

Insect and Wind Pollination in *Urginea maritima* (Liliaceae)

By

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Abstract: Three co-existing pollination mechanisms are found in *Urginea maritima*: insect-, wind-, and self-pollination. The flowers exhibit a typical insect-pollination syndrome; they offer abundant exposed nectar as well as pollen. Out of the many different visitors only a few could be regarded as pollinators: *Apis mellifera*, *Polistes gallicus*, and *Vespa orientalis*. Wind pollination also occurs and generally is responsible for self-pollination.

It is argued that the development of extra wind-pollination accompanied by partial self-incompatibility is an adaptation to increase pollination in an unfavourable season (August–September), when insects are scarce.

Urginea maritima (L.) BAK. is a common geophyte occurring around the Mediterranean (POLUNIN & HUXLEY 1965). Widely distributed in Israel, with the exception of the extreme deserts, it exemplifies a plant with a large ecological amplitude. It grows in large populations and has a conspicuous flowering stem (up to 2 m) and flowers at the end of the summer (August–October). About 25 species flower in this season in Israel, all of which are geophytes with hysteranthous leaves. The “*Urginea* type”, is characterized by: perennial storage organ; distinct flowering stem; onset of flowering preceding leaf development in the winter; seed dispersal immediately after flowering; germination without dormancy, and tropical origin (DAFNI & al. 1981). The flowering season of these geophytes is characterized by poverty of insects (HERRERA 1982) and harsh meteorological conditions (Atlas of Israel, 1957). This study deals with the different devices by which *Urginea maritima* faces its unfavourable pollination environment.

Materials and Methods

The field observations were carried out during September–October 1983–1984 at five localities in Israel: Binyamina (ca. 33 km south of Haifa, abandoned field); Ma'agan Michael (ca. 25 km south of Haifa, an old cemetery); Atlit (13 km south of Haifa, 600 m from the sea shore, roadside); Yagur (12 km south-east of Haifa, garigue of *Quercus calliprinos* at the northern slopes of Mt. Carmel, 100 m a.s.l.), and Shkhem (Nablus) (Samaria, 800 m a.s.l., an abandoned field).

The observations include: diurnal measurements of nectar concentration, expressed as sucrose equivalents and volume; temperature and relative humidity in comparison to the pollinator's visits and behavior. The insects were caught for determination and for examination of the presence of *Urginea* pollen load on their bodies. Self-pollination was examined in plants covered before flowering by fine mesh nets which precluded insect visits. Nectar quantity was measured by calibrated micro pipettes and sugar concentration with Bellingham and Stanley's pocket refractometer.

Pollen traps were made of perspex boards (20 × 20 cm) covered on one side by gelatine-glycerine 5%. The traps were exposed at midnight and collected before the commencement of insect activities at 6 a.m. In order to examine possible U.V. reflection, the flowers were photographed using U.V. sensitive film (plus-x-pan) and a suitable filter (Kodak Wratten Filter 18A).

Results

Flowers and Flowering. Flowering commences in mid-August and terminates at the beginning of October, with slight differences in timing throughout the country. The flower open at about 1:00 a.m. and close the following night at 19:00. The flowering stem bears 50 to 250 flowers, 30 of which are open simultaneously. The white perigon (ca. 10 mm) reflects ultra-violet irradiation (Figs. 1A, B). The nectar is secreted from three septal nectaries located at two-thirds of the ovary. Its secretion continues from the opening of the flower till about 5:00, and the maximal quantity per flower is 3 to 7 μ l. The nectar drains to the base of the ovary and accumulates there into mucilaginous droplets, one for each nectary. The nectar is initially very dilute, but by mid-day is almost crystalline. Nectar concentration is affected directly by both temperature and relative humidity (Figs. 2A, B), being higher in dry conditions. The maximal nectar volume of about 7 μ l came at 5:00 and dropped to 1 μ l at 9:00. Dry, windy nights could show a maximum accumulated quantity of less than 1 μ l.

The pollen is exposed immediately with the flower's opening and is quite conspicuous. Every slight vibration of the flowering stem (especially at low humidity) may cause dispersal of pollen by wind. The pollen availability is thus reduced considerably with time and by about mid-day the anthers are almost empty.

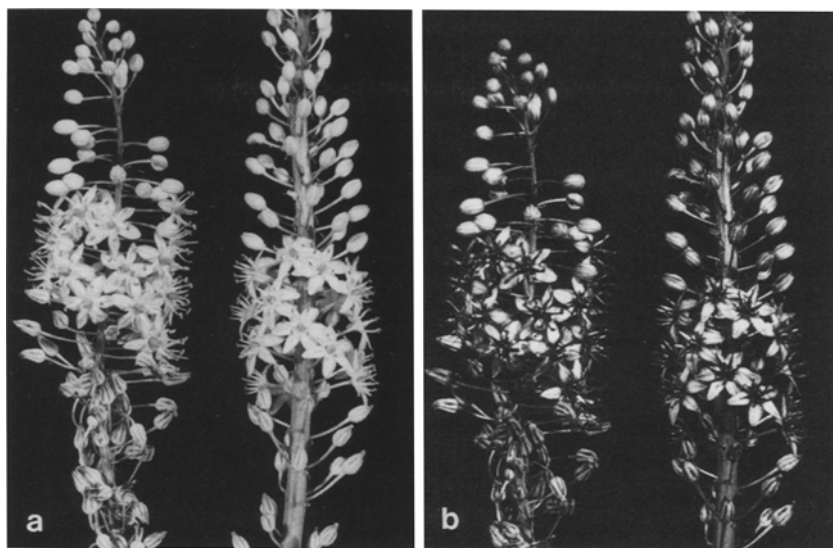


Fig. 1. *Urginea maritima*. a Under daylight; b ultra violet reflection. — Phot. A. Shoub, $\times 0.29$

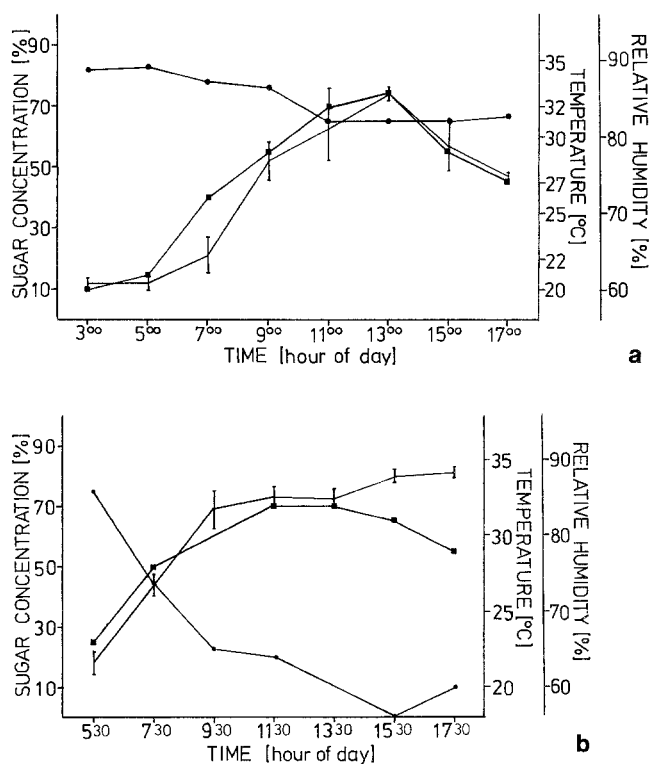


Fig. 2. *Urginea maritima*. Nectar concentration changes in relation to temperature and humidity. a at Yagur 15. 9. 1983; b at Atlit 31. 8. 1983. — ● Relative humidity, ■ temperature, I: nectar concentration

Table 1. Self-pollination in *Urginea maritima*. The observation was carried out at Ma'agan Michael in Oct.–Nov. 1983

Plant No.	No. of flowers	No. of capsules	Percentage of flowers with capsule production
1	220	110	50.0
2	157	27	17.1
3	144	24	16.6
4	101	6	5.9
5	122	38	31.1
6	254	69	27.1
	166.3 ± 58.9	45.6 ± 37.7	$24.6 \pm 15.2 (\mu \pm SD)$

Table 2. Pollen loads on stigmata of *Urginea maritima* under fine mesh nets. Accumulated results of three replicas 6, 26, 28. 9. 1984 at Ma'agan Michael. The stamens of 6 plants were removed at midnight prior to the flowers' opening. The stigmata examination for pollen load was done at 15:00 to 16:00

The treatment:	No. of pollen grains on the stigmata
Castrated flowers:	2.1 ± 3.8
Intact flowers:	50–200
	n = 50

Breeding System. Of flowers that were covered by fine mesh nets (1 mm), which prevent insect visits, prior to the beginning of flowering, only 24.6% yielded capsules (Table 1). Ten flowering plants which were kept under room conditions, (18–22 °C) without insects or wind, did not produce even one capsule. This means that wind is needed to enhance self-pollination, which is not spontaneous.

Comparison of castrated and intact flowers (Table 2) indicated that most of the pollen grains on the stigmata originated from the same flower, signifying a high potential for self-pollination. These results indicate also the existence of partial self-incompatibility as was demonstrated by EISIKOWITCH (1970).

Wind Pollination. Five pollen traps were placed vertically at a distance of 40–50 cm from the flowering stems of the *U. maritima* from midnight to

Table 3. Pollen loads on stigmata of *Urginea maritima* due to wind pollination. The observation was carried out on 8. 10. 1983 at Ma'agan Michael. The previous night there were stormy winds, above 8 m/sec, which prevented any insect activity. The stigmata were collected at dawn, before the commencement of insect activity

Plant No.										
Flower	1	2	3	4	5	6	7	8	9	10
1	114	224	185	235	249	257	477	159	75	168
2	131	201	398	332	201	241	232	77	45	65
3	129	202	55	292	234	392	312	242	88	269
4	162	229	83	224	198	271	317	258	117	35
5	129	151	120	308	294	280	278	81	162	145
$\mu \pm \text{SD}$	133 ± 17	201 ± 31	168 ± 137	278 ± 40	235 ± 40	288 ± 60	323 ± 92	163 ± 85	97 ± 44	136 ± 92
										$\mu = 202 \pm 98$

dawn (on 8. 10. 1983 at Ma'agan Michael). Each trap contained 528 ± 469 ($\mu \pm \text{SD}$) pollen grains, evidence of its dispersal by wind. Counts of the number of pollen grains transferred by the wind to the stigmata (Table 3) show an average of 202 ± 98 ($\mu \pm \text{SD}$) grains per stigma.

Insects as Visitors and as Pollinators. A large gallery of various unrelated insects visit the flowers of *Urginea maritima* (Fig. 3) but only a few of them can be regarded as potential pollinators:

Apis mellifera collects both pollen and rarely nectar, but only a limited amount of nectar is taken per visit perhaps because of its high viscosity. In general it shows low activity on the flowers although it is potentially a very efficient pollinator (Table 4).

Polistes gallicus feeds its brood with nectar in addition to meat, which explains its numerous visits to flowers (FAEGRI & VAN DER PIJL 1979, 107). The body of this wasp is almost bald. Examination shows that it bears few or no pollen grains. However, since it is very common and because of its dimensions it is quite likely to insure pollen transfer to the stigma (Table 4), and thus can be regarded as a pollinator.

Vespa orientalis visits the flowers at low frequency. Because of its hairiness it bears numerous pollen grains on its body and may serve as an efficient pollinator.

Noctuidae, moths of several genera were active on the flowers from their opening at 1:00 till dawn. The moths visited few flowers, out of the 15 that were caught only one bore a few pollen grains.

Others: many ants reached the flowers to collect nectar and since they move on the anthers as well as on the stigma it may be that they play some

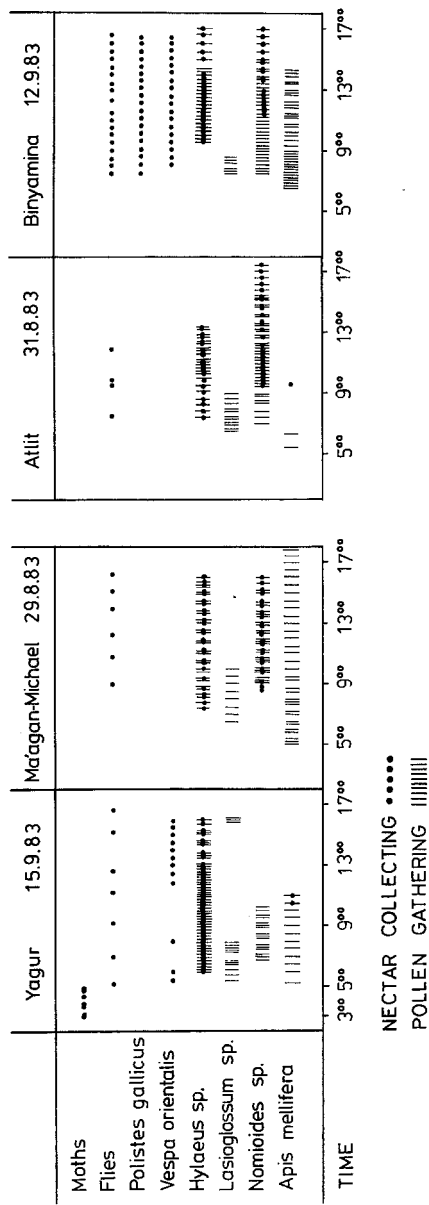


Fig. 3. Insect's daily activity on *Urginea maritima* at four localities

Table 4. Insects' behavior patterns on *Urginea maritima*. Accumulated data from Ma'agan Michael 18. 8. 1984 7:00 to 10:00 and Sh'khem (Nablus) 22. and 23. 8. 1984 10:00 to 12:00, totally 7 hours of observation

The insect	No. of nectar collecting visits	No. of pollen collecting visits	No. of nectar and pollen collecting visits	No. of stigma's touch
<i>Apis mellifera</i>	0	0	59	55
Various flies	50	0	0	2
<i>Polistes gallicus</i>	59	0	0	27
<i>Vespa orientalis</i>	50	0	0	42
<i>Nomiodes</i> spec.	0	0	52	1
<i>Hylaeus</i> spec.	0	0	61	1
<i>Lasioglossum</i> spec.		0	50	0

role in pollination. Flies of several genera (*Sarcophaga* spec., *Musca domestica* and others) visited the flowers randomly and licked nectar. Most of them are too small to serve as pollinators. Three solitary bee genera (*Nomioides* spec. *Hylaeus* spec. and *Lasioglossum* spec.) were found at all five localities in large numbers. They showed high activity (Fig. 3) but could not be considered as pollinators. Their body size is about 5 mm while the stigma is 11 mm above the nectar droplet. These bees were not observed touching the stigma (Table 4) and are, thus, nectar thieves.

Capsule Production under Natural Conditions. At the end of the flowering season (Nov. 1983) 10 flowering stems were counted in several localities, and the percentage of capsule production out of the total number of flowers was estimated. The results are as follows: 65 ± 15 at Ma'agan Michael, 78 ± 21 at Yagur, 55 ± 14 at Binyamina, and 49 ± 19 at Atlit (the results present the mean \pm SD).

Discussion and Conclusions

The main flowering season under Mediterranean conditions is between February and May (ZOHARY 1962, 27). It is assumed that in this season there is a high competition for pollinators, and it has been argued that a change of the flowering season could reduce such a competition (MOSQUIN 1971, HEINRICH 1975, WASER 1983). Competition for pollinators was regarded as a possible selective pressure leading to the shift of the flowering season from spring to autumn, as it occurs in some geophytes with hysteroanthous leaves, which includes *Urginea maritima* (DAFNI & al. 1981).

An increase in pollination possibilities in this harsh season for insects (HERRERA 1982) could be realized by several independent devices: Long exposure of flowers (day and night), polyphily, wind-pollination and self-pollination. All these aspects were found simultaneously in *Urginea maritima*.

U. maritima exposes to the pollinators both its pollen and its nectar. The nectar is not replenished after consumption or evaporation. Initially it has a low sugar concentration (shortly after secretion ca. 10–15%), but this increases rapidly (to 75%) towards noon (Figs. 2*A, B*). This range of sugar concentration could attract different pollinators during the period of nectar presentation, as was suggested by CORBET (1978). During the present observations various pollinators were active during the whole day regardless of the nectar concentration (Fig. 3), since alternative nectar resources were very scarce. The nectar droplet is mucilaginous and remains suspended on the base of the ovary due to its high viscosity. The flowers are horizontal; this feature prevents leakage of the nectar and enables it to be consumed easily by the visitors.

The patterns of insect activity on the flowers of *Urginea maritima* (Fig. 3) show the following descending order: *Hylaeus* spec., *Nomiodes* spec., *Apis mellifera*, *Lassioglossum* spec. and various flies. These visitors were present at all five localities; other visitors were present at some stations only, e.g., *Polistes gallicus* at Atlit and Binyamina, and *Vespa orientalis* at Binyamina and Yagur.

The efficiency of the visitors as pollinators was estimated by the rate of their touching the stigma (Table 2). The efficiency order is decreasingly as follows: *Apis mellifera*, *Polistes gallicus*, and *Vespa orientalis*. The most frequent visitors revealed low efficiency as pollinators, but since they were very abundant it seems that their possible role in pollination must not be neglected.

In accordance with the flower traits – the commencement of anthesis at midnight, the perigon's white colour and the nectar's secretion rhythm – night pollination is also expected. Our observations do not confirm this prediction and it could be that other night pollinators are more abundant in other parts of *U. maritima*'s distribution area. Besides, the *Noctuidae* may be regarded as not always very efficient pollinators since they stay for long periods (up to one hour!) at individual flowers, as was found also by IVRI (1983) for *Capparis spinosa*. These observations are reflected in the low pollen load of these visitors.

The pollen grains of *U. maritima* are smooth and non-sticky (CARPENTER 1938) and the plants are usually in dense colonies due to vegetative reproduction. Both factors can promote wind-pollination. The results indicate a rate of 24.6% of self-pollination under nets. This value

should be taken as a minimal value. The nets prevent much of the wind turbulence around the flowers, which is an important factor in the efficiency of wind pollination (NİKLAŞ 1981). In artificial pollination experiments, EISIKOWITCH (1970) found 57% success of self-pollination in comparison to 93% in cross-pollination, indicating partial incompatibility.

Dual mechanisms of insect and wind-pollination exist in *Calluna vulgaris* (FAEGRI & VAN DER PIJL 1979, 173–174); *Brassica napus* var. *oleifera* (MESQUIDA & BENARD 1982) and *Thalictrum* spp. (KAPLAN & MULCAHY 1971). In the last example the secondary wind-pollination is explained as an adaptation to unfavourable environmental conditions such as drought or scarcity of pollinators, both in a seasonal climate.

The maximizing of insect pollination chances at the end of the summer by attracting a wide range of pollinators also exists in other species. *Sternbergia clusiana* is pollinated by *Apis mellifera* and solitary bees, which collect pollen and nectar from the shorter inner whorl of stamen and from the lowermost part of the funnel-shaped perianth tube. The *Syrphidae*, the other pollinators, visit the osmophores on the perigon and collect pollen at the longer external stamen whorl (DAFNI & WERKER 1982). *Ceratonia siliqua* is a dioecious tree and its flowers have exposed nectar. It is pollinated by Honey bees, *Vespa orientalis*, *Vespula germanica*, *Polistes gallicus*, *Vespula* spec. and various *Syrphidae* along with some degree (10 to 40%) of wind pollination (DAFNI, in prep.).

In conclusion, *Urginea maritima* flowers at the end of a long dry summer and faces a harsh pollination environment which it has overcome by several coexisting strategies: being a generalist, exposing flowers day and night, developing additional wind and self-pollination. The cost of generalism is expressed by the ratio between visitors and pollinators, resulting in a high waste of both pollen and nectar. At least in Israel, night pollination is negligible and it would be of interest to examine it in other places. The partial self-incompatibility limits the efficiency of wind pollination. But the ultimate result is a high degree of capsule production (49–78%). Wind pollination thus substantially contributes to the plant's reproductive success, as this was reported in other *Liliaceae*, e.g., *Paris quadrifolia* and the *Lomandreae* (DAUMANN 1959).

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