

THE ANNUAL CYCLE OF *OSYRIS QUADRIPARTITA*, A HEMIPARASITIC DIOECIOUS SHRUB OF MEDITERRANEAN SCRUBLANDS

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SUMMARY

(1) The growth, flowering and fruiting phenology of a southern Spanish population of *Osyris quadripartita* (Santalaceae), an evergreen dioecious shrub of Mediterranean habitats, has been studied over a 5-year period.

(2) The growth season encompasses the period November–August for females and virtually the entire year for males. Males resume growth shortly after the autumn rains, at least 1.5 months in advance of females. The mean length of the growing period was significantly longer for males.

(3) The flowering period lasts for nearly 6 months (March–September) for females and nearly the entire year for males, with a peak in May–June. The flowering peak of males encompassed that of females in all years. The mean length of the flowering period was significantly longer for males.

(4) Ripe fruits are produced throughout the year, with a major peak in winter and a minor one in spring.

(5) The phenological pattern of *O. quadripartita* seems to be shared only by species from tropical forests or by others that, like itself, are survivors of an old evergreen tropical flora currently living in Mediterranean refugia. Its phenology seems, therefore, not to have experienced substantial variation since the initiation of the Mediterranean climate in the Pliocene. The hemiparasitic habit must have contributed to the persistence, in a strongly seasonal climate, of virtually continuous physiological activity throughout the year.

(6) Sexual differences in phenology are interpreted in terms of the constraints imposed on the organization of the female annual cycle by fruit development and maturation. Males are relieved of this function and allocate the available time among fewer activities. As a result, they exhibit longer average durations of individual functions, greater seasonal spacing of functions, and more flexible integration of activities, than do female plants.

INTRODUCTION

This paper reports on the results of a study on the seasonal pattern of growth, flowering and fruiting in a southern Spanish population of *Osyris quadripartita* Salzm. ex Decne (Santalaceae), a hemiparasitic dioecious shrub of warm Mediterranean scrublands. In addition to describing the unusual seasonal cycle exhibited by this species, further objectives of this paper are documenting sex-related differences in phenology and exploring the possible constraining effects of the female-exclusive function (fruit production) on the temporal organization of the whole female annual cycle. No investigation of this type has been conducted previously on plants of Mediterranean forests or scrublands, where the high incidence of dioecious taxa among woody species is similar to that found in some tropical dry forests (Herrera 1982, 1984c). Furthermore, comparisons of the entire annual cycle (growth, flowering, fruiting) of male and female plants have been not performed previously for any woody dioecious species.

STUDY SITE AND METHODS

This study was conducted from October 1978 to November 1983 in a 3.5-ha plot vegetated by dense Mediterranean scrub on nearly level terrain near El Viso del Alcor (Sevilla province), at 100 m altitude (37°26'N, 5°45'W), where *Osyris quadripartita* accounts for 6.1% of the woody plant cover. Further details on the composition and ecology of vegetation at the site have been presented elsewhere (Herrera 1981, 1982, 1984a). General descriptions of the region may be found in Anonymous (1962) and Ministerio de Agricultura (1975).

Data used to characterize the local climate were taken from the nearest meteorological stations at similar altitude and with at least 30 years of uninterrupted records. These stations are 3 km (rainfall) and 15 km (temperature) away from the study site. There are slight discrepancies between mean values presented below and those in Herrera (1984a), as the latter were taken from the literature and came from different stations.

The phenology of *O. quadripartita* was investigated by means of regular observations (at intervals of 1–4 weeks, mostly 2-weekly) on marked individual shrubs (twenty-seven females and twenty-two males). For the purpose of this paper, records of growth (November 1980–November 1983), flowering (April 1980–November 1983 for females; December 1980–November 1983 for males) and fruiting (October 1978–November 1983, with a gap of October 1979–April 1980) activity of individual shrubs have been analysed. 'Fruiting', refers exclusively to active production of ripe fruits; 'flowering' to the presence of open, functional flowers (unless otherwise stated); and 'growth' to active stem elongation and production of new leaves. An individual plant was considered to be growing if at least 5% of its stems showed elongation and the production of leaves, and to be fruiting or flowering if some open flower or newly-ripe fruit were present, respectively.

The significance of sexual differences in the time of growth and flowering were tested with a Kolmogorov-Smirnov two-sample test (Estabrook *et al.* 1982) using the χ^2 approximation (Siegel 1956).

CLIMATE

The climate of the study site is a warm Mediterranean type (Fig. 1). The mean monthly temperature of the coldest (January) and hottest (August) months are 10.5 °C and 26.8 °C, respectively. There are an average of 7 frost days per year (range 0–20; median 5 days; $n = 33$ years). The temperature varies little between years; the coefficient of variation (C.V. = 100 S.D./mean) of the mean annual temperature (18.1 °C) is only 2.6%.

The average annual precipitation ($n = 43$ years) is 613 mm, but there is substantial between year variation (C.V. = 32.6%; range 243–1103 mm; variation 4.5-fold). On average, 76.4% of the annual precipitation falls in the period October–March, but there are important deviations from this seasonal pattern in particular years, since monthly rainfall values are extremely variable between years. The C.V. of the mean monthly rainfall ranges from 67% in March to 322% in July; most fall between 80% and 100% (Fig. 1). The amount of rainfall is most predictable in the rainy winter months, and least predictable in the dry summer, but in absolute terms it is fairly unpredictable at any time of year. The strong variability of rainfall at the study site, therefore, involves both the annual total and its seasonal distribution.

The amount and seasonality of the rainfall in the 1980–83 main study period deviated substantially from the average conditions (Fig. 2). These years correspond to a period of

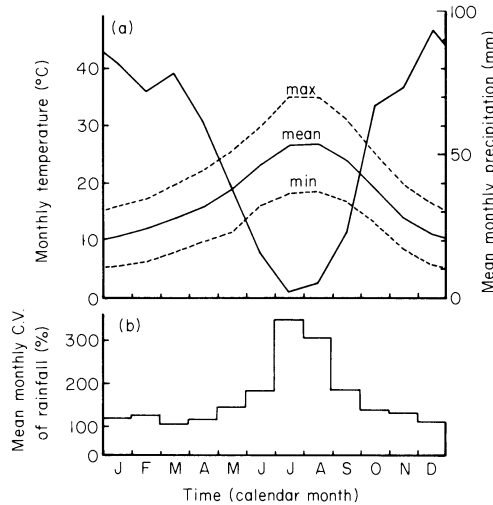


FIG. 1. Mean monthly (a) precipitation (—) and temperature (---); (b) coefficient of variation of monthly rainfall, for the study site in Mediterranean Spain.

extreme and persistent drought, with annual rainfall totals of 356 mm, 328 mm and 531 mm (1980–82), well below the 613-mm mean. The time of rainfall varied greatly in these years and 83% of the monthly rainfall figures were inferior to the respective monthly averages for the preceding 43-year period.

PLANT NATURAL HISTORY

Osyris quadripartita is an evergreen, root-hemiparasitic shrub up to 3 m in height (mostly 1–2 m) occurring in a variety of Mediterranean-type scrublands. In the Iberian Peninsula it is almost restricted to coastal areas south of 40°N (Jalas & Suominen 1976; C. M. Herrera, unpublished), and the northern limits of its distribution closely coincide with the 10 °C mean January isotherm and the 350-days frost-free period isoline (Linés Escardó 1970).

Root hemiparasites which obtain water and nutrients through haustorial connections with their hostplant's roots, but which perform photosynthesis are prominent in the Santalaceae (Kuijt 1969). Hemiparasitism has been demonstrated for some *Osyris* species (Kuijt 1969), and for *O. quadripartita* in particular (C. M. Herrera, unpublished). As in other woody hemiparasites (Kuijt 1969; Lamont 1982), seedlings of *O. quadripartita* are able to survive on their own water and mineral supply for up to 1 year, but eventually die if they fail to establish haustorial connections with other plants (C. M. Herrera, unpublished). In southern Spain, *O. quadripartita* parasitizes evergreen and summer drought-deciduous shrubs of many species.

Its sex ratio did not differ significantly from 1:1 in a random sample of individuals at the study locality (sixty-four males : seventy-eight females; $\chi^2 = 1.38$, $P = 0.24$).

The relative spatial distribution of males and females in this population did not depart significantly from randomness, as determined by an analysis of nearest-neighbour relationships (Pielou 1961) ($\chi^2 = 0.83$, $P = 0.36$). Male plants (height = 1.63 ± 0.36 (S.D.) m, $n = 73$) were significantly taller than females (1.34 ± 0.36 m, $n = 85$) ($t = 4.25$, $P \ll 0.001$).

Small and medium-sized flies are the principal pollinators of *O. quadripartita* in southern Spain (J. Herrera, personal communication). The flowers are yellowish-green, inconspicuous (perianth diameter *c.* 3.5 mm), and their size (as estimated by weight) differs for the two sexes (0.9 mg and 2.25 mg mean dry weight for staminate and pistillate flowers, respectively). Pistillate flowers are produced singly or, rarely, in pairs at the axil of leaves. Staminate flowers are produced in loose inflorescences bearing up to ten flowers. Flowers of both sexes secrete nectar. Female plants produce fleshy one-seeded fruits (*c.* 7.5 mm transverse diameter and 0.25 g wet weight). The orange-red ripe fruits are ingested, and seeds dispersed, by several frugivorous passerine birds in the genera *Turdus* and *Sylvia* (see Herrera 1984a).

Annual cycle of the population

The soil water deficit prevailing during Mediterranean summers greatly limits the physiological activity of woody plants (e.g., Mooney, Parsons & Kummerow 1974; Mooney, Harrison & Morrow 1975; Baker, Rundel & Parsons 1982). For many species, the autumn rains constitute an environmental cue triggering the initiation of vegetative or reproductive activity. For this reason, and although growth, flowering and fruiting overlap extensively in *O. quadripartita*, the description of its annual cycle considers first the growth period that follows autumn rains.

Growth

The growing season encompasses the period November–August for females and virtually the entire year for males, although most plants are growing in winter and spring (Fig. 2). Males resume growth at least 1.5 months in advance of females, and stop growth at the same time (as in 1981), a little earlier (1983), or much later (1982), than females.

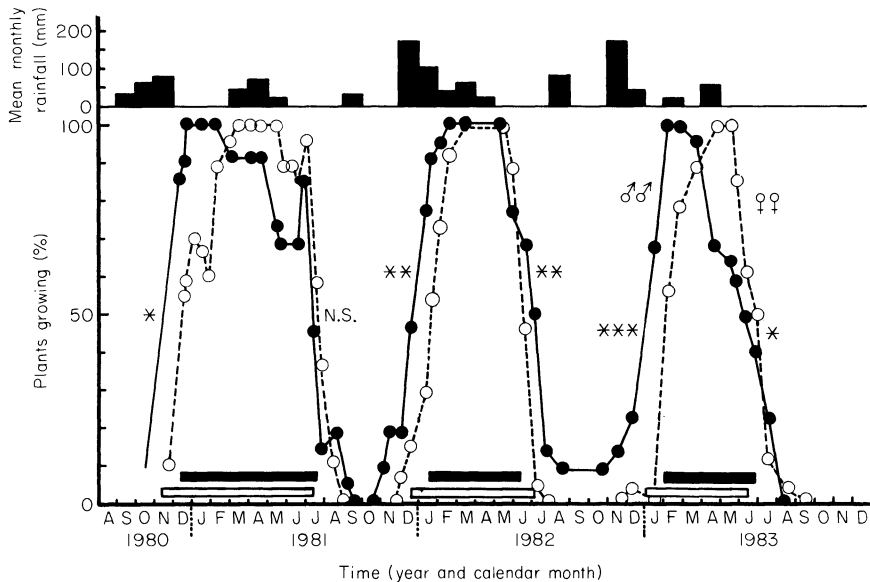


FIG. 2. Seasonality in growth activity of *Osyris quadripartita* (—, males; ---, females) in Mediterranean Spain. Horizontal bars indicate the period during which at least 50% of individuals are growing (□, males; ■, females). Asterisks denote significance levels of observed differences in the initiation and completion of growth between males and females: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; N.S., not significant. The rainfall has been represented only for months having at least 10 mm.

The population growth peak of males occurred 3 months before that of females in 1981 and 1983, while the peaks of the two sexes were coincident in 1982. The length of the period during which at least 50% of the individuals were growing was 5.5–8 months for males and 4.8–7 months for females, with substantial between-year variation (Fig. 2). In any one year, however, this period was nearly one month longer for male plants. The shortening of the growing season from 1981 to 1983 suggests a progressive impairment in growth conditions, attributable to the persistence of the severe drought noted earlier. No one *O. quadripartita* plant, however, died in the study population during the period 1978–83, in contrast with the (up to 50% individual) mortality attributable to drought experienced the same years by other southern Spanish scrubland plants (C. M. Herrera, unpublished).

The timing of the population peak of females varies little between years and is apparently unrelated to the time of the autumn rainfall (Fig. 2). In contrast, the peak for males varies between years (December–February, February–May, and February; 1981, 1982, 1983, respectively) in a way related to between-year variation in the time of the first autumn rain (Fig. 2). Males are therefore more flexible than females in the timing of their growth, and, apparently, are able to adjust it to the occurrence of favourable environmental conditions. This is supported by the uninterrupted growth of some males, but not females, in the summer of 1982, a year with unusual precipitation in August (Fig. 2).

The long growth seasons recorded for the population reflect the long periods exhibited by individual plants. These grow for an average of about 25 weeks every year (Table 1). The mean length of the growing period of male individuals exceeded significantly that of females in the 2 years with complete data for the two sexes (Table 1). This indicates that males have longer growth periods than females at both the population and individual levels.

Flowering

Male plants begin to produce closed flowers in late autumn–early winter, and the frequency of individuals bearing them rises slowly to 100% in mid- or late-March. On female plants, in contrast, closed flowers are first visible in February, and are present on all individuals in late April–mid May (Fig. 3). Population curves for closed flowers and initiation of flowering are much more separated in time for males than for females (Fig. 3), indicating that flowering follows flower formation more rapidly among females than among males.

TABLE 1. Mean (± 1 S.D.) length (weeks) of the growth and flowering periods of individual male ($n = 22$) and female ($n = 27$) plants of *Osyris quadripartita* in Mediterranean Spain.

Year		1980	1981	1982	1983
Growth	Males	—	—†	27.9 \pm 8.5	25.1 \pm 9.0
	Females	—	30.3 \pm 4.8	21.4 \pm 4.7	20.4 \pm 5.7
	Probability of significant difference*	—	—	0.002	0.035
Flowering	Males	—	21.4 \pm 6.8	23.7 \pm 6.4	22.0 \pm 8.3
	Females	14.4 \pm 3.0	16.3 \pm 4.4	12.7 \pm 3.7	15.1 \pm 3.5
	Probability of significant difference*	—	0.003	\leq 0.001	0.0004

* Student's *t*-test.

† Observations commenced when some individuals were already growing.

— No data.

Phenology of Osyris quadripartita

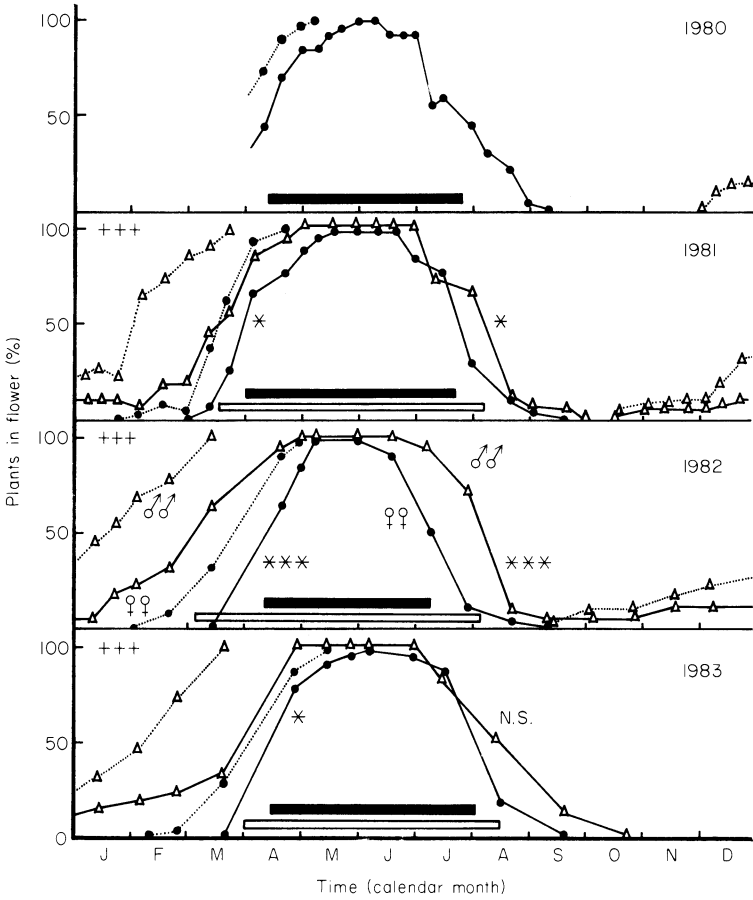


FIG. 3. Sexual differences in flowering phenology of *Osyris quadripartita* in Mediterranean Spain. Continuous lines refer to actual flowering and horizontal bars indicate the periods during which at least 50% of individuals are flowering: (□), males; (●), females. Interrupted lines indicate closed flowers: (●), females; (△), males; only the increasing section of the curves are shown for clarity. Asterisks denote significance levels of observed differences in the phenology of males and females: asterisks refer to curves for closed flowers: *, $P < 0.05$; *** and †††, $P < 0.001$; N.S., not significant.

The flowering period (open flowers) is very long, lasting for nearly 6 months (March–September) for females and the entire year for males (Fig. 3). All marked individuals of each sex flowered every year, and were simultaneously in flower during 0.5–1.5 (females) and 1.6–2.0 (males) months. The periods during which at least 50% of individuals were in flower were 3.0–3.6 and 4.5–5.0 months for females and males, respectively, encompassing from mid-spring to mid-summer. The flowering period of males has a long autumn-winter tail during which a few individuals (<15%) are always in flower.

The population flowering curves are narrower for females, and are included within those for males (Fig. 3). With the exception of relatively short periods (0.5–1.0 months) at the population flowering peaks, during which all plants of both sexes are in flower, the fraction of individuals in flower is always greater among males. There is a long period (September–March) during which flowering males do not overlap with any flowering female, but flowering peaks are largely coincident for both sexes (Fig. 3). Female plants

flower more synchronously than males, as indicated by differences in the slope of the rising sections of population curves. There appear to be similar levels of between-individual synchrony in the completion of flowering by the two sexes.

The average length of the flowering period of male plants was significantly longer than that of females in the 3 years with complete data for the two sexes (Table 1). Males have, therefore, longer flowering seasons than females at both the population and individual levels.

Flowers are produced exclusively on the new growth of the current year. Flower buds appear continuously as actively growing shoots elongate, and cessation of growth arrests flower bud production. One should expect, therefore, an association between the time and duration of flowering and growth, and this is supported by Figs 2 and 3. Variation between sexes and years in flowering phenology is consistent with the observed variation in the time and duration of growth. The lag between the peaks of growth and flowering differs between the sexes; it was of 4.5, 3.0 and 3.0 months for males, and 2.0, 2.0 and 1.75 months for females (1981, 1982, 1983, respectively).

Fruiting

All southern Spanish populations of *O. quadripartita* display an unusual fruiting pattern. Ripe fruits are continuously produced in the population throughout the year. On individual plants, the stock of developing ovaries resulting from the single flowering episode is ripened slowly and gradually over an entire year. Fruits resulting from the previous year's flowers are still being produced when the earliest ripe fruits of current year's flowers appear in the population. In more than 110 inspections of marked female plants conducted over 5 years, in no single instance were newly-ripe fruits absent from the population (Fig. 4). There is some seasonality, however, in the fraction of plants ripening fruits.

There is a major late autumn-winter peak in which 90% (1978) and 100% (1980–82) of marked plants are fruiting (Fig. 4). The time of this peak varies slightly (from early November to late January), but its magnitude (in terms of the number of plants involved) remains almost constant over the years. A second fruiting peak takes place in spring. The time of this peak (from early May to early June) varies very little, but its magnitude does exhibit important between-year variation (60, 80, 70, 90 and 80% of individuals in 1978–82, respectively). The two fruiting peaks differ, therefore, in their time and magnitude: the

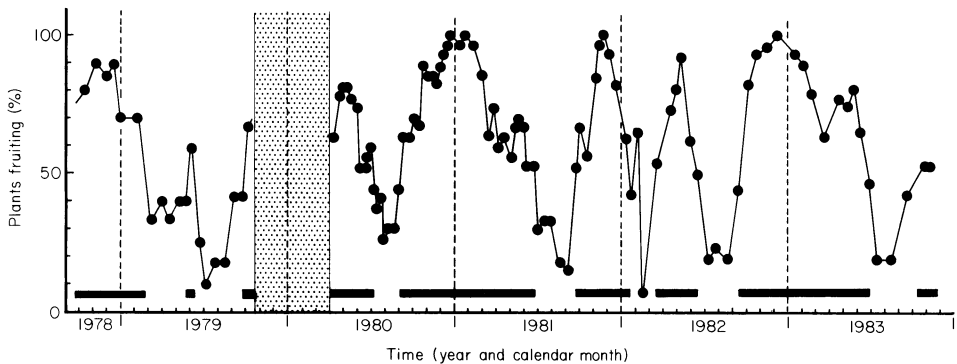


FIG. 4. Seasonality of fruit production (ripening) by female *Osyris quadripartita* plants in Mediterranean Spain. The stippled area corresponds to a gap in the data. Horizontal bars indicate the period during which at least 50% of individuals are ripening fruits.

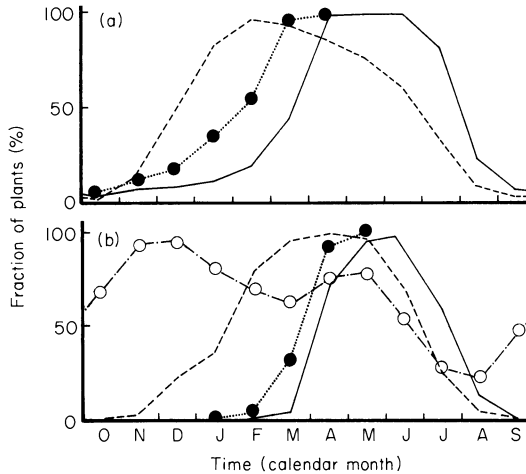
Phenology of Osyris quadripartita

FIG. 5. Comparison of (a) male and (b) female 'average' annual cycles of *Osyris quadripartita* in Mediterranean Spain. Symbols: (---) growing; (●.....●), closed flowers, (—), flowering; (O---O), ripening fruit.

spring peak is variable in magnitude and constant in time, while the winter peak is constant in magnitude and variable in time.

The smallest proportions of fruiting females occur consistently in summer (July–August). A minor low usually separates the winter and spring fruiting peaks, except for the drastic reduction in the proportion of fruiting females that took place in February 1982.

Between-year variation in population fruiting patterns seems to be unrelated to variation in the time and amount of rainfall. The time of winter fruiting peaks does not correlate well with the time of occurrence of autumn rains.

Overall organization of the annual cycle

An average annual cycle has been obtained for plants of each sex by combining the data from all study years and calculating the monthly means for the proportion of plants growing, bearing closed flowers, flowering, and fruiting (Fig. 5). Both sexes share a marked cessation of all activities in mid-summer that, in the case of males, extends well into the autumn. Autumn and early winter is a period dominated by fruiting in the case of females, while in the same period the males are already growing and producing flower buds. These two latter activities occur later in the case of females, simultaneously to a transitory decline in the frequency of fruiting. Growth, production of flower buds, and flowering, are temporally much more tightly packed in females than in males, as illustrated by differences in the lag between the growth and flowering peaks and between flower bud initiation and flowering. In short, males tend to uniformly stagger growth, production of closed flowers, and flowering from late autumn to early summer, while females tend to concentrate all these activities in the spring and use the autumn and winter almost exclusively to ripen fruits.

DISCUSSION

General phenology

Most Mediterranean-type climates impose on plants a moderate-to-light cold stress in winter and a moderate-to-heavy drought stress in summer. Their relative importance is

variable among localities, and Mitrakos (1980) has suggested that a cold-stress–drought-stress environmental gradient regulates compositional variation in Mediterranean plant communities. Conditions at my study site are very close to the predominantly drought-stressed extreme of this gradient, with cold stress exerting a negligible influence on plants (see also Montero & González 1974). Generalized fruit maturation and growth by *O. quadripartita* in winter, and the abrupt cessation of activities during summer, indicate that seasonal water shortage is the only abiotic factor seriously constraining physiological activity of this species at study site. This is further supported by: (i) the variable time of the onset of male growth is related to the time of the rains; (ii) males had an extended growth the single study year with summer rainfall; and (iii) growth, flowering and fruiting of a group of twenty-seven individuals (not considered in this study) of both sexes growing adjacent to a summer-irrigated fruit grove in the same locality did not cease in summer (C. M. Herrera, unpublished).

As compared with other shrub species so far studied in the Mediterranean Basin (Martín & Escarré 1980; Moreno Rodríguez 1982; Herrera 1984a) or in other Mediterranean-climate areas (Mooney, Parsons & Kummerow 1974; Thrower & Bradbury 1977; Hoffmann & Walker 1980; Kummerow, Montenegro & Krause 1981; Mooney & Kummerow 1981; Baker, Rundel & Parsons 1982; Kummerow 1983), this phenology of *O. quadripartita* is unique in having extremely long growth, flowering and fruiting (fruit ripening) periods and an extensive temporal overlap of all these activities. The time of growth and flowering peaks relative to the rainy season falls within the range observed in most Mediterranean-climate evergreen species, but continuous production of ripe fruits throughout the year sets *O. quadripartita* apart from all these species (see references above). This fruiting pattern is not known for any plant species away from the tropics; see Sherburne (1972), Halls (1973), Thompson & Willson (1979) and Sorensen (1981) for temperate forests. In tropical and subtropical habitats, year-round production of ripe (fleshy) fruits at the population level has been often reported, but in the vast majority of cases it is the consequence of continuous or intermittent flowering; see Medway (1972), Frankie, Baker & Opler (1974), Crome (1975), Monasterio & Sarmiento (1976), Hilty (1980), Opler, Frankie & Baker (1980), Lieberman (1982) and Godschalk (1983). Species with single, definite flowering episodes and year-round fruiting, in the pattern of *O. quadripartita*, are extremely rare even in tropical habitats. In a large sample of shrub and tree species of tropical Costa Rican forests studied by Frankie, Baker & Opler (1974) and Opler, Frankie & Baker (1980), only nine species (1.8% of total) have patterns apparently similar to that of *O. quadripartita*.

Many woody species of Mediterranean-climate regions have not evolved under current winter-rain, summer-drought climatic conditions, but rather have been selected out of a diverse array of species evolved under a different, tropical-like climate (Walter 1979; Lamont 1982). As expressed by Raven (1973), much of the present woody species are just the 'survivors of a richer, tropical-margin vegetation that developed ... through the Tertiary' (see also Herrera 1984c). The colder climates and the spread of aridity over the Mediterranean and adjacent Africa during the drier interglacials eliminated this vegetation along with many component species (Raven & Axelrod 1974). The Canary Islands, the warmest portions of the Mediterranean, Madagascar, and the Cape Region, are current refugia for some of the species which still survive (Raven & Axelrod 1974; see also Thorne 1972). The genus *Osyris* fits in this scheme, as its range is mostly circum-Mediterranean (plus Canary Island) and eastern and southern African (Thonner 1915; Bramwell 1974; Jalas & Suominen 1976), and *O. quadripartita* has itself a broadly

disjunct distribution. In the taxonomic literature (Hendrych 1964) this specific name is considered synonymous with *O. lanceolata* Hochst & Steudel, a plant confined to southern Africa whose characteristics (Palmer & Pitman 1972–73; Coates Palgrave 1977) actually coincide with those of *O. quadripartita* from southern Spain. No data are available on the phenology of South African *O. lanceolata* plants, but the annual fruiting and flowering cycle of *O. quadripartita* seems very similar to that of another southern African Santalaceous shrub, *Colpoön compressum* Berg. (= *Osyris compressa* (Berg.) A.DC.) as described by Rowan (1967, p. 89).

The peculiar flowering and fruiting cycle of *O. quadripartita* seems, therefore, to be shared only by plants currently living in tropical forests or by plants that, like itself, are the survivors of an old evergreen tropical flora. This suggests that, most likely, some aspects of the phenology of *O. quadripartita* have not experienced substantial variation since the initiation of Mediterranean climatic conditions in the Pliocene. Accordingly, its evolution would be difficult to interpret strictly as a result of present day selective pressures (see also, Herrera 1984a, b, c).

The few species of present day tropical forests with single flowering episodes and year-round fruiting are distributed among several non-parasitic plant families (Frankie, Baker & Opler 1974; Opler, Frankie & Baker 1980). On the other hand, holo- and hemiparasitic plants in Mediterranean habitats and elsewhere generally depart from this phenological pattern. Its *evolution*, therefore, is not associated with parasitism. Under a Mediterranean climate, in which water and nutrient availability fluctuate strongly, long-term persistence of a phenology involving virtually continuous physiological activity seems, however, to have been favoured by hemiparasitic nutrient and water uptake. Hemiparasitic plants form root grafts with a majority of the species and individuals that surround them (Kuijt 1969; Atsatt 1970; Atsatt & Strong 1970; C. M. Herrera, unpublished). The array of species present in local Mediterranean scrublands exhibit a broad variety of root depths and seasonal patterns of physiological activity, even though all tend to share the summer-drought pause (Diamantoglou & Meletiou-Christou 1978, 1980; Kummerow 1981; Poole, Roberts & Miller 1981; Kummerow, Montenegro & Krause 1981; Gray 1982; Baker, Rundel & Parsons 1982). I suggest that *O. quadripartita*, by parasitizing a range of species, partly shares a broad variety of the phenological patterns of its host species and is thus able to maintain sustained physiological activity for a period encompassing the phenological cycles of its various hosts. This hypothesis will be examined in detail in a subsequent publication.

Sexual differences

It is by now firmly established that, in dioecious species, male and female plants may differ substantially in life history, spatial distribution, competitive ability, phenology, and resource allocation patterns: see Lloyd & Webb (1977) for review; and also Freeman, Klikoff & Harper (1976), Brockmann & Bocquet (1978), Onyekwelu & Harper (1979), Wallace & Rundel (1979), Barrett & Helenurm (1981), Bullock & Bawa (1981), Conn & Blum (1981), Cox (1981), Bawa, Keegan & Voss (1982), Meagher & Antonovics (1982) and Zimmermann & Lechowicz (1982). One of the principal conclusions emerging from these studies is that, directly or indirectly, differential costs and commitments associated with male and female reproduction are responsible for observed ecological differences between the sexes.

Some sexual differences in phenology reported in this study are consistent with this idea. If 'time' is considered a limiting resource which has to be allocated among several

functions, male and female reproduction differ in terms of their time-associated costs. Males are relieved from fruit development and maturation, hence they may allocate available time among fewer functions, and one would expect longer average durations of every individual function, and greater seasonal spacing of functions, than among females. These expectations are confirmed by the results. The various activities of female *O. quadripartita* virtually saturate the annual cycle, whereas males have a distinct resting period in late summer and early autumn (Fig. 5). One should therefore expect the female phenological cycle to be internally much more rigidly integrated, and the timing of individual phases to be less sensible to variation in external conditions, than the male cycle. The sustained growth of some males following unusual summer rainfall and the relation between initiation of male growth and rainfall occurrence, along with the absence of responses of this kind among females, support these expectations.

Males and females may organize their activities differently, but the annual cycles of the two sexes should be in phase at the time of flowering. In *O. quadripartita*, divergence between sexes in the time of growth and the initiation of flowers is much greater than the divergence in the flowering period. Although the population flowering peak of males encompassed that of females in all years, females tended to begin flowering later in the season and finish earlier, than males. This pattern is identical to that documented in detail by Bawa (1980) and Bullock & Bawa (1981) for *Jacaratia dolichaula* (Caricaceae), a small tree of neotropical lowland rain forest, and is perhaps representative of most dioecious species (see Lloyd & Webb 1977).

The earlier flowering of males was attributed by Bawa (1980) to competition between the males, presuming that access to females would be greater for males that are 'best known to' or are most frequented by pollinators because they flower before their competitors. In a later paper, Bullock & Bawa (1981) suggested that the pattern 'is consistent with the notion of mate selection by females'. Female plants could increase their fitness by concentrating flowering during the time when the variety of available mates is greatest. To the extent that these explanations depend on the species-specific reproductive features of *J. dolichaula* (e.g., ostensible mimicry of male flowers by females; female flowers non-rewarding to pollinators; pollination by large sized, specialized trapliners; Bawa 1980), they cannot apply to *Osyris quadripartita* (flowers of the two sexes produce nectar; pollination by small unspecialized pollinators; no apparent mimicry). On the other hand, the regular production of flowers by *O. quadripartita* males at times of year when no female is flowering (Fig. 3), is hard to relate to any immediate reproductive benefit for these earliest flowering males. Due to species-specific developmental constraints (production of flowers restricted to new growth), the time of flowering depends to some degree on the time of growth of *O. quadripartita*. Nevertheless, the earlier flowering of males may not be attributed solely to earlier growth, since males delay flower opening for a longer period after flower initiation than do females (Fig. 3).

Plant phenological studies have most often emphasized aspects related to the time of particular functions, while patterns of time allocation among various functions and the integration of different, often conflicting, activities into particular phenological sequences have received less attention (but see, e.g., Mooney & Bartholomew 1974). The time and duration of every activity an individual plant performs has some influence on its fitness, but it is the successful seasonal combination of all these activities that ultimately has the greatest influence. The present study has shown that, in dioecious plants, sexual differences in the time and duration of particular activities should be examined in relation to the differential, sex-related organization of the entire annual cycle. On the other hand, sexual

differences in phenology may help to illustrate the nature of some functional or ecological conflicts underlying observed phenological patterns.

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