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Insect dispersal of pollen and fruits in *Ajuga*

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RÉSUMÉ

LÜÖND, B. & R. LÜÖND (1981). Dissémination du pollen et des fruits par les insectes chez *Ajuga*. *Candollea* 36: 167-179. En anglais, résumé français.

Les principaux pollinisateurs d'*Ajuga reptans* et d'*A. genevensis* sont des bourdons, des faux-bourdons et des Syrphides. Ils ne distinguent pas les deux espèces et effectuent des croisements interspécifiques. Les abeilles ne visitent qu'*A. reptans*. La composition de la faune pollinisatrice peut influencer le sens du "gene-flow" entre les espèces et leurs hybrides, et fonctionner comme régulateur du degré d'introgression. Les fourmis fréquentent souvent les fleurs d'*Ajuga*; elles sont attirées par une substance sécrétée par les papilles glandulaires de la lèvre inférieure de la corolle. La signification biologique de ce comportement reste obscure. Les fourmis n'en sont pas moins d'importants agents de dissémination des méricarpes d'*Ajuga*. La myrmécochorie autorise une dissémination à bien plus longue distance que la reproduction végétative. Les faibles exigences des graines d'*Ajuga* pour leur germination s'accordent parfaitement avec le comportement des fourmis.

ABSTRACT

LÜÖND, B. & R. LÜÖND (1981). Insect dispersal of pollen and fruits in *Ajuga*. *Candollea* 36: 167-179. In English, French abstract.

The main pollinators of *Ajuga reptans* and *A. genevensis* are bumble-bees, *Syrphidae* and *Bombyliidae*. They do not discriminate between the two species and effect interspecific crosses. Honey-bees visit only *A. reptans*. The composition of the pollinator fauna can influence the direction of gene-flow between the species and their hybrids and thus regulate the degree of introgression. Ants frequently visit *Ajuga* flowers and are attracted by a substance secreted by glandular papillae on the lower lip of the petals. The biological significance of this behaviour is obscure. Ants are however important as dispersal agents of *Ajuga* mericarps. Ant dispersal can cover considerably longer distances than vegetative spread. The somewhat restricted requirements for germination of *Ajuga* seeds are well adjusted to the behaviour of ants.

Introduction

The two widespread blue-flowered species *Ajuga reptans* L. and *A. genevensis* L. were chosen for this work. *Ajuga reptans* is common in Switzerland and occurs from the lowlands to the subalpine level. *Ajuga genevensis* has partly the same distribution but is much less frequent than *A. reptans*.

Hybrids between these two species have been recognized for a long time (KERNER, 1874; BORBÁS, 1889; SANIO, 1890; BECKER, 1901; SCHULZ, 1902; DRUCE, 1916). Information on the extent of this hybridization under different ecological conditions and experimental crossing have been documented by LÜÖND & LÜÖND (1979, 1980).

The present work deals with some of the factors that permit this hybridization. Of particular interest in this respect are the information about the flowering time of the two species and observations on flower visitors and their frequency. Of equal interest is the frequent presence of ants in *Ajuga* flowers in connection with their role in seed dispersal. The extent of sexual reproduction by seedlings in both species is small compared to the vegetative propagation by runners and root buds. Germination experiments are described to show the reason of the restricted seed reproduction.

Flowering time

Ajuga reptans blooms from about mid April to the end of May, *A. genevensis* from the end of April to the middle of June. Blooming overlaps for about one month. At favourable sites a second series of inflorescences of *A. genevensis* appear about six weeks after the main flowering time. The frequency of flowering during one growing season is illustrated in Fig. 1.

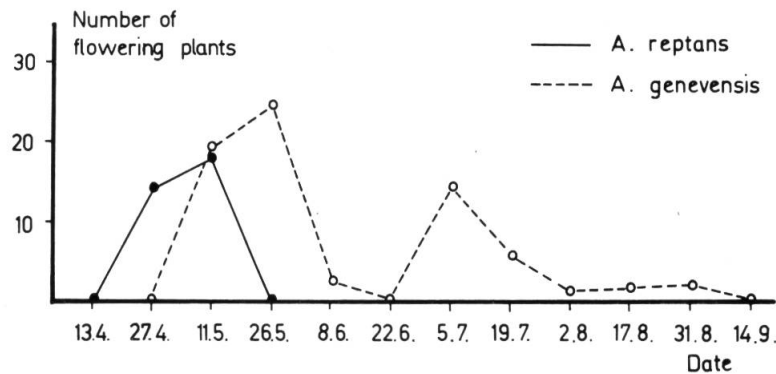


Fig. 1. — Flowering times. Number of flowering plants of a total of 40 plants of each species in an experimental plot in 1977.

Gynodioecy

Gynodioecy was found in *A. reptans*. In all populations investigated by us some plants were found with sterile, sometimes partly reduced or petaloid anthers. The proportion of male sterile plants in samples of different populations cultivated in the garden was similar. The average of male sterile plants is just about one fifth of all plants in the population ($18.55\% \pm 7.8$). Plants with partly sterile anthers occur sporadically. Comparison of the seed set of bisexual and male sterile inflorescences in the field did not show any significant differences.

Visitors to *Ajuga reptans* and *A. genevensis* flowers

In works on pollination biology numerous insects are listed as visitors of *Ajuga* (KNUTH, 1898-1905; KUGLER, 1970; PROCTOR & YEO, 1973). Our investigations showed, that representatives of the families of *Apidae*, *Syrphidae* and *Bombyliidae* are the most frequent visitors. The frequency of the visitors depends on the site, season, weather, frequency and distribution of *Ajuga* plants and competition offered by other flowers in the associated vegetation.

The following insects were observed exclusively to collect nectar:

Apidae

- *Bombus agrorum* F. (most frequent);
- *B. equestris* F. (sporadic);
- *B. terrestris* L. (sporadic);
- two further unidentified species of *Bombus*;
- *Apis mellifica* L. (very frequent on *A. reptans*);
- *Osmia bicornis* L. (rare to frequent depending on the site);
- *O. sp.* (rare to frequent depending on the site);
- *Anthidium manicatum* L. (rare to frequent depending on the site).

Bombyliidae

- *Bombylius major* L. (sporadic);
- *B. minor* L. (sporadic).

Lepidoptera

- *Pieris brassicae* L. (occasional);
- two further unidentified species (occasional).

Exclusive pollen collectors are:

Apidae

- representatives of the genus *Halictus* Latr. (very frequent at certain sites).

Syrphidae

- *Chilosia* sp. (rare);
- *Neoascia podagrica* Fabr. (rare);
- *Pipiza* sp. (rare);
- *Melanostoma ambiguum* Fall. (rare).

The following visitors collect both pollen and nectar:

Syrphidae

- especially *Rhingia campestris* Meig. (in general the larger representatives of the *Syrphidae*).

Syrphidae, ants and occasionally house-flies were often observed to feel papillae at the entrance to the corolla tube with their mouth parts. The ants do not effect pollination. The efficient pollinators are the representatives of the *Apidae* (bees and bumble-bees) and *Bombylius minor* L. The other visitors effect only chance pollinations. *Bombylius major* L., the larger of the observed bee-fly species, must be considered as nectar thief, because the animals put their long proboscis horizontally into the corolla tube and hardly touch the anthers and stigmas.

Discrimination of species by honey-bees

The most frequent visitors, hover-flies, bee-flies and bumble-bees, with the exception of honey-bees have been observed on both *Ajuga* species. In contrast to the honey-bees they have been found at sites with mixed *Ajuga* populations visiting the inflorescences of both species, but also making occasional side-trips to other genera (e.g. *Vicia*). These insects do not discriminate the two *Ajuga* species. Honey-bees however show a more differentiated behaviour towards the two species. They visit almost exclusively *A. reptans*. The visitor lists in KNUTH (1898-1905) do not contain any observations of honey-bees on *A. genevensis* either. Individual plants of *A. reptans* with small or male sterile flowers with short corolla tubes are often preferred by honey-bees. When visiting normal flowers, the honey-bees press their heads powerfully into the corolla tubes. After anthesis of *A. reptans* is finished, honey-bees sometimes visit inflorescences of *A. genevensis*. In these cases the animals regularly show a particular searching behaviour. Large, attractive and well developed flowers are ignored. The bees search the inflorescences for flowers which are partly eaten by snails or otherwise damaged and have incomplete petal tubes. We have also observed selection of small flowers in *Glechoma hederacea* L., which has flowers of markedly different sizes. Differences in size of the flowering parts of the two species are the reason why honey-bees almost exclusively visit *A. reptans*. It is not yet known, which characters other than size are used by honey-bees to

distinguish the two species. Colour and nectar guide pattern of the flowers are not very different. Honey-bees avoid flowers of *A. genevensis* even when they approach them from the front. What influences their decision for or against a visit is probably not the length of the corolla tube but the general appearance of the extended lower lip. UV is known to be the brightest colour for bees. Our investigations showed, that the UV flower patterns of the two species are not very different. On the other hand it is possible that even small difference in UV reflection in combination with the other slight differences in colour and pattern could produce distinctly different impressions to the bees.

Comparisons between proboscis length of the insects and the petal tube length and nectar level showed, that *A. reptans* flowers with up to 9.2 mm long and *A. genevensis* flowers with up to 9.5 mm long corolla tubes can be exploited by honey-bees. Table 1 shows, that all *A. reptans* populations have a large percentage of flowers with nectar accessible to bees. In relatively "pure" or non-introgressed *A. genevensis* (population Randen) the flowers are physically too long for the bees' mouthparts. Hybridized populations of *A. genevensis* (Strahlegg, Disentis) however have a large proportion of flowers with corolla tubes short enough to be exploited by honey-bees. In these populations honey-bee visits to undamaged *A. genevensis* flowers have actually been observed.

Population *	n	Range of corolla tube length (mm)	Percentage of exploitable plants
<i>A. reptans</i>			
Pfannenstiel	14	5.25-10	85.7
Sattel	19	8.25-10.25	68.4
Böbikon	15	6.5 -10.75	73.3
Schönau	17	8 -10.25	58.8
Strahlegg	12	8 -10	83.8
<i>A. genevensis</i>			
Randen	19	10 -13.3	0
Pfannenstiel	15	8.5 -12.8	6.6
Böbikon	25	9 -14	4
Strahlegg	16	7 -11.5	31.2
Disentis	20	6.5 -11.5	65

*Population sites are described in LÜÖND & LÜÖND (1979, 1980). In the populations of *A. reptans* male steriles are included.

Table 1. — Petal tube length and exploitation by honey bees

The relation between the length of proboscis and petal tubes also explains the behaviour of honey-bees on damaged flowers of *A. genevensis*; the nectar is accessible by the damage to the petal tube.

Ants as visitors of flowers

Ants, especially *Formica fusca* and *Lasius niger* were frequently observed in flowers of *Ajuga*. Their activities however are slightly erratic. They often penetrate deeply into the petal tube, but rarely advance far enough to reach the nectar. More often however they lick the papillae of the lower lip with their maxillae, spreading the mandibles sideways. They do this especially in the region of the entrance of the corolla tube. The papillae are short multicellular glandular hairs on the epidermis (Fig. 2) secreting a substance which is apparently attractive to ants. The secretion accumulates under a cuticular blister. Ants cannot be considered to be pollinators. They do not

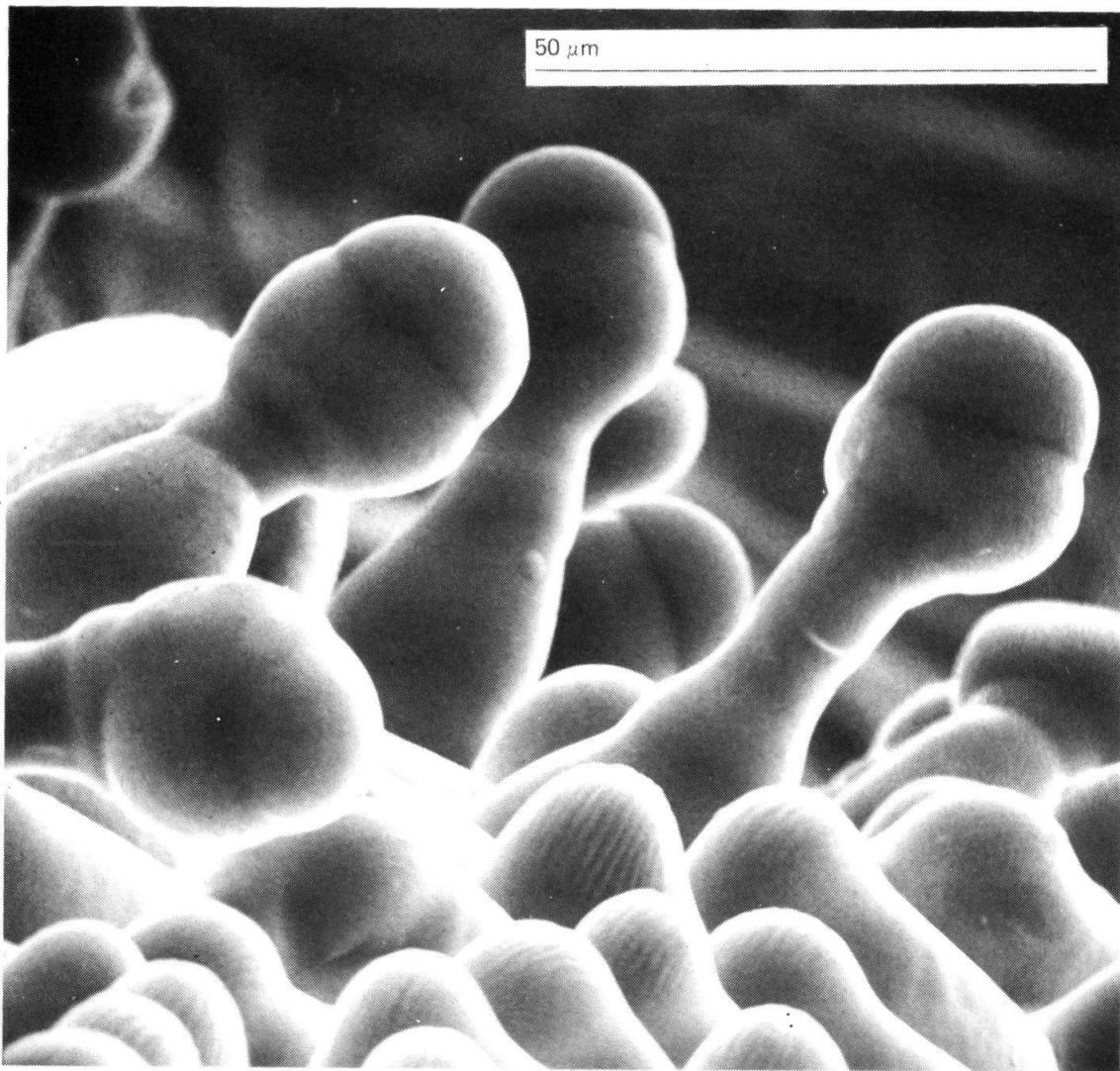


Fig. 2. — Scanning electron microscope picture of the glandular papillae on lower lip at the entrance to the corolla tube.

touch either the anthers or the stigma. A possible explanation for the relationship between ants and *Ajuga* is, that the plants keep their prospective diaspore dispersal agents close at hand by providing an attractive glandular secretion and stimulate them to build nests.

Seed set in *Ajuga*

Investigations showed, that the actual seed set was considerably lower than the possible maximum: the average seed set within populations of *A. reptans* and *A. genevensis* ranged from 17.8 ± 7.7 to $49.1 \pm 15.7\%$. Crosspollinations between the species are not the reason for the low seed sets, because in experimental interspecific crosses much higher seed set was often reached. Competition of pollen from other genera on the stigmas of *Ajuga* also cannot explain this fact, because the foreign pollen in most cases adheres to parts of the insect body, which do not come into contact with the stigmas of *Ajuga*. Comparison between seed sets of bisexual and male sterile plants of *A. reptans* did not yield any significant differences. Therefore geitonogamy cannot be made responsible for the low seed set. A poor seed set was also recorded in some experimental crosses between conspecific individuals from the same or different populations. Seed set in crosses between individuals of *A. reptans* ranged from 0 to 87%. This suggests, that an incompatibility system reduces the possibility of genetic exchange between individuals of the species.

Seed ecology

Fruit dispersal

The fruit of *Ajuga* consists of up to four mericarps. Ants are the most important dispersal agents of *Ajuga* mericarps. Ants develop their greatest mericarp collecting activity in late spring and early summer when they are nest building and raising their brood. *Ajuga* meets the most important requirements for myrmecochorous plants (ULBRICH, 1928): early flowering and quick fruit ripening. In the present work experiments with *Formica fusca* L., *Formica polyctena* Först. and *Lasius niger* L. were conducted. All these species readily collect *Ajuga* mericarps (Fig. 3). It is generally considered in our latitudes, that ants collect *Ajuga* mericarps as an energy rich food. Ants are always present on *Ajuga* plants from the onset of flowering, because they are attracted by glandular secretions of the papillae on the lower lip. They are therefore on the spot, when the fruits ripen and often collect them directly from the calyces without waiting for them to drop to ground. When ripe, the fruits often split in the middle and the elaiosomes

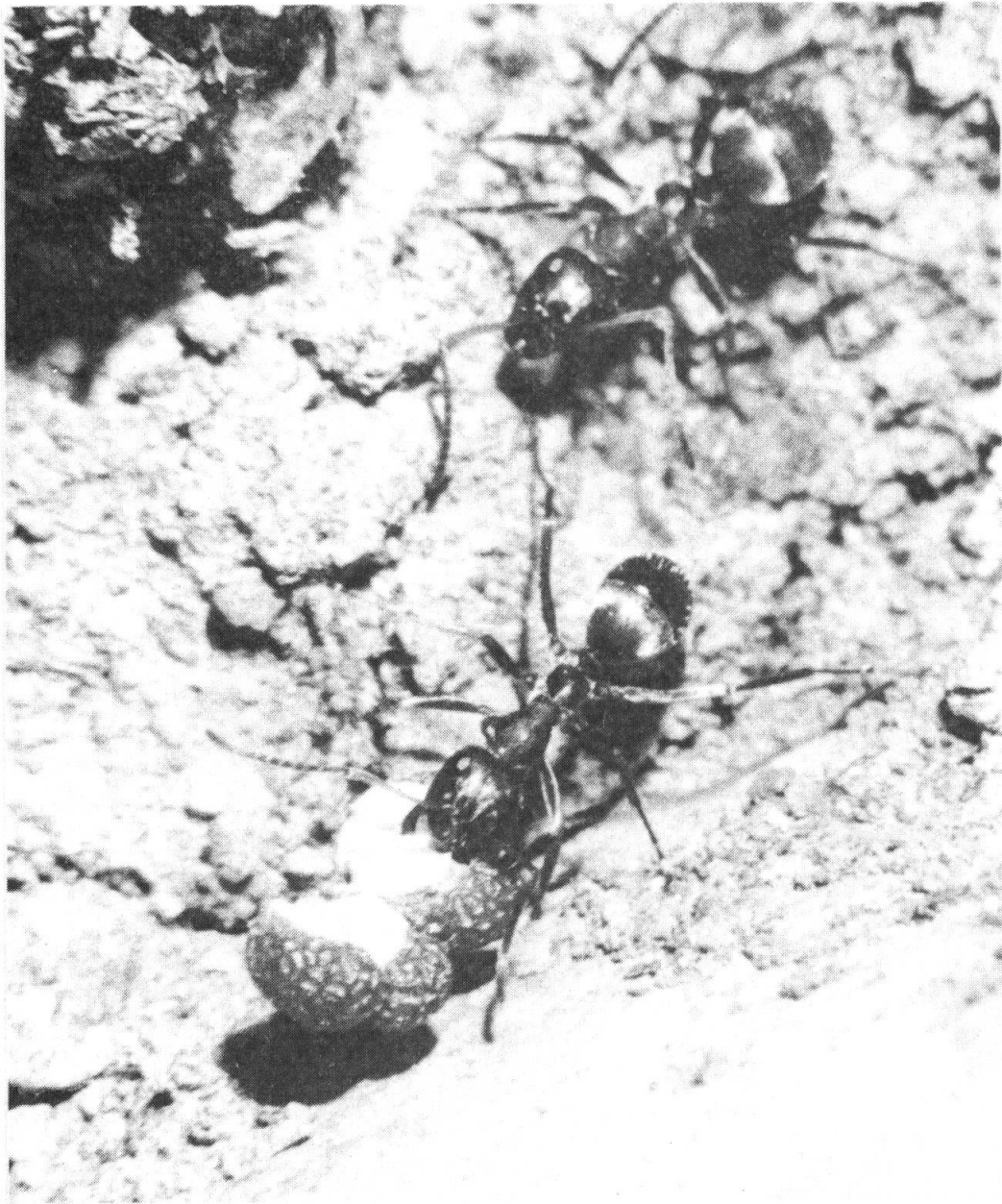


Fig. 3. — *Formica fusca* carrying an *Ajuga* fruit.

on the inner side of the mericarps become exposed. The elaiosomes consist of yellowish white fatty tissue on both sides of the conductive tissue of the funiculus. ULBRICH (1928) called this kind of elaiosome "Ajuga- Typus". Observations of the collecting behaviour of ants in natural sites and in an artificial nest showed, that the seeds are normally thrown out of the nests after the fatty tissue has been eaten off (Fig. 4). The seeds can then be found on the waste heaps of the ants. This makes sense biologically, because the *Ajuga* seeds are obligate light germinators (LÜÖND & LÜÖND, 1979). The

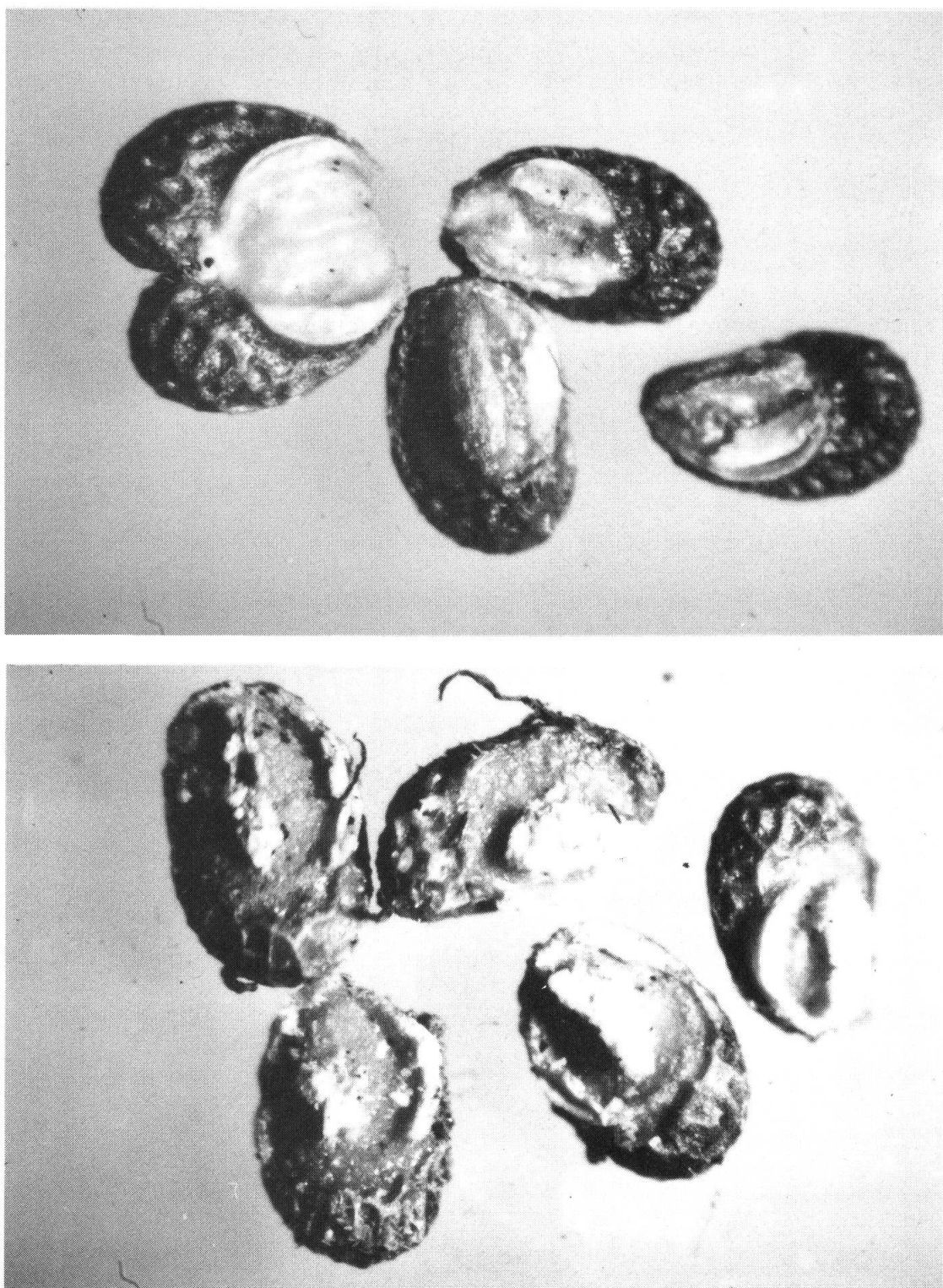


Fig. 4. — Mericarps of *Ajuga*.
Above: intact; below: fatty tissue removed by ants.

differences of the mericarp size of the investigated species obviously do not influence the harvesting behaviour of the ants. In an experiment *Formica polyctena* did not show a preference for either of the species. Deception experiments with pieces of cork proved, that neither colour nor shape, but the smell of the fatty tissue induced the harvesting behaviour of the ants. The distance of dispersal varies considerably. Often the ants built nests within the experimental plots of *Ajuga*. In these cases distance of dispersal was accordingly small. On the other hand, individuals of *Formica fusca* have been observed to cover distances of ca. 8 m from the harvesting place to their nest. Not all the sites around ants' nests are favourable for germination. The waste heaps of ants tend to be on bare soil which quickly dries up. In such habitats, seedlings of *Ajuga* are much less frequent than in moister places with sufficient light. On inhabited nests of *Formica fusca* no plants of *Ajuga* were found.

Seed germination

The ability of the mericarps to germinate is very variable and varies in summer from 15 to 90%. Experiments showed, that many factors are responsible for this variation. Of importance are the species of the plant, the age of the mericarps, their origin, climatic conditions during fruit formation, photoperiod at sowing time, the moisture content of the substrate and within limits also the temperature (LÜÖND & LÜÖND, 1979). The reaction to photoperiod is of particular interest. Only seeds exposed to light germinated, and only in long-days were higher germination percentages reached (Fig. 5). As experiments showed, exposure to only one long day was sufficient for

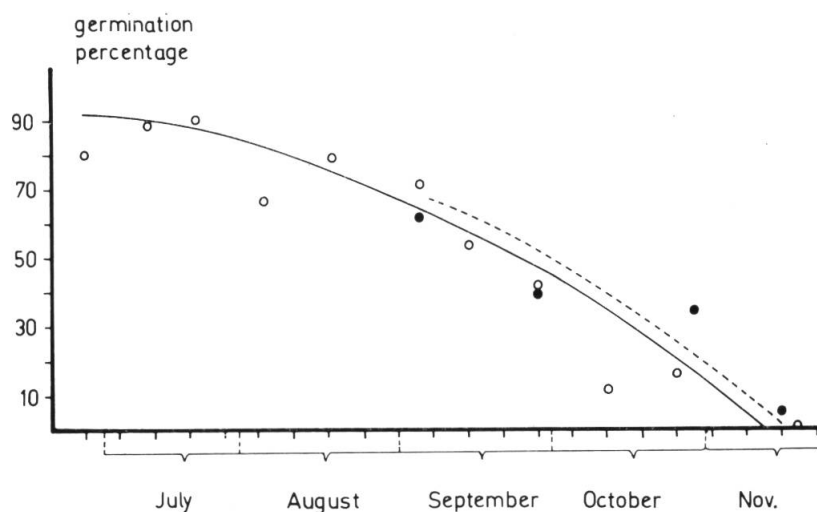


Fig. 5. — ○——○ Decrease of germination percentage during the summer and autumn of 1978 in *A. reptans* (in the field). ●-----● Values at constant temperature (ca. 20°C) but day-length as in the field.

germination of some mericarps. But for higher germination rates, several days of exposition with interjected dark phases were necessary. The mericarp coat is responsible for the light requirement in germination. Without this coat, the seeds also germinated in the dark. AXENTJEV (1929) has observed the same in *Rumex crispus* and SMITH (in HEYDECKER, 1973) in *Lactuca sativa*. Several authors like TOOLE & al. (1955), SCHEIBE & LANG (1965), CÔME (1970) and McCULLOUGH & SHROPSHIRE (1970) attach great importance for germination to the phytochrome system of the diaspores.

Discussion

The spread of *A. reptans* and *A. genevensis* at the population level is mainly vegetative by the means of runners or root buds. Sexual reproduction is comparatively insignificant for local increase in rosette numbers, because most seeds fail to germinate or germinate in places unfavourable for the development of seedlings. Sexual reproduction in *Ajuga* is important in two ways. It provides means for the colonization of new areas and permits genetic recombination.

Ajuga species are myrmecochorous and the transport of mericarps by ants covers far greater distances than is possible by runners or root growth and allows invasion into new suitable areas. Field observations on populations in disturbed sites showed that sexual reproduction can quickly produce a variety of new genotypes, especially where hybridization is possible (LÜÖND & LÜÖND, 1980).

The obligate light germination of *Ajuga* seeds is well attuned to the ant dispersal, because the ants throw the seeds out of their nests after having eaten the elaiosomes. The considerable variation found in the percentage of germination might be due to environmental factors. It could be partly determined by the mother plant during the ripening of the diaspores as McCULLOUGH & SHROPSHIRE (1970) report for *Arabidopsis thaliana*. Variable demands on environmental factors for germination may have survival value for the species. The risk, that the most of the viable seeds die during sudden outbreaks of unfavourable conditions is decreased. The selection of long photoperiods by means of the phytochrome system increases the chance of germination before the onset of winter.

All the pollinators of *A. reptans* and *A. genevensis* except honey-bees visit both species without discrimination and are capable of effecting interspecific crosses. Thus a considerable number of hybrid seeds are produced in sympatric populations. Given the presence of suitable ecological conditions, these seeds can grow into hybrid populations which may exchange genes with the parents. The composition of the pollinator fauna is variable and can affect the direction of the gene-flow between the species in sympatric populations, particularly in places where honey-bees are the most frequent pollinators, because *A. reptans* and *A. reptans*-like hybrids are

intensively visited. An indiscriminant insect visitor carrying pollen from *A. genevensis* will very probably find, that the stigmas of *A. reptans* have already been pollinated by honey-bees. As the honey-bees themselves only visit *A. reptans* and *A. reptans*-like hybrids a cross fertilization of *A. reptans* by pollen of *A. genevensis* is probably a rare event. *Ajuga genevensis* on the other hand is only visited by indiscriminant insects. Especially in places, where *A. reptans* is predominant, they will often carry pollen of this species to still unpollinated stigmas of *A. genevensis*. Therefore the probability of *A. genevensis* being "infected" by genes of *A. reptans* is high. In places, where honey-bees dominate, gene-flow apparently takes place predominantly from *A. reptans* to *A. genevensis*. In other places, where honey-bees are missing and all pollinations are carried out by indiscriminant insects, gene-flow may take place in both directions.

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