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Published in:
Acta Botanica Neerlandica

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Document Version
Publisher's PDF, also known as Version of record

Publication date:
1988

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

Kwak, M. M. (1988). Pollination ecology and seed-set in the rare annual species *Melampyrum arvense* L. (Scrophulariaceae). *Acta Botanica Neerlandica*, 37(2), 153-163.

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Pollination ecology and seed-set in the rare annual species *Melampyrum arvense* L. (Scrophulariaceae)

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SUMMARY

Pollination of *Melampyrum arvense* L., a large-flowered hemiparasitic annual, was investigated in populations in The Netherlands, Germany, France and Switzerland. Pollination is achieved by bumblebees, with varying tongue lengths, collecting pollen and/or nectar. Long- and medium-tongued workers pollinate the flower nototribically (head–thorax pollination) and pollen-collecting short-tongued bumblebees sternotribically (venter pollination), as analysed by the actual transfer of fluorescent powder. Short-tongued bumblebees collect nectar by robbing the flowers, and sometimes also destroying the pistil. Nectar was present in a volume of 0.26 µl, with a sugar concentration of 30% and a ratio of fructose:glucose:sucrose = 1:0.67:0.73. *M. arvense* is self-fertile, but caged flowers do not produce seeds by the absence of auto-deposition. Artificial pollination showed that increasing pollination intensity increased fruiting, although after three pollinations fruiting did not increase and the number of seeds per fruit did.

Observations in plots with variable plant density showed that during a low visitation intensity, flowers were visited at least 6.7 times during the flower's life span (7 days), and at a high visitation intensity 39.3 times. The additional effect on the seed-set of one-hand pollination during the flower's lifetime was low. Plants in low-density plots are highly branched in contrast to plants in high density. Branching of plants, resulting in more flowers per plant, and the fact that flowers on branches produce more seeds per flower, influence the total seed production per plant. The *M. arvense* population in The Netherlands had a rather high fruiting percentage and seed production per plant compared to three French populations.

Key-words: bumblebees, *Melampyrum arvense*, nectar, pollination, robbery, seed production.

INTRODUCTION

The genus *Melampyrum* (Scrophulariaceae, Rhinanthoideae, 20–30 species) has two main areas of distribution, one in Europe extending into Asia and the other in East Asia extending into tropical regions. One species, *Melampyrum lineare* Desr., has a wide distribution in North America (for a review on population biology see Ter Borg 1985). *Melampyrum arvense* L., field cow-wheat, is a hemiparasitic, annual species, which is very

rare in The Netherlands; it is restricted to the southern parts (Mennema *et al.* 1980). It is also found in neighbouring countries such as Belgium, Germany (Matthies 1985, 1986) and France, where it is more common, but also has a low frequency. *M. arvense* is a characteristic species of Caucalidion (Hartl 1974). *M. arvense* prefers warm sunny, dry to semi-dry sites. It is found on road verges, margins of farm lanes, chalk grasslands and very occasionally in cereal fields, the main habitat in the past before efficient methods of seed cleaning were introduced. The seeds of *M. arvense* have the same size, shape and colour as cereal caryopses. The recent decrease in the number of populations may also be due to a reduction in the possible habitats (chalk grasslands) and the use of herbicides.

Although the flowering plants are very conspicuous due to the flower and bract colour, only aspects of germination, parasitism and distribution have received attention (Gislen 1949, Oesau 1973, 1975, Weber 1976, Matthews 1985, 1986). This study on the pollination of *M. arvense* was undertaken in order to increase our knowledge on the floral ecology of other Rhinanthoideae than species of *Pedicularis*, *Rhinanthus* and *M. pratense* (Kwak 1977, 1979). The rarity of the species in The Netherlands was an added incentive to carry out this survey in order to contribute to the ecology of rare species. The behaviour of pollinators (bumblebees) on *M. arvense* and their effect on the seed production is described. A comparison is made of the seed-set in populations with different numbers of individuals, including one Dutch population.

MATERIALS AND METHODS

In 1977 and 1978 insects were observed visiting populations of *M. arvense* in Switzerland (Crusch, Unterengadin) and Germany (ruins Nolle near Wertheim am Main). In 1986 and 1987 additional observations were made in populations (Assen, Bovensmilde in the north of The Netherlands) which had originated from seeds derived from a population near Verdun (France).

In 1987 the population in Bovensmilde was divided into three plots of 50 × 50 cm each. Bumblebee visitors to the plots were observed for a period of 15 min, eight times per observation day, for 4 days in the period from 6th to 21st July. The density of the flowering axes and the number of flowers per plot per observation day were recorded.

The effectiveness of pollen transfer by bumblebees was studied by touching the pollen sites on the bodies of the visiting bumblebees with a brush containing fluorescent powder ('Daylight' Fluorescent Heffner and Co.). These bumblebees continued their foraging trips. Visited flowers were collected and the styles examined with a portable UV lamp for the presence of fluorescent powder (population Crusch 1977).

In 1986 and 1987 plants in bud were caged in order to determine self-pollination potentials. In 1987 two experiments on artificial pollination were carried out on caged, intact flowers.

Experiment 1: self- or cross-pollination only once, or cross-pollination twice per flower.

Experiment 2: three or six self- or cross-pollinations per flower (three pollinations per day with an interval of approximately 5 h).

Pollination success was determined after 3–4 weeks. In 1987 the seed production was measured in the Dutch population (Limburg) and three French populations (Verdun, Toul, Dieu). Nectar was collected from open flowers by inserting a 2 µl capillary tube (Drummond microcaps) into the nectary. Concentration of the solutes was estimated with a pocket refractometer (Bellingham and Stanley, Tunbridge Wells), modified for small volumes, and expressed as a percentage (grams glucose/100 g solution). The

method described by Kwak *et al.* (1985) was used for the analysis of the sugar composition.

RESULTS

Flower morphology

The flowers of *M. arvense* are pink-magenta coloured with a yellow band, which varies in size. The flowers are arranged two by two in a dense spike which also has magenta-coloured bracts. The inflorescence is very conspicuous. The bracts also bear extra floral nectaries that attract ants (Fig. 1).

The zygomorphic flowers (20–25 mm) are two-lipped (Fig. 1). The lower lip is pressed to the upper one in young flowers but forms a more or less small flat landing platform in older ones. Before putting their heads into the corolla, the visiting insects must push the lower lip downwards. The upper lip forms a narrow, laterally flattened hood enclosing the four stamens. The two pairs of stamens (3.0–3.5 mm) are opposite each other and form a pollen chamber in the galea, which is positioned more or less longitudinally (Fig. 2). Pollen grains only drop out of the chambers if these are opened by the bumblebees or later when the flower becomes senescent or wilted. The life span of the flower is 7.1 ± 1.04 days ($n=23$, population Assen 1987). The corolla tube is about 19 mm long and it forms a distinct curve 10 mm from the basis. The nectary is placed under the ovary at the bottom of the corolla tube. A rather long tongue is therefore necessary to reach the nectar legitimately. The very slender pistil has a protruding stigma of about 1 mm (Figs 1 and 2).

The fruit is about 10 mm long, without hairs and contains four ovules. The seeds are large, nearly 6 mm long and 2–3 mm broad with a thick elaiosome.

Insect visitors

Insect visitors on *M. arvense*, foraging for pollen, were divided into two groups: nototribic (head-thorax pollination) and sternotribic (venter pollination) visitors. When foraging for nectar two groups can also be distinguished: the legitimate nectar collecting individuals and the nectar robbers.

Nototribic pollinators. Long- and medium-tongued bumblebees were seen to place their heads and tongues into the corolla tube to secure nectar, foraging in the normal, legitimate way. The sides of the flower hood and the anthers were pressed apart by the tongue and head of the visiting bumblebees. The pollen dropped out of the pollen chambers onto the head and thorax, while the stigma nototribically contacted residual pollen (Figs 4 and 5). When introducing their heads, the bumblebees can cross-pollinate the flower; when leaving the flower they may bring about self-pollination. Pollen was groomed from the body and deposited in the corbiculae and was visible as light-yellow clumps. Workers of the long-tongued *Bombus hortorum* L., *B. pascuorum* Scop. and *B. sylvarum* L. were observed to behave in this way (Table 1). *B. pascuorum* workers particularly visited flower buds with a length of 15 mm or more (calyx slips as long as flower). In this phase the stigma started to be receptive. Short-tongued bumblebees, e.g. *B. terrestris* workers, sometimes visited the flower in a normal position, introducing their heads without unfolding their tongues, and then vibrating their wings to stimulate the grains to fall out of the pollen chamber. The same individuals collected nectar as robbers (see below).

Sternotribic pollinators. Pollen-collecting short-tongued bumblebees approached the flowers, landed upside-down on the upper lip, supported their inverted bodies by grasping

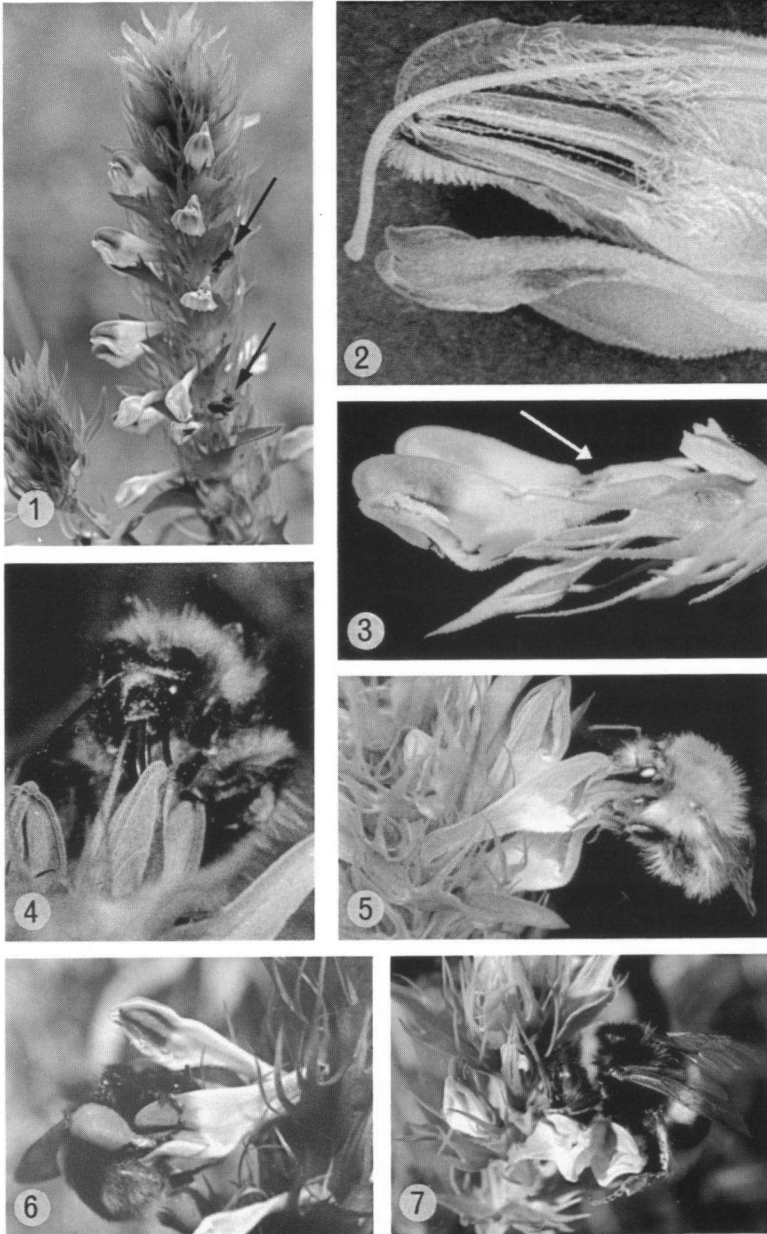


Fig. 1. Inflouescence of *Melampyrum arvense*; arrows indicate ants on extra floral nectaries. **Fig. 2.** Longitudinal section through the upper lip of *Melampyrum arvense*, showing protruding pistil and enclosed anthers. **Fig. 3.** Two flowers of *Melampyrum arvense* showing holes in the corolla tube (arrow) with an intact pistil. **Figs 4 and 5.** A *Bombus pascuorum* worker visits *Melampyrum arvense* nototribically. **Fig. 6.** A sternotribic visiting *Bombus terrestris* worker on *Melampyrum arvense*. **Fig. 7.** A nectar-robbing *Bombus terrestris* worker on *Melampyrum arvense*.

the galea with their legs, and curved their abdomen under the pollen chamber. They opened the pollen chamber by grasping the edge of the galea with their mandibles and tearing it apart (Fig. 6). Wing vibrations, causing a hissing sound, released the pollen

Table 1. Bumblebee species (only workers) and their foraging positions in *Melampyrum arvense* populations, arranged according to tongue lengths (data derived from Pekkarinen 1979)

Species	Tongue length (mm)	Bovensmilde 1987 (The Netherlands)	Nolle 1976 (Germany)	Crusch 1977 (Switzerland)
<i>Bombus hortorum</i>	12.42	N	—	N
<i>Bombus sylvarum</i>	7.93	—	—	N
<i>Bombus pascuorum</i>	7.89	N	—	N
<i>Bombus terrestris</i>	7.85	}	N, S, r	S, r
<i>Bombus lucorum</i>	6.37			
<i>Bombus pratorum</i>	7.11	—	—	r

N = nototribic, S = sternetribic, r = robbing, — = no observation.

that was deposited at the venter. Pollination was achieved when the stigma touched the pollen-covered venter of the inverted bumblebee. The bumblebee groomed the pollen from the venter after one or several flowers and transported it to the corbiculae. Flowers visited by sternetribic pollinators often showed signs of damage, visible as brown spots or the complete destruction of flower parts, caused by the tearing and grasping of the insect's mandibles. The bumblebees species *Bombus terrestris* L., *B. lucorum* L., *B. pratorum* L. visited the flowers sternetribically (Table 1).

The pollination efficiency differed between noto- and sternetribic visitors (measured as transfer of fluorescent powder). Of the nototribically visited flowers, 44.2% ($n=43$) had a fluorescent stigma and of the sternetribically visited flowers 25.9% ($n=27$) had a fluorescent stigma (population Crusch in 1977), but this difference is not significant ($\chi^2 = 2.32$).

Nectar robbers. Flowers of *Melampyrum arvense* have a very long corolla tube (± 19 mm), which is too long for several bumblebee species to reach the nectar. *B. terrestris* workers were seen to make holes in the tube just in the curve to reach the nectar (primary robbers). Other short-tongued species used these holes (secondary robbers).

In the robbing position the bees sit on the upperlip or they use neighbouring flowers or bracts for their support (Fig. 7). They do not pollinate the flower, and therefore reduce seed production. Of the flowers of the Nolle population (26 July 1977) 78.4% had a hole ($n=88$) but 19.3% of the flowers also had a pistil that was bitten through; thus fertilization had become impossible.

Nectar

Nectar was present in a volume of 0.26 μ l (range 0–0.69 μ l, $n=21$) and a sugar concentration of 30% (range 17–36%, $n=8$, population Assen 1987). Three main nectar sugars were present in the ratio fructose:glucose:sucrose = 1:0.67:0.73 (population Crusch, 20-7-1977).

Seed production

In Table 2 seed-set and fruiting of open pollinated flowers in various populations is shown. Generally fruits on branches produced more seeds per flower than fruits on the main axis

Table 2. Numbers of flowers on main axis and branches, seed-set per flower and per plant in populations of *Melampyrum arvense* 1987; the estimated population size is given for natural populations, the density per plot (50 × 50 cm) is given for the artificial population Bovensmilde

Population	Size	Number of flowers		Seeds per flower		Percentage fruiting per plant	Seed-set per plant
		On main axis	On branches	On main axis	On branches		
Limburg	14	26.9	13.3	1.08	1.88	71.3	54.06
Verdun	100	29.7	16.8	0.56	0.83	49.5	30.58
Toul	300	ND	ND	1.17	1.98	78.6	ND
Dieu	> 1000	28.1	56.1	0.95	0.75	41.4	68.76
Bovensmilde							
Plot 1	26	24.7	29.0	0.57	0.92	57.4	40.73
Plot 2	103	11.0	1.8	0.48	ND	37.1	6.43*
Plot 3	107	11.2	2.0	0.49	0.63	42.0	6.73

*The value of plot 3 (flowers) is used for calculation; ND = not determined.

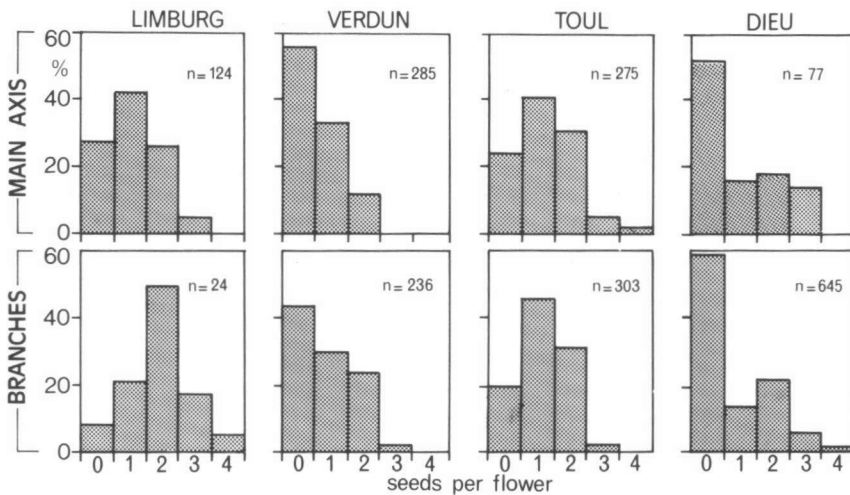


Fig. 8. Frequency distributions of seeds per flower per main axis and branch in four bumblebee-pollinated *Melampyrum arvense* populations in 1987.

except in the population Dieu. Plots with high plant density in the artificial population Bovensmilde showed a low seed (and flower) production compared to the low-density plot (per 1 m² the production was: plot 1, 4236; plot 2, 2649 and plot 3, 2880 seeds). Therefore, fewer plants per area resulted in more branched (and more flowers per) plants producing more seeds per square metre. The number of seeds per flower in the plots did not differ in this way. Three or four seeds per capsule were quite rare (Fig. 8), and they were found more often in fruits on branches than on the main axis.

Caged flowers had a very low percentage of fruits (1.9–4.3%) and seed-set per flower (0.02–0.05) (Table 3) compared to the open pollinated flowers (45.8–88.2%), thus indicating the importance of insect visits for seed-set.

Table 3. Fruit and seed production in open-pollinated and caged flowers in artificial populations of *Melampyrum arvense*

Location	Year	Open-pollinated			Insect-exclosure		
		Number of flowers	Percentage fruiting	Seeds per flower	Number flowers	Percentage fruiting	Seeds per flower
Assen	1986	170	88.2	1.32	211	3.8	0.05
Bovensmilde	1986	177	76.3	1.14	257	4.3	0.04
Bovensmilde	1987	794	45.8	0.60	574	1.9	0.02

Table 4. Fruiting percentages and seed set in artificial pollinated, caged *Melampyrum arvense* flowers in the Bovensmilde population 1987

	Self-pollination		Cross-pollination	
	1 ×		1 ×	2 ×
Experiment 1				
<i>n</i>	42		28	32
Percentage fruiting	21.4		32.1	59.4
Experiment 2	3 ×	6 ×	3 ×	6 ×
<i>n</i>	21	21	24	19
Percentage fruiting	57.1	47.6	45.8	36.8
Seeds/flower	0.86	0.71	0.54	0.58
Seeds/capsule	1.50	1.50	1.18	1.57

The results of artificial pollinations are summarized in Table 4. Experiment 1 showed a better fruiting if flowers were cross-pollinated instead of self-pollinated and two artificial cross-pollinations resulted in a higher fruit-set than one.

In Experiment 2 pollination took place three to six times a day. Fruiting decreased when the frequency of pollination increased whereas cross-pollinated fruits seemed to produce more seeds at a higher pollination frequency. The age of the flower at the time of pollination had no effect on the seed-set: pollination of the youngest flowers ($n = 29$) gave a fruiting of 41.4% and a seed per flower ratio of 0.59, whereas pollination of the oldest flowers ($n = 29$) resulted in a fruiting percentage of 37.9% and a seed per flower ratio of 0.55.

Plot observations

Visitation. In the population Bovensmilde only two bumblebee species were important visitors (nototribic pollinators): *B. hortorum* and *B. pascuorum* workers. Several times workers of *B. pratorum* and *B. terrestris* visited the inflorescences but they did not succeed in entering the flowers. On the 9th July visitation was low in all the plots, resulting in approximately one visit per flower per day (0.96–1.11) (Table 5). On the 13th July visitation was high (4.91–5.11) in all plots. The flower life span was 7 days. Visitation

Table 5. Numbers of flowers and bumblebee visits per flower per day (=9 h activity period) in three *Melampyrum arvense* plots (50 × 50 cm). Bovensmilde population 1987

	6 July	9 July	13 July	21 July
Plot 1 (26 plants)				
Flowers	97	154	198	317
Visit/flower/day	5.01	1.11	4.91	3.59
Plot 2 (103 plants)				
Flowers	151	193	202	230
Visit/flower/day	2.89	0.98	5.61	1.60
Plot 3 (107 plants)				
Flowers	174	294	221	358
Visit/flower/day	1.32	0.96	5.11	1.60

Table 6. Fruiting percentage and seed-set per flower per day in three *Melampyrum arvense* plots, population Bovensmilde 1987

	6 July	9 July	13 July	21 July
Plot 1				
Fruiting	77.8	86.7	78.9	48.0
Fruiting +	83.3	86.7	73.7	56.0
Seed-set	1.28	1.80	1.42	0.8
Seed-set +	1.39	1.60	1.32	0.8
Plot 2				
Fruiting	50.0	71.4	44.4	17.6
Fruiting +	78.6	64.3	50.0	11.8
Seed-set	0.79	0.79	0.56	0.18
Seed-set +	0.93	0.86	0.78	0.12
Plot 3				
Fruiting	83.3	44.4	28.6	0
Fruiting +	61.1	61.1	47.6	7.1
Seed-set	0.89	0.67	0.33	0
Seed-set +	0.89	0.67	0.52	0.07

+ = One additional hand-pollination on the observation day, *n* per treatment per day varies between 14 and 25.

per flower lifetime during low visitation happened 6.72 times as a minimum and for high visitation 39.3 times as a maximum. The actual visitation per flower lifespan lies somewhere between these ranges.

Seed-set and fruiting. The results on seed-set and fruiting of the flowers that flowered during the observation days are summarized in Table 6. If an increase of at least 7% in the fruiting percentage is considered to be the effect of one additional hand-pollination per flower per day, then a positive effect was observed in five cases, no effect in five cases, and even a negative effect was observed on 2 days. If a difference of 0.15

seeds/flower is considered to be the effect of one additional hand-pollination per flower per day then a positive effect was only observed in three cases and no effect was observed in nine cases.

DISCUSSION

The flowers of *M. arvense* are the largest among the genus in Europe. They need visitors with a long tongue because of the long corolla tube and because the galea is usually closed they need visitors that are able to open it. Long- and medium-tongued bumblebees (workers) were observed as visitors but in some cases short-tongued species, such as *B. terrestris*, *B. lapidarius* and *B. pratorum* workers were also visitors, either as nectar robbers or as sternotribic pollen collectors. It is striking that only long- and medium-tongued bumblebees were visitors in the Bovensmilde population, although short-tongued species were present and sometimes tried to visit the flowers. This situation corresponds to Werth's (1955) idea that a division could occur between long-tongued bumblebees visiting *Rhinanthus serotinus* and short-tongued bumblebees visiting *R. minor*. The pollination efficiency of nototribic visitors was higher than that of sternotribic visitors (44% and 26%, respectively, of the pistils showed the presence of fluorescent powder). This may be due to the difficulties experienced by sternotribic visitors in positioning their bodies correctly under the galea, which must first be opened. The position on the body where pollen is deposited can vary because the whole underside contained pollen grains. *M. arvense* flowers are attractive to bumblebees for both pollen and nectar. A moderate volume of nectar was present (0.26 μ l) with a sugar concentration of approximately 30%. The volume is larger compared to *M. pratense* but the concentration is lower (*M. pratense* in Sweden: volume 0.12 μ l \pm 0.01 ($n=250$), concentration 39.2% \pm 1.31 ($n=35$); M. M. Kwak unpublished data). *M. arvense* nectar may be more attractive than *M. pratense* nectar because of its composition of the three sugars in equal amounts, the most attractive mixture for bumblebees (Pouvreau 1974). *M. pratense* has a ratio of 1:0.26:1.18. *M. pratense* is also very attractive for bumblebees for both pollen and nectar. The robber bumblebees may have a negative effect on the seed-set of *M. arvense* by destroying the pistil. It is only the corolla which is bitten and not the calyx. After the flower has fallen off it is impossible to trace whether the flower had been robbed or not (in *Rhinanthus* spp. the calyx also had holes).

The lifespan of the flower is relatively long (7 days) compared to *M. pratense* (4 days). The additional effect of a single hand-pollination in open flowers is, therefore, less important. For instance, if the visitation frequency is low a flower only receives 6.7 visits, and if the visitation frequency is high a flower received 39.3 visits, hand-pollination is only 13.0% and 2.5%, respectively.

The two experiments on artificial pollination showed that increasing pollination frequency stimulated fruiting but that after about three pollinations fruiting decreased. In this case the time interval between two pollinations was approximately 5 h (during the day). It is therefore possible that if only one pollination was applied each day, fruiting and seed-set would increase. In Experiment 2 no observations were made of fruits with three and four seeds per capsule. The occurrence of three and four seeds per capsule is also rare in the field situation. The Limburg and Dieu populations had the highest percentages (4.8 and 14.3) for the main axes, 16.7 and 5.4 for the branches, respectively). Matthies (1986) found 10–40 seeds per plant. The lowest value found here was only six seeds per plant and the highest 69 seeds per plant. Branching had a great influence on the total seed production

per plant because more flowers were produced per plant and the flowers on the branches generally produced more seeds per flower. The branching of the plants may be the result of a good habitat with convenient host plants, and not too high a density of other hemiparasitic individuals.

Matthies (1986) mentioned a density-dependent effect on the reproduction. High-density plants (112 plants per m²) produced fewer seeds per plant than low-density plants (16 plants per m²). The same was found for plants in plots 2 and 3 compared to plot 1 and here the densities were much higher (412, 428 compared to 104 plants/m²). Matthies (1986) found that the performance of *M. arvensis* was better along farm lane edges than in chalk grasslands, which can be attributed to more fertile conditions and different host species. This conclusion cannot be confirmed by the data presented here (Table 2). The highest seed production per plant was found in the Dieu population, a road side on the edge of a forest. The Toul population was also isolated from agricultural land and had the highest fruiting percentage. Matthies (1986) only described populations in chalk grassland vegetations and not in cereal fields. The populations in this study are also situated in this type of vegetation. *M. arvensis* was only observed once in a cereal field (Barrême, Haute Provence, France).

The field situation of the populations and the presence of other species that are attractive to bumblebees may influence the number of species and the number of individual insects. In the Bovensmilde population many other plant species that attract bumblebees were present. It was therefore possible to make a distinction between plants visited by long- and short-tongued bumblebees. The Nolle population had very few other flowering species present. The population was very isolated, surrounded by vineyards. O. Jennersten (unpublished data) found that in the case of *Dianthus deltoides* anthophilous insect's diversity was lower in the population isolated within an agricultural area than in the population surrounded by a mixture of forests and abandoned farmland. If other plant species visited by bumblebees are present, then insects may combine several food plants in one foraging trip. If an attractive species is present with few individuals then this combination of various simultaneously flowering species is likely. This combination must have taken place in the case of the Limburg population (only 14 plants). In that habitat other plants which are attractive to bumblebees were *Vicia cracca*, *Lotus corniculatus*, *Ononis spinosa* and *Centaurea jacea*.

M. arvensis is not self-sterile. A lack of seed production in caged plants must be due to the absence of a mechanism for auto-deposition. The style did not curve backwards as was found, for instance, in *Rhinanthus serotinus* (Kwak 1979) and what is described for both *M. arvensis* and *M. pratense* (Heukels 1910). *M. arvensis* will maintain its population as long as it occurs in a habitat with sufficient host plants, where the surrounding vegetation is not too high and possibly in the presence of other plant species attractive for bumblebees.

The studied, natural population in The Netherlands has maintained itself at least since 1950. Its number of plants varies but in 1987 only 14 plants were present. If the percentages of survival of *M. pratense* are applied (1–6% of the seeds will result in an adult plant Masselink 1980) one can expect 7.6–45.6 plants of *M. arvensis* in 1988.

ACKNOWLEDGEMENTS

The author wishes to express her gratitude to Drs Ben Hoentjen (Bovensmilde), who looked after the plants in the artificial populations and counted seeds, to Yolande

Holthuijzen for the nectar composition analysis, to Dr P. Rasmont (Gembloux, Belgium) for the determination of the *Bombus* species and to Dr C. L. Plate (Leiden) for additional information on the rarity of the species. Dr S. J. ter Borg (Wageningen) and Professor Dr J. van Andel commented on the earlier draft of the manuscript. Mr E. Leeuwinga prepared the diagram and Mrs J. M. Purdell-Lewis corrected the final English text. All their contributions are gratefully acknowledged.

The investigations were supported by the Foundation for Fundamental Biological Research (BION), which is subsidized by The Netherlands Organization for the Advancement of Pure Research (WO).

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