

**A comparative study of reproduction and biomass allocation between spring and autumn flowering Mediterranean geophytes**

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E-mail [gneeman@research.haifa.ac.il](mailto:gneeman@research.haifa.ac.il)Keywords: Phenology, Hyacinthaceae, *Scilla hyacinthoides*, *Urginea maritima***Abstract**

Spring is the optimal growing season, the peak of flowering and of pollinator abundance in the Mediterranean climate. However, several geophyte species bloom in autumn, before the rainy season, during the driest months of the year. It was suggested that these species evolved from spring flowering species and that the evolutionary driving force was the escape from competition for pollinators. The aim of this work was to test the hypothesis that the shift from spring to autumn flowering season in *Urginea maritima* resulted in some reproductive advantage to this species. This was done by comparing: fruit set, pollen to ovule ratio, seed to ovule ratio, mating systems, effect of supplementary pollination, relative biomass allocation to pollinator attraction (flowers) and reproduction (seeds) in two closely related species: *Urginea maritima*, an autumn flowering species and *Scilla hyacinthoides* a spring flowering species. The results demonstrate an advantage in the efficiency of male function in *U. maritima* over *S. hyacinthoides*. Therefore, we can support the hypothesis that the shift from spring to autumn flowering resulted in a reproductive advantage. However, this shift in flowering season had also cost in higher allocation for pollinator attraction and a lower female reproductive success in *U. maritima* than in *S. hyacinthoides*.

**Introduction**

The geophytes, or in their original name cryptophytes (Raunkaer, 1934), are plants well adapted to extreme conditions of cold or drought and persist because they regenerate from buds, bulbs and rhizomes that are completely buried in the soil (Archibald, 1995). This is a relatively infrequent life form in most vegetation types of the world (Raunkaer, 1934). However, geophytes growing in the Mediterranean and semi-desert parts of Israel comprise 8-17% of the flora (Orshan, 1983; Shmida & Dafni, 1989). Most Mediterranean geophytes are summer dormant, a life habit that can be explained as a drought avoiding mechanism, and is the key for their relative abundance in semi-arid climates (Gali, 1961). The leaves of all these geophytes appear after the beginning of winter rainy season. Production and storage take place mainly during the mild winter and continue as long as local growing conditions are favorable. Leaves usually dry up in late spring, at the beginning of the dry season (Dafni *et al.*, 1981a).

The various species of geophyte species in Israel are flowering almost all year round. Some species flower from the end of summer into autumn, some during winter and others in spring

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and early summer (Shmida & Dafni, 1989). In most geophyte species the leaves emerge immediately after the onset of the rainy season and flowers appear later in the season simultaneously with the leaves. These species, in which the leaves and flowers share a common period are defined to have synanthous foliage (Dafni *et al.*, 1981a). Another distinct ecological group of Mediterranean geophytes is the 'Lily group' that flowers in end summer or autumn, before the first rains, when climatic conditions are most extreme. This group of geophytes is the major component (80%) of all autumn flowering species in Israel (Shmida & Dafni, 1989). All these species, that flower before the onset of the winter rains and do it with no leaves were defined to have hysteranthous foliage (Dafni *et al.*, 1981a). Shortly after the end of flowering, these species disperse their non dormant seeds that germinate soon after the first winter rains (Dafni *et al.*, 1981b).

Spring time is the peak season of flowering for all plant life-forms in Mediterranean areas because of climate conditions, plant life cycle and the abundance of pollinators (Zohary, 1976; Shmida & Dafni, 1989). Correspondingly, the distribution of the number of flowering plant species in Israel has a peak in spring (Auerbach & Shmida, 1987;

Shmida & Dafni, 1989). However, although insect species richness and abundance is greatest during spring, there might be a relative shortage of pollinators per flower. Therefore, spring flowering plants species seem to compete for pollinators by means of advertisement and reward (Cohen & Shmida, 1993).

Competition for pollination was suggested to be one of the selective forces acting on blooming time and blooming of different species in any one ecosystem is thought to have evolved so as to reduce competition for pollination (Mosquin, 1971; Heinrich & Raven, 1972). This idea is also supported by experimental field research showing that the result of competition for pollinators is a reduction in the pollinator visitation rate and disruption of conspecific pollen flow (Gentry, 1974; Waser, 1978, 1979; Pleasant, 1980; Campbell, 1985; Campbell & Motten, 1985). However, Kochmer & Handel (1986) stated that competition can not push species flowering time beyond seasonal boundaries imposed by phylogenetic constraint.

In South Africa, transitional forms, concerning flowering phenology, grow in transition zones from xero-tropical regions to Mediterranean-type climate regions (Letty *et al.*, 1962). This may indicate that flowering season can be modified by selection. Flowering time has been shown to change rapidly under natural regimes, and in cultivated species grown under climatic condition different from those in their area of origin (Waser, 1983).

Hysteranthous (flowering with no leaves) autumn flowering geophytes were proposed to have evolved from synanthous (flowering with leaves) species by delaying flowering time (*Urginea* type) or by advancing it (*Crocus* type) (Dafni *et al.*, 1981b). Hysteranthous foliage in autumn flowering species evolved convergently in some families, and even in some genera like *Cyclamen*, *Scilla* and *Urginea* (Dafni *et al.*, 1981b). In Israel, most of the populations of *Cyclamen persicum* and *Narcissus* sp. flower in winter with synanthous foliage. However, in rocky hot and dry habitats, autumn flowering hysteranthous populations grow (Arroyo & Dafni, 1995).

Plant energy reserves for flowering are stored in many species and expended at an appropriate time, i.e. when flowers can be pollinated adequately (Heinrich, 1975). According to optimal allocation theories, plants adjust phenology and life history patterns to acquire resources when they are cheap,

store them internally, and utilize them when conditions are most favorable (Bloom *et al.*, 1985; Kozlowski, 1992). Reproductive effort, growth, and maintenance are the three parts of plant life history and energy budget with tradeoff relation among them (Willson, 1983). Reproduction may cost in terms of stored energy, current growth, future growth, future reproduction or even survival (Shon & Policanski, 1977; Evenson, 1983; Primack & Hall, 1990).

As mentioned above the autumn flowering species evolved from spring flowering ones. Since conditions in autumn are harsh, such a shift in flowering season seems to contradict optimal allocation theories, unless some ecological advantage was coupled to this process and served as the evolutionary driving force for this transit. Three such advantages were proposed: 1) decreasing competition for pollinators during autumn, 2) reduced risk of seed predation resulting from shorter time in the soil seed bank, 3) lower rate of improper pollen flow as a result of forced pollinators constancy, because there are only very few plant species flowering simultaneously (Dafni *et al.*, 1981b; Shmida & Dafni, 1989). However, no field data are available to demonstrate any actual advantage in any plant species that will support these assumptions.

Related species with similar life habits which grow in the same habitat but with different flowering seasons, allow for comparisons of their different adaptations to the flowering seasons. The aim of this work was to test the hypothesis that the shift from spring to autumn flowering in *Urginea maritima* resulted in some reproductive advantage to this species in comparison to *Scilla hyacinthoides* a closely related spring flowering species.

## Materials and methods

### Studied species

*Scilla hyacinthoides* L. (Hyacinthaceae) is a typical geophyte in open oak woodland of *Quercus calliprinos* and *Q. ithaburensis* found in the northern Mediterranean part of Israel. An adult plant has an underground bulb and a rosette of about 10 leaves (5cmX30cm) that emerge from the ground just after the first winter rains. The scape emerges at the end of February, it grows to a height of about 1m, and is comprised of about 150 high-blue, small (1 cm diameter), open flowers. The flowers are

arranged in whorls and flowering advances upwards with stem elongation. The flowering season is April-May. The flowers are pollinated by honey bees, small solitary bees and flies (pers. observ.). Following seed dispersal, as summer heat begins, all the above ground parts dry up until the beginning of the next rainy winter.

*Urginea maritima* (L.) BAKER. (Hyacinthaceae) is a very common geophyte typical to open fields and dwarf-shrub vegetation. It ranges from the mountains in the northern Mediterranean parts of Israel, throughout the whole country, along the decreasing humidity gradient, down to favorable sites in the Judean Desert and the high mountains of the central Negev. Adult plants have bulbs up to 20 cm in diameter located near soil surface. A rosette of about 10 leaves (10cm x 50cm) that emerge from the ground soon after the first winter rains. The leaves remain green until June when summer heat begins at which time they dry up. However, in the midst of the dry summer, from the end of August, the scape emerges from the dry soil. The scape is about 1.5 m high and supports about 300 white, small (1cm diameter), open flowers. The flowers are pollinated by honey bees, wasps, flies and to some extent, also by wind (Dafni & Dukas, 1986). Fruit ripening is very rapid and the seeds are dispersed by the end of October. Seeds are non-dormant and germinate immediately after the first winter rains.

#### *The study sites and monitoring plants*

The study was carried out in the Upper and Lower Galilee, Israel, under typical Mediterranean climate. *S. hyacinthoides* was studied at Amirim (500m above sea level) and at Alon-Hezilil (200m a.s.l.). *U. maritima* was studied at Shorashim (200m a.s.l.) and Tivon (100m a.s.l.). The sites ranged from 10 km (Tivon) to 30 km (Amirim) from the Mediterranean sea. Thirty plants in Amirim and 40 at all other sites were tagged, numbered and monitored between August, 1990 and June, 1991. Monitoring included: 1) Non destructive measurement of bulb diameter (i.e. by digging to reveal the upper half of the bulb). 2) Counting the number of leaves. 3) Estimating leaf area by copying their shape on paper, cutting the shapes, weighing them multiplying their by the weight of 1cm<sup>2</sup> of paper. 4) Measuring height and diameter of scape. 5) Counting the number of flowers. 6) Counting number of fruits, and the mean num-

ber of seeds in ten randomly chosen fruits from each individual. The number of fruits and flowers were used for calculation of fruit set (Fr/FI). All monitored plants were naturally pollinated.

#### *Pollination treatments*

About 20 plants of each species were numbered. In each plant about 40 flowers were artificially cross-pollinated in the early morning of their first flowering day, as supplementary pollination treatment. These flowers were exposed to natural pollination before and after treatment. Forty untreated flowers on the same plants, served as natural pollination control. Other untreated plants with free naturally pollinated flowers served also as control. Forty flowers on each of 5 plants in both species were bagged to prevent insect visits, and also to check the presence of spontaneous self-pollination or agamospermy. Forty flowers on each of 5 plants of both species were similarly bagged, but artificially cross pollinated in order to validate the effectiveness of the supplementary artificial cross-pollination. Fruit set served as a measure for the efficiency of pollination treatments.

#### *Pollen to ovule ratio, seed to ovule ratio and relative reproductive success*

Just before opening 20 young flowers of *U. maritima* and 40 of *S. hyacinthoides* were collected and preserved in FAA. The carpels were dissected and ovules counted. Two anthers of each flower were opened and the pollen suspended and stained by Aniline Blue in a known volume of liquid. The number of pollen grains were counted in a haemocytometer slide with a known volume and the total number of pollen grains per flower was calculated. Pollen to ovule ratio (P/O) was calculated on a single flower basis. For the calculation of seeds to ovules ratio (S/O), the mean number of seeds per flower in the monitored plants were used. The fecundity, or relative reproductive success (RRS) was calculated ( $RRS = Fr/FI * S/O$ , where Fr/FI is the fruit to flower ratio) (Wiens, 1984).

#### *Biomass allocation*

Ten additional bulbs of each species were obtained from the studied populations during winter. Their diameter was measured and the bulbs were dried in a ventilated oven at a constant temperature of 80° C

for one week, until steady weight was reached for biomass (dry weight) determination. The regression equation between bulb diameter and biomass of these 10 plants was used to estimate the biomass of the bulbs of monitored plants from their diameter that was measured undestructively. Leaf biomass (dry weight) was calculated by multiplying the leaf area measured for each monitored plant by the dry weight of 10 cm<sup>2</sup> of fresh leaf for each species. Regression equations between the diameter and the dry weight were calculated also for 10 cm long parts of the scape for each species. Flower dry weight was determined for both species. These data were used for non destructive calculation of biomass allocation to scape and flowers of the monitored plants in both species. Mean dry weight of seeds of both species was measured for the calculation of biomass allocation to seed in each monitored plant.

#### Data analysis

The effects of treatments within each species were tested by one-way analysis of variance (ANOVA). A significant one way ANOVA ( $P < 0.05$ ) was followed by Duncan's multiple range test for comparison among the individual treatments. T-tests were used for comparisons of each variable between the two species. Coefficient of variation (CV) was calculated ( $CV = \text{STD}/\text{mean}$ ) to compare the variation of any variable between species. Whenever ANOVA revealed no significant effect of a treatment on a tested variable in both species, the results of both treatment and control, of each species separately, were pulled together for a t-test comparison between the species. All statistical analysis were done on transformed proportions (arcsin of square root) with GLM (general linear model) and t-test procedures of SAS program on PC (SAS, 1988).

#### Results

##### Pollination treatments, fruit set and seed numbers

Fruit set (Fr/FI in Table 1) in untreated plants as a result of free and natural pollination was  $89\% \pm 11.4\%$  and  $35.5\% \pm 30.0\%$  in *S. hyacinthoides* and in *U. maritima* respectively and this difference was significant ( $F_{(5,1)} = -10.0701, P = 0.0001$ ). In *U. maritima*, no significant ( $F_{(3,46)} = 1.47, P = 0.2356$ ) differences were found in fruit set among the various

Table 1. Mean numbers ( $\pm$ std) of pollen grains per flower, ovules per flower, seeds per capsule, proportions of pollen grains number over ovule number per flower (P/O), proportions of fertilized ovules (S/O), proportions of fruit set per plant (Fr/FI) and relative reproductive success (RRS) in *Urginea maritima*, and *Scilla hyacinthoides*.

Variable	<i>Urginea maritima</i>		<i>Scilla hyacinthoides</i>	
	n	mean $\pm$ std	n	mean $\pm$ std
Pollen	20	26580 $\pm$ 2977	40	21060 $\pm$ 2652
Ovules	20	39.6 $\pm$ 2.6	40	6.3 $\pm$ 1.2
Seeds	68	9.33 $\pm$ 3.58	67	3.83 $\pm$ 0.97
P/O	20	6.76 $\pm$ 1.00	40	3.435 $\pm$ 0.618
Fr/FI	80	0.355 $\pm$ 0.300	70	0.890 $\pm$ 0.114
S/O		0.221		0.513
*RRS		0.0785		0.4566

\*Calculated from means.

pollination treatments (Fig. 1), while in *S. hyacinthoides* pollination treatments had a significant ( $F_{(3,25)} = 17.6, P = 0.0001$ ) effect on fruit set (Fig. 1). Fruit set as a result of spontaneous self-pollination in both species, or wind pollination in flowers under cover of fine mesh net (1 mm) was low in both species. Supplementary pollination did not increase fruit set in either species, and the variation in natural fruit set relative to the mean was much higher in *U. maritima* ( $CV = 0.845$ ) than in *S. hyacinthoides* ( $CV = 0.128$ ).

The mean number of seeds per capsule in untreated flowers was  $3.16 \pm 1.13$  in *S. hyacinthoides*, and  $9.33 \pm 3.58$  in *U. maritima*, and this difference was significant ( $T_{(37,9)} = 9.6988, P = 0.0001$ ). The average total number of seeds produced by a

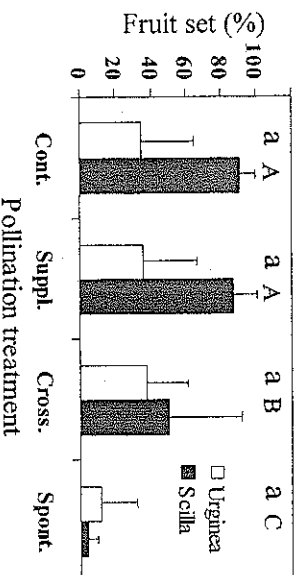


Fig. 1. Percentage of fruit set in *Urginea maritima*, and *Scilla hyacinthoides* as affected by pollination treatments: Control untreated plants (Cont.). Supplementary pollination of open flowers (Suppl.). Artificial cross pollination of bagged flowers (Cross.). Spontaneous self pollination of bagged flowers (Spont.). Columns with identical letters are not significantly different (Duncan's test  $p < 0.05$ ).

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whole plant was  $35.2 \pm 21.4$  and  $170.4 \pm 170.4$  for *S. hyacinthoides* and *U. maritima* respectively, and this difference was also significant ( $t_{(33,8)}=4.5992$ ,  $P=0.0001$ ). Seed number per fruit (Fig. 2) was not affected by pollination treatments in *S. hyacinthoides* ( $F_{(3,49)}=2.35$ ,  $P=0.0842$ ), but in *U. maritima* fruits of self pollination produced significantly ( $F_{(3,37)}=3.15$ ,  $P=0.0361$ ) fewer seeds than fruits of cross or open free pollination (Fig. 2).

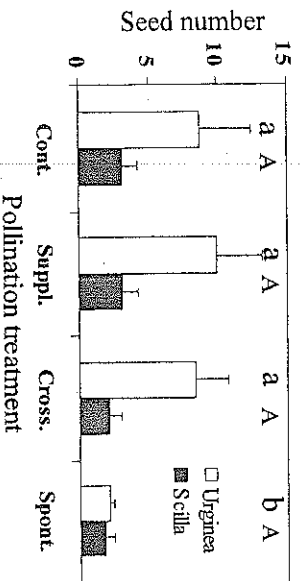


Fig. 2. Seed number per fruit in *Urginea maritima*, and *Scilla hyacinthoides* as affected by pollination treatments: Control untreated plants (Cont.). Supplementary pollination of open flowers (Suppl.). Artificial cross pollination of bagged flowers (Cross.). Spontaneous self pollination of bagged flowers (Spont.). Columns with identical letters are not significantly different (Duncan's test  $p < 0.05$ ).

#### Pollen to ovule ratio, seed to ovule ratio and relative reproductive success

The number of pollen grains per flower (Table 1) were not significantly different in both species ( $T_{(58,0)}=7.28$ ,  $P=0.4997$ ). However, the number of ovules per flower was significantly higher and the P/O significantly lower in *U. maritima* than in *S. hyacinthoides* (Table 1,  $T_{(22,8)}=54.5$ ,  $P=0.0001$  and  $T_{(42,9)}=-27.52$ ,  $P=0.0001$  respectively). The mean percentage of ovules that produced seeds (S/O) was higher for *S. hyacinthoides*, as was the relative reproductive success (RRS) (Table 1).

#### Biomass allocation

Table 2 presents the overall allocation of dry weight to the various plant organs, in both species. Because there is a large difference in size and thus in the total biomass of the two species, the allocation in each species was normalized as percentage of total biomass (Table 2). Although the bulbs of *U. maritima* had greater biomass, the relative alloca-

Table 2. Mean ( $\pm$ std.) biomass (g; dry weight) and relative allocation (% of total biomass) to the various plant organs in *Urginea maritima* and *S. hyacinthoides*.

	<i>Urginea</i> (n=70)		<i>Scilla</i> (n=60)	
	dry weight (g) $\pm$ std.	% (g) $\pm$ std.	dry weight	%
Bulb	66.6 $\pm$ 16.0	61.7	47.6 $\pm$ 10.9	84.2
Leaves	20.4 $\pm$ 8.36	18.9	3.1 $\pm$ 1.33	5.5
Stem	15.6 $\pm$ 3.27	14.5	2.1 $\pm$ 0.47	3.7
Flowers	2.5 $\pm$ 0.93	2.3	1.1 $\pm$ 0.37	1.9
Seeds	2.8 $\pm$ 1.34	2.6	2.6 $\pm$ 1.29	4.6
*Total	107.9	100	56.5 $\pm$	100

\*Calculated from the means.

tion to the bulbs was lower than in *S. hyacinthoides* (Table 2). The relative allocation to leaves, stem and flowers in *U. maritima* was higher than that of *S. hyacinthoides*, while relative allocation to seeds was lower. The allocation to inflorescence stem and flowers was much higher in *U. maritima*, and the allocation to pollinator attracting structures (stem and flowers) per seed was 1.94 g in *U. maritima*, but only 0.84 g in *S. hyacinthoides*.

#### Discussion

The total fitness of a plant species in its natural environment is the outcome of many vegetative and reproductive traits. Therefore, if one wants to compare the fitness of two species, he must compare separately each aspect of their reproductive success. However, similar reproductive success (e.g. number of seeds produced) could result from different absolute or relative allocation of energy. Therefore, I compared the two species from several aspects of their reproductive biology and the biomass allocated to achieve that level of reproductive success. By this comparison I want to address the hypothesis that the possible evolutionary shift of the flowering season from spring to autumn in *U. maritima* might have resulted in some reproductive advantage to the species.

#### Pollination treatments, fruit-set and seed numbers

Percentage of fruit set in natural populations is a major factor determining reproductive success because it is a result of resources and pollination limiting factors. *U. maritima* had lower fruit set in

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untreated plants than *S. hyacinthoides* reflecting an overall reproductive disadvantage. The higher variation in this fruit set in *U. maritima* may indicate a sub-optimal rate of fruit set due to microhabitat heterogeneity in resource availability or pollinator activity. The low level of fruit set that resulted from spontaneous self-pollination or wind-pollination, indicate that fruit set in both species was depended mainly on pollinator's activity.

Supplementary artificial pollination of flowers can reveal whether resource or pollinators are the limiting factors for fruit set (Stephanson, 1981; Zimmerman & Pyke, 1988). In cases where this treatment increases fruit set, in comparison to control on the tested plants as well as on other plants, it may be a evidence that shortage in pollination is the limiting factor for fruit set. However, supplementary pollination did not increase fruit set in both tested species, indicating that pollinators' activity was not limiting fruit set, in either spring or autumn (but see Young & Young, 1992).

Seed number per fruit and per plant were higher in *U. maritima* than in *S. hyacinthoides*. This fact must be considered together with the fact that *U. maritima* has smaller and lighter seeds. This difference, in seed mass and number, might be the result of life history difference associated with seed germination and the fact that *U. maritima* is typical to sunny habitats, whereas *S. hyacinthoides* grows generally in more shaded areas. The lower seed number per fruit in the spontaneous self-pollination treatment in *U. maritima*, might be the result of partial self-incompatibility (Eisikowitch, 1970). However, the fact that in all other treatments, in both species, seed number per fruit was not affected by pollination treatments, coincide with the sexual selection theory that predicts male rather than female limitation on reproduction in hermaphrodite flowers (Queller, 1984; Brunet, 1992).

#### *Pollen to ovule ratio, seed to ovule ratio and relative reproductive success*

P/O ratio is a good indicator of breeding system in flowering plants as well as of energy allocation to male/female floral functions (Queller, 1984). P/O decreases along a gradient from obligatory outcrossing species to cleistogamous ones (Cruden, 1977). P/O ratio varies with pollination syndrome, being higher in inefficient pollination syndromes (wind) and lower in more efficient systems, and is affected by many other factors (see Dafni, 1992).

However, when comparing two related species with similar floral morphology, P/O can serve as a general measure for pollination efficiency, and for male success. The lower P/O ratio in *U. maritima* may indicate on a more efficient pollination system and higher male success. This result do not coincides with the partial wind-pollination found in this species (Dafni & Dukas, 1986)

Percentage of fruit set (FV/Fr) and seed per ovules (S/O) are both parameters of female success (Charlesworth, 1989) which can be multiplied to obtain overall female relative reproductive success (RRS) (Weins, 1984). The values of all these parameters, and especially RRS, were higher in *S. hyacinthoides* indicating a higher rate of female success than in *U. maritima*. Since female success is often affected by resource availability, this result may reflect the differences in the environmental conditions when fruit maturation takes place. Favorable growing conditions prevail in spring when *S. hyacinthoides* is fruiting and harsh conditions prevail in autumn when *U. maritima* is fruiting.

#### *Biomass allocation*

*U. maritima* is a bigger plant with larger bulbs than *S. hyacinthoides*, this agrees with two predictions made by Dafni *et al.* (1981a), that geophytes adapted to more arid unpredictable conditions will have more stored reserves, and that hystereanthous geophytes (flowering before leaf sprouting) will have more than synanthous (flowering after leaf sprouting). However, if we look on the normalized allocation relative to total biomass, the picture reverses. *S. hyacinthoides* allocates higher proportion of its biomass to storage than *U. maritima*. Relative allocation to seeds was also higher in *S. hyacinthoides*. What is most interesting is that relative allocation to leaves in *S. hyacinthoides* was lower, indicating a more efficient production than in *U. maritima*.

Allocation to attractive structures was found to decrease with increase in selfing rate, and allocation to a certain organ in the flower is proportional to its exponent of the gaining curve (Brunet, 1992). Attraction of pollinators to flowers was found to be correlated to the flower biomass (Bell, 1985). Therefore, in case of competition for pollinators, the allocation to attractive structures is expected to be higher than in the absence of such competition. Our results show that allocation to scapes and flow-

ers, which serve as pollinator attraction structures, was lower in *S. hyacinthoides*. This means that much less allocation in attraction structures in *S. hyacinthoides* than in *U. maritima*, resulted in the production of similar seed mass. The allocation to attracting structures needed for the production of a single seed, was also lower in *S. hyacinthoides* than in *U. maritima*. This means that the relative allocation for attracting pollinators is more efficient in *S. hyacinthoides* although it flowers in spring when competition for pollinators is higher than in autumn – the flowering season of *U. maritima*.

## Conclusions

We may state that: A) pollination is not a limiting factor for fruit set in the autumn flowering *U. maritima*, a sign that there is enough pollinator activity; B) pollination is not a limiting factor for fruit set also for the spring flowering *S. hyacinthoides*, C) male function of *U. maritima* seems to be more efficient than that of *S. hyacinthoides*, D) *S. hyacinthoides* has a higher rate of female success and E) The relative allocation of biomass, for the attraction of pollinators needed to achieve these rates of reproductive success is lower *S. hyacinthoides*.

The results demonstrate an advantage in the efficiency of male function in *U. maritima* over *S. hyacinthoides*. Therefore, we can support the hypothesis that the shift from spring to autumn flowering resulted in a reproductive advantage. However, this shift in flowering season had also cost in higher allocation for pollinator attraction and a lower female reproductive success.

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