placed beneath the canopy of *N. oleander* shrubs. In addition to this, 200 individual seedlings were tagged and numbered in 12 patches distributed across the population. Tags were made of a small piece of plastic sheet loosely fastened to the hypocotyl with a fine copper wire. All plots were within 2 m from the watercourse since no seedlings appeared beyond this distance. Locations encompassed most visible variability in microsites: rock fissures, sandy soil, layers of litter, beneath the canopy of shrubs (mostly *N. oleander* shrubs), or in the open. I checked seedling survival periodically during spring and summer and determined the cause of death.

#### PHENOLOGY

The phenology of *N. oleander* at El Garrobo is pictured in [Fig. 1](#) together with a plot of the climatic pattern in the site. Typically, most rain falls from October to April, while the period May—September, when temperature is at its maximum, is usually very dry. Because of heavy rainstorms, however, the spring and early summer of 1988 were unusually wet. Flowering and growth occur simultaneously and once every year within any individual, but the processes are restricted to different plant parts: while some branches elongate and produce new leaves on terminal buds, others form a terminal inflorescence. Leaf buds become active by April, and growth may continue until September—October. Simultaneous to flowering and, to a great deal, growth, the lowermost leaves on any stem become yellow and are dropped. The pattern of leaf shedding

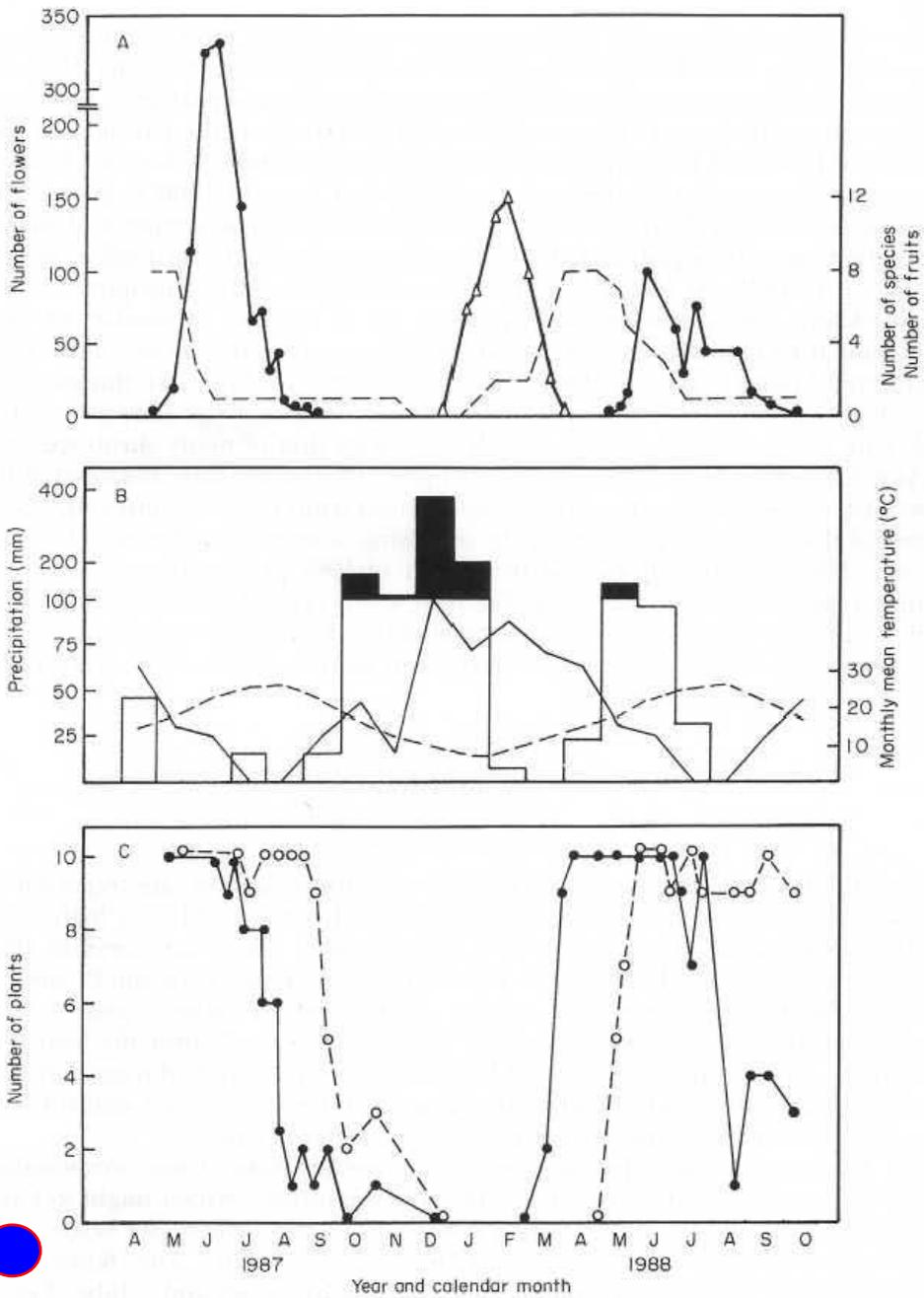


Figure 1. Phenology of *N. oleander* and climatic pattern at El Garrobo, southern Spain. A. Number of flowers (●), of fruits liberating seeds (△), and of other shrub species in bloom (---). B. Monthly precipitation during the period of study (vertical bars), and monthly average for ten years. (solid line). Precipitations above 100 mm are represented by blacked areas. The dashed line indicates mean monthly temperature. C. Number of plants flushing new (●) and shedding old leaves (○).

paralleled, with a 2-month delay, that of leaf flushing during both 1987 and 1988.

As is usually the case with Mediterranean communities, most scrub species at the main study site (El Garrobo) flower at the beginning of spring (Fig. 1). However, *N. oleander* starts flowering in May, when a major portion of blooming in the community is past. The period of peak bloom spans the customarily dry months of June and July, while some flowering occurs until as late as October. Unusually intense precipitations during May and June of 1988 had a clearly deleterious effect on flowers and inflorescences that had just started to develop. Many buds were dropped, and this caused flowering intensity in 1988 to be low compared to 1987. At Grazalema, the site with high average precipitation (see Study Sites), the phenological behaviour of *N. oleander* is similar to that occurring at El Garrobo, except in that blooming starts later (June), peaks later (July and August), and concludes earlier (September). Since, at this elevated site, flowering of most scrub species is delayed until summer (Arroyo, 1985), flowering of *N. oleander* overlaps considerably with that of many shrub species.

At El Garrobo one can observe initiated pods a few weeks after the onset of the flowering season and, by the end of August, most fruits have definitive size. Seed dispersal does not take place until the following winter, from January through March (Fig. 1). Although during the winter of 1988 precipitations were lower than average, dispersal occurred at the time when rainfall is usually most likely and, as a result, streams and rivers were high. By April 1988 marked fruits from 1987 flowers had liberated all their seeds, and plants were ready to start a new season of growth and flowering.

## POLLINATION

### *Flower description*

General features of *N. oleander* flowers and inflorescences are reported in Table 1. A medium-sized plant (about 2 m of diameter and 2 m high) may produce from eight to more than 100 inflorescences. These are corymbs that, when large, have 3–5 lateral branches and may produce between 12 and 44 flowers. Individual flowers are showy (52 mm of diameter), and a peak blooming inflorescence may bear up to 17 open flowers. Against the brown or dull-green background typical of Mediterranean landscapes during summer, flowering plants are readily visible from large distances even when isolated. The visual impact of tens of plants arranged along banks is striking.

All flowers from any population lacked nectar disks. Close examination revealed no trace of either nectar or any other substance which might act as a reward. Pollen is scarce and so tightly concealed by the anthers (see below) that only with difficulty could an insect have access to it. The flowers are hermaphroditic and have a pink corolla with five free lobes and a tube (Figs 2, 3). In addition to the lobes, the corolla presents five petal-like perianth scales irregularly dissected into narrow, acute segments that project from the tube mouth. Scales exhibit a pattern of deep-pink, parallel lines descending into the tube, which is about 20 mm long (Table 1) and funnel-shaped in the upper half. The lower half, below the level of anthers, is relatively narrow and densely hairy inside. The fresh biomass of a *N. oleander* flower averages 426 mg and mean dry

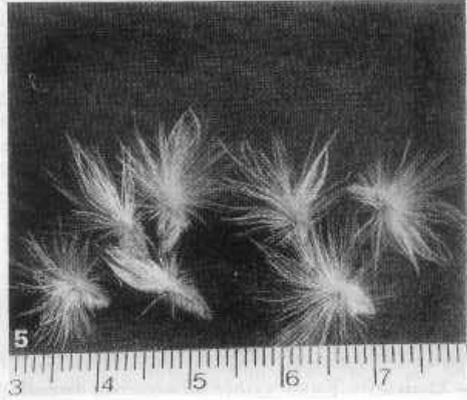
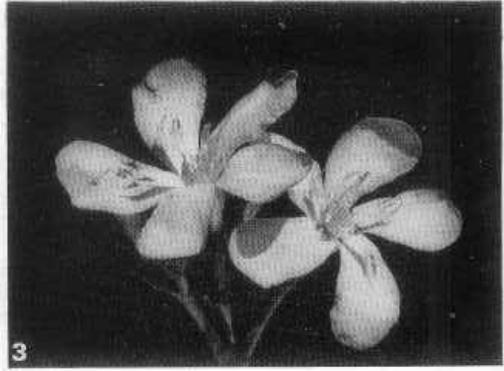
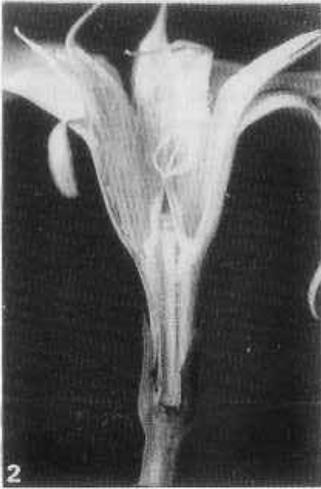
TABLE 1. Characteristics of the inflorescences, flowers, fruits and seeds of *Nerium oleander*. Masses are in mg and measurements in mm. C.V., Coefficient of Variation; SE, standard error

Variable	N	$\bar{x} \pm SE$	Range	C.V.
Inflorescences per plant	25	38+5	8—108	67.2
Total flowers per inflorescence	20	22+2	12—44	33.9
Open flowers per peak blooming inflorescence	20	10±0.7	3—17	31.3
Corolla diameter	10	52+2	45.5—59.7	12.2
Tube length	10	21+0.3	19.4—23.4	4.5
Tube mouth width	10	8+0.2	7.5—9.4	7.6
Pollen grains per flower	5	11 595 + 383	10 600—12 800	7.4
Ovules per flower	5	370 ± 26	304—442	15.7
Pollen : ovule ratio	5	32+3	24—38	17.4
Fruit length	15	90+5.4	47—142	23.3
Seeds per fruit	15	181+22	36—325	47.7
Mass of:				
Whole fresh flower	10	426±13	377—489	9.7
Whole dry flower	10	79 ± 1.1	72—83	4.4
Dry corolla	10	68±1	60—73	5.7
Dry pistil plus receptacle	10	8±0.3	7.2—10.5	12.8
Dry anthers	10	2.8 ± 0.1	2.3—3.3	11.1
Fresh fruit	15	3992+458	1060—6473	44.4
Dry fruit	9	1602+190	622—2345	35.6
Individual seed	90	3.3+0.1	1.8—4.4	28.7

weight is 79 mg (i.e. 18% of fresh weight). Within a flower, most dry biomass (86%) is allocated to the corolla, while anthers (appendages included) and pistil-plus-receptacle respectively account for 4% and 10%.

The stamens have their filaments fused to the corolla for most of their length. The anthers are sagittate (arrow-shaped), hairy on the outer side, and form a tent over the tip of the style (Fig. 6). Pollen grains, in a number of 11 600 per flower on average, are shed inwards. Each anther is prolonged into a hairy process which is longer (7—9 mm) than the anther itself (5 mm). The style is slightly longer (11 mm) than the narrow part of the corolla tube, its tip bearing long papillae embedded into a sticky drop. Below the papillae there is a narrow rim to which anthers are firmly attached. Upon release from anthers, pollen rests on the mucilage (Fig. 7). At the lower end of the style there is a tiny ovary with two carpels and numerous (370 on average) ovules. Mean pollen : ovule ratio is 32 (Table 1). Flower predation occurs rarely, although Tettigonidae were observed to eat the hairy appendages of anthers. The corolla, pistil and fertile parts of anthers are seldom damaged.

Observation under UV-light of aniline-blue stained styles revealed that pollen grains germinate readily when deposited into a groove below the rim that surrounds the style end, but do not if placed above it (Fig. 7). In any flower, self pollen adheres to the sticky drop and cannot reach the receptive area if left undisturbed. Old flowers may present scattered grains germinated on the drop but, apparently, pollen tubes do not grow far enough to penetrate the style. Thus, automatic selfing is prevented by spatial separation of pollen and stigma. The style-anther arrangement and the way in which pollen is presented are very similar to that of *Vinca minor* (Apocynaceae) as it was described by Darwin (1861; see Proctor & Yeo, 1973: 188). Besides, there is no sign of a separation in



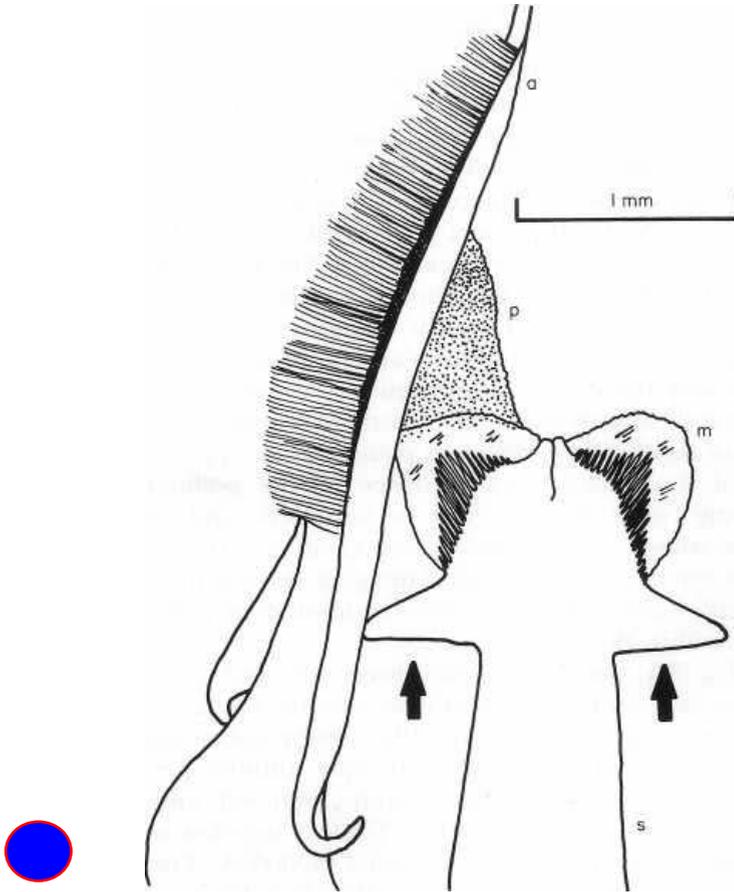


Figure 7. Drawing of anther-stigma ensemble. Only one anther is represented for simplicity. a, Anther; p, pollen; m, mucilage drop embedding papillae; r, stylar rim; s, style. Arrows point to the receptive area.

time of male and female functions: at flower opening, pollen has been shed and the stigma is fully receptive, so that the flower may both donate and receive pollen.

Newly-opened, unbagged flowers were checked for corolla abscission after being either hand-pollinated or left untreated. Three days after anthesis, most (14/16, 87%) pollinated flowers had shed their corollas, but only three out of eight (37%) untreated flowers had. Proportions are significantly different among treatments ( $G = 6.333$ ,  $P < 0.025$ , d.f. = 1). No hand-pollinated flowers kept their corollas a week after anthesis, while one untreated flower did.

### Compatibility

*Nerium oleander* seems to be fully self-compatible. Selfing resulted in fruit being set in all five experimental plants (Table 2), and differences among pollen sources in overall fruit set were not significant (Yates corrected Chi-square = 0.271, d.f. = 1,  $P = 0.602$ ). Self-pollination is easily achieved artificially by inserting a clean, thin bristle into the corolla tube and forcing it to pass between two anthers. First, as the bristle moves downwards, a mixture of mucilage and pollen (320—1710 grains; see Methods) sticks to it. Second, as the bristle is moved upwards, it rubs the edge of the style-rim. A portion of the mixture is scraped from the bristle and thus deposited on the receptive area (i.e. the lower side of the style-rim; Fig. 7). At both El Garrobo and Grazalema plants, manipulation of flowers in this way resulted in huge numbers of pollen tubes penetrating to the middle of the style after 6 hours. If a bristle previously inserted into a flower is used to pollinate another on a different plant, one can effect cross-pollination. Nevertheless, and as a logical consequence of the pollination system just described, 'crossing' most likely results in both self- and cross-pollen being transferred to the stigma. (Since anthers are firmly attached to the stylar rim, flowers cannot be emasculated without damaging the stigma.) Styles of crossed flowers did not differ from selfed in either the number of pollen tubes or in the distance covered within the style.

As shown in Fig. 8A, pods originating from self- and self- plus cross-pollen grow at a similar rate and reach definitive size 40—45 days after pollination. Mean definitive size (as length) does not differ among pollen sources ( $t = 0.5406$ , d.f. = 28,  $P > 0.5$ ), and neither does mean seed number per pod ( $t = 1.064$ , d.f. = 14,  $P > 0.2$ ). Mean masses of seeds coming from self- and cross-pollination for three individual plants are reported in Table 3 together with results of the two-way (treatment and plant), mixed-model ANOVA. For plants 3 and 9 crossed seeds are significantly heavier than selfed, but this is not so for plant 11. As a result, the ANOVA reflects a highly significant plant  $\times$  treatment interaction. Overall, however, crossed seeds were heavier than selfed ( $t = 3.072$ ,  $P = 0.002$ , d.f. = 178).

Figure 8B depicts cumulative germination curves for selfed and crossed seeds.



TABLE 2. The number of hand-pollinated flowers setting fully-developed fruits according to pollen source in five *N. oleander* plants

Plant	Pollen source			
	Self		Cross	
	Flowers	Fruits	Flowers	Fruits
1	2	1	2	0
3	10	5	10	8
8	2	2	2	1
9	6	1	6	3
11	12	10	12	10
Total	32	19 (59%)	32	22 (68%)

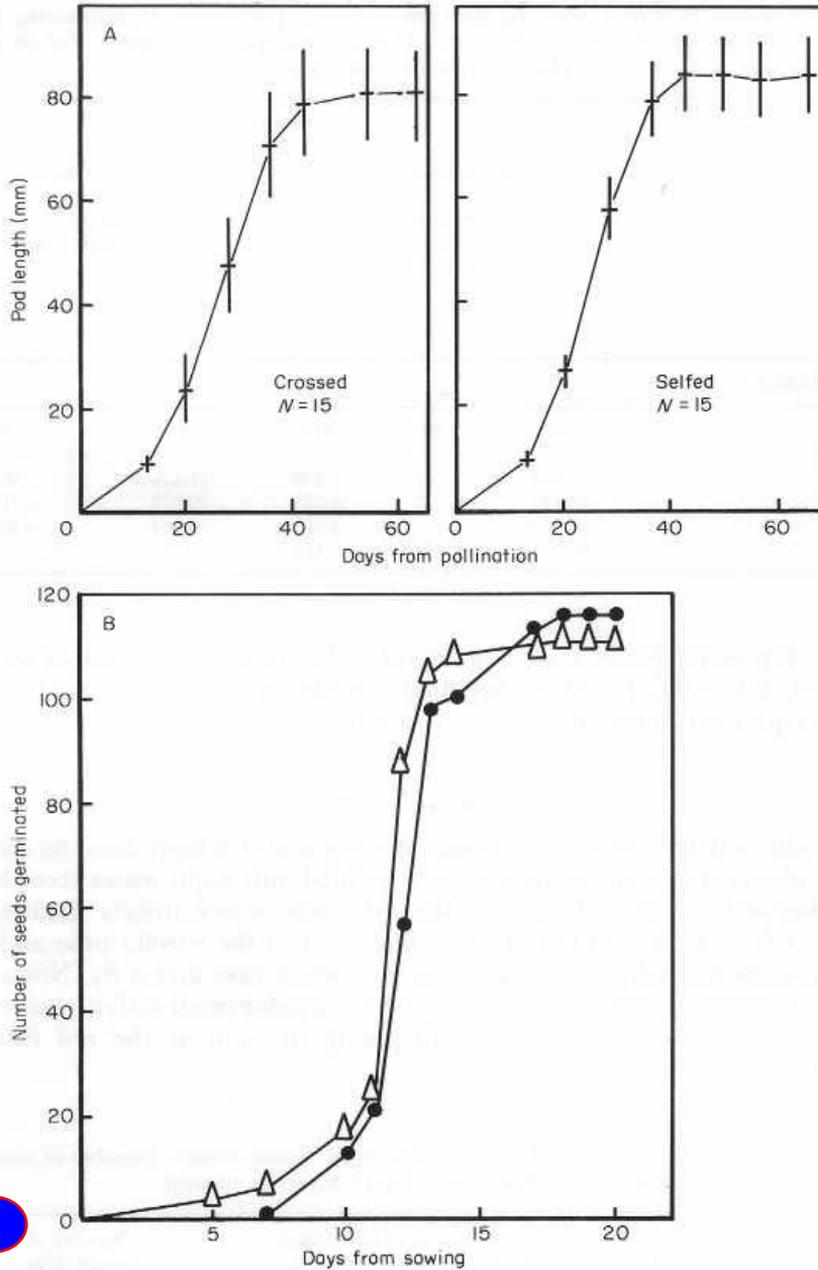


Figure 8. A. Growth of crossed and selfed fruits of *N. oleander*. Horizontal lines indicate the mean, and vertical lines  $\pm 1$  standard error of the mean. B. Cumulative number of germinating seeds from selfed (solid circles) and crossed fruits (open triangles).

Crossed tend to germinate slightly earlier than selfed, the delay being statistically significant (Kolmogorov-Smirnov statistic  $D = 0.286$ ,  $P < 0.01$ ). Twenty days after sowing, germination was near 100% for both seed types, proportions not being significantly different ( $\chi^2 = 0.06$ , d.f. = 1,  $P = 0.812$ ). The size, measured as the distance from the tip of radicle to the base of cotyledons, of seedlings

TABLE 3. Mean masses of seeds resulting from self- and cross-pollination. Means sharing the same letter do not differ significantly at  $P = 0.05$  (Duncan multiple range test).  $N = 30$  for each plant x treatment combination

Plant	Treatment	
	Self-pollination	Cross pollination
11	3.36a,b	3.08a
3	3.07 a	3.89 b,e,d
9	3.55 b, c	4.04 d
Overall	3.33	3.67

ANOVA TABLE

Source	SS	DF	MS	F	P
Treatment	5.339	1	5.339	11.479	0.001
Plant	10.114	2	5.057	10.873	< 0.001
Treatment x Plant	9.640	2	4.820	10.364	< 0.001
Error	80.927	174	0.465		

grown in tap water for 30 days was found to be similar regardless of seed type ( $t = 1.573$ , d.f. = 98,  $P > 0.2$ ). Seedling samples were approximately normal and had equal variances ( $F = 1.239$ ,  $P > 0.05$ ).

#### *Insect visitation*

Pollinator activity around *N. oleander* flowers was strikingly low. As shown in Table 4, observations spread over 2 years yielded only eight insect records. This figure does not consider thrips nor the otherwise scarce insects landing on a flower to rest or bask, but only those which probed the corolla tube and could thus be considered pollinators. These include seven bees and a fly. Not a single visit was recorded at night, although nocturnal lepidopteran activity was evident from numerous moths approaching the lamp as soon as the red filter was removed.

TABLE 4. Potential pollinators recorded at the flowers of *Nerium oleander*. Number of visitors and observation efforts have been lumped by months

Locality	Year	Month	Observation effort (min)	Number of visitors (type)
El Garrobo	1987	May	25	1 (Halictidae)
		June	170	0
		July	390	3 ( <i>Xylocopa violacea</i> , Anthophoridae)
	1988	June	300	1 (Halictidae)
		July	330	1 (Calliphoridae)
		August	120	0
Grazalema	1987	September	60	0
		July	60	0
	1988	July	200	2 ( <i>Bombus lucorum</i> , Apidae)

Large bees inserted their proboscis deeply into the tube as if seeking nectar. In doing so, they undoubtedly effected pollination. On July 12 1987, a single *Xylocopa violacea* at El Garrobo was observed to visit, in a rapid sequence, approximately 40 flowers on four widely spaced plants. Then, it abandoned the site. Three days later, another(?) *Xylocopa* visited an indeterminate number of flowers on two plants before flying out of sight. Whether these bees had obtained some unknown reward from flowers, or they were just starving or naive insects looking for food is a matter of conjecture. When the observations were made no other shrub species was in bloom within a radius of 100 m.

On July 1988, at the elevated study site of Grazalema, *N. oleander* was in bloom together with several nectariferous (*Rubus ulmifolius*, *Antirrhinum majus*, *Origanum virens*) and polliniferous (*Adenocarpus telonensis*, *Clematis flammula*) species, individuals of all these taxa being intermingled. While the rewarding taxa were heavily visited by an insect array which included Syrphidae, Pieridae, Halictidae, Apidae (*Apis* and *Bombus*) and Anthophoridae (*Xylocopa* and *Ceratina*), the showy flowers of *N. oleander* remained largely ignored. On July 1, however, a *Bombus lucorum* worker was observed to visit three flowers of *N. oleander* within a single inflorescence and, on July 8, two flowers within an inflorescence.

Results from fluorescent dye experiments revealed that visitation rates were indeed low. Besides the 10 'source' flowers receiving the powder 3 days before on plant 1, only six from a total of 80 checked flowers showed signs of dye inside the broad part of the corolla tube and/or the outside of anthers. (The innermost, narrow part of the corolla tube (Fig. 2) was not checked for the presence of dye.) Furthermore, three of these six flowers were within the same inflorescences containing source flowers. On plant 2, five from a total of 55 checked flowers showed some dye, of which three were on source inflorescences. Overall, six of eleven flowers showing some dye inside the tube were on source inflorescences, which suggests that a relatively great fraction of the few visits occurred between adjacent flowers. In spite of being close to each other (4 m), there was no sign of between-plant visits, as inferred from lack of coloured dye transfer from one plant to another. Note that the presence of dye at the broad part of the corolla tube did not necessarily imply that the flower had been pollinated. Thus, the number of effective fertilizations probably was even lower than indicated.

## FRUITING

### *Fruit description*

If pollinated, the ovary may develop into a double follicle, each half originating from one of the paired carpels (Fig. 4). Fruits are similar to those of, for example, *Asclepias*, except that the two follicles are parallel and fused together from bottom to tip. Both carpels elongate at the same rate, and I have never observed a fruit to be produced from just one carpel. Seed dispersal takes place through twisting and curling of the follicle walls.

A ripe fruit about to liberate seeds is 90 mm long on average (Table 1). Mean number of seeds per fruit was 181 in the studied sample, but there is ample variation in this respect, with some fruits containing less than 40 and others more than 300 seeds. In fact, this trait has a coefficient of variation (47.7) which is

among the highest reported in Table 1. Seed number is positively correlated with fruit length (Spearman rank correlation,  $r = 0.931$ ,  $P < 0.001$ , d.f. = 13). Developing pods are sometimes pierced by sap-sucking Hemiptera, which often causes deformations, but not abortion. Distorted fruits were observed to continue growing and, later, to liberate seeds in the usual way. On occasions pods are preyed on by chewing insects (probably Tettigonidae), but this has been observed in just three out of 100 fruits tracked from pollination through dispersal.

#### Fruit- and seed-set

If unvisited, *N. oleander* flowers do not set fruit, as demonstrated by lack of fruiting in inflorescences bagged to exclude pollinators (Table 5). Flowers left exposed for natural pollination, on the other hand, only rarely set fruit. If hand-pollinated, however, the probability that a flower will set a fruit increases dramatically. Artificial pollination at El Garrobo caused fruit-set to increase by a factor of ten in 1987, and by a factor of 100 in 1988. At Grazalema, hand-pollination increased fruiting by a factor of 300 in 1988 (Table 5). Rarity of pollination events on a per inflorescence basis is shown in Fig. 9. Open-pollinated inflorescences often set no fruit or, at most bore two ( $x = 0.2 + 0.03$ ), while those that were both artificially and open pollinated bore from one to eight ( $x = 3.8 + 0.32$ ). Means are significantly different (Mann-Whitney statistic  $U = 27.22$ ,  $P < 0.001$ ).

Table 6 shows average female reproductive effort of medium-sized plants. Mean fruit production differed significantly among years at El Garrobo ( $t = 4.257$ , d.f. = 18,  $P < 0.001$ ), with the later, rainier year, exhibiting the poorer fruit crop. Among-year comparisons for Grazalema are inadvisable since plants differed between years. Overall, plants from El Garrobo produced larger fruit crops than those from Grazalema (respectively  $43 \pm 6$  and  $11 \pm 2$  fruits per plant for pooled years). In spite of the low fruit set (see Table 5), the absolute seed output on a per plant basis is usually high. Because of (1) the large flower complement of plants, and (2) the large seed complement of fruits, medium-sized individuals often liberated thousands of seeds (Table 6).

#### Abortion

As shown in Fig. 10, not all hand-pollinated flowers set fruit. Between 20% and 60% of treated flowers abscised without enlarging their ovaries, perhaps owing

TABLE 5. Percent fruit set of *Nerium oleander* under various pollination treatments,  $\pm$  SE, standard error of the mean. N1 is the number of individual plants, and N2 the number of flowers

Locality	Year	Open-pollination			Bagged			Hand-pollination		
		+ sE	NI	Nz	+ sE	NI	N2	+ sE	NI	N2
El Garrobo	1987	4.9-1.3	9	827	0	5	260	47.7 $\pm$ 9.8	8	76
	1988	0.5+0.2	5	985	--	--	--	50.8+3.5	5	243
Grazalema	1987	1.1 + 0.3	15	12 185						
	1988	0.1 + 0.1	10	502	0	5	112	34.4+ 6.7	10	35

TABLE 6. Female reproductive effort of medium-sized *Nerium oleander* individuals. SE, Standard error of the mean; N, number of plants

Locality	Year	N	Fruits per plant		Seeds per plant, in thousands*	
			$\bar{X} + sE$	(range)	$\bar{X} + sE$	(range)
El Garrobo	1987	10	63.4+7.7	(27-107)	11.5 + 1.4	(4.9-19.4)
	1988	10	22.1+5.9	(8-63)	4.0 + 1.1	(1.5-11.4)
Grazalema <sup>1</sup>	1987	15	7.6+2.1	(0-29)	1.4+0.4	(0-5.3)
	1988	10	16.2+3.4	(5-33)	2.9±0.6	(0.9-5.9)

\*Based on an average of 181 seeds per fruit.

<sup>1</sup>Individual plants used to count fruits differed between years.

to inadequate pollination. The rate of 'late' abortions (i.e. the difference of initiated- minus fully-grown pods), on the other hand, was low during May and June (0-8%), but increased noticeably on July (28-54%), when most inflorescences were bearing several developing fruits. As a result, as few as 7% of flowers pollinated at the end of July set a fruit, while about 40% of those pollinated in May did. Aborted pods were usually 20 mm long or smaller, and did not show signs of being damaged in any way. They simply turned from red to blackish and stopped growth without abscising. Besides, open-pollinated flowers rarely, if ever, initiated a pod, which demonstrates that the contribution of insects to fruit set in treated, unbaggged flowers, should be considered negligible.

#### DISPERSAL AND GERMINATION

Seeds range in mass from 1.8 to 4.4 mg (mean 3.3 mg; Table 1) and are covered by numerous short hairs (Fig. '5). In addition, there is a tuft of longer hairs that expand radially when relative humidity is low. The rate of descent in still air of seeds with a fully extended pappus is  $82.5 + 1.33 \text{ cm s}^{-1}$  ( $N = 15$ ). When relative humidity is high around a seed, such as on a rainy day or if placed on water, all the long hairs of the pappus fold along the main axis of the seed. Since folding of the hairs greatly decreases the wing-loading of the seed (i.e. weight/area; Augspurger, 1986), such seeds fall much faster than those with the hairs extended.

*Nerium oleander* seeds germinate well when placed on a wet substrate, but they do so faster (see Fig. 8B) if placed directly on water, where they can float for months. Apparently because of the short, unwettable hairs that cover the testa, clipping of the long hairs do not lower a seed's ability to float: after 20 days, there was no significant difference among treatments (clipped or intact pappus) in the proportion of sunken seeds ( $G = 0.512$ ,  $P > 0.5$ , d.f. = 1). Seeds germinate, form fairly long (8-15 mm) radicles and even unfold the cotyledons while floating. Seedlings, however, do not anchor to the substrate unless water depth is less than 10 mm, and they unavoidably sink upon detachment from the testa. Experimental seedlings remained submerged and alive for up to 5 months. Floating seeds and seedlings are also commonly observed in the wild.

Just after follicle opening, density of seeds on the ground within the vertical projection of *N. oleander* shrubs was high. From February onwards they

TABLE 7. Major causes of seedling death through spring and summer of 1988. Although seedlings were censused at approximately weekly intervals, results are reported on a per month basis for clarity

Cause of death	Calendar month					Total	of initial number
	April	May	June	July	August		
Rotten	1	0	0	0	0	1	0.5
Trampled on	3	0	0	0	0	3	1.5
Eaten	0	12	4	0	0	16	8.0
Desiccated	40	13	1	12	26	92	46.0
Missing	4	81*	2	1	0	88	44.0
Total	48	106	7	13	26	200	100

\*Buried by sand and gravel after flood.

germinated massively and, at the peak moment (April), seedling density rose to 1066, 533 and 500 seedlings per square metre, as estimated from counts in three permanent plots. Later on, seedling density decreased noticeably. The fate of 200 numbered individual seedlings was tracked from April through August 1988 (Fig. 11). Seedlings in open sites (without cover) died shortly after germination, with no seedlings surviving later than May. Although seedlings in shady places lived longer on average, none survived August. Major causes of seedling death are reported in Table 7. In spite of many seeds having germinated in very damp places, shallow soil moisture was soon unavailable to seedlings during spring and summer, and this resulted in 46% dying because of desiccation. Rotting, trampling and herbivory were responsible for few deaths (10%). The highest mortality of seedlings (41% of total) took place in May after flooding by heavy rainstorms (see Fig. 1).

#### DISCUSSION

The seeds of *N. oleander* depend on a generous supply of water for optimal germination, while young seedlings (less than 1 year old) are extremely sensitive to drought. This is enough to explain why under a summer-dry, Mediterranean climate the individuals of this species are restricted to stream banks. In addition, the diaspores can float for long periods and be thus transported far downstream, which must facilitate the colonization of banks and development of the dense stands that characteristically constitute *N. oleander* populations. Although seeds exhibit a tuft of long hairs and may be primarily dispersed by wind, a relatively large rate of descent ( $RD = 82 \text{ cm sg}^{-1}$ ; c.f. Levin & Kerster, 1974), together with a moderate height of release (2–3 m; c.f. Augspurger, 1986) causes most seeds to land very close to the parent plant. It is a known fact that anemochory results in strongly leptokurtic distributions (Levin & Kerster, 1974), but it is even more pronounced for this species since the pappus folds hygroscopically and seed release occurs during the rainiest period of the year. Decreased dispersal ability has been claimed to be advantageous for plants inhabiting small spots of land surrounded by vast extensions of unsuitable habitat, as often may happen in desert plants (Elmer & Shmida, 1984; Pijl, 1972; Shmida, 1985). In a similar

way, a large rate of descent in *N. oleander* diaspores may help to avoid the excessive spread of wind-carried propagules far away from the proximity of the stream. Occasional episodes of long-distance dispersal through wind gusts cannot be completely ruled out, but it seems likely that anemochory is of lesser importance (at least in terms of the number of seedlings generated) while secondary transportation through water plays a major role in the ecology and distribution of the species. The fact that both seed dispersal and germination take place at the rainiest season and, consequently, at the moment when most temporary streams run high is undoubtedly an essential attribute in the reproductive ecology of this shrub.

Individuals are self-compatible and liberate numerous seeds on a per plant basis. Self-compatibility makes it possible for a single plant to colonize a wide area, while generating a heavy 'rain' of seeds is probably the only way of finding the new suitable, summer-moist sites formed after or during intense precipitations. Such reproductive attributes are widespread among weedy plants from habitats with intense disturbance regimes (Baker, 1974; Harper, Lovell & Moore, 1970), and the strategy is shared, at least in part, by many temperate and Mediterranean woody taxa inhabiting riparian or, in general, open habitats (Pijl, 1972). As regards dispersal, species in genera unrelated taxonomically to *Nerium* such as *Salix*, *Populus*, *Alnus*, *Betula*, *Fraxinus* and *Tamarix*, for example, behave in a similar fashion. The striking point is that while in the former group of taxa the flowers are usually small, inconspicuous, often anemophilous and grouped in catkins, *N. oleander* presents large, showy flowers with ovaries containing numerous ovules. Dispersal characteristics may appear similar, which might be due to a phenomenon of ecological convergence under similar selective pressures, but the process by which *N. oleander* achieves this end (i.e. the system of pollination) is quite unusual.

Although most zoophilous angiosperms have flowers that provide an energetic reward for food-seeking animals (pollen, nectar, or both; Simpson & Neff, 1983) pollination in some species is achieved not by providing a reward, but by bearing flowers with a set of visual and olfactory cues that makes them look like truly rewarding ones (Batesian mimicry), a substrate for oviposition (reproductive deception) or an insect mate (pseudocopulation); see Little (1983) and Dafni (1984) for reviews on mimicry and deceit in pollination. The most outstanding pollination-related features of *N. oleander* can be summarized as follows: there is a massive flower display of large, scantily aromatic, long-lasting (up to 7 days if unpollinated), tubular, although nectarless flowers. Insect visits are rare, and percent fruit-set low in spite of full self-compatibility. All these circumstances taken together point to the plant relying on 'false advertising' (Slater & Calder, 1988) for pollination. That cheating is not restricted to pollinators is demonstrated by the fact that most people have to be persuaded that such a 'showy and elaborate' flower is nectarless. It is also interesting to note that most people take the long appendages of anthers for stamens (Figs 2, 6), which leads one to speculate about the possibility that, for insects, these might act as stamen mimics.

In the strict sense, nectarless hermaphroditic flowers are not completely unrewarding since some pollen can always be obtained from them. Observations of visitors at *N. oleander* flowers suggest that their aim was to obtain food in the form of nectar, but possibly pollen acted as a secondary reward under certain

circumstances. If so, the profitability of *N. oleander* is likely to be low because (1) pollen is concealed by the anthers, which increases both the time and effort necessary for an insect to gather the food, and (2) the maximum amount of harvestable pollen on a per flower basis (11 600 grains on average) is low in comparison with genuine pollen flowers) in the vicinity (although these mostly flower at other times of the year to *N. oleander*). To exemplify this, the large-flowered *Cistus salvifolius* (Cistaceae) liberates, on average, 106 000 pollen grains per flower; *Cytisus grandiflorus* (Fabaceae, Genisteae) 69 000 grains per flower; and *Myrtus communis* (Myrtaceae) 599 000 grains per flower (Herrera, 1987). Dividing the number of grains by flower dry weight to correct for flower size differences, yields 2244, 3080 and 35 654 grains per mg of flower respectively for these species, but just 146 for *N. oleander*. It seems likely, therefore, that the species is not a good pollen source. In spite of this, and although pollen collection has not been observed so far, it cannot be ruled out that some pollination is achieved by insects attempting to gather pollen, perhaps in conditions when alternative food sources are lacking. Otherwise, it is difficult to explain why large bees visit *Nerium* flowers as reported above, moving between up to four plants consecutively. Given that few shrub species flower during summer in southern Spain (Arroyo, 1985; Herrera, 1986) and that bee diversity and activity are often high at this time (Herrera, 1988), summer flowering and starving (or naive?) bees probably are the key point in the pollination of *N. oleander*. Coleman (1935) reports on blowflies visiting and getting trapped (!) by their mouth parts at the flowers of cultivated *N. oleander* in Australia, a fact not observed by me in southern Spain. Some attributes of flowers, such as the long tube, may well have evolved in response to lepidopteran visitors, and day-flying hawkmoths have sometimes been observed visiting cultivated plants in southern Spain (*Macroglossum stellatarum* L.; C. M. Herrera, personal communication). My own observations in the wild during 1987 and 1988, on the other hand, suggest a shift to pollination by large bees, but since the time spent on night observations during this study was relatively short, visitation by moths cannot be completely ruled out.

Many pollination-related features of *N. oleander* are similar to those of a related species, *Plumeria rubra* L. (Apocynaceae), a mass flowering tree from dry tropical forests. According to Haber (1984), the flowers of *Plumeria* are large, white, aromatic and unrewarding, and pollination results from deceit of nectar-seeking hawkmoths. Also the arrangement of anthers and stigma of *Plumeria* is similar to that of *Nerium*, except in that reproductive parts are at the bottom of the corolla tube. The observations that anthers liberate pollen apparently onto the stigma but that fruit set is consistently low (less than 0.1%) led Haber (1984) to suggest that *Plumeria* is self-incompatible. Results for *Nerium oleander*, however, demonstrate that genetic self-incompatibility does not need to be invoked to explain low fruit set. In fact, small fruit crops are produced by *N. oleander* in spite of full self-compatibility, which simply indicates very low visitation rates. I suggest that an investigation of where the receptive stigmatic surface is situated in *Plumeria* would reveal that self pollen cannot arrive there by its own means. Darwin's (1861) observations on *Vinca minor* did not overlook this fact.

Haber (1984) stated that *Plumeria rubra* lacks a specific model in Costa Rica, but convincingly reasoned that odour and visual cues make its flowers resemble those of many typical hawkmoth-pollinated species in the neighbourhood. Thus,

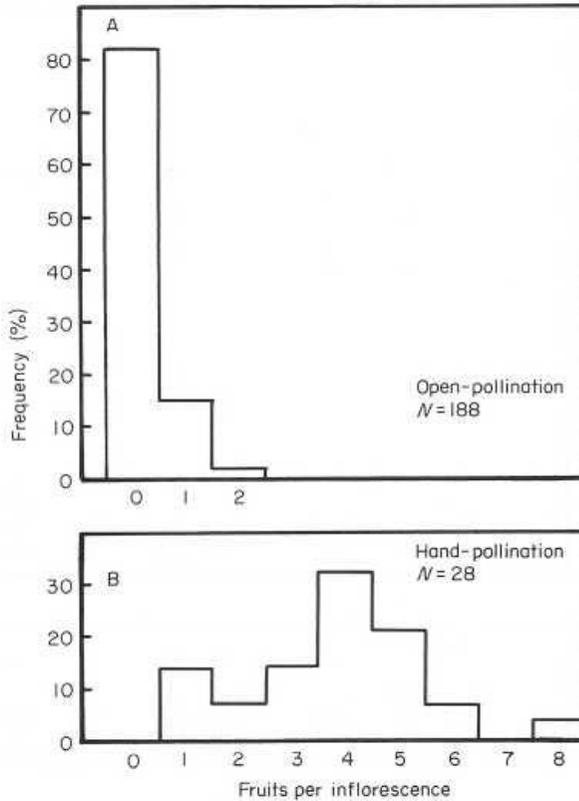


Figure 9. Frequency distribution of the number of fruits per inflorescence in *N. oleander*.

*Plumeria* would be a generalized mimic. *Nerium*, however, represents a quite different case since its flowers are exceptional among Mediterranean scrub species with regard to size, morphology and blooming date. Speculations on possible models for *N. oleander* should consider large, pink-flowered nectariferous species inhabiting stream banks. No common occurring tree, shrub or herb species can, to my knowledge, be claimed to be a model. My hypothesis is that the supposedly crucial points for mimicry, namely (1) a model and (2) low occurrence of the mimic (Little, 1983; Dafni, 1984) are in fact necessary for the evolution of this pollination system, but are not thereafter. If the model vanishes, mimicry just changes into mere deception. In other words, *N. oleander* flowers would imitate those of an extinct, or nearly extinct model. The same would apply to other food-deceptive systems reported in the literature where a likely model is absent (e.g. Ackerman, 1981, 1983; Nilsson, 1980). A supposedly Tertiary relict, the at-present very rare *Rhododendron ponticum*, may be proposed to represent a model for *N. oleander*: it has large, moderately nectariferous pink flowers, and inhabits stream banks across the southernmost part of Spain. Curiously, according to Collins' English Dictionary, the name oleander derives 'from Medieval Latin, variant of arodandrum, perhaps from latin *Rhododendron*'. To my knowledge, the identity of insects pollinating *R. ponticum* in Spain is not known.

There are examples of deceit pollination in several plant families (see Little,

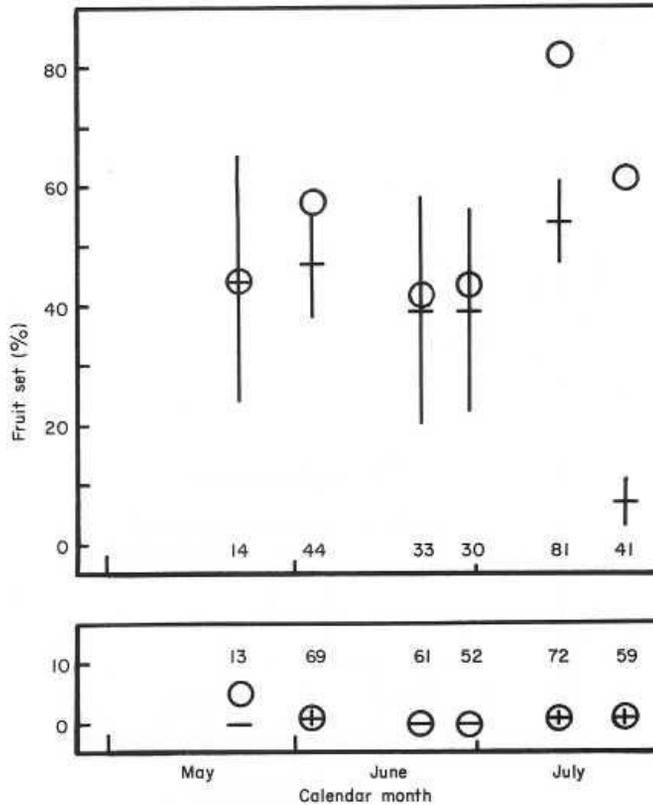


Figure 10. Variation of the number of initiated (open circles) and fully-grown pods (horizontal lines) in hand- (top) and open-pollinated flowers (bottom) according to the date of anthesis. Values are means for five individuals. For any date and treatment numerals indicate the number of flowers, and the vertical line plus-minus one standard error of the mean for fully grown fruits.

1983), but the highest incidence occurs among orchids where, in addition to well-known examples of pseudocopulation (e.g. *Ophrys* spp.; Pijl & Dodson, 1966; Proctor & Yeo, 1973), there seems to exist numerous cases of nutritive deception Batesian mimicry (Bierzuchudek, 1981; Dafni & Ivri, 1981; Dafni, 1983; Dafni & Calder, 1987; Kjellson, Rasmussen & Dupuy, 1985). According to Dafni (1984: 270) floral deception is widespread, too, among the Asclepiadaceae. Both orchids and asclepiads present many seeded fruits and large numbers of pollen grains dispersed on a per-visit basis (pollinia). The correlation of deception with these traits is remarkable and, certainly, one would not expect deception to evolve in plant groups exhibiting few-seeded fruits. *Nerium oleander* presents ovaries containing numerous (300–400) ovules and pollen dispersed collectively by aggregation into a sticky substance and, as in most other cases of floral deception, this enables large numbers of seeds to be generated from a single, probably rare pollination event. Since massive pollen deposition also occurs in nectariferous Apocynaceae (e.g. *Vinca minor*; Proctor & Yeo, 1973: 188), this trait should be regarded as a precondition for, but not as consequence of, floral deception.

Fruit abortion has been shown to occur among flowers pollinated late in the

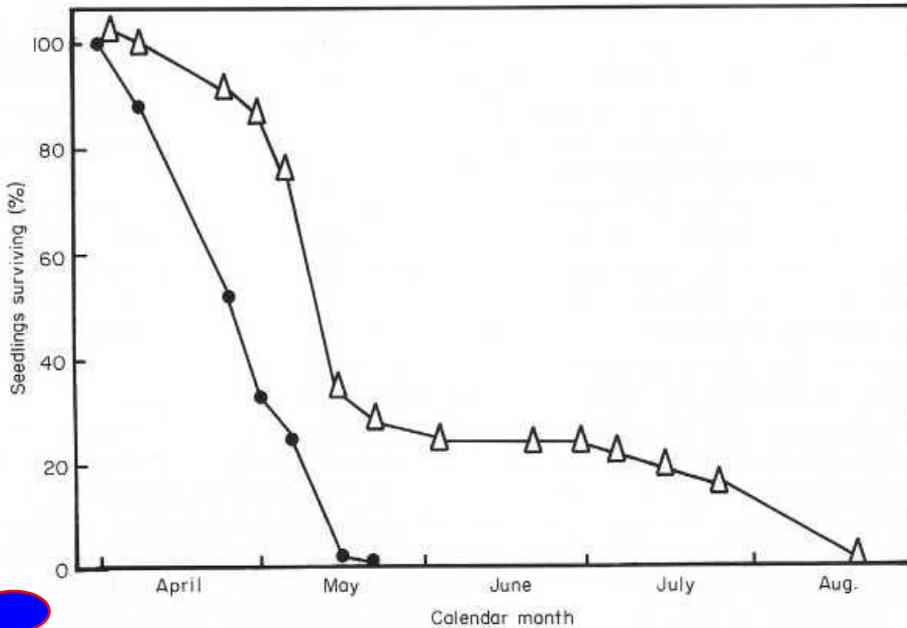


Figure 11. The survival of *N. oleander* seedlings appearing on sites without cover (●;  $N = 40$ ) and on shady places (△;  $N = 160$ ).

season on experimental inflorescences (Fig. 10), which points to resource-limited reproduction. This phenomenon, however, would only occur in nature if the conditions of the experiment are met, namely that a relatively large fraction of the ovaries in an inflorescence have been pollinated. This seems a quite unrealistic situation given the unrewarding nature of flowers. It seems more likely that rarely, if ever, will developing pods compete for resources and that, instead, fruiting is consistently pollen-limited. This is strongly supported by observed differences in percent fruit set of open- and hand-pollinated flowers (Table 5), and by the finding that fruits with as few as 40 seeds can develop successfully. Although growth and reproduction overlap in time to a great deal within any individual (Fig. 1), the possible conflict between these processes must be attenuated by the fact that inflorescences and leaf buds are terminal and appear on different branch-ends.

Artificial pollinations indicated that, on average, four is the maximum number of fruits produced within any inflorescence (see Fig. 9). Since inflorescences bear 20 flowers on average, 80% of all flowers in any inflorescence would be 'in excess', or, in other words, will not set a fruit even if pollinated. Flower overproduction is a quite common phenomenon in angiosperms on which there is an extensive literature (see Stephenson, 1981; Sutherland, 1987). Customary explanations of its evolution include fitness increase of individuals through increased pollinator attraction (Stephenson, 1979; Willson & Price, 1977), increased pollen donation (Bawa & Webb, 1984; Queller, 1985; Willson & Price, 1977), adjustment to unusually good pollinator service or resource availability (Stephenson, 1980) and improvement of progeny quality through selective fruit abortion (Stephenson, 1984; Stephenson & Winsor, 1986). In this

self-compatible (although not automatically self-pollinating), nectarless, and rarely visited species, selective fruit abortion is unlikely to operate often, while compensation for variations in resource availability remains a possibility, provided that such variations exist. The evolution of flower overproduction and an impressive floral display should probably be explained in terms of increased pollinator attraction and pollen donation.

Deceit pollination is far from common among southern Spanish scrub species. The typically Mediterranean, species-rich group taxa in the Cistaceae, Fabaceae, and Lamiaceae, for example, most often are either heavy pollen producers or nectariferous (Herrera, 1985, 1987). The possession by *N. oleander* of unrewarding flowers is, to my knowledge, exceptional. Next, I will discuss the hypothesis that deceit pollination in this species has little to do with extant, Mediterranean-type life conditions. The flowers are unrewarding because (1) they lack nectar and (2) pollen is largely inaccessible to visitors. Inaccessibility of pollen results from a special arrangement of style and anthers which is typical of the Apocynaceae. This is unlikely to occur in *N. oleander* as a result of recent selective pressures, but rather because of phylogenetic constraint within the family. Lack of nectar, on the other hand, is not a matter of nectary malfunction or environmental commitments, but of nectar-disk absence. Since this a generic trait (Bentham & Hooker, 1873) shared by congeneric, non-Mediterranean species, it seems possible again that phylogenetic constraints play a major role in *N. oleander* flowers being unrewarding. Furthermore, according to Bentham & Hooker (1873), 40 out of 100 apocynaceous genera lack nectar disks, which suggests that the associated trait (no nectar) has evolved on several occasions. (A high incidence of pollination systems based on deceit among the poorly studied, mainly tropical Apocynaceae could thus be reasonably predicted.) As stated above (see Introduction), fossil remains of *Nerium* date from the Tertiary, and it is appealing to think of pollination-related characteristics in this old, pre-Mediterranean taxon as having changed little since that time.

#### ACKNOWLEDGEMENTS

This study was supported during 1988 by a post-doctoral fellowship from the Spanish Plan Nacional de Perfeccionamiento de Doctores y Licenciados. The author thanks Carmen Blazquez and Adolfo Munoz for help during field work, Peter Gibbs for indicating Darwin's method of hand-pollinating vincas, and P. Gibbs, L. A. Nilsson and S. Talavera for critically reading the manuscript.

#### REFERENCES

- ACKERMAN, J. D., 1981. Pollination biology of *Calypso bulbosa* var. *occidentalis* (Orchidaceae): a food-deception system. *Madrono*, 28: 101-110.
- ACKERMAN, J. D., 1983. Euglossine bee pollination of the orchid *Cochleantes lipscombiae*: a food source mimic. *American journal of Botany*, 70: 830-834.
- ARROYO, J., 1985. *Fenología de la floración en matorrales de Andalucía Occidental*. Unpublished Ph.D. thesis of the University of Sevilla.
- AUGSPURGER, C. K., 1986. Morphology and dispersal potential of wind-dispersed diaspores of neotropical trees. *American journal of Botany*, 73: 353-363.
- AXELROD, D. I., 1975. Evolution and biogeography of the Madrean-Tethyan sclerophyll vegetation. *Annals of the Missouri Botanical Garden*, 62: 280-334.

- BAKER, H. G., 1974. The evolution of weeds. *Annual Review of Ecology and Systematics*, 5: 1-24.
- BAWA, K. S. & WEBB, C. J., 1984. Flower, fruit, and seed abortion in tropical forest trees: implications for the evolution of paternal and maternal patterns. *American Journal of Botany*, 71: 736-751.
- BENTHAM, G. & HOOKER, J. D., 1873. *Genera Plantarum* 2. London: Lovell Reeve & Co.
- BIERZYCHUDEK, P., 1981. *Asclepias*, *Lantana*, and *Epidendrum*: a floral mimicry complex? *Biotropica*, 13 (Suppl.): 54-58.
- COLEMAN, E., 1935. More insect tragedies. *The Victorian Naturalist*, 52: 20-22.
- CUISANCE, P. & SEABROOK, P., 1970. *Les arbustes d'ornement*. Paris: Larousse.
- DAFNI, A., 1983. Pollination of *Orchis caspia*-a nectarless plant which deceives the pollinators or nectariferous species from other plant families. *Journal of Ecology*, 71: 467-474.
- DAFNI, A., 1984. Mimicry and deception in pollination. *Annual Review of Ecology and Systematics*, 15: 259-278.
- DAFNI, A. & CALDER, D. M., 1987. Pollination by deceit and floral mimesis in *Thelymitra antennifera* (Orchidaceae). *Plant Systematics and Evolution*, 158, 11-22.
- DAFNI, A. & IVRI, Y., 1981. Floral mimicry between *Orchis israelitica* Baumann & Dafni (Orchidaceae) and *Bellevalia fexuosa* Boiss. (Liliaceae). *Oecologia*, 49: 229-232.
- DARWIN, C., 1861. Fertilization of Vincas. *Gardeners' Chronicle*, 552.
- ELLNER, S. & SHMIDA, A., 1984. Seed dispersal in relation to habitat in the genus *Picris* (Compositae) in Mediterranean and arid regions. *Israel Journal of Botany*, 33: 25-39.
- ENGLER, A., 1964. *Syllabus der Pflanzenfamilien*, 2. Berlin: Gebrüder Borntraeger.
- FONT-QUER, P., 1973. *Plantas medicinales*. Barcelona: Labor.
- GREUTER, W., BURDETT, H. M. & LONG, G. (Eds), *Med-checklist*, 1. Geneve: Editions des Conservatoire et Jardin Botaniques de la ville de Geneve.
- HABER, W. A., 1984. Pollination by deceit in a mass-flowering tree *Plumeria rubra* (Apocynaceae). *Biotropica*, 16: 269-275.
- HARBORNE, J. B., 1982. *Introduction to Ecological Biochemistry*, 2nd edn. London: Academic Press.
- HARPER, J. L., LOVELL, P. H. & MOORE, K. G., 1970. The shapes and sizes of seeds. *Annual Review of Ecology and Systematics*, 1: 327-356.
- HERRERA, C. M., 1984. Tipos morfológicos y funcionales en plantas del matorral mediterráneo del sur de España. *Studia Oecologica*, 5: 7-34.
- HERRERA, J., 1985. Nectar secretion patterns in southern Spanish mediterranean scrublands. *Israel Journal of Botany*, 34: 47-58.
- HERRERA, J., 1986. Flowering and fruiting phenology in the coastal shrublands of Donana, south Spain. *Vegetatio*, 68: 91-98.
- HERRERA, J., 1987. Flower and fruit biology in southern Spanish mediterranean shrublands. *Annals of the Missouri Botanical Garden*, 74: 69-78.
- HERRERA, J., 1988. Pollination relationships in southern Spanish mediterranean shrublands. *Journal of Ecology*, 76: 274-287.
- HEYWOOD, V. H., 1978. *Flowering Plants of the World*. Oxford: Oxford University Press.
- HOOKER, J. D. & JACKSON, B. D., 1895. *Index Kewensis*, 2. Oxford: Oxford University Press.
- KJELSSON, G., RASMUSSEN, F. N. & DUPUY, D., 1985. Pollination of *Dendrobium infundibulum*, *Cymbidium insigne* (Orchidaceae) and *Rhododendron lyi* (Ericaceae) by *Bombus eximius* (Apidae) in Thailand: a possible case of floral mimicry. *Journal of Tropical Ecology*, 1: 289-302.
- LEVIN, D. A. & KERSTER, H. W., 1974. Gene flow in seed plants. *Evolutionary Biology*, 7: 139-220.
- LINES-ESCARDO, A., 1970. The climate of the Iberian Peninsula. In C. C. Wallen (Ed.), *Climates of Northern and Western Europe*: 195-239. Amsterdam: Elsevier.
- LITTLE, R. J., 1983. A review of floral food deception mimics with comments on floral mutualism. In C. E. Jones & R. J. Little (Eds), *Handbook of Experimental Pollination Biology*: 294-309. New York: Scientific and Academic Editions.
- MARTIN, F. W., 1959. Staining and observing pollen tubes in the style by means of fluorescence. *Stain Technology*, 34: 125-128.
- NILSSON, L. A., 1980. The pollination ecology of *Dactyloctenium aegyptium*. *Botaniska Notiser*, 133: 367-385.
- OZENDA, P., 1977. *Fiore du Sahara*, 2nd edn. Paris: Centre National de la Recherche Scientifique.
- PIJL, L. VAN DER, 1972. *Principles of Dispersal in Higher Plants*, 2nd edn. Berlin: Springer-Verlag.
- PIJL, L. VAN DER & DODSON, C. H., 1966. *Orchid Flowers. Their Pollination and Evolution*. Coral Gables: University of Miami Press.
- PONS, A. & QUEZEL, P., 1985. The history of the flora and vegetation and past and present human disturbance in the Mediterranean region. In C. Gomez-Campo (Ed.), *Plant Conservation in the Mediterranean Area*: 25-43. Dordrecht: Dr W. Junk.
- PROCTOR, M. & YEO, P., 1973. *The Pollination of Flowers*. London: Collins.
- QUELLER, D. C., 1985. Proximate and ultimate causes of low fruit production in *Asclepias exaltata*. *Oikos*, 44: 373-381.
- QUEZEL, P., 1985. Definition of the Mediterranean region and the origin of its flora. In C. Gomez-Campo (Ed.), *Plant Conservation in the Mediterranean Area*: 9-24. Dordrecht: Dr W. Junk.
- RIVAS-GODAY, S. & PINIES, M., 1949. Acerca del area ecologica de la Adelfa, *Nerium oleander* L. *Annales Instituto Jose Celestino Mutis*, 9: 223-230.

- ROTHSCHILD, M., 1972. Some observations on the relationship between plants, toxic insects and birds. In J. B. Harborne (Ed.), *Phytochemical Ecology*: 1-12. London: Academic Press.
- SHMIDA, A., 1985. Why do some Compositae have an inconsistently deciduous pappus? *Annals of the Missouri Botanical Garden*, 72: 184-186.
- SIMPSON, B. B. & NEFF, J. L., 1983. Evolution and diversity of floral rewards. In C. E. Jones & R. J. Little (Eds), *Handbook of Experimental Pollination Biology*: 142-183. New York: Scientific & Academic Editions.
- SLATER, A. "1". & CALDER, D. M., 1988. The pollination biology of *Dendrobium speciosum* Smith: a case of false advertising? *Australian journal of Botany*, 36: 145-158.
- STEPHENSON, A. G., 1979. An evolutionary examination of the floral display of *Catalpa speciosa* (Bignoniaceae). *Evolution*, 33: 1200-1209.
- STEPHENSON, A. G., 1980. Fruit set, herbivory, fruit reduction, and the fruiting strategy of *Catalpa speciosa* (Bignoniaceae). *Ecology*, 61: 57-64.
- STEPHENSON, A. G., 1981. Flower and fruit abortion: proximate causes and ultimate functions. *Annual Review of Ecology and Systematics*, 12: 253-279.
- STEPHENSON, A. G., 1984. The regulation of maternal investment in an indeterminate flowering plant (*Lotus corniculatus*). *Ecology*, 65: 113-121.
- STEPHENSON, A. G. & WINSOR, J. A., 1986. *Lotus corniculatus* regulates offspring quality through selective fruit abortion. *Evolution*, 40: 453-458.
- SUTHERLAND, S., 1987. Why hermaphroditic plants produce many more flowers than fruits: experimental tests with *Agave mckelveyana*. *Evolution*, 41: 750-759.
- WILLSON, M. F. & PRICE, P. W., 1977. The evolution of inflorescence size in *Asclepias* (Asclepiadaceae). *Evolution*, 31: 495-511.