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PLANT SIZE, SPACING PATTERNS, AND HOST-PLANT SELECTION IN *OSYRIS QUADRIPARTITA*, A HEMIPARASITIC DIOECIOUS SHRUB

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SUMMARY

(1) Sex ratio, plant size, spatial distribution and host-plant selection have been examined in three south-western Spanish populations of *Osyris quadripartita* (Santalaceae), a hemiparasitic dioecious shrub of mediterranean habitats. The three populations are distributed along an environmental gradient characterized by variation in water availability and soil fertility.

(2) Sex ratios do not depart significantly from 1:1 in any of the populations studied. There is no significant spatial segregation of plants of the two sexes in any population, as assessed by nearest-neighbour analyses.

(3) Significant dimorphism in plant size was found at one of the sites, where males were significantly larger than females.

(4) The positive correlation between combined plant size and distance of separation of neighbours provides evidence for intraspecific competition in this species. The effect of intersexual competition is greater than the effect of intrasexual competition between males, but it is similar to the effect of intrasexual competition between females. Females apparently have a greater competitive effect on males than other males.

(5) Males and females are similar in their proportional use of host-plant species at two sites, and differ significantly at the other locality.

(6) These results provide no evidence for niche differentiation of the sexes of *O. quadripartita* along an environmental gradient defined by abiotic factors (moisture, soil nutrients), but favour the view of small-scale segregation based on differential utilization of host-plants. It is suggested that niche differentiation in parasitic dioecious plants is most likely to occur along biologically rather than physically defined environmental gradients.

INTRODUCTION

Male and female individuals of dioecious plant species often differ in vegetative and reproductive features (Lloyd & Webb 1977; Wallace & Rundel 1979; Hancock & Bringhurst 1980; Conn & Blum 1981; Bullock 1982; Herrera 1984b; Allen 1986), and in proportional occurrence along environmental gradients (Freeman, Klikoff & Harper 1976; Grant & Mitton 1979; Cox 1981; Fox & Harrison 1981; Melampy 1981; Freeman & Vitale 1985). This latter phenomenon is known as the Jack Sprat effect (Onyekwelu & Harper 1979) or intersexual niche partitioning (Cox 1981). Males tend to be over-represented in resource-limited environments, whereas no bias or female preponderance is found in environments with more abundant resources. These sex-related niche differences may be the result of selection against deleterious intersexual competition, or a consequence of selection for increased interspecific competitive ability (Cox 1981).

This paper examines sex ratio, plant size, spatial distribution and host-plant selection in *Osyris quadripartita* Salzm. ex Decne (Santalaceae), a hemiparasitic dioecious shrub of mediterranean scrublands, along an environmental gradient. Most previous studies on

the comparative ecology of the sexes of dioecious plants have been conducted on tropical trees or temperate forest herbs. Dioecy is prominent in some southern European scrubland communities (Herrera 1982), yet there are few studies on the ecology of dioecious mediterranean plants (Herrera 1984b, 1985). Furthermore, dioecious hemiparasites have received little attention from the viewpoint of the ecology and evolution of dioecy (but see Barlow *et al.* 1978; Wiens & Barlow 1979; Nixon & Todzia 1985), despite the fact that this breeding system is well represented among parasitic plant families (e.g. Olacaceae, Santalaceae, Viscaceae, Misodendraceae, Rafflesiaceae) and the study of these species may help to understand the ecological basis for niche partitioning between the sexes of non-parasitic plants as well. The relations of parasitic plants with important, potentially limiting resources of the physical environment (water, nutrients) are mediated, and to some degree also buffered, by the physiology of their hosts (Kuijt 1969). One should thus expect that parasitic dioecious plants will exhibit less niche differentiation with respect to the physical environment than with respect to the host-plant environment.

*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 scrubland. A general account of the natural history and distribution of this species may be found in Herrera (1984b). Other studies have dealt with the reproductive biology of female plants (Herrera 1985), phenology of both sexes at the population level (Herrera 1984b), and seed dispersal ecology (Herrera 1984a, 1988).

STUDY SITES

This study was conducted at two south-western Spanish localities, in the lowlands of the lower Guadalquivir River valley ('Doñana' and 'El Viso' hereafter). The two sites have a warm mediterranean climate, with rainy mild winters and dry hot summers. (Herrera (1984b) and Díaz Paniagua (1983) present climatological details for El Viso and Doñana, respectively.)

The Doñana study site was the Sabinar del Marqués, in the north-western corner of the Reserva Biológica de Doñana, at 10 m altitude (Parque Nacional de Doñana, Huelva province; 37°1′ N, 6°31′W). The area consists of old stabilized dunes less than 1 km from the Atlantic coast, and is vegetated by sparse scrub with scattered juniper trees (*Juniperus phoenicea*), growing on very nutrient-poor sandy soils (see, e.g. Ramírez Díaz *et al.* (1977), García Novo (1979) and Merino & Martín Vicente (1981) for descriptions of the ecology of the vegetation in this dune system). The sandy nature of the soils, coupled with the mediterranean climatic regime, make water availability an important factor for plants, particularly during the severe summer drought. Extreme water potentials of up to −8 MPa have been reported for some shrub species in the area, and fluctuations of water potential from winter to summer commonly encompass a range of 4 MPa (Merino, García Novo & Sánchez Díaz 1976). In these conditions, even slight variations in ground elevation have a pronounced effect on the water balance of plants, by influencing the depth of the water table in summer (Ramírez Díaz *et al.* 1977; García Novo 1979). For this reason, two populations of *Osyris quadripartita* were selected for study at this site, one growing on the most elevated portion of the dune ('dune ridge' hereafter) and the other on the lowermost portion of the dune slope and the adjacent level area ('dune bottom'). The difference in elevation between the two zones is relatively small (2·5–4·5 m), but values in this range have been shown to produce important intraspecific variations in the water

* Nomenclature follows *Flora Europaea* (Tutin *et al.* 1964–80).

potential of several woody species in this locality (Merino, García Novo & Sánchez Díaz 1976; Ramírez Díaz *et al.* 1977).

The El Viso study site was a 3·5-ha patch of dense mediterranean scrub on nearly level terrain near El Viso del Alcor (Sevilla province), at 100 m altitude (37°26′N, 5°45′W). Details on the composition and ecology of vegetation at the site have been presented in Herrera (1984a), and general descriptions of the area in Ministerio de Agricultura (1975). The shrub layer is dominated by *Pistacia lentiscus, Quercus coccifera* and *Myrtus communis*, and there are scattered *Arbutus unedo* and *Pinus pinea* trees. The substrate consists of fertile, very productive alluvial soils (Anon. 1962), as evidenced by the extensive cultivations surrounding the study scrub patch (Ministerio de Agricultura 1975). No quantitative data are available on the magnitude of summer water deficiency in plants in this locality. Indirect evidence (depth of water table in irrigation wells in summer; C. M. Herrera, pers. observ.) suggests that it is roughly similar to that experienced by plants growing in the dune bottom area of Doñana. Virtually the whole local population of *Osyris quadripartita* in El Viso was examined for this study. Previous studies on this species (Herrera 1984b, 1985, 1988) were conducted on this population.

METHODS

Observations and measurements reported in this paper were performed in June 1980 (El Viso) and May 1983 (Doñana), unless otherwise stated. These dates roughly coincide with the local flowering peak of *O. quadripartita* at these localities (Herrera 1984b; J. Herrera 1986). This facilitated identification of the sex of plants.

For each population, all *O. quadripartita* plants found within the boundaries of a previously determined area (3·5 ha in El Viso, 2·5 ha in Doñana), were examined individually. The size of the survey area was determined in function of the local density of plants, in order to contain approximately 150 (El Viso) or 100 (each Doñana site) individual plants. Sex, height, associated host-plant species (see below) and sex of the nearest neighbour were recorded for every plant examined. In El Viso, further measurements taken were major and minor axes of the shrub's vertical projection (by assimilating it to an ellipse), distance to the nearest neighbour, and height and vertical projection dimensions of the neighbour. Neighbour distances were measured on a straight line from the points where single or multiple trunks entered the ground. Only plants exceeding 50 cm in height have been considered in the analyses below. Smaller plants were never observed to bear flowers or fruits, thus their sex could not be determined.

Parasitism has been demonstrated in at least seventeen genera of the family Santalaceae, including *Osyris* (Ferrarini 1950; Kuijt 1969, and references therein). A detailed account was presented by Ferrarini (1950) for *O. alba*, and observations based on root excavations confirm the parasitism in *O. quadripartita*. Root excavation (which has to be made by hand, to avoid breaking fine, haustorium-producing roots) involves a vast amount of work; thus, it was impractical to excavate the root systems of every sampled plant. For this reason, analyses of host-plant use performed in this paper have been confined to the fraction of sampled individuals that were found rooted in close contact with the main root(s) of other woody plants. This procedure assumes that the plant in contact with an *O. quadripartita* shrub is used, or was used in the past, as a host (without implying, however, that it is, or was, its single host). This assumption is supported by observations. Excavation of the root system of ten *O. quadripartita* plants, growing on the loose sandy soils of Doñana and rooted in contact with other woody plants, demonstrated

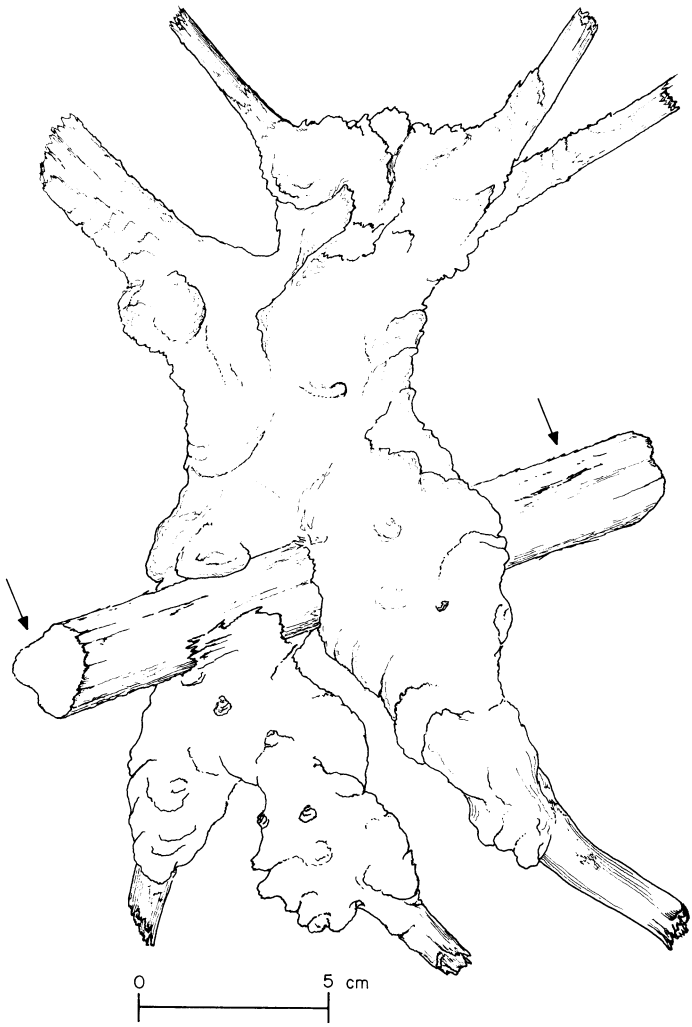

FIG. 1. Rootstock of a medium-sized *Osyris quadripartita* plant, almost completely surrounding one of the main roots (marked by arrows) of the *Juniperus phoenicea* treelet with which it was closely associated (Doñana study site, south-western Spain).

in all cases that the roots of *O. quadripartita* and those of its close associate had extensive areas of contact. One such case is depicted in Fig. 1. Functional haustoria were infrequently observed in the close vicinity of the parasite's rootstock, as fine roots were rare in this zone, but they were observed on roots of the associate 1–2 m away. Furthermore, transverse sections of the associate's root near the zone of contact with the parasite's rootstock revealed distinctive internal scars, demonstrating old haustorial connections healed up by the host (by comparison with descriptions, drawings and photographs in Herbert 1925, Ferrarini 1950, Kuijt 1969). From these observations, it

TABLE 1. Sex ratio and spatial relationships between female and male plants of *Osyris quadripartita* at sites in south-western Spain.

Population	Base plant	Nearest neighbour		Total	Deviation from 1:1	
		Male	Female		Chi-square	*P*
El Viso	Male	27	37	64	1·38	0·24
	Female	26	52	78		
		$G=1{\cdot}18$; $P=0{\cdot}28$				
Doñana:						
Dune ridge	Male	15	29	44	0·01	0·92
	Female	27	18	45		
		$G=6{\cdot}06$; $P=0{\cdot}014$				
Dune bottom	Male	23	22	45	0·17	0·68
	Female	23	26	49		
		$G=0{\cdot}16$; $P=0{\cdot}69$				

seems safe to infer a host–parasite relationship from observations of close basal contact (Herbert 1925 reported similar findings for some species of Australian Santalaceae).

Excavations of root systems mentioned earlier and supplementary observations did not reveal any evidence for underground vegetative propagation of *O. quadripartita* plants. Separate shrubs must thus be considered as distinct individuals.

Spatial relationships between male and female plants were examined according to Pielou's (1961) nearest-neighbour method (see also Levin 1974, Bawa & Opler 1977). Meagher & Burdick (1980) have shown that this method may produce erroneous results, leading to assignment of statistical significance where none exists. This effect, however, does not apply to the results presented below, as no significant segregation between sexes has been found.

Interference between conspecifics was analysed in the El Viso population examining the relationship between the summed volumes and distances between neighbouring plants (Pielou 1960; Phillips & MacMahon 1981). Shrub volume was computed (after Phillips & MacMahon 1981) as $\pi W_1 W_2 h/6$, where W_1 and W_2 are the lengths of the major and minor axes of the vertical projection, and h is shrub height.

Throughout this paper, averages are presented as mean $\pm$ 1 standard deviation (S.D.).

RESULTS

Sex ratio and spatial distribution

All the plants larger than 50 cm in height surveyed in El Viso ($n=152$) were in flower or had recently finished flowering by the time of observations, while in Doñana the proportion of individuals of this size exhibiting signs of reproductive activity (flowers, young fruits) was 93% ($n=216$ plants, dune bottom and dune ridge combined; there is no difference between these populations, $P=0{\cdot}17$, Fisher exact probability test). The difference between the two localities is statistically significant ($P=0{\cdot}0003$, Fisher test).

Sex ratios are not significantly different from 1:1 in any of the three populations studied (Table 1). Ascribing all the non-reproductive individuals of the Doñana populations to either sex does not result in significant departure from a 1:1 ratio ($P>0{\cdot}65$, chi-square tests). The slight differences observed between populations in the proportion of plants of the two sexes are not statistically significant ($G=0{\cdot}45$, $P=0{\cdot}80$).

TABLE 2. Average height (±1 S.D., in cm) of male and female *Osyris quadripartita* plants (sample sizes in parentheses) at sites in south-western Spain.

	Males	Females	Difference t	P
El Viso	163±49 (73)	134±36 (85)	4·25	<0·0001
Doñana:				
Dune ridge	162±59 (47)	148±50 (54)	1·28	0·20
Dune bottom	150±57 (47)	172±67 (53)	1·74	0·08
Difference between populations				
F-statistic	0·90	9·22		
P	0·41	0·0002		

Nearest-neighbour analyses do not reveal significant departures from randomness in the relative distribution of males and females in the populations of El Viso and Doñana dune bottom (Table 1). Plants of the two sexes are not randomly distributed in the Doñana dune ridge population. There, the nearest neighbour of a plant tends to be an individual of a different sex more frequently than expected by chance. Plants of the two sexes, therefore, rather than being spatially segregated in the dune ridge, tend to occur there regularly intermixed.

Plant size

The average height of male plants remains fairly constant between populations (range 150–163 cm), and the differences observed are not significant (Table 2). Average height of females varies more widely (range 134–172 cm), and there is significant heterogeneity among populations. The smallest females are those of El Viso, while the tallest ones are those of the Doñana dune bottom. Female shrubs are significantly shorter than males in El Viso, and tend to be taller than males in the Doñana dune bottom population, although the difference is only marginally significant (Table 2). The two sexes do not differ in average shrub height in the Doñana dune ridge. In El Viso, the mean volume of males ($1·86 \pm 2·29$ m^3, $n=64$) significantly exceeds that of females ($0·73 \pm 0·75$ m^3, $n=78$) ($t=4·07$, $P=0·0008$).

In Doñana, non-reproductive plants larger than 50 cm in height (79 ± 25 cm, $n=15$) are significantly smaller than reproductive conspecifics (158 ± 59 cm, $n=201$; the two sexes and two populations combined) ($t=5·05$, $P<0·0001$). This result, and the observation that in El Viso all plants exceeding 50 cm were reproductive, suggest that regular reproduction starts at larger plant size in Doñana.

Size and spatial distribution

The relationship between plant size and spatial distribution was examined in detail for the El Viso population. For the two sexes combined, a significant positive correlation exists between the summed volumes and distance between neighbouring *O. quadripartita* plants ($r=0·379$, $n=142$, $P<0·0001$). Intraspecific spacing and plant size are thus interrelated in this population, with large shrubs tending to occur further apart than small ones.

Neighbour pairs were classified into three mutually exclusive categories depending on the sex of the two plants concerned: male–male, female–female and mixed (plants of different sexes). Separate linear regressions were run for these three groups, using summed volumes as the dependent (Y, in m^3), and distance as the independent (X, in m) variable (Fig. 2). The regressions for male ($Y=0·44+2·17X$; $n=27$, $F=7·20$, $P=0·12$), female

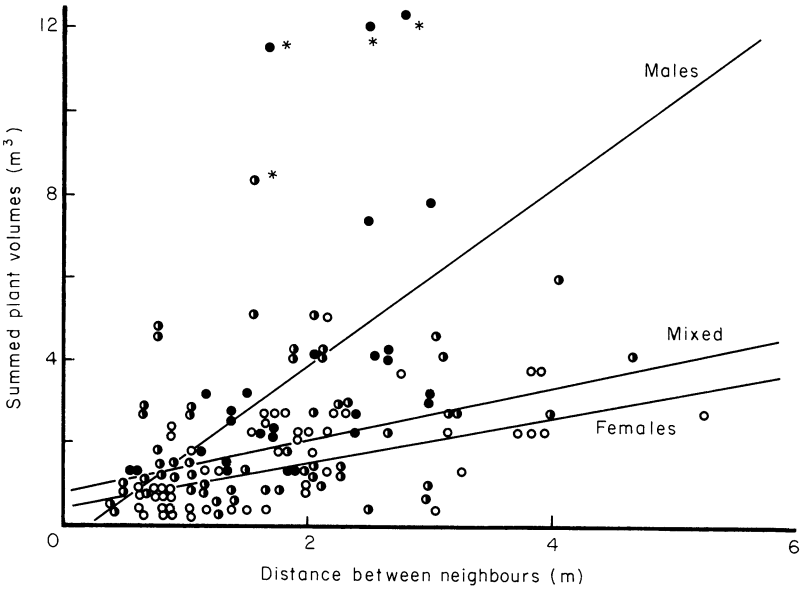

FIG. 2. Variation of summed plant volumes with distance between plants for nearest neighbour pairs of *Osyris quadripartita* at El Viso study site in south-western Spain. Separate regression lines are shown for male–male (●), female–female (○) and mixed-sex (◑) pairs. Outliers mentioned in the text are marked with asterisks. See text for regression equations.

($Y=0{\cdot}39+0{\cdot}58X$; $n=52$, $F=25{\cdot}8$, $P<0{\cdot}0001$), and mixed ($Y=0{\cdot}88+0{\cdot}65X$; $n=63$, $F=10{\cdot}0$, $P=0{\cdot}003$) plant pairs are all statistically significant. An analysis of covariance demonstrates significant heterogeneity in regression slopes for the three groups ($F=4{\cdot}92$, d.f. $=2,136$, $P=0{\cdot}009$). Heterogeneity of slopes remains significant after removing from the regressions four apparent outliers (Fig. 2; three male and one mixed pairs) ($F=3{\cdot}07$, d.f. $=2,132$, $P=0{\cdot}048$). This heterogeneity is due to the significantly steeper slope of male pairs relative to both female ($F=8{\cdot}06$, d.f. $=1,75$, $P=0{\cdot}006$; with outliers removed, $F=7{\cdot}69$, d.f. $=1,72$, $P=0{\cdot}007$) and mixed ($F=5{\cdot}94$, d.f. $=1,86$, $P=0{\cdot}017$; with outliers removed, $F=3{\cdot}95$, d.f. $=1,82$, $P=0{\cdot}047$) pairs. These latter two groups do not differ significantly in regression slope ($F=0{\cdot}078$, d.f. $=1,112$, $P=0{\cdot}78$), although they do differ in Y-intercept ($F=6{\cdot}16$, d.f. $=1,112$, $P=0{\cdot}015$). The regression for male pairs is significantly steeper than that for female and mixed pairs combined ($F=9{\cdot}87$, d.f. $=1,137$, $P=0{\cdot}002$; with outliers removed, $F=6{\cdot}07$, d.f. $=1,133$, $P=0{\cdot}01$). These results indicate that, per unit of plant volume, male–male pairs are spaced closer together than female–female and mixed pairs. With increasing distance between neighbouring shrubs, the rate of increase in plant size is greatest for male pairs. Mixed pairs are indistinguishable from female pairs in this respect.

There are no significant differences between categories of neighbour pairs (male, female, mixed) in average distance between neighbours ($P>0{\cdot}05$, Student–Newman–Keuls test). Spacing of neighbours is thus independent of the sex of the plants involved.

The volumes of individual plants in neighbouring pairs are not significantly correlated either for all plants combined ($r=0{\cdot}141$, $P=0{\cdot}09$) or for any of the three sex-based categories considered separately ($r=0{\cdot}063$, $P=0{\cdot}57$; $r=0{\cdot}144$, $P=0{\cdot}47$; $r=0{\cdot}098$,

TABLE 3. Proportional utilization (%) of host species by the sexes of *Osyris quadripartita* at the three study sites in south-western Spain.

	El Viso		Doñana ridge		Doñana bottom	
Host species	Males ($n=62$)	Females ($n=50$)	Males ($n=22$)	Females ($n=33$)	Males ($n=14$)	Females ($n=18$)
Pistacia lentiscus	45·2	70·0				
Phillyrea angustifolia	32·3	12·0				
Myrtus communis	11·3	8·0				
Rosmarinus officinalis	1·6	4·0	4·5	9·1		16·7
Juniperus phoenicea			63·6	75·8	78·6	77·7
Corema album			13·6	3·0	14·3	5·6
Others*	9·6	6·0	18·3	12·1	7·1	
Difference between sexes						
G-statistic	9·11		2·64		4·05	
d.f.	3		2		2	
P	0·028		0·27		0·13	

*Includes *Erica scoparia*, *E. arborea*, *Daphne gnidium*, *Quercus coccifera*, *Pinus pinea*, *Rhamnus lycioides*, *Cistus libanotis*, *Stauracanthus genistoides*, *Ulex parviflorus* and *Cytisus grandiflorus*.

$P=0·44$; female, male and mixed pairs, respectively). Plants of all sizes thus tend to occur randomly intermixed in the population.

Host-plants

The analyses to follow are restricted to those plants for which a host could confidently be identified (on the basis of observations described in the Methods section). This fraction of the total number of plants examined was similar for males and females in all the populations studied (El Viso: $G=3·53$, $P=0·06$; Doñana ridge: $G=2·08$, $P=0·15$; Doñana bottom: $G=0·83$, $P=0·36$).

Sixteen different species of woody plants were recorded as hosts of *O. quadripartita* (Table 3). The most frequent hosts were *Pistacia lentiscus* and *Phillyrea angustifolia* in El Viso, and *Juniperus phoenicea* in Doñana. The number of host species recorded was roughly similar for the two sexes in each population. Males and females do not differ significantly in proportional utilization of the various host species at the two Doñana sites, but they do differ in El Viso (Table 3). At this locality, females concentrate heavily on *P. lentiscus* as host, while males tend to use this species and *P. angustifolia* much more equitably.

All host-plants were in healthy condition in El Viso. In Doñana, 16·1% of hosts were dead ($n=87$, dune ridge and bottom combined; there is no significant difference between the two populations in the proportion of dead hosts; $P=0·13$, Fisher test). There is no significant difference in the proportion of hosts which were dead for males (11·1%, $n=36$) and females (19·6%, $n=51$) ($P=0·22$, Fisher test).

DISCUSSION

Sexual dimorphism in plant size has been reported for a number of dioecious plants (Lloyd & Webb 1977; but see Melampy & Howe 1977; Bullock 1982; Kaul & Kaul 1984; Cavigelli *et al.* 1986). In this study, significant sex-related differences in size were found only in El Viso, where females were significantly shorter than males.

The three *O. quadripartita* populations studied are distributed along an environmental gradient characterized by variation in water availability and soil nutrients. Resource limitation increases in the direction El Viso (little nutrient limitation, moderate water shortage — dune bottom (moderate nutrient limitation, moderate water shortage) — dune ridge (strong nutrient limitation and water shortage). Above-ground plant biomass and productivity (all woody species combined), and soil nutrient content are substantially greater in the dune bottom than in the ridge (Merino & Martín Vicente 1981). The water potential values reported for several shrub species in the dune area (Merino, García Novo & Sánchez Díaz 1976) fall in the range observed for species from North American deserts (MacMahon & Schimpf 1981).

Despite the differences between sites in water and nutrient limitations, and the extremely unfavourable conditions faced by plants growing at the dune ridge, no significant differences in sex ratio exist between the three *O. quadripartita* populations. Proportions of the two sexes do not depart from 1 : 1 at any site. Furthermore, there is no significant spatial segregation of sexes in any population. These results are contrary to expectations of spatial niche partitioning between the sexes of *O. quadripartita*, either along the steep gradient in abiotic factors (moisture, nutrients) or at a smaller spatial scale (within populations). Earlier studies in arid habitats have almost invariably shown spatial niche partitioning of the sexes of dioecious plants along gradients of water availability, with males being over-represented at the xeric ends of moisture gradients (Freeman, Klikoff & Harper 1976; Freeman & Harper 1980; Fox & Harrison 1981; Waser 1984; but see Wallace & Rundel 1979; Shaw, Bern & Winkler 1987).

The only evidence suggestive of niche partitioning between the sexes of *O. quadripartita* is the different proportional use of host species found in El Viso. There, females tend to concentrate on *Pistacia lentiscus*, while males are distributed more equitably among this species and *Phillyrea angustifolia*. Male and female plants do not differ significantly in proportional utilization of host species in Doñana. This may be due to insufficient sample sizes, as combining host-plant records for the two Doñana populations into a single sample reveals a marginal, non-significant trend toward sex-related differentiation in host use ($G = 5{\cdot}90$, d.f. $= 3$, $P = 0{\cdot}11$). In El Viso, a positive correlation exists between combined plant size and distance of separation of nearest-neighbour pairs. This pattern has been usually considered as indicative of the existence of competition between plants (Pielou 1960; Yeaton & Cody 1976; Yeaton, Travis & Gilinsky 1977; Yeaton 1978; Phillips & MacMahon 1981; Smith & Grant 1986). In addition to supporting the notion of intraspecific competition, size–distance regressions for *O. quadripartita* in El Viso suggest that the magnitude of competitive effects is sex-dependent. The slope of regressions may be considered inversely related to the size-depressing effect of competitive interactions between neighbours. The steeper the slope, the more spatially restricted the competitive interference. According to this interpretation, female *O. quadripartita* plants in El Viso have a spatially more extensive influence on female neighbours than male plants have on male neighbours (Fig. 2). In other words, size–distance regressions suggest that females compete more between themselves than do males. The slope of the regression for mixed-sex neighbour pairs is statistically indistinguishable from that for pure female pairs. This suggests that the outcome of the interaction between males and females is equivalent to that of the interaction between females. In short, the effects of intersexual competition seem to be greater than the effects of intrasexual competition between males, but similar to the effects of intrasexual competition between females; and females have a much greater effect on males than other males.

Cox (1981) suggested that niche differentiation should be favoured if intersexual competition is more deleterious than intrasexual competition. Although the effects of competition have been evaluated very indirectly in this study, the results for the El Viso population are consistent with this view. For males, intersexual competition seems more important than intrasexual interference. Sex-related differences in host-plant selection observed in this population may therefore be interpreted as a case of niche partitioning, potentially reducing intersexual competition via differential microsite (host species) utilization.

The relationships between parasitic plants and some potentially limiting resources of the physical environment (water, nutrients) take place via their hosts. Host-plants may thus be seen as buffers between the parasite and the physical environment. In a sense, hosts *are* the environment of parasitic plants, and they even modify the expression of genetic variability in the parasites (Atsatt 1970; Atsatt & Guldberg 1978). On the other hand, the parasitic habit has been interpreted as an adaptation to enhance nutrient uptake in nutrient-poor soils of mediterranean habitats (Lamont 1982, 1983). In this context, the results presented in this paper are not unexpected. No evidence has been found suggesting niche differentiation of the sexes of *O. quadripartita* along an environmental gradient defined by abiotic factors. In contrast, small-scale segregation based on differential use of host species takes place in the population most thoroughly sampled, and this finding is in agreement with the relative magnitudes of inter- and intrasexual competitive effects observed in that population. Nixon & Todzia (1985), in a study in which sex and distribution among hosts were simultaneously recorded for a dioecious plant parasite, provided data for the mistletoe *Phoradendron tomentosum* which demonstrate differential host use of males and females. Recomputation of their figures for the five major host trees reveals a significant sex-related difference in proportional use of host species by the parasite ($G = 16{\cdot}97$, d.f. $= 4$, $P = 0{\cdot}002$). These data and the results of the present study thus support the view that niche differentiation in parasitic dioecious plants is likely to occur along biologically rather than physically defined environmental gradients.

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