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Reproductive biology in the Iberian taxa of the genera *Sonchus* and *Aetheorhiza* (*Asteraceae*: *Lactuceae*)

Abstract

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Aspects of the reproductive biology of the 9 wild Iberian species of *Sonchus* and *Aetheorhiza*, plus one additional subspecies and an interspecific hybrid, have been studied. Comparison between fruit set in bagged and freely pollinated flower heads indicates that xenogamy is prevalent in most species, but that some taxa are preferentially autogamous. There is a clear correlation between reproductive system and life cycle. The pollen-ovule index is similarly correlated but also shows clinal differences within single capitula. Xenogamy appears to be the primitive condition within the group. The evolutionary shift to self-fertility has entailed a change in flower head diameter, in floral pigmentation, and in longevity of the florets and flower heads.

Introduction

Launaea Cass., *Sonchus* L., *Aetheorhiza* Cass. and *Reichardia* Roth constitute a group of closely related genera (Gallego & al. 1980, Stebbins 1953), although Sell (1975) considers *Sonchus* to be taxonomically isolated. *Launaea* seems to be the oldest genus, with a probable origin in tropical Asia (Kilian 1988), but presently extending to Africa and southern Europe. *Sonchus* may have arisen from *Launaea* in tropical Africa (Saad 1961) or may be related with *Launaea* through a common ancestor (Boulos 1974b, Pons & Boulos 1972). It comprises three subgenera: *S.* subg. *Dendrosonchus*, subg. *Origosonchus* and subg. *Sonchus* (Boulos 1972). The last-named has a worldwide distribution and is the only subgenus represented on the Iberian Peninsula. *Aetheorhiza* is a monospecific genus widely distributed around the Mediterranean Sea and in south-western Europe, with two additional subspecies in Majorca and in the eastern Mediterranean (Rechinger 1974). It has probably originated from the group of *Launaea* and *Sonchus* since they have similar morphological characters. *Reichardia* is probably closely related to *Launaea* with which it constitutes a very natural group.

The Iberian Peninsula is an important centre of diversification of the group (Tomb 1977). As part of a biosystematic study, observations have been made on the reproductive biology of taxa occurring in that area. The results obtained for *Sonchus* and *Aetheorhiza* are presented here; those for *Launaea* and *Reichardia* will be published subsequently. The work has two aims. The first is to investigate the extent of inbreeding and outbreeding within the Iberian taxa. The second is to study certain aspects of the biology of the capitulum in relation to the mode of sexual reproduction that have been regarded as interconnected or closely correlated with the breeding system: the ability to self-fertilize, flower size and coloration, and pollen/ovule (P/O) ratio. In addition, flower longevity has been observed casually, being thought to be important from the point of view of pollination, as a dynamic process.

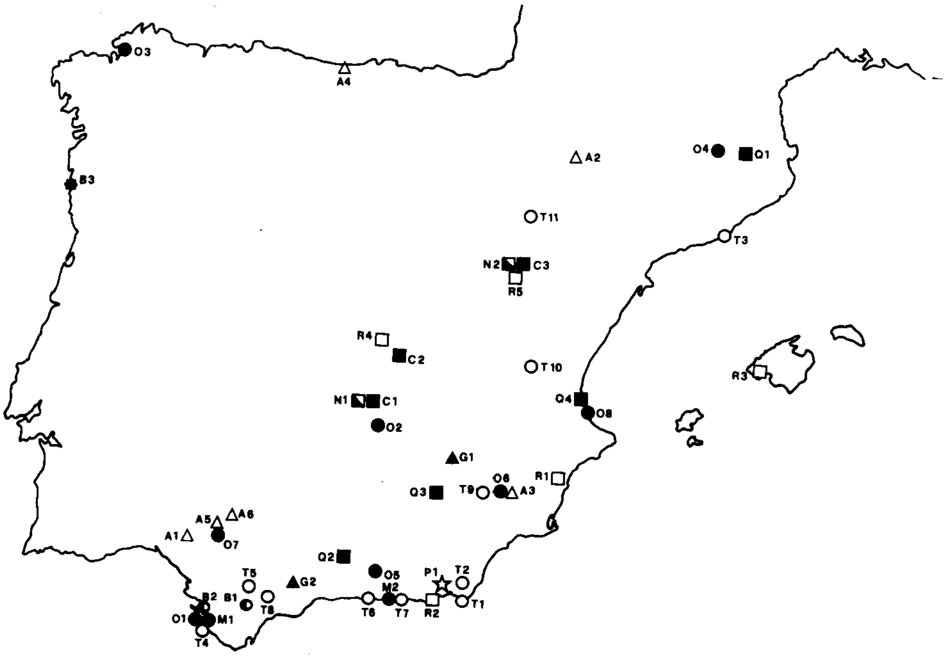

Fig. 1. Geographical localization of the populations studied: *Sonchus oleraceus* (●) , *S. microcephalus* (◉) , *S. tenerrimus* (○), *S. asper* subsp. *asper* (△), *S. asper* subsp. *glaucescens* (▲) , *S. maritimus* (□), *S. aquatilis* (▣) , *S. crassifolius* (■), *S.* x *novocastellanus* (◧) , *S. pustulatus* (☆), *Aetheorhiza bulbosa* subsp. *bulbosa* (◐) .

Even though *Sonchus* and *Aetheorhiza* have been the subject of important studies from the taxonomic and caryological points of view (Babcock & Stebbins 1943, Boulos 1973, 1974a, 1974b, Roux & Boulos 1972), few observations have been made on their reproductive biology. Some suggestions are found in the literature on the occurrence of self-fertilization in *S. oleraceus*, *S. asper* and *S. arvensis* (Hsieh & al. 1972, Percival 1955).

The two genera are represented in the region by 10 non-hybrid taxa and one interspecific hybrid. They all show herbaceous growth habit but diverse life-forms, and so constitute a suitable group for testing their reproductive biology. The non-hybrid taxa are: *Sonchus oleraceus* L. (annual, sometimes biennial), *S. microcephalus* Mejías (1991; annual), *S. tenerrimus* L. (variable life span, but mainly perennial according to the literature), *S. asper* (L.) Hill subsp. *asper* (annual), *S. asper* subsp. *glaucescens* (Jordan) Ball (annual, sometimes biennial), *S. maritimus* L. (rhizomatous perennial), *S. aquatilis* Pourret (rhizomatous perennial), *S. crassifolius* Pourret (rhizomatous perennial), *S. pustulatus*

Willk. (perennial, woody at the base), and *Aetheorhiza bulbosa* (L.) Cass. subsp. *bulbosa* (perennial, with rhizomes and tubers). The hybrid *S.* x*novocastellanus* Cirujano (1983; rhizomatous perennial), probably a cross between *S. maritimus* and *S. crassifolius* (Cirujano 1982, 1983, Mejías & Valdés 1988), has also been considered.

Material and methods

Most of the plants investigated (indicated in the Tables by an identification code;, see Appendix) were raised in the experimental grounds of the University of Seville from seeds collected in the wild, or were transplanted from natural populations. In some cases (indicated by asterisks in Tables 4 and 6), observations were made in the wild. Voucher specimens are deposited in the Herbarium of the Department of Plant Biology and Ecology (formerly Dept. of Botany), Faculty of Biology, University of Seville (SEV).

Self-fertility tests were performed by bagging of synflorescences (1-9 flower heads). These were covered by a nylon bag prior to anthesis to prevent the access of pollinators. Some flower heads were also covered after anthesis to serve as controls. Bags were collected when cypsela had matured and had been shed into the bag. Some flower heads (marked AA in Table 1) were self-pollinated artificially with a brush every day during anthesis. For those, bags with an opening at the top but closed by a knot were used. In both cases, fruit set was calculated as the percentage of florets which yielded fruits. The number of florets was determined by counting the dry ligules in each bag.

Seed germination tests were performed during the autumn or winter following harvest. Seeds were sown on a filter paper in Petri dishes with 8 ml of tap water. Germination was considered to have occurred when well-developed cotyledons were observed. Where possible, the number of germinated seeds was plotted against time on a germination chart to estimate the time (hours) needed to achieve 50 % (t_{50}) and 90 % (t_{90}) germination.

The P/O index (Cruden 1977) was calculated from buds collected shortly before anthesis in the wild. The buds were fixed in Farmer's fluid (Löve & Löve 1975) and preserved at 4°C until usage.

The counting procedure was different depending on the number of pollen grains per floret. When it was lower than 1000, single florets were crushed onto a slide in a drop of water plus safranine and detergent, and the grains were counted under a microscope (x80).

When the number was higher, 1 or 2 florets were softened in 5 ml of the same solution and the number of grains included was calculated from the count of 5-8 0.1 ml samples of the homogeneous pollen grains suspension. Since the number of seminal primordia, as in the whole family, is always 1, in this particular case the P/O index coincides with the number of pollen grains per floret.

Studies on flowering patterns included counts of the number of days that each flower head invested in flowering and of the number of hours they remained open in a single day. For the first kind of study some flower heads were marked before blooming. Each day, a note was made as to whether the head was open or not, and the position of the open florets in the capitulum was noted.

For the second kind of study, flower heads were marked the previous day and observed all throughout the day, from dawn until sunset. Periodically, the diameter of the circle formed by the tips of the outer ligules was measured, and notes were taken on pollen presentation and stigma exposure. Some further observations were made at night, to make sure that no flowers had opened. The duration of daily exposure of the florets in the flower heads was defined as the period during which the measured diameter exceeded 5 mm. This value, judging from observation of insect behaviour, may be considered as the threshold of insect access to flower heads.

Table 1. Fruit set in Iberian taxa of *Sonchus* and *Aetheorhiza* . BP, flower heads bagged before anthesis; FP, freely pollinated flower heads; n, number of individuals tested; % frt., mean value of fruit set, and the variance found (s); AA, artificially self-pollinated capitula.

SAMPLE		BP			FP	
	n	% frt .	(s)	n	% frt.	(s)
S. oleraceus						
O2	6	52.07	(18.67)	5	69.92	(27.02)
O3	4	60.16	(37.05)	4	73.80	(23.36)
O4	4	62.77	(13.33)	4	79.68	(13.80)
O5	4	79.76	(5.02)	4	88.71	(9.50)
O6	4	89.75	(4.13)	4	97.55	(2.08)
O7	6	80.87	(11.44)	6	81.00	(20.98)
O8	6	82.32	(19.05)	6	92.87	(8.49)
S. microcephalus						
M1	4	90.53	(13.23)	4	90.76	(8.41)
M1 (raised from cypselas produced after selfing)						
	6	75.52	(12.55)	6	92.46	(7.17)
M2	7	69.06	(19.74)	8	79.24	(10.72)
S. tenerrimus						
T1	7	0.00		7	56.27	(28.89)
	(AA)3	0.00				
T2	5	2.30	(4.26)	5	87.57	(9.49)
T3	7	0.33	(0.65)	6	78.04	(20.49)
T4	6	6.20	(14.93)	6	59.09	(31.76)
T5	6	3.70	(9.05)	6	56.62	(11.72)
T6	5	0.51	(1.15)	5	83.55	(14.65)
T7	9	6.87	(18.51)	9	68.75	(19.91)
T8	6	0.00		6	88.70	(6.69)
T10	6	18.10	(36.71)	6	50.47	(37.07)
S. asper subsp. *asper*						
A2	3	4.27	(4.72)	3	8.76	(4.69)
A4	7	20.72	(26.08)	7	65.92	(16.97)
A5	4	59.32	(23.61)	3	96.23	(2.59)
A6	4	66.94	(20.63)	3	82.42	(8.59)
S.asper subsp. *glaucescens*						
G1	5	29.62	(16.33)	4	57.25	(23.54)
G2	5	63.64	(29.78)	5	91.60	(3.75)
S. maritimus						
R1	6	0.00		6	51.49	(26.23)
R2	6	0.00		4	55.06	(16.70)
R3	4	0.00		4	54.53	(26.41)
R5	5	5.99	(15.25)	5	73.44	(16.91)
	(AA)3	0.31	(0.54)			
S. aquatilis						
Q1	7	24.10	(23.17)	7	70.74	(15.58)
	(AA)3	22.40	(38.79)			
Q2	6	1.53	(3.75)	6	55.65	(25.80)
Q3	4	0.00		4	54.12	(27.84)
Q4	3	0.00		2	24.44	(14.04)
S. crassifolius						
C1	2	0.44	(0.63)	2	79.48	(6.34)
C3	1	0.00		-	-	-

SAMPLE		BP			FP	
	n	% frt .	(s)	n	% frt.	(s)
S. crassifolius	(AA)1	0.00				
S. x*novocastellanus*						
N1	4	0.51	(0.63)	4	41.66	(7.51)
N2	2	0.00		2	65.76	(23.83)
	(AA)1	0.00				
S. pustulatus						
P1	8	0.00		7	21.19	(17.25)
	(AA)3	0.00				
A. bulbosa subsp. *bulbosa*						
B1	4	0.96	(1.11)	4	77.95	(12.85)
B2	6	0.00		6	27.41	(33.59)
B3	5	3.82	(6.09)	3	74.41	(23.77)

Results

Fruit set observed in the studied taxa is summarized in Table 1. For flower heads bagged before anthesis, the values represent the frequency of autogamy including geitonogamy. Since genetically the consequence of strict autogamy and geitonogamy is exactly the same, no distinction was considered necessary. For freely pollinated flower heads the values represent the fruit set under natural conditions, i.e., the natural fertility of the plant. It should be noted that the plants were growing in an experimental garden in the urban area of Seville, where climatic features and pollinator activity may not have been the most suitable for some of the populations studied. Fruit set in freely pollinated flower heads was, however, usually high enough.

Table 1 indicates that xenogamy is the most frequent mode of sexual reproduction in perennials: 6 of the 10 non-hybrid taxa, viz., *Sonchus tenerrimus. S. maritimus*, *S. crassifolius*, *S. aquatilis*, *S. pustulatus* and *Aetheorhiza bulbosa* subsp. *bulbosa*. Some populations of *S. tenerrimus* colonizing disturbed areas seemed to be composed of annual or biennial members (Lucainena de las Torres: T2 and Muel: T11; see Appendix), but their cultivation in the experimental grounds over three years has shown they are in fact perennials. In most of the individuals studied, no cypselas were produced after self-fertilization, but in many populations, individuals with the capacity of giving some fruits in bagged flowers were found. In these cases, autogamous fruits were yielded by one or two plants only. This explains the high intra-population variance found, which was always higher than the mean value of fruit set except in the *S. aquatilis* population from Sárdenas (Q1). It is noteworthy that brushing stigmas of a flower head with their own pollen (AA, forced autogamy) did not alter the results.

In the other 4 taxa, mainly annuals, self-fertility prevails. *Sonchus oleraceus*, *S. microcephalus*, *S. asper* subsp. *asper* and *S. asper* subsp. *glaucescens* produced large numbers of fruits in the flower heads that were bagged before anthesis. In 13 out of 16 populations, the fruit set after self-fertilization was higher than 50 %; in two (*S. asper* subsp. *asper* from Rioturbio: A4 and *S. asper* subsp. *glaucescens* from Bienservida-Villaverde: G1) it ranged between 20 % and 30 %, and in only one (*S. asper* subsp. *asper* from Lanavé: A2) was the percentage very low. In general, all individuals tested set fruits significantly, which is reflected by the comparatively low variance values. Fruit production in the freely pollinated flower heads always exceeded that in the bagged ones, but usually by not more than 20 %.

Sexual reproduction seems to be important in the hybrid taxa *Sonchus* x*novocastellanus*, too, as fruit set in freely pollinated flower heads was fairly high, and comparable to that of the putative parents species.

Self-fertility data presented in Table 1 agrees with the few published records. *Sonchus oleraceus* and *S. asper* were considered to be self-compatible by Hsieh & al. (1972) and Percival (1955). No indications relating to other taxa have been found.

Vegetative reproduction was found in the group, but only in some taxa. *Sonchus maritimus*, *S. aquatilis*, *S. crassifolius* and *S.* x*novocastellanus* have a vigorous rhizome (all are interrelated, and are included in *S.* sect. *Maritimi* (Kirp.) Boulos). Nevertheless, sexual reproduction seems to be important in these species since they usually produce notable amounts of well-formed cypselas in the wild.

Rhizomes are also found in *S. tenerrimus*, but here the level of vegetative reproduction is not very high. *Aetheorhiza bulbosa* subsp. *bulbosa* usually has a large number of tubers, but high variability in the production of flower heads has been observed between populations in the wild; some flower freely, but in many others flower heads are absent or are formed only in very low number. In some populations very few (if any) well-formed cypselas are produced, probably because they really constitute clones, and self-fertilization hardly yield fruits in this taxa (Table 1).

Most fruits of self-compatible species produced after selfing germinate properly (Table 2), yielding well-developed seedlings. Thus they may be assumed to be able to give rise to perfect adult plants as has been observed in *S. microcephalus*. In this species, the cypselas produced after selfing of plants from Sancti Petri (M1) were found to originate perfect adult plants with high level of fertility (Table 1).

Germination tests in basically allogamous taxa of *Sonchus* gave low values; in the assay of *S. tenerrimus* from Valcarca-Garraf (T3), cypselas resulting from self-pollination produced a little radicle, but no true seedlings were ever developed, so that the germination index was considered zero. It is notable that germination in *S. oleraceus* and *S. asper* seems to be quick, and no kind of pretreatment is needed (Fig. 2).

Time required for achieving 50 % of germination oscillates between 50 and 79 h, i.e., 2 to 4 days, and the 90 % level was always reached within a week. Germination in sect. *S.* sect. *Maritimi* (*S. maritimus*, *S. aquatilis* and *S. crassifolius*) was usually slow, both in cypselas collected in the wild and in fruits produced after selfing. This must be due to some kind of seed dormancy. Germination in *S. microcephalus* was not so easy as in its relative *S. oleraceus*, so that some seed dormancy mechanism may also be assumed.

P/O index values were found to correlate with self-fertilization levels, being higher when flowers are basically allogamous (Table 3), although they do not fit well with Cruden's classes (Cruden 1977). In the genus *Sonchus*, the P/O rates in autogamous species (*S. oleraceus*, *S. microcephalus* and *S. asper*) range between 285 and 563 in the populations tested, which could thus be considered halfway between facultative autogamous and facultative xenogamous according to Cruden. In other species which are basically xenogamous, the P/O rate always exceeds 2000 and attains 4353 in *S. pustulatus*. These values approach those of Cruden's obligate xenogamous species class. In *Aetheorhiza* the xenogamous character of sexual reproduction is similarly reflected by a P/O index in excess of 2000. The number of pollen grains per floret is not homogeneous within each capitulum. It depends on position of the florets, and usually increases gradually towards the centre. Differences are more pronounced in flower heads with numerous florets, as can be well observed in *Sonchus oleraceus* and *S. asper*. Here the central florets have double the pollen content of outer florets. Differences are smaller when the flower heads have relatively few florets as exemplified by *S. tenerrimus* and *S.pustulatus*.

Table 2. Germination of cypselas yielded by bagged flower heads in some of the studied *Sonchus* and *Aetheorhiza* populations; n, number of cypselas tested; % germ., final percentage of germination obtained; t_{50}, t_{90}: estimated time as necessary to achieve 50 % and 90 % germination, respectively (in hours); SC, self-compatible; X, xenogamous probably self-incompatible.

SAMPLE	n	% germ.	t_{50}(h)	t_{90}(h)
S. oleraceus (SC)				
O4	120	98.33	50	91
O6	50	98.00	53	103
O8	140	98.57	79	151
S. microcephalus (SC)				
M1	139	80.60 (see text)		
M2	100	0		
S. tenerrimus (X)				
T3	25	0		
T9	120	35.83 (after 168 h)		
S. asper subsp. *asper* (SC)				
A5	87	100	51	84
A6	50	98.00	59	102
S. asper subsp. *glaucescens* (SC)				
G1	100	99.00	65	106
G2	100	98.00	59	101
S. maritimus (X)				
R5	50	38.00 (after 3 months)		
S. aquatilis (X)				
Q1	90	53.33 (after 3 months)		
A. bulbosa subsp. *bulbosa* (X)				
B3	6	100 (after 360 h)		

This is not, however, a very clear trend; in particular, it does not hold in *S.* sect. *Maritimi*. It has been possible to demonstrate that some flower characters are linked to the method of sexual reproduction in the taxa studied (Tables 4-6). Table 4 shows that the diameter of the fully expanded flower heads is smaller in autogamous than in basically xenogamous taxa. Mean values range between 14.8 (*Sonchus microcephalus*, Sancti Petri: M1) and 22.5 (*S. oleraceus*, Calasparra: O6) in the former, and between 23.1 (*S. aquatilis*, Sárdenas: Q1) and 33.3 (*S. maritimus*, Elche: R1) in the latter. These differences are reinforced by colouring, since *S. oleraceus*, *S. microcephalus* and *S. asper* florets are yellow -often pale yellow and sometimes almost white- with brown or grey stigmas, while xenogamous taxa have bright yellow or yellow-orange florets. The flower heads are exposed for several days (Table 5), during which new florets open daily, but the florets of the day before are not accessible to insects. Exposure takes place for some hours each day. The time during which flower heads are exposed for pollination thus depends on two factors: the number of days needed for completing the exposure of all florets, and the duration of their daily opening. In the taxa studied, anthesis of the florets in a single capitulum can occur over 1 to 4 days.

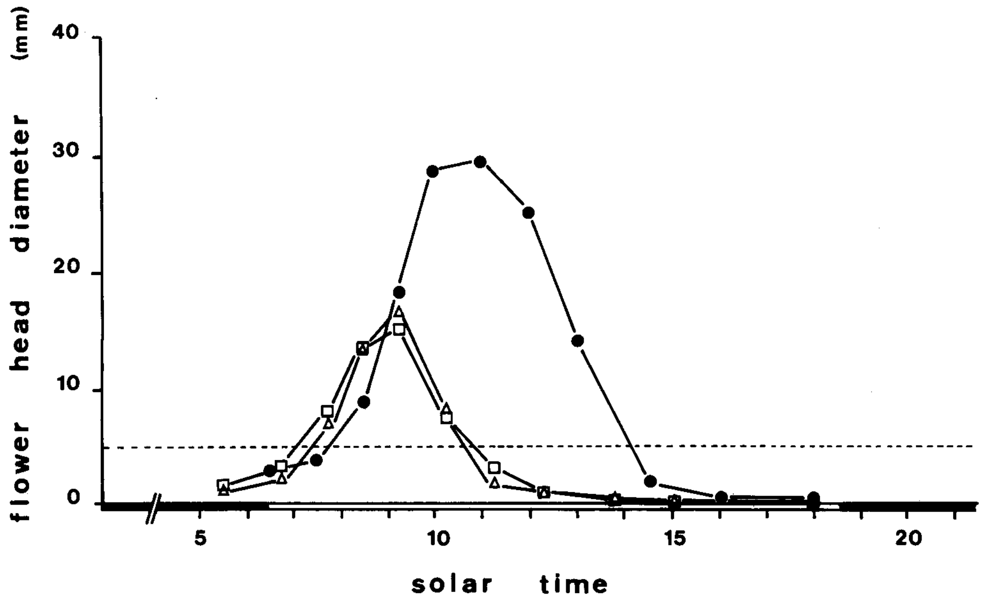

Fig. 2. Flower head diameter variations along a day in *Sonchus oleraceus*, *S. microcephalus* and *Aetheorhiza bulbosa*. Mean values of 18 heads from *S. oleraceus* (□), 12 heads from *S. microcephalus* (△), and 20 heads from *A. bulbosa* (●) are represented; (- - -) threshold of insect access to flower heads. Observations were made in the wild, simultaneously, in plants exposed to the sun, on 23 March 1988.

In preferentially autogamous taxa (*S. oleraceus* and *S. asper* subsp. *asper*) the exposure usually takes place on 2 days, often a single day and rarely 3 days. In contrast, the taxa in which the ability for self-fertilization is very reduced expose their flower heads for 2, 3 or 4 days, although in general the number of florets per capitulum is lower. The daily period during which flower heads expose their florets is very variable, with mean values ranging between 168 and 380 minutes in flower heads exposed to the sun (Table 6). From own experience, variation in flower exposure tends to be considerable between different days, depending on environmental conditions as temperature, humidity, day length and light intensity (variations due to sun and shade exposition are exemplified by *Aetheorhiza bulbosa* subsp. *bulbosa*, Table 6). However, differences attributable to species have also been detected. Few data are here brought forward to make any definite conclusions, but duration of daily exposure was shorter in autogamous taxa than in xenogamous ones in observations made simultaneously under the same conditions. This is evident when one compares the values for *Sonchus tenerrimus* with those for *S. asper* and *S. oleraceus* (10 May 1986). Even more pronounced differences were found between *A. bulbosa* subsp. *bulbosa*, *S. oleraceus* and *S. microcephalus* on 23 March 1988 (Fig. 2).

Discussion

The study of the reproductive systems in Iberian *Sonchus* and *Aetheorhiza* taxa shows that xenogamy is prevalent. It has been found to be the main reproductive mode in 7 taxa (64%), whereas self-fertilization predominates in 4 taxa (36%). It is assumed that self-pollination is a derived character (see Stebbins 1957, 1974, and some particular cases documented by Rollins 1963, Lloyd 1965, Solbrig 1976, Solbrig & Rollins 1977, and

Table 3. Pollen grain number (P/O ratio) in florets and flower heads in Iberian taxa of *Sonchus* and *Aetheorhiza*. n, number of flower heads studied; P/floret, mean pollen grain number per floret in outer, central and (sometimes) intermediate florets; P/O, mean pollen-ovule ratio; fl./head, mean number of florets per head (see also Table 5); P/fl. head, mean pollen grain number per flower head; SC, self-compatible; X, xenogamous probably self-incompatible.

SAMPLE	n	P/floret			P/O	fl./ head	P/ fl. head
		outer	interm.	central			
S. oleraceus (SC)							
O6	3	427 (n = 3)		699 (n = 3)	563		---
O7	11	297 (n = 6)	438 (n = 6)	522 (n = 6)	419	139	58241
S. microcephalus (SC)							
M1	6	238 (n = 6)		332 (n = 6)	285	114	32461
S. tenerrimus (X)							
T1	10	2526 (n = 6)	2975 (n = 6)	3318 (n = 6)	2940	74	217560
T5	6	2815 (n = 6)		3992 (n = 6)	3403	101	343703
S. asper subsp. *asper* (SC)							
A1	10	221 (n = 7)	344 (n = 7)	440 (n = 7)	335	240	80400
A3	8	198 (n = 8)		447 (n = 7)	322	289	93058
A4	3	132 (n = 3)		213 (n = 3)	172	267	45885
S. asper subsp. *glaucescens* (SC)							
G2	3	165 (n = 3)		448 (n = 3)	302	159	48018
S. maritimus (X)							
R2	5	2547 (n = 5)	2910 (n = 5)	3010 (n = 5)	2748	144	395712
S. aquatilis (X)							
Q2	5	2547 (n = 5)		3143 (n = 5)	2840	108	306720
S. crassifolius (X)							
C1	8	2059 (n = 5)	2026 (n = 5)	2129 (n = 5)	2071	100	207100
C2	3	2189 (n = 3)		2526 (n = 3)	2353	94	221558
S. pustulatus (X)							
P1	6	3619 (n = 5)		5087 (n = 5)	4353	66	287298
A. bulbosa subsp. *bulbosa* (X)							
B1	5	1816 (n = 5)		2417 (n = 5)	2117	80	169360

Table 4. Diameter and colouring of flower heads in Iberian taxa of *Sonchus* and *Aetheorhiza*. n, number of flower heads; dia. fl. head, diameter of fully expanded flower heads, indicating the minimum (min.) and maximum (max.) values found and the mean value ($\overline{x} \pm s$); *, observations made in the wild; SC, self-compatible; X, xenogamous probably self-incompatible.

SAMPLE	n	dia.	fl. head	$\overline{x}\pm s$	flower colouring
		min.	max.		
S. oleraceus (SC)					
O1, 1987*	53	13.0	25.0	19.1 ± 2.9	Yellow or white(grey stigma)
O1, 1988*	18	13.1	21.8	17.2 ± 2.5	Yellow or white(grey stigma)
O5	7	17.5	24.2	20.8 ± 2.3	Yellow or white(grey stigma)
O6	4	21.0	23.6	22.5 ± 1.3	Pale yellow (dark grey stigma)
O7, 1985*	10	15.7	23.0	19.8 ± 2.6	Pale yellow (dark grey stigma)
O7, 1986*	20	15.5	23.5	19.2 ± 2.1	Pale yellow (dark grey stigma)
S. microcephalus (SC)					
M1, 1987*	30	12.0	18.5	14.8 ± 1.7	Yellow
M1, 1988*	12	12.7	17.2	15.2 ± 1.3	Yellow
S. tenerrimus (X)					
T1	17	22.6	37.3	29.1 ± 4.9	Yellow-orange
T2	5	28.0	29.8	28.7 ± 0.7	Brigth yellow
T3	21	18.7	27.5	23.7 ± 3.0	Brigth yellow
T5	5	28.2	37.2	32.6 ± 3.8	Brigth yellow
T7	15	22.0	33.0	27.5 ± 3.0	Brigth yellow
T9	5	28.3	34.4	31.5 ± 2.4	Brigth yellow
S. asper subsp. *asper* (SC)					
A2	5	16.5	20.6	18.4 ± 1.6	Yellow (grey stigma)
A3	10	18.0	20.2	18.6 ± 1.2	Yellow (grey stigma)
S. maritimus (X)					
R1	21	22.5	37.5	33.3 ± 3.8	Yellow-orange
R5	31	17.0	34.5	27.8 ± 4.1	Yellow-orange
S. aquatilis(X)					
Q1	43	19.5	28.6	23.1 ± 2.6	Yellow
Q2	22	17.5	29.5	23.6 ± 3.8	Yellow
Q3	6	20.4	26.4	23.9 ± 2.8	Yellow
S. crassifolius (X)					
C1 *	23	19.0	28.0	23.8 ± 2.1	Yellow
S. x*novocastellanus* (X)					
N1	6	20.5	27.7	24.6 ± 2.3	Yellow
N2	6	23.1	33.5	28.5 ± 4.0	Yellow
S. pustulatus (X)					
P1	25	23.9	32.5	27.9 ± 2.7	Yellow-orange
A. bulbosa subsp. *bulbosa* (X)					
B2, 1987*	36	25.0	36.5	30.6 ± 3.3	Yellow-orange
B2, 1988*	30	26.2	36.5	30.8 ± 3.2	Yellow-orange

Table 5. Blooming duration of the flower heads in the Iberian taxa of *Sonchus* and *Aetheorhiza*. n, the number of capitula tested; days of exposure, the number of capitula for each period of days; n fl./head, number of florets included in the inflorescences, the mean value and the range (see also Table 3, with a different set of measurements); SC, self-compatible; X, xenogamous, probably self-incompatible.

SAMPLE	date	n	days of exposure				fl./head	
			1	2	3	4	$\bar{x}$	range
S. oleraceus (SC)								
O4	May 1986	10		9	1		143	(125-175)
O5	Jume 1985	7	4	3			144	(112-166)
O6	May 1986	6		6			129	(112-164)
O7	June 1985	10	8	2			166	(92-248)
S. tenerrimus (X)								
T1	June 1985	4		2	2		69	(57-79)
T1	May 1986	5			4	1	99	(80-113)
T2	June 1985	6		4	2		59	(57-66)
T3	May 1985	12		2	10		79	(55-98)
T5	June 1986	6		4	2		59	(50-72)
T7	June 1986	15		10	3	2	79	(63-115)
T8	June 1985	5		5			67	(61-74)
T9	May 1985	12		2	10		87	(72-111)
S. asper subsp. *asper* (SC)								
A3	May 1986	10	2	8			262	(226-299)
A4	May 1986	15	1	13	1		183	(114-225)
S. maritimus (X)								
R1	Aug.-Sept.1985	9		4	5		172	(145-197)
R3	Aug.-Sept.1985	5		3	2		140	(140-160)
R4	July-Aug.1986	8		7	1		135	(113-189)
R5	July-Aug.1986	14		8	6		128	(98-172)
S. aquatilis (X)								
Q1	July-Aug.1986	12		10	2		65	(45-85)
Q2	Aug.-Sept.1986	9	1	8			85	(86-101)
Q3	July-Aug.1986	4	1	3			68	(52-80)
S. x*novocastellanus* (X)								
N1	Aug.-Sept.1985	7		6	1		116	(73-110)
N2	July-Aug.1986	4		1	3		145	(139-152)
S. pustulatus (X)								
P1	May 1986	10			8	2	63	(45-69)
A.bulbosa subsp. *bulbosa* (X)								
B1	May.1986	4			2	2	72	(52-97)
B2	May.1986	3			2	1	76	(59-97)
B2	March.1988	12		1	9	2	100	(72-120)

Wyatt 1986). In the species studied, the florets are perfectly hermaphroditic and there is no spatial handicap for self-fertilization. As is general in *Asteraceae*, they show protandry which contributes to cross-pollination but does not prevent self-fertilization (Knuth 1908, Müller 1883). The data here presented supports this statement, since flowering duration is very short, and dichogamy (protandry in this case) is incomplete (Lloyd & Webb 1986). Since all our attempts to carry out artificial self-fertilization in basically allogamous taxa failed, the existence of a self-incompatibility system must be postulated, probably of the sporophytic type as has been indicated in several species of the family *Asteraceae* (Hughes

& Babcock 1950, Gerstel 1950, Crowe 1954, Kirmam 1963, cited from Nettancourt 1977, Brewer 1968, Imrie & al. 1972, Drewlow & al. 1973, Ronald & Ascher 1975). However, in basically xenogamous taxa we found some individuals capable of yielding fruits in bagged flower heads. They were probably plants in which the self-incompatibility reaction fails or is weak. Fruit set in freely pollinated flower heads has been remarkably high in general. Sutherland & Delph (1984) found an average of 22.1 % among data from 187 species of self-incompatible plants, which is clearly lower than the results presented here, except for *Sonchus pustulatus*.

In 4 taxa the level of fruit set in bagged flower heads is usually high and no self-incompatibility system appears to operate. The low levels of self-fertilization found in some populations of *S. asper* (from Rioturbio: A4 and Bienservida - Villaverde: G1) may be due to ecotypically differential reaction to the physical conditions in the experimental garden. The observed increase of fruit set in freely pollinated flower heads (particularly notable in *S. asper*) is thought to be due to pollinator activity and to reflect fertilization by foreign pollen. In contrast, Ottaviano & al. (1983) found that in autogamous strains of maize the pollen tubes of the plant's pollen grow faster than those of foreign pollen as a result of a natural selection, so that xenogamy is considered a rare event. Our own results show that the situation in *Sonchus* is different.

Many floral and biological characteristics are linked to the mode of reproduction. Some authors have described differences in related cross- and self-pollinated taxa (Ornduff 1969) or characteristics of self-pollinated colonizing species (Allard 1965, Baker 1974, Stebbins 1957). In the first place, life cycle and mode of sexual reproduction are clearly correlated. It has been shown that colonizing species are usually annuals and self-compatible. Sutherland (1986) found a significant relationship between breeding system and life form in a sample of 447 species of flowering plants. Among the species studied here, all perennials are basically xenogamous, whereas annual to biennial, weedy species show high levels of self-fertility. This general trend has been found in many different plant groups; for example in the *Plumbaginaceae* (Baker 1966), in the *Biscutella* (*Brassicaceae*, Olowokudejo & Heywood 1984), *Carduus* (*Asteraceae*, Devesa & Talavera 1981), *Eupatorium* (*Asteraceae*, Baker 1967), *Leavenworthia* (*Brassicaceae*, Lloyd 1965), *Melilotus* (*Fabaceae*, Sano 1977), *Damasonium* and *Baldellia* (*Alismataceae*, Vuille 1987a, 1987b) and in different subspecies (Vuille 1987b) or varieties and strains of a single species, as in *Baldellia ranunculoides* (*Alismataceae*, Vuille 1987b), in *Oryza perennis* (*Poaceae*, Oka & Morishima 1967) and in *Picris echioides* (*Asteraceae*, Baker 1974)

Features of floral morphology and biology are often indicative of the mode of sexual reproduction. Sometimes they determine the sexual system, but in plants without non-specific pollinators and/or without effective separation of pollen presentation and stigma exposure, as in the group studied here, they provide mechanisms of attraction. Among the most important such characters are blossom size and colour, flowering duration and P/O index, which is related to pollination efficiency.

The flower head size during anthesis may determine insect attraction. Table 4 shows that the diameter of fully expanded flower heads is larger in the allogamous taxa than in the self-compatible ones. Flower size and reproductive system were found to be correlated in *Arenaria* (*Caryophyllaceae*, Wyatt 1984), *Baldellia* (*Alismataceae*, Vuille 1987b), *Githopsis* (*Campanulaceae*, Morin 1983), *Leavenworthia* (*Brassicaceae*, Lloyd 1965), *Melilotus* (*Fabaceae*, Sano 1977), *Senecio* (*Asteraceae*, Gibbs & al. 1975), etc. This is probably a general feature in many evolutionary lines. Flower colour also acts as an insect attractant in association with blossom size. In *Sonchus*, many self-fertile taxa have pale yellow flowers.

Table 6. Observed daily exposure of flower heads to pollination in Iberian taxa of *Sonchus* and *Aetheorhiza*; n, number of flower heads observed; exposure, the range of exposure times observed (in minutes) with their mean values ($\bar{x} \pm s$); *, observations made in the wild; SC, self-compatible; X, xenogamous probably self-incompatible.

SAMPLE	date	n	exposure (min)	$\bar{x} \pm s$
S. oleraceus (SC)				
O1 *	23 March.1988	18	156 -339	206 ± 39.1
O6	10 May 1986	4	148 -210	168 ± 28.9
S. microcephalus (SC)				
M1 *	23 March.1988	12	135 -249	198 ± 37.4
S. tenerrimus (X)				
T1	10 May 1986	12	273 -546	346 ± 76.3
T9	10 May 1986	5	228 -333	274 ± 44.4
S. asper subsp. *asper* (SC)				
A2	10 May 1986	5	195 -225	209 ± 10.8
A3	10 May 1986	10	160 -244	205 ± 25.5
S. maritimus (X)				
R5	August 1986	5	183 -259	234 ± 44.1
S. aquatilis (X)				
Q1	August 1986	5	350 -435	380 ± 30.7
A. bulbosa subsp. *bulbosa* (X)				
B2 *:				
In the sun	23 March 1988	20	250 -570	367 ± 71.4
In the shade	23 March 1988	10	420 - 655	530 ± 68.6

It would however be desirable to consider flower colour as viewed by the insect eye before drawing definitive conclusions. The duration of exposure of flowers and flower heads is a very important factor since a long period of exposure increases the chances of cross-pollination. Table 5 shows that in the taxa studied, the flower heads are exposed for 1 - 4 days. These values are similar to those (1 - 3 days) observed by Estes & Thorp (1975) in *Pyrrhopappus carolinianus* (*Asteraceae*: *Lactuceae*), but are low in comparison with those indicated by Primack (1983, 1985) for some *Asteraceae* from Chile and New Zealand, where the flower heads are exposed for 3 - 15 days. Observations of this kind are unfortunately scarce in the literature surveyed. The xenogamous taxa here studied spend more days in exposing their flower heads, in spite of the lower number of florets per head, than their autogamous counterparts (Table 5). Primack (1985) found evidence to the same effect in *Calandrina* (*Portulacaceae*), as did Wyatt (1984) in *Arenaria uniflora* (*Caryophyllaceae*) and Morin (1983) in *Githopsis* (*Campanulaceae*). Our data also demonstrates that the period during which flower heads are accessible daily to insects is shorter in self-compatible taxa than in xenogamous ones (Table 6). Since presentation of pollen grains and exposure of stigma occur on the same day in an individual floret, the level of dichogamy is relatively low in our plants. The dichogamy barrier is further lowered by an increase in the number of florets that are simultaneously functional within a capitulum. Successful autogamy is therefore enhanced by a combination of high number of florets per head with a short exposure period for individual heads -exactly what we find in autogamous species.

P/O index is clearly correlated with breeding system, although high levels of variation have been found among taxa with similar systems. It is noteworthy that the position of a floret within the capitulum affects its pollen grain content: the number of pollen grains is lower in outer florets than in the central ones. This decrease seems to be gradual, so that the pollen grain number in intermediate florets is usually close to the average between the extremes. Differences in P/O ratio within the same inflorescence have been described in *Lamium amplexicaule* (*Lamiaceae*, Lord 1980), but in this taxon they are related to changes in the sexual system.

In our case the differences are hard to explain, but may be considered as pertaining to the overall sexual function of the composite flower head, bearing in mind that in many taxa of the *Asteraceae* the outer florets are exclusively female. Differences in the reproductive system imply fundamental differences in life strategy. Autogamous plants are usually annual and behave as colonizers and weak competitors (Allard 1965, Willson 1983).

Quick germination allows them to colonize disturbed environments effectively, so that they are considered "r" strategists (Solbrig 1976), as is the case of *Sonchus oleraceus* and *S. asper*, two of the most widespread weeds. In contrast, basically allogamous taxa are often perennials that engender vigorous offspring with a long life cycle, usually occupying well-defined niches. Exceptions do occur however: for example, many populations of *S. tenerrimus* behave as active colonizing weeds in the Mediterranean region.

Appendix. — Origin of the material (and voucher specimens)

Taxa	Origin of the material	Identification code
Sonchus sect. *Sonchus*		
S. oleraceus		
	Cádiz: Sancti Petri (SEV 126623)	O1
	Ciudad Real: Valdepeñas (SEV 126624)	O2
	Coruña: Ferrol, Playa de Doniños (SEV 133009)	O3
	Gerona: Bruguera (SEV 126459)	O4
	Granada: Sierra Nevada (SEV 126482)	O5
	Murcia: Calasparra (SEV 126469)	O6
	Sevilla: Sevilla (SEV 126485)	O7
	Valencia: Cullera - Favareta (SEV 126470)	O8
S. microcephalus		
	Cádiz: Sancti Petri (SEV 126496)	M1
	Granada: Calahonda (SEV 126500)	M2
S. tenerrimus		
	Almería: Cabo de Gata (SEV 120972)	T1
	Almería: Lucainena de las Torres (SEV 120974)	T2
	Barcelona: Valcarca - Garraf (SEV 120976)	T3
	Cádiz: Cabo Roche (SEV 120977)	T4
	Cádiz: Olvera, Peñón de Zaframagón (SEV 120989)	T5
	Granada: Almuñécar - Salobreña (SEV 120980)	T6
	Granada: Calahonda - Castell de Ferro (SEV 120982)	T7
	Málaga: Igualeja (SEV 120984)	T8
	Murcia: Moratalla, Puerta de Moratalla (SEV 120985)	T9
	Valencia: Embalse de Loriguilla (SEV 120989)	T10
	Zaragoza: Muel (SEV 120990)	T11

Taxa	Origin of the material	Identification code
Sonchus sect. *Asperi*		
S. asper subsp. *asper*		
	Huelva: Hinojos (SEV 126473)	A1
	Huesca: Lanavé (SEV 126453)	A2
	Murcia: Calasparra (SEV 126488)	A3
	Santander: Rioturbio (SEV 126625)	A4
	Sevilla: Salteras (SEV 119569)	A5
	Sevilla: Villanueva del Río y Minas (SEV 119570)	A6
S. asper subsp. *glaucescens*		
	Albacete: Bienservida - Villaverde (SEV 126463)	G1
	Málaga: El Burgo - Alora (SEV 126466)	G2
Sonchus sect. *Maritimi*		
S. maritimus		
	Alicante: Elche (SEV 121008)	R1
	Almería: Punta Entinas (SEV 121009)	R2
	Baleares: Palma de Mallorca (SEV 121013)	R3
	Madrid: Aranjuez, Mar de Ontígola (SEV 121012)	R4
	Zaragoza: Laguna de Gallocanta (SEV 121015)	R5
S. aquatilis		
	Gerona: Sárdenas, ermita de S. Aniol (SEV 121021)	Q1
	Granada: Riofrío (SEV 121020)	Q2
	Jaén: Sierra de Cazorla (SEV 121001)	Q3
	Valencia: Silla, La Albufera (SEV 121002)	Q4
S.crassifolius		
	Ciudad Real: Laguna de las Yegüas (SEV 126626)	C1
	Toledo: Lagunas del Altillo (SEV 119568)	C2
	Zaragoza: Laguna de Gallocanta (SEV 121007)	C3
S. xnovocastellanus		
	Ciudad Real: Alcázar - Villafranca (SEV 126521)	N1
	Zaragoza: Laguna de Gallocanta (SEV 126627)	N2
Sonchus sect. *Pustulati*		
S. pustulatus		
	Almería: Almería (SEV 126629)	P1
Genus *Aetheorhiza*		
A. bulbosa subsp. *bulbosa*		
	Cádiz: Puerto Gális (SEV 125406)	B1
	Cádiz: Sancti Petri (SEV 125402)	B2
	Minho: Viana do Castelo (SEV 125409)	B3

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