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Autumnal and winter pollination adaptations under Mediterranean conditions

Abstract

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The Mediterranean autumn and winter pose environmental constraints on pollination which result in a low frequency of flowering species as well as pollinators. The various floral adaptations by which plants overcome the harsh pollination environment are discussed in the light of new observations and existing literature.

Introduction

The Mediterranean autumn (September to November) is characterized by high temperatures at the end of a long drought period starting in May or June (Anonymous 1957). The majority of species flowering in autumn are geophytes with hysteranthous leaves (Dafni & al. 1981a-b). The Mediterranean winter (December to February) is characterized by spells of rain (rarely hail or snow) accompanied by relatively low temperatures (Anonymous 1957). Geophytes are prominent among plants flowering in this season; the first flowering annuals are rarely seen before December or January (Shmida & Dafni 1989). Relatively few insects, mainly solitary bees, are active – in species as well as in numbers (Herrera 1982; Shmida & Dukas 1990; Dafni & O'Toole 1994; Petanidou, pers. comm.). Generally, in any single habitat only 2-4 species of solitary bees and 1-3 species of *Syrphidae* are present (Shmida & Dafni 1989), as compared with 100-200 species of solitary bees and 5-30 species of hover flies at the peak of the spring flowering season (O'Toole, pers. comm.).

Possible advantages of autumn and winter flowering

The storage organs in geophytes provide them with a potential ecological advantage: the ability to separate between the vegetative and reproductive phases and bloom beyond the growing season (Burtt 1970; Dafni & al. 1981a-b). Many geophytes in the

Mediterranean region flower in spring, like most other plants. However, they are relatively prominent when flowering between September and February, when other plants in flower are rare (Shmida & Dafni 1989). The possible advantages of flowering outside the main season (spring) are twofold:

- A shift to the autumn and winter may be advantageous in terms of competition for pollinators (Burtt 1970; Dafni & Werker 1982; Dafni & Dukas 1986). It has been assumed that due to reduced competition the visitation frequency per flower is higher when flowers are scarce.
- The few simultaneously flowering species and the small number of pollinators may enhance the chances for a "non-mixed" visit in the same foraging bout (Shmida & Dafni 1989). This will lead to a high degree of "forced" pollinator constancy and in a low rate of improper pollen transfer (sensu Rathcke 1983).

The present paper is an attempt to elucidate the various adaptations which may help flowers to overcome the adverse conditions of the Mediterranean autumnal and winter pollination environment.

Flower mechanisms and adaptations

Discovery advertisement

The factors which determine the nature of the "pollination market" (Selten & Shmida 1991) change through the year, thus imposing different selective pressures on advertisement (flower size) and reward in the various seasons (Cohen & Shmida 1993). In the autumn there is a "truncated pollination market", characterized by relatively few flowering species pollinated by a reduced number of pollinators, mainly small bees and hover flies. Typical of this season are the showy flowers of large, stemless geophytes (*Colchicum* and *Crocus* species) that appear in low abundance. Shmida & Dafni (1989) present

Table 1. Visitors of autumnal flowers and their behavioural patterns. – Sources: Dafni & Werker (1992, on *Sternbergia*); Dafni & Dukas (1986, and unpublished, on *Urginea*); and Dafni (unpublished).

Species	*Floral adaptations*	*Pollinator*	*(n°)*	*pollen gathering %*	*nectar sipping %*	*pollen & nectar %*	*stigma hits %*
Colchicum stevenii	heteranthery (short and long)	solitary bees	(275)	33.0	86.5	25.0	38.8
	several types of stigma length	syrphids	(193)	82.8	0.01	0.0	59.8
	semi-concealed nectar	*Apis mellifera*	(55)	78.1	30.7	12.7	33.3
Pancratium parviflorum	osmophores on the perigon	*Nomioides* sp.	(85)	100.0	0.0	0.0	17.0
	concealed nectar	*Amegilla* sp.	(45)	87.0	13.0	6.0	23.0
Sternbergia clusiana	heteranthery	solitary bees	(21)	42.8	76.2	23.8	23.8
	osmophores on perigon tips	syrphids	(78)	2.6	93.5	0.0	17.9
	concealed nectar	*Apis mellifera*	(67)	37.3	97.0	25.3	35.8
Urginea maritima	exposed pollen and nectar	*Apis mellifera*	(59)	0.0	0.0	100.0	93.2
		various flies	(50)	0.0	100.0	0.0	4.0
		Polistes gallicus	(59)	0.0	100.0	0.0	96.6
		Vespa orientalis	(50)	0.0	100.0	0.0	84.0
		Nomioides sp.	(52)	0.0	0.0	100.0	1.9
		Hyalaeus sp.	(61)	0.0	0.0	100.0	1.6
		Lasioglossum sp.	(70)	28.6	0.0	100.0	0.0

data which indicate that average flower size in autumnal geophytes is larger than in plants flowering in any other season. Because flowers in autumn are few in number, the mean distance between them, in the field, is large. Thus the situation is not one of "competitive advertisement" but rather of "discovery advertisement".

"Competitive advertisement" occurs in the spring where an abundance of flowers compete on the market for a limited number of pollinators. Each species tries, by the colour, size and arrangement of the flowers on the plant, to attract more pollinators than do other species.

In the autumn large flowers act as "discovery advertisement", as signposts that can be detected by pollinators from a distance. The low nectar quantities of *Colchicum* and *Crocus* species, or *Sternbergia clusiana*, indicate that their large flowers are a means of "discovery advertisement", not "competitive advertisement". In a competitive market one may expect a higher investment in reward than in advertisement, meaning that even large flowers will offer a high reward (Milgrom & Roberts 1986; Cohen & Shmida 1993).

Reward partitioning

Various species which bloom at the end of the summer and whose flowering season extends into the autumn (after the first showers) show adaptations to simultaneous attraction of various pollinators that exploit different rewards (nectar or pollen) or/and forage on various parts of the flower. The compartmentalization of rewards may be achieved by variation in anther length (heteranthery) and/or by simultaneous attraction of unrelated pollinators.

Colchicum stevenii. - This species with synanthous leaves flowers in November, after the first showers. The whitish-lilac flowers (2-5 cm long) are arranged in dense clumps of 2-10 on the plants (n° of plants = 25). In general only 1-2 flowers per plant are blooming at any one time. The whole flowering season lasts 31 ± 5 days (n° = 5). The longevity of an individual flower is 6.1 ± 2.4 days (n° = 100) if not damaged by rain. The nectaries are borne on the axis between the filament insertion and the base of the corresponding perigon lobe. Nectar is scarce (≈ 0.1 μl per nectary) and dilute (20.3 ± 6.8 % sucrose equivalent, n° = 100). Pollen is ample.

Morphological analysis of various populations shows that different floral types occur together in varying proportions, as follows: long stigmas (high above the anthers), medium stigmas (± in the height of the anthers), short stigmas (below the anthers), male flowers (no stigmas) and female flowers (no functional anthers). Various pollinators forage on the flowers, showing different patterns of reward harvesting (Table 1); the chances for pollination depend on the flower type (Table 2).

Pancratium parviflorum. - This species has hysteranthous leaves, and flowers in September to November; it has whitish flowers (2.5-4 cm long) that are borne in umbels by 4-12. The flower presents nectar at the base of the floral tube (originating from septal nectaries on the ovary). On the average the amount of nectar is 2.3 ± 1.2 μl (n° = 20) and contains 19.3 ± 7.3 % sucrose equivalent (n° = 20). The flowers are not fragrant to humans, but the perigon lobes are equipped with glandular hairs at the tip and outer margin that react positively with neutral red and, thus, may be regarded as osmophores.

Table 2. Percentage of visitors of *Colchicum stevenii* touching the stigmas, out of the total number of visits (Σ n°) of the different floral types (cumulative results, 7 Nov to 5 Dec 1988, from 6 populations in Israel).

Pollinator	Σ *n°*	*long stigmas*	*medium stigmas*	*short stigmas*
Solitary bees	416	20.9	74.2	89.1
Syrphids	419	65.7	68.3	06.4
Honey-bees	146	31.6	87.9	92.6
Σ n°		533	363	85

Each flower lasts 1.2 ± 1.3 days (n° = 50), but most of the pollen and nectar may be harvested during the first hour of flower opening, which may occur at any time during the day. The flowers are exploited by various pollinators showing different patterns of reward collecting but similar pollination efficiency, as can be concluded from the percentage of stigma hits (Table 1).

Sternbergia clusiana (Dafni & Werker 1982). – This is a species with hysteranthous leaves which flowers before the rains (August to October). The stamens are borne in two whorls (heteranthery); the outer dehisce earlier than the inner, and their length (4.0-4.3 cm) exceeds that of the inner ones (3.0-3.2 cm). A large amount of pollen accumulates at the bottom of the flower cup. Nectar is secreted by septal nectaries at the top of the ovary. Since the ovary is located underground, the points of secretion are separated from the point where the nectar is presented, viz., the mouth of the perigon tube. The various pollinators (Table 1) show different patterns of reward exploitation and stigma hits.

Syrphids are the most common visitors (47 %), but are relatively inefficient as pollinators due to the low percentage of hits to the stigma (32.6 %). Honey-bees account for 40.4 % of the visitors and 55.8 % of possible pollination events. Solitary bees represent 12.7 % of the visitors but only 11.6 % of possible pollination, according to the number of times they hit the stigma.

The syrphids are attracted by special glandular hairs at the tip of the outer perigon segments, which function as osmophores and probably direct the flies into the flower bowl where they harvest pollen on the longer stamens. The bees visit the nectar presentation site and shorter stamens, and in addition collect pollen shed on the flower bottom. In this way, both pollinators are attracted simultaneously, exploit different resources, and perhaps avoid competition.

Urginea maritima (Dafni & Dukas 1986). – This is an hysteranthous species which flowers from mid-August to the beginning of October and has whitish flowers c. 10 mm across. The nectar (4.2 ± 1.8 µl per flower; n° = 50) is secreted from three septal nectaries located on the ovary and has a concentration of 15.3 ± 7.1 % of sucrose equivalent (n° = 50). It is drained to the base of the ovary and accumulates there.

The pollen is exposed immediately upon anthesis (at about 1 a.m.) and is quite conspicuous. Self- and wind-pollination as well as insect-pollination (Table 1) have been observed. Although a large array of insects visit the flowers, only few of them can be regarded as potential pollinators (Table 1):

Table 3. The influence of rain on flowers, and the plants' adaptations.

Rain effect	*Plant adaptation*	*Example*
Damage to pollen	flower opening only in good weather	*Crocus hyemalis*
	pendulous flowers	*Muscari* spp.
	pollen germination inhibitors	*Primula* spp.
	germination in rain water	*Narcissus serotinus*
	hydrophobic floral parts	*Narcissus tazetta*
Mechanical damage	flower opening between showers	*Colchicum stevenii*
	few simultaneous flowers	*Crocus hyemalis*
	long flowering season	*Colchicum* spp.
Nectar dilution	hairs inside the flower tube	*Mandragora autumnalis*
	pendulous flowers	*Bellevalia* spp.
	unwettable rims	*Narcissus tazetta*

Apis mellifera collects both pollen and nectar, but only a limited amount of the latter is taken per visit. *Polistes gallicus* bears few or no pollen grains. However, since it is very common and because of its dimensions it is quite likely to ensure pollen transfer to the stigma and can thus be regarded as a pollinator. *Vespa orientalis* pays few visits to the flowers. Because of its hairiness, however, it can bear numerous pollen grains on its body and may act as an efficient pollinator. Three solitary bee genera *(Nomioides, Hylaeus, and Lasioglossum)* show high activity but cannot be considered as pollinators. Their body size is about 5 mm, while the stigma is 11 mm above the nectar droplet.

Flowers and rain

The rainy season is considered by many authors as unfavourable for flowers and pollinators alike. Rain may impose several constraints on pollination success:

- contact with free water can cause irreversible damage to pollen grains (Kerner 1886-1891; Percival 1955);
- pollen grains of many species explode when exposed to rain drops (Lidforss 1896; Kerner 1886-1891; Daumann 1970; Eisikowitch & Woodell 1975; Corbet & Plumridge 1985);
- rain may prevent pollen germination on the stigma (Akamine & Girolani 1959);
- rain may reduce pollen availability for collecting, notably in buzz-pollinated species (Corbet & al. 1988);
- there is a risk of nectar dilution (Müller 1873; Eisikowitch 1979; Corbet 1990);
- rain can cause mechanical harm to flowers (Pacini & Franchi 1984);
- continuous rains may reduce the number of pollen-bearing insects and, thus, affect the reproduction potential of the species (Pacini & Franchi 1984);
- bad weather may cause a scarcity of pollinators (Pacini & Franchi 1984; Eisikowitch & al. 1992).

Table 4. Pollen germination (%) at various concentrations of sucrose solution, and data on flower position. – n° = 100 × 6 pollen grains; B = pollen burst; ± = standard deviation.

	Sucrose concentration (%)							*Flower position*
	0	5	10	20	30	40	50	
Summer species:								
Dianthus pendulus	2.7 ± 3.2	7.8 ± 2.5	16.7 ± 2.7	43.0 ± 7.0	56.7 ± 7.0	57.0 ± 6.8	20.5 ± 2.5	horizontal
Foeniculum vulgare	B	B	B	B	34.8 ± 5.0	38.1 ± 2.7	31.5 ± 1.5	erect
Ceratonia siliqua	B	B	B	B	38.2 ± 3.0	24.5 ± 6.9	18.5 ± 4.6	erect
Pancratium parviflorum	B	B	B	B	51.7 ± 8.0	20.6 ± 2.4	9.4 ± 0.7	erect
Hypericum triquetrifolium	26.5 ± 6.5	46.0 ± 4.2	52.7 ± 2.9	65.3 ± 6.3	75.7 ± 3.7	46.0 ± 6.8	26.3 ± 5.6	erect
Atractylis comosa	3.0 ± 1.1	2.2 ± 1.5	2.7 ± 2.1	3.3 ± 3.9	2.8 ± 1.3	7.7 ± 2.1	60.2 ± 2.1	erect
Autumn and winter species:								
Crocus ochroleucus	8.7 ± 2.3 B=36.0±6.2	6.0 ± 2.8 B=45.0±9.2	7.1 ± 1.7	18.2 ± 7.2	5.9 ± 1.5	6.2 ± 3.0	4.7 ± 1.6	erect
Smilax aspera	24.3 ± 7.8	32.2 ± 2.6	6.2± 2.6	2.5 ± 1.8	0.2 ± 0.4	0.0	0.0	erect
Scilla autumnalis	1.54 ± 5.6	32.4 ± 7.2	56.2 ± 9.1	24.8 ± 10.8	2.8 ± 2.2	2.1 ± 2.2	0.0	erect
Cyclamen persicum	9.2 ± 4.1	20.1 ± 5.2	45.6 ± 10.1	51.7 ± 16.1	32.3 ± 8.9	18.1 ± 4.1	8.3 ± 3.7	pendulous
Colchicum stevenii	20.8 ± 7.8	69.5 ± 7.5	80.5 ± 9.1	79.8 ± 12.4	66.0 ± 8.9	23.0 ± 3.6	12.0 ± 3.4	erect
Crocus hyemalis	7.5 ± 1.9	11.8 ± 4.5	15.2 ± 3.1	8.8 ± 3.0	6.2 ± 1.6	1.8 ± 1.7	0.7 ± 0.4	erect
Narcissus serotinus	50.8 ± 4.8	35.8 ± 10.3	44.7 ± 10.0	27.3 ± 11.4	5.0 ± 2.1	3.7 ± 2.1	1.1 ± 0.7	erect
Muscari parviflorum	0.0	0.0	0.0	9.7 ± 0.6	44.7 ± 1.2	53.3 ± 1.9	54.6 ± 3.1	erect
Narcissus tazetta, hill ecot.	29.2 ± 14.2	39.3 ± 17.9	52.3 ± 22.8	55.2 ± 18.9	49.7 ± 18.6	20.7 ± 17.6	0.0	± horizontal
id., marsh ecotype	18.0 ± 9.1	29.2 ± 8.4	54.9 ± 10.2	72.0 ± 8.3	81.9 ± 10.4	57.5 ± 19.0	0.0	± horizontal

Plants may show several different adaptations, either morphological (1-2), or physiological-developmental (3-5), or chemical (6-7), or other (8) that can be interpreted as reducing possible rain damage (Table 3):

1. pendulous flowers, in which the flower mouth points downward or to the side (*Narcissus tazetta, Scilla cilicica, Bellevalia, Muscari,* and *Leopoldia* species);
2. floral parts which protect the inner organs from direct exposure to the rain (Corbet 1990), e.g., upper corolla lip in *Lamium amplexicaule,* corona in *Narcissus tazetta,* and tuft of dense hairs in the floral tube of *Mandragora autumnalis;*
3. cleistogamy (*Lamium amplexicaule,* Eisikowitch 1979);
4. closure of the flower during rain (Kerner 1886-1891), e.g., *Crocus hyemalis, Anemone coronaria, Stellaria media;*
5. resistance of pollen grains to humidity (Eisikowitch & Woodell 1975);
6. presence of pollen germination inhibitors during rain (Zeroni & Galil 1965; Eisikowitch & Woodell 1975);
7. unwettable rims that repel water around the narrow flower tube (Corbet 1990), e.g., the corona in *Narcissus tazetta* and *N. serotinus;*
8. vigorous vegetative reproduction and reduction in flower production (e.g., *Muscari parviflorum,* Eisikowitch 1979).

Pollen grain behaviour under varying osmotic conditions

Autumn- and winter-flowering plants are exposed to rain, which may affect the pollen grains. To study the behaviour of pollen grains under rain conditions (simulated by distilled water) and on the stigma (simulated by sucrose solutions), autumn- and winter-flowering plants were compared to summer-flowering ones. The pollen grains of various species were germinated at sucrose concentrations of 0 %, 5 %, 10 %, 20 %, 30 %, 40 %, and 50 %. According to the results (Table 4), one may recognize three patterns of pollen grains behaviour:

1) burst in distilled water as well as in low sucrose concentrations, optimum germination in high concentrations (30-40 %), e.g. in *Dianthus pendulus* (Fig. 1), *Foeniculum vulgare, Ceratonia siliqua, Pancratium parviflorum, Hypericum triquetrifolium,* and *Atractylis comosa.* All these species are typical summer-flowering species, their flowering period usually terminating before the onset of the rainy season (October or November);

2) low (0-10 %) germination in distilled water, but no bursting; optimum pollen germination with various sucrose solutions, e.g. in *Crocus ochroleucus, Scilla autumnalis* (Fig. 2), and *Muscari parviflorum.* These species flower at the end of the summer, their flowering period extending into the rainy season;

3) high germination rate (> 30 %) and no bursting in distilled water, low sucrose concentration (10-20 %) for optimal germination, as in *Smilax aspera, Cyclamen persicum, Narcissus tazetta* (both ecotypes), *Crocus hyemalis,* and *Narcissus serotinus* (Fig. 3). These species flower during the rainy season and may therefore face pollen wetting.

According to Lidforss (1896) and Eisikowitch & Woodell (1975), differences in pollen behaviour were to be expected between pendulous and erect flowers, due to the uneven probability of exposure to rain damage. Our results show that pollen behaviour in distilled water and sucrose optimum for germination do indeed reflect the likelihood of the pollen being wetted by rain. It is thus logical to assume that rain-caused pollen damage acted as a selective pressure, resulting in different patterns of pollen resistance to wetting, and different osmotic optima for pollen germination.

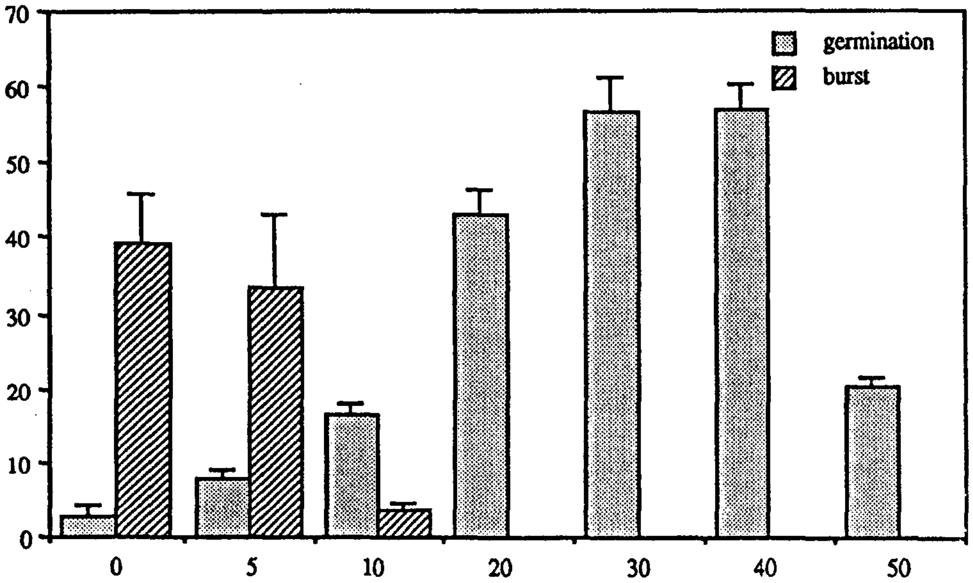

Fig. 1. Germination and bursting (ordinate, in %) of *Dianthus pendulus* pollen in solutions with various concentrations (0-50 %) of sucrose.

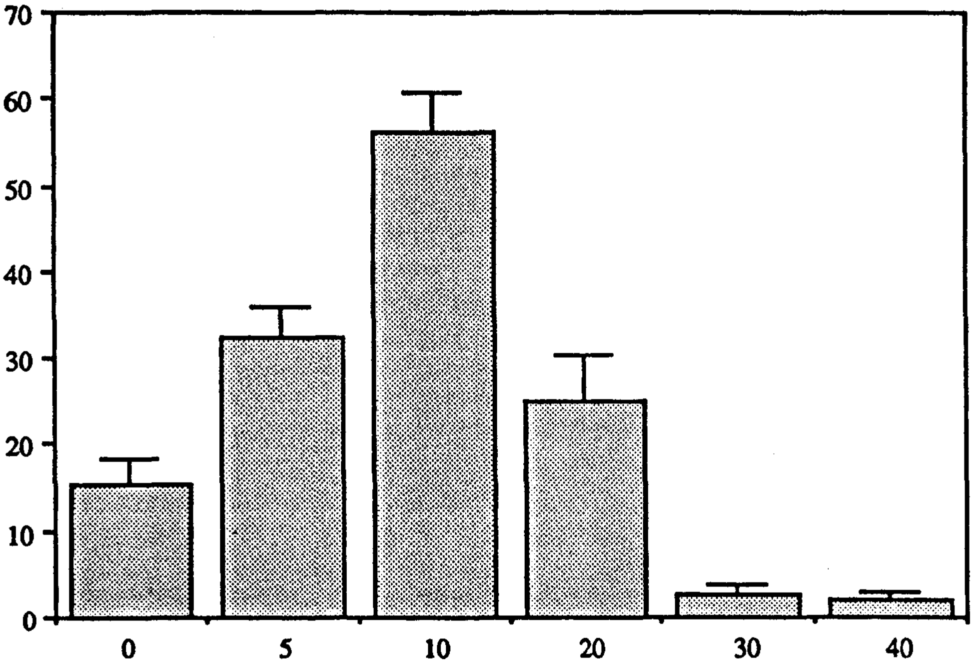

Fig. 2. Germination (ordinate, in %) of *Scilla autumnalis* pollen in solutions with various concentrations (0-40 %) of sucrose.

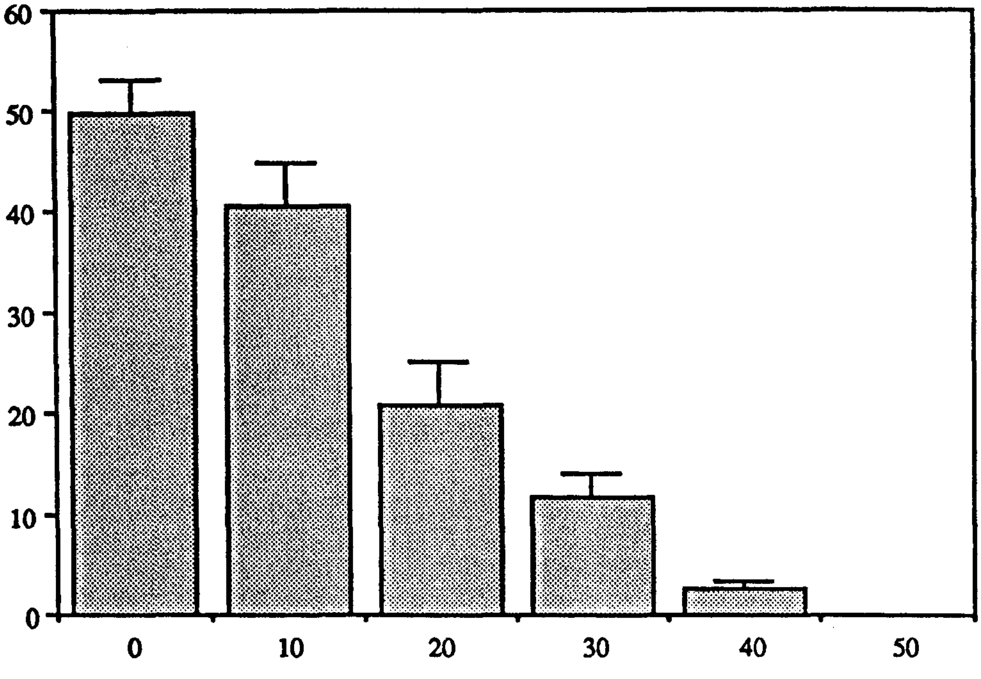

Fig. 3. Germination (ordinate, in %) of *Narcissus serotinus* pollen in solutions with various concentrations (0-40 %) of sucrose.

Discussion

The autumnal and winter pollination market is considered an "oligopolistic market", which implies that pollinators as well as flowers are few (Shmida & Dafni 1989; Cohen& Shmida 1993). These seasons are also harsh from an environmental point of view, as there are risks of exposure to heat (end of the summer, beginning of the autumn) and/or rain (autumn and winter).

An increase in pollination success during a season harsh for insects may be realized by several independent devices: long exposure of flowers, combined pollination mechanisms, wind pollination, and self-pollination (Herrera 1982). All these adaptations can be found in autumnal and winter-flowering species.

Combined pollination mechanisms enable compartmentalization of pollen and nectar in the flower, allowing simultaneous use of floral resources by unrelated pollinators. The efficiency of different pollinators (as inferred from the number of stigma hits) is species-specific (Table 1) as well as flower-type dependent. In the plant species here mentioned, the most frequent visitor is not necessarily the most efficient pollinator. *Urginea maritima* (Dafni & Dukas 1986) exemplifies an extreme case of generalism by combining insect-, self- and wind-pollination. One may conclude that combined pollination mechanisms are a common adaptation to the unpredictable autumnal season, maximizing pollination chances by using all possible pollen vectors.

The large flowers of autumnal and winter-flowering, stemless geophytes seem to be peculiar to the Mediterranean region (Dafni & O'Toole 1994). The appearance of large flowers is explained in terms of "discovery advertisement" (Shmida & Dafni 1989), a choice strategy at a time when there are few species of flowers and insects present at low densities. The most important factor in attracting pollinators over a long distance, in this season, is a large visual signal; this contrasts with the reward-based "competitive advertisement" of spring and early summer.

Our results corroborate the conclusion, by other authors (Hagerup 1950; Eisikowitch & Woodell 1975; Heslop-Harrison 1985), that pollen grains are not as a rule damaged by rain. It was found that pollen behaviour in distilled water and pollen germination at various concentrations of sucrose reflect the probability of rain in the flowering period. The higher the natural probability of being wetted, the lower the damage actual rain will cause.

In conclusion, autumnal and winter-flowering species in the Mediterranean region show some common characteristics, including large flowers, combined pollination mechanisms, pollen germination in rain water, and optimal pollen germination at low concentrations of sucrose solutions. All these features may serve to overcome pollinator scarcity and to reduce rain damage.

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