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Generative reproduction in *Allium oleraceum* (Alliaceae)

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The field garlic *Allium oleraceum* is reproducing by subterraneous bulbs, and above ground by bulbils and seed. Two chromosome numbers, tetraploid (2n = 32) and pentaploid (2n = 40) have been found in Finland and Sweden. The seed production was studied in some populations of *A. oleraceum* mainly in south Finland. The fruits mature only if visited by insects and the seed ripen only in favourable, that is warm and not too dry, summers. Several insect species of the orders Hymenoptera, Diptera and Lepidoptera were found to visit flowers of *Allium oleraceum*. The most frequent visitors were *Bombus lapidarius* (Apidae), *Dolichovespula norwegica* and *D. saxonica* (Vespidae), *Eumenes* spp. (Eumenidae), *Volucella* spp. and *Syrphus* spp. (Syrphidae), *Pieris napi* (Pieridae) and *Autographa gamma* (Noctuidae). Wasps of the family Vespidae are very regular visitors in the flowers of *Allium oleraceum*. Thus we suggest that *Allium oleraceum* is a species which has "wasp blossoms". Both tetraploid and pentaploid plants are visited by insects and they both produce viable seed. The seed is described. In germination tests most of the seeds of both ploidy levels germinated well.

Key words: *Allium oleraceum*, germination, pollination, seed, Vespidae, "wasp blossom"

Introduction

The field garlic *Allium oleraceum* is a bulbous geophyte with sympodial branching. The development of an individual plant begins in the autumn, when the offset bulb begins to develop roots, and lasts for almost one year. The plant either hibernates as a bulb below the ground or develops a short green leaf sheath above ground during warm and long autumns and stays over winter at this stage. The further development of the plant starts in spring, in southern Finland at the end of April or beginning of May, when the scape and its foliage of three or four vegetative leaves begins to elongate. The terminal umbel-like mass of young bulbils and flower buds develop enclosed by two spathe bracts of unequal length with broad base and elongated tip. As the bulbils grow in size they burst between the bracts and occasionally also through their bases. This happens several weeks before the anthesis. The young flower buds develop between the young bulbils and are protected by them at an early stage. Later on, the flower pedicels elongate and the flower buds begin to stand out in different directions between the bulbils. At this stage the green foliage begins to die back. In SW Finland, the anthesis begins in late July or early August and continues in an individual for about two weeks. The flowers are protandrous.

At anthesis the pedicels of the campanulate flowers are curving downwards.

The number of flowers per plant is usually rather low. It varied between 0 and 41, with mean numbers between 2.0 and 9.3 in thirteen population samples studied by us (C.-A. Hæggström & H. Åström unpubl. data). However, a maximum number of 50 flowers was seen in a voucher specimen collected in the Botanical Garden of Helsinki (herbarium TMP). The number of bulbils normally exceeds the number of flowers; in our study it varied between 5 and 65 with means between 17.1 and 33.0 in nine population samples (C.-A. Hæggström & H. Åström unpubl. data).

Four chromosome numbers are reported in *Allium oleraceum*: triploid (2n = 24; Vahtina 1985), tetraploid (2n = 32; Levan 1931), pentaploid (2n = 40; Geitler & Tschermak-Woess 1946) and hexaploid (2n = 48; Pastor 1982). We have found both tetraploid and pentaploid specimens in Finland and Sweden (H. Åström & C.-A. Hæggström unpubl. data). The tetraploid and pentaploid specimens are morphologically discernible, especially during anthesis. This was not known to us before August 2000.

In late July and early August 1997, the author C.-A.H. observed that flowers of *Allium oleraceum* were regularly visited by wasps of the family Vespidae at Nåtö Biological Station in the Åland Islands, SW Finland. Later it was observed that some flowers were seemingly developing into fruits; they had risen more or less straight up, the campanulate flowers were constricted and the pedicel seemed to be thicker than in flowers still curving downwards. In late August and early September, some of the flowers had developed capsules with one to three seeds. More than 350 seeds could be gathered from the *A. oleraceum* population comprising over one thousand specimens in the meadow area next to Nåtö Biological Station.

Qualitative studies on insects visiting flowers of *A. oleraceum* and the development of fruit and seed were continued in 1998–2001 by both authors.

The aim of this study was to investigate which insects visit the flowers of *Allium oleraceum* and if these visits lead to fruiting. Further, our aim was to study the seeds, especially their germination. As the populations of flowering *Allium oleraceum* specimens vary in size from a few specimens to thousands, and the number in a certain population fluctuates from one year to another, quantitative studies are extremely difficult to do in this species. Further, drought periods often put an end to fruit and seed development.

Material and methods

Insect visits in flowers of *Allium oleraceum* were studied in the island of Nåtö in 1999 in two populations: (1) in an open rock meadow and dry and mesic meadow at Nåtö Biological Station (NBS) and (2) in a previously dense *Fraxinus* and *Corylus* stand at Själskatsudden belonging to the Nåtö-Jungfruskär Nature Reserve. Occasional observations were also made at Tvärminne Zoological Station on the south coast of Finland in 1999, in southern Sweden 2000, in the Botanical Garden in Helsinki in 2001 and at NBS 2001–2003. Some of the flower visitors were collected for later identification.

To elucidate the role of insects visiting the flowers of *Allium oleraceum*, well developed flower and bulbil heads were enclosed in mid-July 1998 and 1999 before anthesis in pergamine and tulle bags (Fig. 1). In 1998, 10 pergamine and 8 tulle bags were used at NBS. In 1999, 10 pergamine bags and 3 tulle bags were used at NBS and 3 pergamine and 5 tulle bags at Själskatsudden. The bagged plants were collected and inspected for possible fruits in late August.

The pollen viability was studied on pentaploid plants from the Åland Islands. Fresh pollen grains were dyed with methylgreen-phloxin (according to Gurr 1965), which stains the cytoplasm of the pollen grains red and the walls green. In the pollen of *Allium oleraceum*, the cell walls were only faintly stained. Wholly red coloured pollen grains were regarded as viable, faintly and unevenly coloured lacking a homogenous cell content were regarded as non-viable. Pollen grains were also tested for pollen tube development on agar with added nutrients (10% sucrose, 0.03% $CaCl_2$ and 0.01% boric acid in 1% agar).

Fruiting plants were searched for in numerous localities in the Åland Islands, in the south-

Fig. 1. Unbagged and bagged *Allium oleraceum* specimens at Nåtö Biological Station. A few taller specimens of *Allium scorodoprasum* are seen, too. Photo: C.-A.H., 6.VIII.1998.

ern part of mainland Finland and in southern and mid Sweden. Seeds were collected whenever found. In order to get ripe seed from localities that could not be revisited, plants with unripe fruits were cut, placed in vessels with tap water and kept either out-of-doors or in the laboratory. In such a way many more seeds were gathered. Two batches of seeds, one from Germany and one from Italy, were received through the exchange of the Botanical Garden, University of Helsinki.

Seeds were germinated on moist soft paper in petri dishes, if not otherwise stated. In some germination experiments air dry seeds were pretreated by storing them in a refrigerator at 7 °C. Germination was carried out at two temperatures: (1) in dark (the petri dishes were covered by aluminium foil) and cool (7 °C) in a refrigerator and (2) at 21–23 °C in the laboratory in dark.

Results

Insects visiting *Allium oleraceum* flowers

The flowers of *Allium* have septal nectaries in their ovary (Daumann 1970, Rahn 1998). This is also the case with *Allium oleraceum*. The nectaries are elongate (about 2.8–2.9 mm long), narrow sack-like furrows in the ovary septas; they are of Daumann's (1970) position type e (*Lagetyp e*). Percival (1961), who studied the nectar composition of *Allium fistulosum, A. schoenoprasum, A. triquetrum* and *A. ursinum*, reported that the nectar of these species was of the dominant fructose and glucose type also containing some sucrose. In the two first mentioned species maltose was found, too. No study on the sugars of the nectar of *A. oleraceum* is known to us.

Insects of the orders Hymenoptera, Diptera and Lepidoptera were observed to visit flowers of *Allium oleraceum* (Table 1). 30 and 31 July 1999, were sunny and warm (25 °C) days in Nåtö. Some species of bumblebees (*Bombus lapidarius, B. pascuorum, Psithyrus bohemicus* (Apidae) visited flowers of *Campanula rotundifolia, Centaurea jacea, Lathyrus pratensis* and *Trifolium pratense* at NBS. Only one of these, namely queens and workers of *Bombus lapidarius*, frequently visited flowers of *Allium oleraceum*. One other bumblebee species was once seen in an *Allium oleraceum* flower; it could not be caught for identification.

Bombus lapidarius visited several (2–10) flowers in each *Allium* plant. The duration of the visit lasted only 1–2 seconds in each flower. After that the bumblebee moved on to a neighbouring plant. After visiting one, few or several *Allium* plants, the bumblebee shifted to one of the other plant species mentioned above.

The wasps *Dolichovespula norwegica* and *D. saxonica* (Vespidae) were frequent visitors in *Allium* flowers. A wasp usually visits only a single flower of a single *Allium* plant. The wasp approaches the flower from beneath and creeps into the bell-shaped flower. With its head and thorax inside the flower and the abdomen sharply bent outside the flower (Fig. 2), the wasp's visit lasts usually 5–10 seconds. Then the wasp flies to the next plant, often several metres apart from the previous one. The wasps were only seen visiting flowers of *Allium oleraceum*. The wasps find the flowers easily also in dense meadow vegetation. They are probably led to the flowers by their scent.

Table 1. Insects visiting flowers of *Allium oleraceum*. Abbreviations: f = females; m = males; w = workers; – = no observation. Most of the insects were caught for identification; * = insects only observed. — NBS1 = Nåtö Biological Station, 30 and 31 July, and 11 August 1999; NBS2 = Nåtö Biological Station, 28 July–5 August 2001; SJÄ = Själskatsudden, 31 July, 1 and 11 August 1999; TVÄ = Tvärminne Zoological Station 9 August 1999 and 1 August 2001; KÅG = Kågeröd, Sweden, 4 August 2000; BOT = Botanical Garden, Helsinki, 25 and 30 July 2001.

Taxon	NBS1	NBS2	SJÄ	TVÄ	KÅG	BOT
Hymenoptera						
Apidae						
Apis mellifera L.	–	–	–	–	–	2w
Bombus lapidarius (L.)	2f, 3w	*	1w	–	–	3w
Andreidae						
Evylaeus fratellus (Panzer)	2f	–	1m	–	–	–
Halictus sp.			1f			
Hylaeus communis Nylander	1f	–	–	–	–	2f
Vespidae		–				
Dolichovespula norwegica (Fabricius)	1m, 1w	*	4f, 2m, 2w	–	–	–
Dolichovespula saxonica (Fabricius)	6f, 11w	*	18f, 1 m, 13w		4w	–
Vespula rufa (L.)	–	–	2 w	–	–	–
Eumenidae						
Ancistrocerus parietinus (L.)	–	–	–	–	1f	–
Eumenes coronatus (Panzer)	–	–	1f	1f	–	–
Eumenes pedunculatus (Panzer)	–	–	1f	2f	–	–
Eumenes sp.	–	–	2*	4*	–	–
Diptera						
Syrphidae, Eristalinae						
Eristalis anthoporina (Fallén)	–	–	1f	–	–	–
Eristalis intricaria (L.)	–	–	1m	–	–	–
Helophilus pendulus (L.)	–	–	1m	–	–	–
Helophilus hybridus Loew	–	–	1f	–	–	–
Syritta pipiens (L.)	1f	–	–	–	–	–
Volucella inanis (L.)	4m	–	1f, 6m	–	–	–
Volucella pellucens (L.)	1f	–	1m	–	–	–
Syrphidae, Syrphinae						
Episyrphus balteatus (De Geer)	–	–	1m	–	2m	–
Eupeodes corollae (Fabricius)	1m	–	–	–	–	–
Melanostoma scalare (Fabricius)	–	–	1f	–	–	–
Parasyrphus lineolus (Zetterstedt)	–	–	–	–	1f	–
Sphaerophoria loewi Zetterstedt	1f	–	–	–	–	–
Sphaerophoria sp.	–	–	1f	–	–	–
Syrphus ribesii (L.)	1m	–	4f, 1m	–	–	–
Syrphus vitripennis Meigen	–	–	2f	–	–	–
Muscidae						
Species indet.	–	–	2	–	–	–
Lepidoptera						
Pieridae						
Pieris napi L.	–	–	3	–	–	–
Noctuidae						
Autographa gamma (L.)	–	*	–	–	–	–

Fig. 2. A wasp of the genus *Dolichovespula* visiting a flower of *Allium oleraceum*. Nåtö Biological Station. Photo: Saskya van Nouhuys, VIII.1999.

Fig. 3. A hoover fly of the genus *Volucella* visiting a flower of *Allium oleraceum*. Nåtö Biological Station. Photo: C.-A.H., 26.VII.2002.

The same flower of an *Allium oleraceum* specimen could be visited dozens of times during one day by both *Bombus lapidarius* and *Dolichovespula* spp., and perhaps by other insects, too.

Other Hymenoptera seen in the flowers were small solitary bees of the genera *Evylaeus, Halictus* and *Hylaeus* (*Prosopis*) (Andrenidae). Honeybees (*Apis mellifera*) were not observed at all.

The Diptera were represented by several species of hoover flies (Syrphidae, subfamilies Eristalinae and Syrphinae; Fig. 3). While the larger species, such as *Volucella inanis* and *V. pellucens*, crept into the flowers, smaller species, such as *Sphaerophoria loewi* and *Syrphus ribesii*, stayed at the entrance of the flower and were perhaps only sucking on the anthers or the edge of the tepals. Both males and females of these flies were visitors in *Allium* flowers.

At Själskatsudden, wasps and other insects were studied on 1 August 1999 during sunny and warm (25 °C) weather and on 11 August 1999 during a cooler (17 °C), partly overcast day with northerly wind. Bumblebees were rarer than at NBS. At least two species were seen, but *Bombus lapidarius* was the only species seen to visit flowers of *Allium oleraceum* in addition to its visits in flowers of *Satureja vulgaris*. Wasps of the family Vespidae were the most frequent flower visitors. It was estimated that up to about 90% of all insects visiting the flowers at Själskatsudden were of these wasps. Numerous individuals of the species *Dolichovespula norwegica* and *D. saxonica* were flying around in the *A. oleraceum* stand. Five to seven wasps could be seen visiting flowers on spots of about 1–5 m^2 at the same time. Two workers of *Vespula rufa* were also caught. Two females of true solitary wasps of the family Eumenidae, *Eumenes coronatus* and *E. pedunculatus*, were caught while visiting *Allium* flowers, while two smaller specimens escaped. The behaviour of these solitary wasps resembles that of the Vespidae. Solitary bees were also visiting the flowers; one specimen of the genus *Halictus* was caught.

Several species of hoover flies were seen visiting flowers of *Allium oleraceum*. Specimens of the fly family Muscidae landed occasionally on the flowers. These flies did not seem to be interested in the nectar inside the flowers.

Two specimens of the butterfly *Pieris napi* (Pieridae) were regularly visiting the flowers of *Allium oleraceum* on 1 August 1999 and one specimen on 11 August 1999. It could clearly be seen that they sucked nectar from the flowers. They did not visit any other flowers at this locality during the observation period.

In early August 2001, an invasion of the moth *Autographa gamma* (Noctuidae) occurred. Several individuals of this moth regularly visited flowers of *Allium oleraceum*. This moth visited both tetraploid and pentaploid specimens of *Allium oleraceum*, as did also *Bombus lapidarius, Dolichovespula norwegica* and *D. saxonica*.

During two hours at Tvärminne Storängsberget on 9 August 1999, six individuals of Eumenidae and one of Syrphidae could be seen visiting flowers of *Allium oleraceum*. Two females of *Eumenes pedunculatus* were caught.

Several wasps of the *Dolichovespula-Vespula* type were seen visiting flowers of *Allium oleraceum* on 1 August 2000, in the town of Trosa, Södermanland, east coast of Sweden. On 4 August 2000, flower visitors were studied in Kågeröd, Skåne, S Sweden. Several individuals of *Dolichovespula saxonica* were seen as well as individuals of Syrphidae (Table 1).

Several insects were seen in the flowers of *Allium oleraceum* in the Botanical Garden in Helsinki in July and August 2001. Among them *Bombus lapidarius* and *Apis mellifera* were identified.

Pollen viability

A total of 2958 pollen grains from fresh flowers collected at NBS and 539 pollen grains from Lemland, Granboda were studied. All pollen studied were taken from pentaploid plants. The pollen viability was fairly good; in several batches of pollen, the percentage of viable pollen grains were 20–76, the mean being about 52% at NBS, and 58% in Granboda. The agar test for pollen tube development was performed on pollen from flowers at NBS. Pollen tubes developed in 9.7% (n = 176) and 22% (n = 341) of the pollen grains from two different anthers after 25 hours. The length of the pollen tubes varied between 8 and 1360 μm, with a mean of 24 μm (n = 17) and 296 μm (n = 83). There was a considerable variation in respect to pollen grain development into pollen tubes between different flowers of the same plant and also between different anthers in the same flower.

Fruit development in Nåtö

Although many flowers seem to develop a capsule, few of them actually reach maturity (Table 2). This is mainly a result of unfavourable weather conditions, especially in August and September. Too long dry periods or too cool and wet weather hampers fruiting. The summer of 1997 was favourable as compared with those in the following years. The proportion of fruits per flower was much higher than in 1999 (Table 2). Also the proportion of specimens without fruits was much lower, being 35% in 1997 and 52%–65% in 1999. A moderate to weak positive correlation between the number of flowers and fruits was found (Table 2).

The precipitation in July–September 1998 was similar to the long term mean (1961–1990), but it rained, at least a little, almost every day. As the monthly mean temperatures were 1–2 °C lower than the long term means and the daily maximum temperatures hardly exceeded 20 °C, the vegetation stayed wet for long periods (ILMKA 1998). In 1998, no fruits could be found anywhere.

The early summer of 1999 was at least as favourable as in 1997, but later on the weather became too dry. The precipitation at the climate station in Jomala Södersunda was in July–September 1999 only about 45% of the 30-year-mean precipitation (ILMKA 1999). Most of the specimens of *Allium oleraceum* began to wilt because of the prolonged drought in August and early September. Further, most of the several thousand plants at Själskatsudden were browsed by some animals, possibly roe deer (*Capreolus capreolus*) in 1999, 2000 and 2001, despite the single barbed wire streched around the study area. This barbed wire kept the cattle grazing in the Nature Reserve outside the study area.

The bagging experiment gave the result that not a single flower developed a capsule in the bagged plants in 1998. As the weather during this summer was generally cool and rainy and no wasps or any other insects could be seen visiting unbagged plants during their anthesis, no fruits could be found in these either. As a contrast the weather during the summer of 1999 was warm and sunny. Numerous insects were frequently seen visiting unbagged flowers of *Allium oleraceum* and the pedicels of hundreds of flowers began to straighten. In the bagged plants, not a single flower had developed capsules or could be seen to have begun development into fruits (straightening of the pedicel). Our interpretation is that without insect visitors, capsules and seeds do not develop.

Seed development

After possible pollination through an insect, the flower pedicel is straightened and thickened (Fig. 4). The thickening of the pedicel is probably due to an increase in the turgor pressure of the cells, since no visible differences in the anatomy could be distinguished between straightened and unstraightened pedicels.

The fruit is a loculicid capsule with three locules (Fig. 5). Each locule has two ovules (Hanelt 1992), of which only one normally develops into a seed (Fig. 6). Thus a ripe capsule usually contains 1–3 seeds. Of fruits studied by us from 11 localities in 2001, only one fruit from NBS ($2n = 40$) had 5 seeds and one fruit from Kökar Hamnö ($2n = 40$) had 4 seeds. All other fruits had 1–3 seeds. Either ovule ("right-hand" and "left-hand") in a locule can develop into a seed. The proportion of "right-hand" and "left-hand" seeds is shown in Table 3.

The seed is elongated and curved like a banana (Figs. 5–7). The micropylar or proximal end of a seed is more or less blunt, the chalazal or distal more or less pointed. The parietal face

Table 2. Minimum, mean and maximum number of flowers and fruits of individual specimens of *Allium oleraceum* in Nåtö. NBS A = dry and mesic meadows at Nåtö Biological Station; NBS B = seaside meadows off NBS; SJÄ = former dense hazel and ash stand at Själskatsudden about 500 m E of NBS. The number of specimens without flowers and fruits in brackets. The percentage of fruits to flowers is calculated on the means. Corr. = Pearson's correlation of flowers and fruits.

Locality, year	Number of flowers min.–mean–max.	Number of fruits min.–mean–max.	Fruits/flowers (%)	Corr.
Nåtö, NBS A, 1997 (n = 200)	0(4)–7.3–21	0(70)–1.4–9	19.2	0.55
Nåtö, NBS A, 1999 (n = 125)	2–9.3–41	0(77)–0.6–5	6.5	0.31
Nåtö, NBS B, 1999 (n = 100)	1–8.8–21	0(52)–0.9–7	10.2	0.42
Nåtö, SJÄ, 1999 (n = 100)	1–5.8–15	0(65)–0.5–4	8.6	0.13

Fig. 4. A flower head of *Allium oleraceum* with nine flowers with more or less straightened pedicels at an early stage of fruit development, about ten flowers in anthesis and one flower bud. Nåtö Biological Station. Photo: C.-A.H., 1.VIII.2001.

is convex, the opposite concave. The seeds are often wrinkled when dry. The testa is black due to phytomelan (Rahn 1998), and about 15–20 μm thick with a surface pattern consisting of small angular warts (Fig. 7).

The length and width of the seeds varied between 3.13 and 5.06 mm and 1.13 and 2.00 mm, respectively (Table 3). The mean length was 3.62–4.66 mm, the mean width 1.38–1.80 mm. The thickness of a seed varies in its different parts, being in the mid area about 0.4–0.7 mm.

The weight of three batches of each 100 seemingly well developed seeds collected at NBS in 1997 was 198 mg, 200 mg and 200 mg. The average weight of an individual seed was thus 1.98–2.00 mg. The average seed weight of different batches of seeds collected in 1999 and 2000 varied between 0.67 and 2.50 mg (Table 3).

The smallest and lightest seeds collected in Finland were those from Svidja. The seeds acquired from Germany and Italy were also small and light. The largest and heaviest were found in Trosa in Sweden. The mean length, width and weight of the three most numerous seed batches from Finland (NBS 1 & 2 1999 and Ekenäs 2000) were almost identical.

The seeds from tetraploid plants were on average both smaller and lighter than those of the pentaploid plants. However, only the mean length of the seeds (t-test: $p \leq 0.001$) differed significantly.

Seed germination

Ten seeds of *Allium oleraceum* collected at NBS were put on moist potflower soil on 5 October 1997. Three of the thus soaked seeds were cut into two longitudinal halves and treated with a 0.1% TTC (triphenyltetrazoliumchloride) water solution on 15 October 1997. The embryos of all three seeds became faintly red, showing that they probably were viable.

On 20 October 1997 two of the seeds on the moist soil germinated. The cotyledons and radiculas developed slowly. On 25 October 1997 the two seedlings were about 3 cm and 1 cm long, respectively. This germination experiment was then terminated.

On 26 October 1997, 43 seeds of habitually inferior quality collected at NBS were put on moist soft paper in a plastic box. The seeds were kept at first in light at indoor temperature (about 20–22 °C) during day-time and in dark in a refrigerator (about 6–7 °C) during night-time. After about two months the box was kept indoors all the time. By 14 February 1998, 26 seeds had germinated, which equals to about 60% of the total number of seeds.

A batch of 100 habitually good quality seeds collected at NBS were put in moist flower pot soil and wrapped in a plastic bag and sealed in brown paper. This parcel was put in the refrigerator for stratification at about 6–7 °C on 16 November 1997. When the parcel was unpacked three months later it contained a mass of about 5 cm long ethiolated seedlings. It was not possible to count the number of seedlings.

The germination experiments were continued on different seed lots collected (Table 4). These

Fig. 5. A capsule of *Allium oleraceum* with two ripe seeds. The left seed is seen from the concave face with its chalazal or distal more pointed end upwards. The right seed is seen from its parietal face. Microphoto: H.Å.

Fig. 6. Of the six ovules in a capsule, one to three usually develop. In this capsule, one seed is normally developed, one is poorly developed and four are abortive. Microphoto: H.Å.

experiments show that the seeds of *Allium oleraceum* germinate much better in dark and cool (7 °C) than in dark and warm (21–23 °C), the germination percentage often rising to 80%–100%. Some seeds germinated in 2–3 weeks. A few of the germination experiments were interrupted after too short a time due to mould contamination of the cultures. Storing the air-dry seeds in the refrigerator at 7 °C as a pretreatment did not improve the germination at 7 °C, but was necessary to result in any germination at all at 21–23 °C. Both tetraploid and pentaploid seeds germinated. However, the pentaploid seeds germinated much better than the tetraploid seeds: 68.1% and 51.8% respectively. If the smallest seed batches (1–2 seeds) are omitted, the mean germination percentage is 67.3 in the pentaploids and 45.2 in the tetraploids.

Discussion

Insects are attracted by the usually showy mass of flowers in many *Allium* species and by nectar, which is produced by the septal nectaries of their flowers (Rahn 1998). Thus, beetles, flies, bees and butterflies have been recorded as pollinators of *Allium* (Müller 1873, 1879, Rahn 1998). Almost twenty bee and bumblebee species of the families Colletidae, Andrenidae, Halictidae, Megachilidae, Anthophoridae and Apidae have been recorded as visitors of *Allium* flowers in

Fig. 7. A seed seen from the concave face with the chalazal or distal more pointed end to the left. The seed is wrinkled and the surface of its testa consists of small angular warts. Microphoto: H.Å.

Finland (Dr. Antti Pekkarinen, Helsinki, information in a letter; *see* also Pekkarinen & Teräs 1998). We found several species of flies, wasps and bees, one bumblebee species and two species of Lepidoptera visiting *A. oleraceum* flowers in our study. No Coleoptera was found by us.

No written information on wasps of the family Vespidae as flower visitors in *Allium* have come to our knowledge. Species of *Dolichovespula* and *Vespula* are primarily animals of prey as their larvae feed chiefly on animal protein. The adult wasps are, however, interested in sugars which they use to maintain their own metabolism. According to Fægri and van der Pijl (1979), the mouth parts of Vespidae are primitive and the tongue (total length) is short as compared with the tongue of bees and bumblebees. Thus the flower visits of Vespidae are restricted to allophilic blossoms with open nectar and these wasps are regarded unreliable and unsteady pollinators (Fægri & van der Pijl 1979).

Some plant species are obviously pollinated

Table 3. Minimum, mean and maximum length and width (mm), length/width ratio (calculated on the minimum, mean and maximum measures) and mean weight (mg) of a seed and the proportion (R/L%) of "right-hand" and "left-hand" seeds of *Allium oleraceum*. Number of seeds studied in brackets. – = not studied.

Locality (number of seeds)	Chr. no.	Length	Width	Length/width	Mean weight	R/L%
Finland						
NBS 1, 1997 (*n* = 100)	2n = 40	–	–	–	2.00	–
NBS 2, 1997 (*n* = 100)	2n = 40	–	–	–	2.00	–
NBS 3, 1997 (*n* = 100)	2n = 40	–	–	–	1.98	–
NBS 1, 1999 (*n* = 50)	2n = 40	3.94–4.49–4.88	1.25–1.60–1.94	3.15–2.81–2.52	1.88	46.0/54.0
NBS 2, 1999 (*n* = 126)	2n = 40	3.94–4.45–5.00	1.13–1.57–2.00	3.49–2.83–2.50	1.78	57.1/42.9
Nåtö, SJÄ 1999 (*n* = 5)	2n = 40	4.00–4.26–4.50	1.38–1.51–1.69	2.90–2.82–2.66	1.40	60.0/40.0
Kökar, Österbygge 2000 (*n* = 11)	2n = 40	4.19–4.52–4.88	1.31–1.52–1.81	3.20–2.97–2.70	1.82	54.5/45.5
Ekenäs 2000 (*n* = 48)	2n = 40	4.06–4.48–4.75	1.25–1.53–1.88	3.23–2.93–2.53	1.77	56.2/43.8
Sjundeå, Svidja 2000 (*n* = 3)	2n = 32	3.13–4.08–4.75	1.13–1.38–1.56	2.77–2.96–3.04	0.67	33.3/66.7
Helsingfors, Sveaborg 2000 (*n* = 5)	2n = 32	3.94–4.19–4.50	1.50–1.64–1.94	2.63–2.55–2.32	1.60	80.0/20.0
Sweden						
Trosa 2000 (*n* = 6)	2n = 40	4.25–4.66–5.06	1.56–1.80–1.94	2.72–2.59–2.61	2.50	50.0/50.0
Germany						
Regensburg (no. 0010) (*n* = 16)	2n = 32	3.29–4.09–4.88	1.22–1.56–1.83	2.70–2.62–2.66	1.29 (*n* = 7)	62.5/37.5
Italy						
Bormio (no. 1909) (*n* = 109)	2n = ?	3.17–3.62–4.15	1.22–1.47–1.70	2.59–2.46–2.44	1.30 (*n* = 89)	46,8/53.2

Table 4. Germination of *Allium oleraceum* seeds from different localities in Finland and Sweden. Pretreatment = storing the air-dry seeds in the refrigerator at 7 °C.

Country, locality and year of seed collection	Approximate germination temperature and possible pretreatment	Germination (%), total number of seed used (*n*) and total germination time in days (d)		Chromosome number
Finland				
Al (*Alandia*)				
Nåtö, NBS, 1999	7 °C, no pretreatment	85%	(*n* = 20, 61 d)	2n = 40
— NBS, 1999	7 °C, no pretreatment	83%	(*n* = 6, 35 d)	2n = 40
— NBS, Sjöstycket, 1999	7 °C, no pretreatment	90%	(*n* = 20, 50 d)	2n = 40
— NBS, Sjöstycket, 1999	7 °C, no pretreatment	100%	(*n* = 10, 21 d)	2n = 40
— NBS, 1999	7 °C, 14 days in 7 °C	85%	(*n* = 20, 26 d)	2n = 40
— NBS, Sjöstycket, 1999	7 °C, 15 days in 7 °C	100%	(*n* = 10, 35 d)	2n = 40
— NBS, 1999	21–23 °C, 8 days in 7 °C	0%	(*n* = 10, 126 d)	2n = 40
— NBS, 1999	21–23 °C, 48 days in 7 °C	20%	(*n* = 10, 18 d)	2n = 40
— NBS, 2000	7 °C, no pretreatment	100%	(*n* = 1, 19 d)	2n = 40
— NBS, Sjöstycket, 2000	7 °C, no pretreatment	100%	(*n* = 2, 21 d)	2n = 40
— NBS, 2001	7 °C, no pretreatment	70%	(*n* = 10, 102 d)	2n = 40
— NBS, 2001	7 °C, no pretreatment	80%	(*n* = 30, 101 d)	2n = 40
— NBS, 2001	7 °C, no pretreatment	50%	(*n* = 10, 96 d)	2n = 40
— NBS, 2001	7 °C, no pretreatment	50%	(*n* = 4, 160 d)	2n = 32
Nåtö, Själskatsudden, 1999	7 °C, no pretreatment	90%	(*n* = 10, 36 d)	2n = 40
Finström, Stålsby, 2000	7 °C, no pretreatment	100%	(*n* = 2, 19 d)	2n = 40
Geta, Isaksö, 2000	7 °C, no pretreatment	100%	(*n* = 2, 19 d)	2n = 40
— Pantsarnäs, 2000	7 °C, no pretreatment	100%	(*n* = 1, 19 d)	2n = 40
Kökar, Hamnö, church, 2001	7 °C, no pretreatment	60%	(*n* = 10, 119 d)	2n = 40
— Hamnö, church, 2001	7 °C, no pretreatment	60%	(*n* = 5, 119 d)	2n = 32
— Överboda, Åström, 2001	7 °C, no pretreatment	80%	(*n* = 20, 154 d)	2n = 40
— Överboda, Åström, 2001	7 °C, no pretreatment	86%	(*n* = 7, 160 d)	2n = 40
— Hellsö hamn, 2000	7 °C, no pretreatment	0%	(*n* = 1, 267 d)	2n = 40
— Hellsö, Loppö, 2000	7 °C, no pretreatment	100%	(*n* = 1, 21 d)	2n = 40
— Österbygge, Västerklis, 2000	7 °C, no pretreatment	73%	(*n* = 11, 244 d)	2n = 40
Sund, Prästgården, 2000	7 °C, no pretreatment	50%	(*n* = 2, 21 d)	2n = 40
Vårdö, Lövö, 2001	7 °C, no pretreatment	71%	(*n* = 14, 154 d)	2n = 40
Ab (*Regio aboensis*)				
Uusikaupunki, Kalanti, Heikkilä, 2001	7 °C, no pretreatment	83%	(*n* = 30, 160 d)	2n = 40
— Kalanti, Heikkilä, 2001	7 °C, no pretreatment	50%	(*n* = 6, 159 d)	2n = 40
— Kalanti, Heikkilä, 2001	7 °C, no pretreatment	40%	(*n* = 20, 160 d)	2n = 32
Rymättylä, Aaslaluoto, Alakylä, 2001	7 °C, no pretreatment	100%	(*n* = 1, 51 d)	2n = 32
Lieto, Vanhalinna, 2000	7 °C, no pretreatment	100%	(*n* = 2, 30 d)	2n = 32
N (*Nylandia*)				
Hangö, Tvärminne, nature trail 1999	7 °C, no pretreatment	83%	(*n* = 6, 31 d)	2n = 40
— Tvärminne, nature trail 2001	7 °C, no pretreatment	100%	(*n* = 2, 27 d)	2n = 40
— Tvärminne, village, 2000	7 °C, no pretreatment	100%	(*n* = 1, 19 d)	2n = 40
Ekenäs, Fabriksgatan, 2000	7 °C, no pretreatment	80%	(*n* = 10, 56 d)	2n = 40
— Fabriksgatan, 2000	7 °C, no pretreatment	65%	(*n* = 20, 39 d)	2n = 40
— Fabriksgatan, 2001	7 °C, no pretreatment	80%	(*n* = 10, 160 d)	2n = 40
Sjundeå, Svidja, 2000	7 °C, no pretreatment	100%	(*n* = 2, 24 d)	2n = 32
Helsingfors, Sveaborg, Walhalla, 2000	7 °C, no pretreatment	50%	(*n* = 2, 275 d)	2n = 32
— Gustavssvärd, 2000	7 °C, no pretreatment	0%	(*n* = 1, 244 d)	2n = 32
— Gustavssvärd, 2000	7 °C, no pretreatment	67%	(*n* = 3, 226 d)	2n = 32
— Vargön, Café Piper, 2000	7 °C, no pretreatment	100%	(*n* = 1, 152 d)	2n = 32
— Degerö, Jollas, 2000	7 °C, no pretreatment	100%	(*n* = 1, 33 d)	2n = 32
— Botanical Garden, 2001	7 °C, no pretreatment	34%	(*n* = 35, 154 d)	2n = 40

Continues

Table 4. Continued.

Country, locality and year of seed collection	Approximate germination temperature and possible pretreatment	Germination (%), total number of seed used (*n*) and total germination time in days (d)		Chromosome number
Ta (*Tavastia australis*)				
Hollola, Noitala 2000	7 °C, no pretreatment	100%	(*n* = 1, 41 d)	2n = 32
— Heinlammi, 2000	7 °C, no pretreatment	0%	(*n* = 1, 267 d)	2n = 32
Riihimäki, Herajoki, 2001	7 °C, no pretreatment	0%	(*n* = 3, 176 d)	2n = 32
Tyrväntö, Lepaa, 2001	7 °C, no pretreatment	95%	(*n* = 20, 154 d)	2n = 40
Sweden				
Skåne				
Sk., Kågeröd, 1999	7 °C, no pretreatment	83%	(*n* = 6, 35 d)	2n = 40
Södermanland				
Trosa, 2000	7 °C, no pretreatment	100%	(*n* = 6, 152 d)	2n = 40
Uppland				
Norrtälje, Älmsta, 2000	7 °C, no pretreatment	100%	(*n* = 1, 11 d)	2n = 40
Grisslehamn, harbour 2000	7 °C, no pretreatment	0%	(*n* = 1, 175 d)	2n = 40
Germany				
Regensburg (no. 0010), 2001	7 °C, no pretreatment	38%	(*n* = 8, 156 d)	2n = 32
Italy				
Bormio (no. 1909), 2001	7 °C, no pretreatment	60%	(*n* = 20, 144 d)	2n = ?

by Vespidae. Since the studies of Müller (1873) a few plant species have been recognised as "wasp blossoms"; they are characterised by dull, brown colours. *Scrophularia nodosa* is the classical case; the author C.-A.H. has also seen that Vespidae regularly visit the flowers of *S. scopolii*. Other species pollinated by Vespidae are orchids of the genus *Epipactis*.

The periant of *Allium oleraceum* is pale greenish or pinkish with darker redbrown veins and small redbrown mottles. In this respect they resemble typical wasp blossoms. Flowers of tetraploid *A. oleraceum* are rather whitish, while flowers of pentaploids are more reddish; this is easily recognised in fresh plants, but hardly discernible in voucher specimens in herbaria.

Our studies disclose that *Allium oleraceum* is visited to such a degree by wasps of the family Vespidae that it should be included in the group of "wasp blossoms".

In his investigations of the cytogenetics of different *Allium* species, Levan (1933) stated that "… *Allium oleraceum* is tetraploid (2n = 32) …" and "in nature entirely seed-sterile." Presumably referring to Levan's studies, Jalas (1958) pointed out that the possibility to reproduce by seed is lacking in *A. oleraceum*, because no fruits are formed. Thus the reproduction is entirely vegetative by means of offset bulbs and bulbils. According to Hylander (1953) and Weimarck (1963), a capsule is not developed and according to Hultén (1958) the development of seed is bad. Clapham *et al*. (1987) stated that fruits are rarely or never produced.

However, several sources set forth that seeds are produced in *Allium oleraceum* and that they also germinate. The oldest which has come to our knowledge is the book on monocotyledons by Raunkiær (1895–99) where he states that the plant of *A. oleraceum* dies shortly after the ripening of the seeds. Korsmo (1925) reported in his book on weeds in agriculture that *Allium oleraceum* reproduces with subterranean bulbs and above ground by seed and bulbils. Further, the germination of seeds is usually good; 64% of seeds sown in the autumn germinated the next spring. Fruits were also observed during the 1940s in pentaploid (2n = 40) *A. oleraceum* in Austria (Geitler & Tschermak-Woess 1946, Tschermak-Woess 1947). The seeds of these could even occasionally germinate. A seed catalogue of 1956 lists seeds of pentaploid (2n = 40) *A. oleraceum* from Alsace in France (Linder & Brun 1956).

According to Geitler and Tschermak-Woess (1946), only pentaploid *Allium oleraceum* was known from Austria. They observed that the meiosis was strongly disturbed with univalents and polyvalents, and inversion bridges. The pollen fertility was, however, high with 5%–10% ripe and normal looking pollen; spontaneous seed formation was noticed by them. Our studies on the pollen viability resulted in 20%–76% viable pollen in two Alandian populations of pentaploid *A. oleraceum*. The development of pollen tubes was fairly good (9.7% and 22%, respectively).

The question is: How does the pentaploid *Allium oleraceum* form seed? Apomixis is perhaps occurring in *A. oleraceum* as apomixis is known in some species of *Allium* (Kojima *et al.* 1992).

According to Cheshmedziev (1997), the fruit in subgenus *Codonoprasum*, section *Codonoprasum* (or subgenus *Allium*, section *Codonoprasum*, e.g. Hanelt *et al.* 1992), to which *Allium oleraceum* belongs, is ovoid or pyriform and tripartite with prominently concave walls and more or less pointed edges; the mean length of the fruit in *A. oleraceum* is 6–7 mm. The seeds in sect. *Codonoprasum* are vaguely trihedral or almost flat-convex, rough with length between 2.3 and 4.4 mm and width between 1.0 and 2.7 mm; the length:width ratio varies between 1.48 and 3.40. The largest seeds in this section are found in *A. oleraceum*, according to Cheshmedziev (1997).

Korsmo (1935) described the fruit of *Allium oleraceum* as a three-celled, six-seeded capsule and he gave a detailed description of the seed. According to him, it is about 4.5 mm long and 1.6 mm wide; the average weight of 1000 seeds is about 2.0 g (Korsmo 1935). Our results of the size and weight are in accordance with those of Korsmo.

In our germination experiments the seeds germinated much better in dark and cold than in warm. A pretreatment with cold did not improve the germination. Temperature requirements for seed germination in *Allium* species vary. Specht and Keller (1997) tested among others 21 species of *Allium*, subgenus *Allium*, at germination temperatures of 5, 11, 16 and 26 °C. Most of the species reached a germination percentage of 60–80 at 5 °C and 90–100 at 11 °C and 16 °C, whereas the percentage was low at 26 °C. *Allium oleraceum* was not, however, among the tested species.

What happens with the seeds in nature? As far as we know, no studies have been done on the seeds of *Allium oleraceum* in the wild. Perhaps some of the seeds are incorporated in the seed bank? Further studies are needed to solve this problem.

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