

# Predispersal reproductive biology of female *Osyris quadripartita* (Santalaceae), a hemiparasitic dioecious shrub of Mediterranean scrublands

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*Received June 1984, accepted for publication November 1984*

HERRERA, C. M., 1985. **Predispersal reproductive biology of female *Osyris quadripartita* (Santalaceae), a hemiparasitic dioecious shrub of Mediterranean scrublands.** Female *Osyris quadripartita* plants exhibit uninterrupted reproductive activity throughout the year, due to the long duration of successive stages in the cycle and marked within-crop developmental asynchrony. Cycles corresponding to the flowering seasons of consecutive years overlap in each individual. Flowering takes place in spring, and fruits develop in the dry summer season and ripen at any time of the year. Variation in flowering time explains a negligible proportion of variation in ripening time. The greatest reproductive losses are incurred in the phase extending from closed flowers through unripe fruits, mostly due to ovary abortion. Only 30% of closed flowers eventually reach this latter stage. In contrast, 75% of unripe fruits complete their development, with subsequent dispersal of seeds. The probability of the setting of ripe fruit steadily decreases from early to late season flowers, due to increased ovary abortion rates. Resource limitation in the dry summer season seems responsible for this pattern of selective fruit maturation.

ADDITIONAL KEY WORDS:—Phenology – selective fruit maturation.

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## INTRODUCTION

The diversity of parasitic angiosperms, both with regard to ecology and taxonomy, is a peculiarity of vegetation on nutrient-poor soils of mediterranean

Australia and S Africa, the parasitic habit apparently contributing to enhanced nutrient uptake (Lamont, 1982, 1983). No investigations on the frequency of parasitic taxa have been conducted in the Mediterranean Basin itself, but regional floras reveal that these plants are also well represented there. Hemi- and holoparasitic species belonging to seven families (Santalaceae, Viscaceae, Balanophoraceae, Orobanchaceae, Rafflesiaceae, Scrophulariaceae and Cuscutaceae) are found in mediterranean SW Spain. Among these, root hemiparasitic shrubs of the genus *Osyris* (Santalaceae) are prominent components of some coastal scrublands on poor soils (Rivas-Martínez, Costa, Castroviejo & Valdés, 1980; Herrera, 1984b).

Detailed ecological studies of root hemiparasites have largely concentrated on herbaceous taxa (e.g. Atsatt, 1965, 1970a, b; Atsatt & Strong, 1970; Cantlon, Curtis & Malcolm, 1963; Kwak, 1977; Lackney, 1981; Malcolm, 1966; Safa, Jones & Musselman, 1984). Woody species have received comparatively little attention, and our knowledge of important aspects of their general biology and ecology is imperfect (see Kuijt, 1969; Lamont, 1983). In the case of the Santalaceae, anatomical and developmental aspects have attracted researchers for more than a century (Griffith, 1845; Guignard, 1885; Herbert, 1925; Iyengar, 1937; Rao, 1942; Sedgley, 1982a), but quantitative information on reproductive ecology and general biology of species in this family is strikingly sparse. *Osyris quadripartita* Salzm. ex Decne is an evergreen dioecious shrub found in SW Spain. The main objectives have been:

- to describe quantitatively the unusual reproductive cycle exhibited by female individuals,
- to assess the relative significance of the various stages in the cycle in determining reproductive rates,
- to identify some factors responsible for observed patterns.

The phenology of both sexes at the population level has been described elsewhere (Herrera, 1984b). A general account of the natural history of *O. quadripartita* may be found in Herrera (1984b), and preliminary information on seed-dispersal ecology in Herrera (1984a).

#### STUDY SITE AND METHODS

A marked population (22 males, 27 females) of *Osyris quadripartita* has been intensively studied from late 1978 through early 1984 in dense mediterranean scrub near El Viso (Sevilla province, 37° 26' N, 5° 45' W), at 100 m elevation. Details on the composition and ecology of vegetation at the site have been presented in Herrera (1984a). Climate is of the warm mediterranean type. Average annual precipitation is 613 mm, with 76% falling in October–March and only 1.2% in July–August. Mean monthly temperature of the coldest (January) and hottest (July) months are 10.5°C and 26.8°C (see Herrera, 1984b, for further details). The severe summer drought is the dominant stress on plants at the site. Winter cold stress is unimportant (Herrera, 1984b; Montero & González, 1974).

In April 1980 six female plants were arbitrarily chosen from the marked population for detailed study of reproductive biology. They were fully representative of the local female population in every respect, including size, phenology and growing conditions. Starting in the first week of May (coincident

with the early phase of the female flowering peak that year), a sample of closed and newly open flowers were individually tagged every week on each plant until the end of its flowering period. A total of 398 closed flowers and 287 newly open flowers were marked. Numbered 8 × 5 mm tags of stiff parchment paper were used, secured to floral pedicels with a piece of thin wire. Complete tags had an individual weight of about 40 mg. Despite the small size of flowers (4 mg wet weight), I had no evidence suggesting that tags could damage floral pedicels, induce abnormal abscission, or alter floral or fruit development in any perceptible way.

From the end of the flowering period through May 1981, samples of developing ovaries and unripe fruits were marked periodically (mostly biweekly) using the same procedure as for flowers. In total, 967 developing fruits were individually marked in this period. Regular fruit marking served to maintain adequate sample sizes throughout the study period, given the important reductions which took place after flowering and the peak of fruit ripening.

Every week (May–August 1980) or nearly so (September 1980–August 1981), all ‘surviving’ tags were examined, and a record was kept of the stage of the marked reproductive structure. Five stages were considered: closed flower, open flower, latent ovary, unripe fruit, and ripe fruit; detailed descriptions of which are presented below. Any sign of damage was annotated and its cause identified whenever possible. Results of the regular examination of tagged structures consisted of timed sequences of events for a total of 1652 individual flowers or fruits, and this information constitutes the basis of the analyses and descriptions to follow. Supplementary data were provided by regular observations of flowering and fruiting phenology of the six study individuals (see Herrera, 1984b, for methods), and counts of standing ripe fruit crops and fallen ripe fruits beneath plants. This information has been used for the estimation of ripe fruit removal rates by seed dispersers. Estimates of the total number of flowers produced over the entire flowering season were obtained for each plant by combining observations in this period with projected figures computed on the basis of total number of ripe fruits produced and flower-to-fruit success rates.

#### REPRODUCTIVE CYCLE

##### *Sequence of stages*

Female flower buds are produced, singly or in pairs, at the axil of new leaves on growing shoots, mostly during March–May (Herrera, 1984b). Buds appear continuously as actively growing shoots elongate, and cessation of growth in late spring–early summer arrests flower bud production.

Flowers are yellowish-green, inconspicuous (perianth diameter about 3.5 mm), and have an average dry weight of 2.25 mg. The inferior, cone-shaped ovary has a single ovule. The receptacle is flat and has a nectar-secreting disk around the base of the centrally placed style. Three staminodes are inserted on the margin of the receptacle, which do not produce pollen but are morphologically almost identical to the stamens of male flowers. Flowers remain open, and apparently functional for 2 weeks (Table 1). There is no difference in duration of flower opening between those which eventually produce a developing ovary ( $2.0 \pm 0.8$  weeks,  $N = 257$ ) and those which do not ( $2.0 \pm 0.9$  weeks,  $N = 84$ ). This suggests a predetermined mean duration of flower opening

Table 1. Duration (in weeks) of stages in the female reproductive cycle of *Osyris quadripartita*, based on observations of individually marked flowers and fruits

Plant	Open flower				Latent ovary				Unripe fruit			
	<i>N</i>	$\bar{x}$	s.d.	range	<i>N</i>	$\bar{x}$	s.d.	range	<i>N</i>	$\bar{x}$	s.d.	range
8	46	2.2	0.7	1-3	51	4.3	1.7	1-9	46	13.4	8.3	7-45
9	73	2.2	1.0	1-3	25	8.7	5.3	1-22	33	14.7	8.0	6-36
15	50	1.8	0.7	1-3	11	4.0	4.0	1-16	12	21.7	8.1	10-35
16	73	1.8	0.7	1-3	15	11.6	6.0	3-25	30	17.7	7.7	6-36
1PG	83	2.0	0.8	1-4	45	6.1	2.6	1-14	48	14.7	3.7	7-24
1PA2	18	1.9	0.8	1-3	28	4.4	2.0	1-10	38	15.3	7.0	5-31
All combined	343	2.0	0.8	1-4	175	6.0	4.0	1-25	207	15.4	7.3	5-45

which is not significantly shortened by pollination. Flowers are rarely visited by insect pollinators (mostly small and medium-sized flies), and tiny droplets of nectar often accumulate in the receptacle (less than 0.05  $\mu$ l per flower). Several ant species have been recorded feeding on this nectar, but they play no role in pollination (Herrera, Herrera & Espadaler, 1984).

After anthesis, flowers either wither and fall, or shed perianth pieces and the ovary becomes modified to what will be termed here a LATENT OVARY. It loses the pale green, somewhat waxy appearance and relatively soft texture, to become tougher and deeper green. It increases slightly in length (up to about 3.5 mm) and width (up to 2.5 mm), but retains its peculiar conical shape. Latent ovaries may remain in this stage for more than 5 months without perceptible external change. Mean duration of latent ovaries which eventually reach the next stage (unripe fruit, see later) is 6 weeks (Table 1), and the observed range is 1-25 weeks. There is considerable inter-individual and within-crop heterogeneity in latent ovary duration (Table 1). Nineteen percent of latent ovaries remain in this stage for more than 2 months (all plants combined).

The transition from latent ovary to unripe fruit takes place rather abruptly. A nearly spherical shape is acquired in 1.0-1.5 weeks, size increasing to 5.5-7.5 mm diameter. The seed coat hardens, and the single seed almost reaches definitive size. Unripe fruits may remain 'dormant', without ripening, for nearly 1 year after the transition from latent ovary. The mean duration of this stage is 15.4 weeks, and there is substantial inter-individual and within-crop heterogeneity (Table 1).

Ripening may occur at any time of year. The pericarp becomes juicy and turns to either an orange or orange-red colour. Fruits produced in autumn-winter are orange and have a thin waxy layer, whereas those produced in spring-summer are orange-red and lack the waxy layer. Individual fruits remain on the plant usually for less than 2 weeks after ripening. Most of them are eaten by frugivorous birds (mainly *Sylvia atricapilla* and *Turdus merula*) which effectively disperse the seeds (Herrera, 1984a). Some fruits fall to the ground, where they rot (in autumn-winter) or are taken by ants or mice (spring-summer). Rodent consumption has not been recorded for ripe fruits borne on plants, but ants sometimes remove the pericarp of these fruits.

Nearly 6 months elapse from anthesis to fruit ripening

(mean  $\pm$  s.d. =  $24.9 \pm 10.0$  weeks,  $N = 48$ , all plants combined), but this magnitude is extremely variable (range 13–54 weeks, all plants combined). Heterogeneity in overall developmental rates is a consequence of the heterogeneity in every successive stage, and is responsible for the extended fruiting period exhibited by individual plants (see below).

### Timing

The reproductive cycle of individual plants encompasses the entire year (Fig. 1), due to long duration of successive stages and strong within-crop developmental asynchrony. Cycles corresponding to consecutive years' flowering seasons overlap in all individuals. In late spring–early summer, individual plants bear the current year's flowers and latent ovaries, along with unripe and ripe fruits resulting from the previous year's flowers. Two different cohorts of unripe fruits may simultaneously be found on the same individual. Latent ovaries are found on plants from May through late summer–early autumn. In all plants, some ovaries experience the transition to unripe fruit very early (May–June), while others do so in autumn. The timing of fruit ripening varies between individuals but all plants ripen the earliest fruits of the current season sometime in the summer, and the latest ones in the early summer of the following year.

The seasonal distribution of the transitions from latent ovary to unripe fruit, and from the latter to ripe fruit, is represented in Fig. 2 for individually marked ovaries resulting from marked flowers, all plants combined. Most ovaries (77%) which developed into unripe fruits did so in July–August, in the middle of the summer dry season, while a small proportion did so in autumn. Most fruits

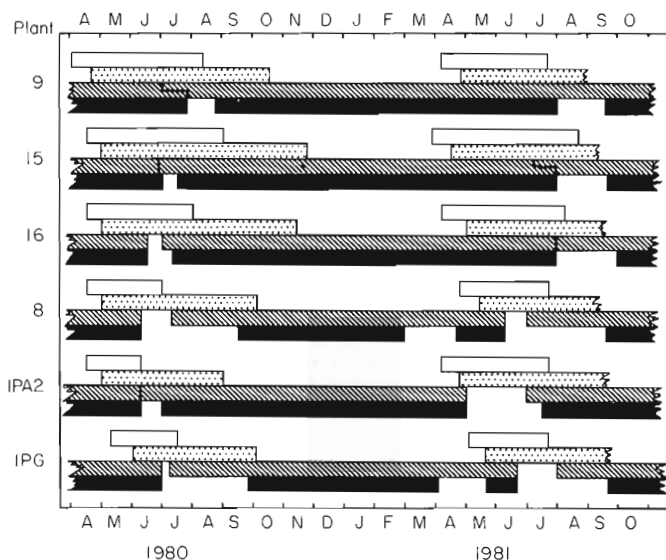


Figure 1. *Osyris quadripartita*. Reproductive cycles of the six female plants studied. The entire study cycle, corresponding to the 1980 flowering season, is shown along with the late phases of the cycle originating in 1979, and the early phases of the 1981 season. Bars extend over the period in which the presence of the corresponding stage has been recorded on the shrub: □, open flowers; ▨, latent ovary; ▩, unripe fruit; ■, ripe fruit.

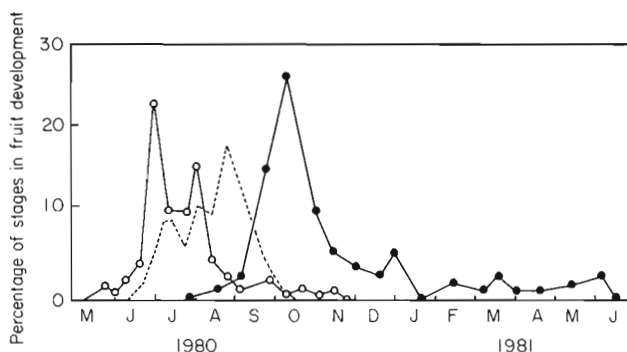


Figure 2. *Osyris quadripartita*. Seasonal distribution of transitions from latent ovary to unripe fruit (○) and from unripe to ripe fruit (●), and abortions of latent ovaries (---), for individually marked ovaries and fruits, all plants combined ( $N = 179, 107$  and  $270$ , respectively).

(59%) ripened in October–November, but the ripening period extended well into the following spring, when a minor peak occurred (see also Herrera, 1984b).

The date when individual unripe fruits reach maturity is largely independent of the time elapsed since flowering, which is consistent with the broad variation in total development time from anthesis to fruit ripening reported above. Fruits originating from flowers on the same plant opening on the same week ripen over the whole fruiting period of the plant. For all plants combined (Fig. 3), there is a significant correlation between the dates of anthesis and fruit ripening ( $r = 0.264$ ,  $N = 101$ ,  $P = 0.008$ ), but variation in flowering time explains only about 7% of the variation in ripening time. The long fruiting periods of individual plants are not, therefore, the consequence of an orderly chronological staggering of ovary and unripe fruit development.

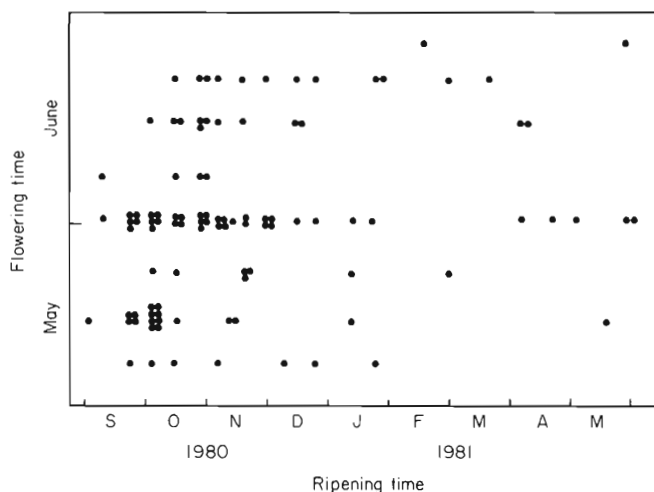


Figure 3. *Osyris quadripartita*. Relation between dates of anthesis and ripening of resulting fruits, for the 101 marked flowers which eventually accomplished the complete cycle.

## REPRODUCTIVE SUCCESS

*Overall patterns*

The proportion of closed flowers, open flowers, latent ovaries, and unripe fruits eventually reaching the respective subsequent stages in the cycle, along with estimates of the fraction of ripe fruits removed by legitimate seed dispersers, are presented in Table 2. For the phase extending from closed flowers through ripe fruits, figures are based only on data from individually marked structures (flowers or fruits). The proportion of ripe fruits removed by seed dispersers was obtained by combining information on the fraction of ripe fruits which were damaged while attached to the plant, together with the fraction of ripe fruits which had fallen to the ground under the parent plant. These two categories of fruit are assumed to have failed at dispersal. Information on the former comes both from individually marked fruits and from regular counts of standing crops on the entire plants. The proportion used in the computations was the mean of values obtained by the two methods, which were closely coincident. Information on the latter comes exclusively from counts of fallen fruits under plants. The proportion of ripe fruits of each individual which falls to the ground was estimated by the ratio of the respective sums, over the entire season, of fallen fruits and standing fruit crops.

Averaged over the six study plants and the whole flowering season, 84.3% of closed flowers eventually reached anthesis. Those which had failed to do so were destroyed by caterpillars feeding on new growth (mostly *Charaxes jaisius* L., Nymphalidae, and an unidentified species of the Tortricidae). Among open flowers, 70% produced latent ovaries, but only 51.2% of the latter eventually became unripe fruits. The majority of missing ovaries (98.3%) were aborted by the plant without any sign of external or internal damage, and very few (1.7%) were destroyed by insect herbivores (mostly caterpillars). A large fraction of unripe fruits (86.4%) eventually ripened. Those which failed to do so were destroyed by insect herbivores (commonly Acridid or Tettigoniid grasshoppers) or fell after drying without apparent damage. A mean of 86.8% of ripe fruits was removed by avian seed dispersers. The remaining 13.2% was accounted for by fruits falling to the ground under the parent plant (8.7%) and destroyed or damaged while on the plant (4.5%). Over the cycle, the greatest losses were incurred in the phase extending from closed flowers through unripe fruits, since only 30% of closed flowers eventually reached this latter stage. In contrast, a mean of 75% of unripe fruits completed their development and eventually lead to dispersed seeds.

Combining multiplicatively the successive proportional losses, only 22% of closed flowers eventually lead to a dispersed seed. However, considerable interindividual variation in this magnitude ('overall relative success', ORS hereafter) existed, ranging from 9.9 (plant 15) to 37.6% (plant 8). Correlations were computed (across individuals) between ORS and each of its five component factors (all log-transformed) to identify the main source of interindividual variation in overall relative reproductive success. The only significant correlation found ( $r = 0.896$ ,  $N = 6$ ,  $P < 0.02$ ) was with the proportion of latent ovaries yielding unripe fruits. This variable explains 80.3% of observed variation in ORS. This demonstrates that this transition was the most directly responsible for interindividual variation in ORS. Plants were most

Table 2. Relative success rates in consecutive transitions of the female *Oryzias quadripartita* reproductive cycle. Figures represent the percentage of flowers or fruits which eventually reach the next stage in the cycle. Sample sizes are shown in parantheses. In the case of seed dispersal rates, the two sample sizes shown correspond to number of individually marked fruits and the sum over the whole season of standing fruit crops, respectively (see text for methods)

Transition	Individual							Mean
	8	9	15	16	1PG	1PA2		
Closed to open flower	90.2 (51)	80.6 (93)	83.0 (59)	93.4 (76)	94.3 (87)	64.3 (28)	84.3	
Open flower to latent ovary	62.0 (92)	63.4 (153)	65.7 (105)	82.1 (105)	78.1 (114)	69.0 (58)	70.0	
Latent ovary to unripe fruit	80.6 (67)	32.2 (115)	24.4 (78)	31.5 (108)	56.0 (100)	82.3 (62)	51.2	
Unripe to ripe fruit	90.0 (130)	75.4 (224)	84.0 (188)	93.6 (219)	90.8 (142)	84.6 (104)	86.4	
Ripe fruit to dispersed seed	92.7 (120; 153)	88.4 (163; 1756)	88.4 (128; 465)	84.9 (140; 583)	79.1 (108; 256)	87.3 (80; 177)	86.8	
Closed flower to dispersed seed (overall relative success)	37.6	11.0	9.9	19.2	29.6	27.0	22.4	



similar with regard to the proportion of ripe fruits which were dispersed (range 79.1–92.7%), and this variable explains only 1.2% of ORS variation. Seed dispersal rate seems, therefore, unimportant in determining individual variation in ORS.

#### *Individual variation*

The small number of individuals studied precludes a detailed analysis of factors responsible for interindividual variation in the components of relative reproductive success. Even with this small sample a marginally significant trend exists relating inversely the percentage of flowers setting latent ovaries and the distance to the nearest flowering male plant (log-transformed) ( $r = -0.640$ ,  $N = 6$ ,  $P = 0.08$ ). This tends to suggest that the proportion of flowers setting latent ovaries is limited by pollination in some individuals.

There is a significant inverse correlation between the percentage of latent ovaries that became unripe fruits and estimates of total number of ripe fruits produced by the plant during the whole season (log-transformed) ( $r = -0.816$ ,  $N = 6$ ,  $P = 0.02$ ). Plants eventually producing small fruit crops were those displaying the higher transition rates from latent ovary to unripe fruit, and vice versa. Since the absolute number of ripe fruits produced and the percentage of flowers setting latent ovaries were uncorrelated ( $r = 0.025$ ,  $P = 0.96$ ), the significant correlation above suggests that eventual abortion rates of latent ovaries depend on the absolute numbers of flowers produced initially. There is a strong negative correlation between the fraction of ovaries developing to unripe fruits and the total number of flowers produced (log-transformed) (Fig. 4;  $r = -0.899$ ,  $P = 0.01$ ). Abundant flowering is, therefore, associated with increased levels of latent ovary abortion.

#### *Phenological correlates*

For all plants combined, the proportion of flowers producing ripe fruits depends significantly on time of anthesis (Table 3). The probability of setting ripe fruit steadily decreases from flowers opening in May (29.6%) through those opening in June (18.4%) and July (0.7%) ( $G = 67.2$ ,  $df = 2$ ,  $P < 0.0001$ ). The decline in success of July flowers is particularly pronounced, and is shared by all

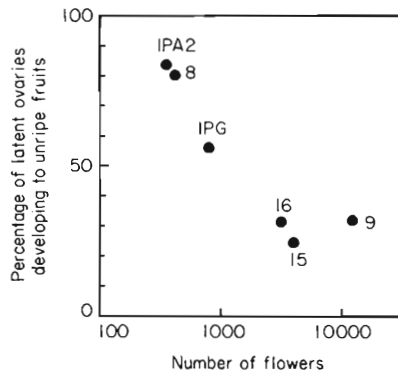


Figure 4. *Osyris quadripartita*. The proportion of latent ovaries which develop to unripe fruits declines with increasing total number of flowers produced by the plant over the entire flowering period.

Table 3. *Osyris quadripartita*: variation with time of anthesis of the proportion of flowers (%) eventually producing ripe fruits. Sample sizes in parentheses

Individual	Time of anthesis		
	May	June	July
8	42.7 (68)	60.5 (43)	— (0)
9	13.3 (83)	8.1 (37)	3.5 (29)
15	11.5 (26)	8.5 (47)	0 (47)
16	42.9 (28)	9.8 (42)	0 (45)
1PA2	43.0 (51)	66.7 (6)	0 (6)
1PG	45.1 (51)	33.9 (59)	0 (17)
All combined	29.6 (307)	18.4 (234)	0.7 (144)

individuals (Table 3). Only a single fruit ripened out of a total of 144 marked flowers opening in July. Three plants (9, 15, 16) exhibited a marked decrease in the success of June flowers. These individuals were those having the longest flowering seasons and largest flower productions (Figs 1 and 4).

Although there is some individual variation, the proportion of flowers setting latent ovaries (and thus presumably pollinated) tended to increase from those opening in May through those doing so in July (Fig. 5) ( $G = 41.6$ ,  $df = 2$ ,  $P < 0.0001$ , all plants combined). In contrast, the fraction of latent ovaries developing into unripe fruits decreased precipitously from those originating from May flowers through those resulting from June and July flowers (Fig. 5). For all plants combined, 69.5, 38.0 and 4.4% of latent ovaries became unripe fruits among those originating from May, June and July flowers, respectively ( $G = 140.2$ ,  $df = 2$ ,  $P < 0.0001$ ). The observed decrease in overall flower success from May to July was, therefore, due to a steadily increasing rate of ovary abortion as the flowering season proceeded, which offset the parallel increase in pollination success. These results also illustrate selective abortion of latent ovaries by the plants on the basis of time of anthesis. In every plant, abortion preferentially affected those ovaries resulting from late flowers.

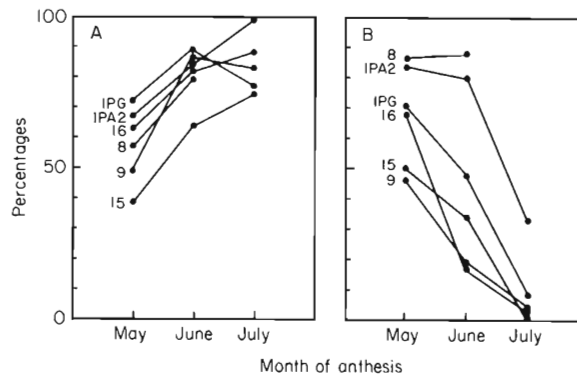


Figure 5. *Osyris quadripartita*. Variation of the proportion of flowers setting ovaries (A) and ovaries developing to unripe fruits (B) with time of anthesis. Each line corresponds to an individual shrub.

## DISCUSSION

*Reproductive success*

The proportion of flowers setting latent ovaries (roughly equivalent to pollination success) is potentially important in determining reproductive rate, but individual variation in this magnitude is later offset by high levels of ovary abortion. The negative relation between percentage of ovaries set and distance to the nearest pollen source suggests limited pollinator movement, and is similar to that reported for other plants (Beattie, 1976; Rust, 1980; Silander, 1978; Wyatt & Hellwig, 1979).

The proportion of latent ovaries which became unripe fruits explains most of the individual variation in overall reproductive success rate (ORS), and this transition is also responsible for the greatest reproductive losses. Ovary abortion rate was highest among those resulting from June and, particularly, July flowers (early dry season), and varied among plants in direct relation to the absolute number of flowers produced (and thus also to the number of latent ovaries set). Most ovary-fruit transitions take place in the first half of the dry season, while most ovary abortions take place in the second half (Fig. 2). These observations suggest that a resource-mediated limitation is operating on the absolute number of unripe fruits set, via modifications in latent ovary abortion rates, and that this limitation operates in the dry season, becoming increasingly restrictive as the latter advances. This is supported by the observation of very low abortion rates in mid and late summer among plants growing adjacent to a summer-irrigated fruit grove in the same locality (Herrera, unpublished data). Information available thus points to a dry-season resource limitation of potential fruit set through influence on ovary abortion rates. The (short-term) effects of biotic factors (pollination, seed dispersal, insect herbivory) are each responsible for a minor fraction of total predispersal reproductive losses (pollination and dispersal failure, flower and fruit destruction), and contribute very little to individual variation in ORS.

As with so many other species (see review by Stephenson, 1981), *O. quadripartita* apparently initiates a greater number of fruit that can be matured with available resources, and aborts 'excess' fruits. The production of a fruit may be determined at three sequential stages: flower determination, ovary development and fruit maturation (Lloyd, 1979, 1980). Different species differ widely in the relative use made of the three control periods (Lloyd, Webb & Primack, 1980). Ovary development is primarily determinant for *O. quadripartita*, truncating the development of ovaries at an early stage. Most fruit ripening takes place in the rainy season, when conditions are favourable to plants, and one should expect those fruits having survived the restrictive summer-drought 'bottleneck' to mature successfully. Unripe fruits have negligible abortion rates, and most of them eventually reach maturity.

*Selective fruit development*

Selective abortion of developing fruits may be based on: pollen source (Bertin, 1982b; Bookman, 1984); outcrossed *versus* selfed progeny (Stephenson, 1981); number of seeds filled/fruit or percentage of fertilized ovules (Bertin, 1982a; Lee & Bazzaz, 1982); order of fruit initiation (Lee & Bazzaz, 1982; Lovett Doust & Eaton, 1982; Stephenson, 1980; Udovic & Aker, 1981). Latent ovaries of

*O. quadripartita* become selectively aborted on the basis of date of initiation. In the most general case of hermaphroditic species with multi-seeded fruits, several of the factors above may be involved simultaneously (e.g. Lee & Bazzaz, 1982), and separation of their effects is difficult without carefully controlled experiments. In *O. quadripartita* the effects of outcrossing and number of seeds/fruit must be ruled out, as all progenies result from outcrossing and all fruits are single seeded. The influence of pollen source remains. Depending on the flowering phenology of males in the population, the diversity of pollen sources represented in pollen loads may differ for female flowers opening in different months. In the study population, all male individuals were continuously in flower from late April through early July (Herrera, 1984b). There was, therefore, a very long period during which pollen source diversity remained at or near the maximum possible level at the locality, yet latent ovary abortion rate increased steadily over this period. The role of pollen source diversity on selective abortion is probably unimportant if it occurs at all. On the other hand, it is difficult to envisage a mechanism of selective abortion based on the diversity of the pollen load deposited on the stigma of a single-ovule flower, since this diversity *per se* cannot originate within-fruit progeny heterogeneity. The relation between ovary abortion rate and time of anthesis may be best explained in terms of resource limitation.

Preferential abortion of ovaries resulting from the latest formed flowers is most likely to be a consequence of the very slow pace of reproduction in *O. quadripartita*. In summer, the youngest and oldest latent ovaries in a plant may differ in age by nearly 3 months. Individual older ovaries have cost the mother plant several arbitrary units more of 'monthly ovary maintenance cost' than younger ones. The best resource-saving strategy for adjusting crop size to available resources would be to eliminate those ovaries which had so far received the smallest investment at the time when conditions become limiting, and force abortion (Lloyd, 1980). If this explanation is correct, the age threshold below which ovaries are aborted when conditions become limiting should increase with decreasing overall abortion rate. This is supported by these results. The two individuals having by far the lowest overall ovary abortion rates and floral productions (1PA2 and 8; Table 2 and Fig. 4) were the only two plants for which abortion rates for ovaries resulting from June flowers did not increase (Fig. 5).

#### *The reproductive cycle*

At the population level, female plants of *O. quadripartita* exhibit a characteristically 'saturated' annual cycle involving uninterrupted reproductive activity, with individual phases of the cycle (flowering, fruiting) lasting for very long periods (Herrera, 1984b). The present study shows that the cycle of individual female plants was similarly organized, with long flowering, fruit development, and fruit ripening periods. Extended reproductive activity in the population is therefore mainly the consequence of the very long individual cycles, with little contribution of interindividual asynchrony in flowering and fruiting times.

The dominant times of flowering (spring), fruit development (summer) and ripening (autumn) in *O. quadripartita* are representative of those exhibited by most fleshy-fruit-producing, bird-dispersed species of S Spanish scrublands

(Herrera, 1984a; Jordano, 1984). The spring, which coincides with the late rainy season, is also the predominant flowering season in other mediterranean scrublands of the world (Kummerow, 1983; Mooney, Parsons & Kummerow, 1974). Fruit development during the severe summer dry season (in *O. quadripartita* and the majority of other coexisting bird-dispersed species; Herrera, 1984a; Jordano, 1984) apparently conflicts with the well-known limiting role of summer water stress in mediterranean vegetation (Baker, Rundel & Parsons, 1982; Gray, 1982; Kummerow, Montenegro & Krause, 1981; Mooney, Harrison & Morrow, 1975; Mooney & Kummerow, 1981; Nilsen & Schlesinger, 1981). Nevertheless, most fleshy-fruit-producing species of S Spanish scrublands are deep-rooted, sclerophyllous evergreens, very resistant to summer drought and temperature, which maintain a positive carbon balance even in summer (see, for example, Diamantoglou & Meletiou-Christou, 1977, 1978, 1979; Konis, 1949; Lange, Tenhunen & Braun, 1982; Tenhunen, Lange & Jahner, 1982). *Osyris quadripartita*, by parasitizing a variety of these species is apparently able to withstand summer drought and develop fruits precisely in this period. However, this does not imply that summer drought is unimportant in limiting reproductive rates, as discussed earlier.

The duration of reproductive stages and their extreme within-plant asynchrony, rather than their timing, is what uniquely characterizes *O. quadripartita*, setting it apart from all other evergreen shrubs in the region. These include the congeneric, and often locally coexisting, *Osyris alba* L., which is also a root hemiparasite. *Osyris alba* has a 'conventional' reproductive cycle, with well-defined, non-overlapping reproductive phases and a long non-reproductive period (Jordano, 1984; Herrera, unpublished data). This fact, along with the sparse information available on the cycle of other santalaceous root hemiparasites in Australia and S Africa (Liversidge, 1972; Palmer & Pitman, 1972-1973; Sedgley, 1982b), rules out any evolutionary interpretation of the cycle of *O. quadripartita* which relies on a consideration of its parasitic habit. On the other hand, the phenological pattern of this species seems to be shared only by a few species from tropical forests or by others that, like itself, are survivors of an old evergreen tropical flora currently living in Mediterranean refugia (Herrera, 1984b). It may be argued that its phenology may not have experienced substantial variations since the initiation of the mediterranean climate in the Pliocene. The hemiparasitic habit must have contributed to the rather unexpected persistence, in a strongly seasonal climate, of a phenology involving continuous reproductive activity throughout the year (see Herrera, 1984b, for further discussion).

Some apparently puzzling ecological traits of *Cneorum tricoccon* L. (Cneoraceae), another very old Mediterranean taxon, have been previously attributed to its being a Tertiary relict evolved in a tropical climate (Müller, 1933, p. 402). Interestingly, both the genus *Cneorum* and *O. quadripartita* have broadly disjunct world distributions (Herrera, 1984b; Raven & Axelrod, 1974) and very restricted geographical distributions in the Mediterranean Basin. The latter are of disjunct, small local populations in warmer coastal areas (Folch i Guillén, 1981; Jalas & Suominen, 1976; and specimens in the herbarium of the Department of Botany, University of Sevilla). (*Osyris alba*, in contrast, extends northwards well beyond the limits of the mediterranean climate.) This seems indicative of a non-equilibrium distributional status of these and other ancient

tropical relicts, which are being affected by a continuing selective extinction process operating on the surviving premediterranean climate flora (see Herrera, in press). Under these circumstances, evolutionary interpretations of the observed reproductive patterns of *O. quadripartita* on the sole basis of current selective pressures would be unwarranted.

## ACKNOWLEDGEMENTS

I thank M. Carrión for making the tags, and J. Herrera and P. Jordano for field assistance.

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