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GERMINATION AND SEED POPULATION DYNAMICS IN MELAMPYRUM PRATENSE L.

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SUMMARY

Dormancy and germination requirements, their variation throughout the year, and aspects of the seed population dynamics are studied in *Melampyrum pratense* L. (Rhinanthoideae), an annual hemiparasite.

Germination occurs at low temperatures. Within this process a considerable period of epicotyl dormancy is involved. Dormancy preceding radicle germination may be present in varying degrees. In the field the germination response changes with time and appears to be related to macroclimatic changes, especially in temperature.

Counts made on a small number of plots show that most seed losses occur on the forest floor during summer and autumn. Small mammals are the most likely and important cause accounting for these losses. The data on survival and germination, supplemented with information on seedlings and mature plants, allow the construction of a life table. It is also attempted to explain the coincidence in distribution which is often found between *M. pratense* and *Deschampsia flexuosa*. Data on the losses indicate that different pressures are exerted upon the seeds in various microhabitats by seed eating animals, leading to a spatial coincidence of *M. pratense* with sites with densely tufted grasses.

Moreover, the possible ecological significance of the prolonged germination is discussed.

1. INTRODUCTION

Cow wheat, *Melampyrum pratense* L. (Rhinanthoideae, Scrophulariaceae), an annual chlorophyllous parasite, is common in the eastern, sandy districts of The Netherlands.

Contrary to the other hemiparasitic Rhinanthoideae in this country, it parasitizes exclusively woody plants (SMITH 1963, HARTL 1974). It could be grown e.g. with *Quercus robur*, *Betula pubescens*, *B. pendula*, *Vaccinium myrtillus* and *V. vitis-idaea* as a host, but did not accept herbaceous plants nor other Ericaceae (unpublished data). Nevertheless, the distribution of plants within its habitat mostly coincides with that of grassy species and especially that of *Deschampsia flexuosa*, a phenomenon which has already long been noticed, though interpreted as a parasite-host relation (WESTHOFF 1937, ELLENBERG 1963). *M. pratense* is restricted to open woods, edges of woodland, hedgerows and wooded roadsides. In The Netherlands it does not occur in heath vegetation types (except those with *Vaccinium*), peatlands and conifer woods (cf. SMITH 1963, HARTL 1974).

Mature plants of *M. pratense* start flowering in June and die in late summer and autumn. Seeds are shed from July to early September. The seeds are large

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(3–6 × 1–2 mm) and newly shed, they may become dispersed by ants (Formicidae), because they have an elaiosome, containing a fatty substance that is attractive to them (e.g. HEUKELS 1910, HARTL 1974). Germination takes place from late September until November. A root system with haustoria develops during winter and seedlings emerge in March.

Various studies deal with the germination of *Melampyrum* species (ZALASKY 1962, CURTIS & CANTLON 1963, 1965 and 1968, HORRILL 1972, OESAU 1973). The extensive studies of CURTIS & CANTLON show that in *M. lineare* germination is of long standing and comprises various stages. Results of other studies indicate this to be a general feature in *Melampyrum*, though detailed information is often wanting. This holds as well for *M. pratense*. Only temperature requirements to start germination have been studied more fully (OESAU 1975).

Like other annual Rhinanthoideae *M. pratense* possesses a pronounced phenotypic variation (SOÓ 1927/28, HARTL 1974). Part of it has been found to be geographically determined (SMITH 1963, JALAS 1967). Another part is likely to be habitat related, as this has been shown to be present in related genera, e.g. *Rhinanthus serotinus* (TOLWINSKA 1962a and b, TER BORG 1972, MIZIANTY 1978) and *Euphrasia* spp. (KARLSSON 1976). However, studies for *M. pratense* are lacking.

To obtain more insight into the variability of *M. pratense* a study was made of populations occurring in the north of The Netherlands, including morphological and ecological aspects. It showed that the populations predominantly belong to the subspecies *pratense*. Out of sixty populations studied, only one had to be placed in another taxon, the ssp. *commutatum* (Tausch ex Kerner) C. E. Britton. Within the ssp. *pratense* no relation between phenotypic variation and habitat factors could be established (unpublished data).

This paper presents the data of a detailed study of dormancy and germination requirements and their variation with time in seeds that have been kept under natural conditions. By combining this information with demographic data, it appeared possible to present an explanation for the coincidence in distribution between *M. pratense* and grasses, mentioned above.

2. MATERIALS AND METHODS

Studies were performed in various populations occurring in the north of The Netherlands (Drenthian district). The populations of Eext, Zeegse, Annen, Appelbergen and Zeijener strubben were situated in open, coppiced oak woodland (*Querco roboris-Betuletum*), mostly bordering upon patches of heath-like vegetation. The population of Norg grew along a young oak plantation in the State forest Zeijenerveld, that of Amen along a hedgerow in a small brook valley among meadows. All occurred on poor, acid, sandy soils.

A single experiment was also performed with seeds from Scandinavian populations (Sandby (Öland), Karlshamn (Blekinge), Arvika (Värmland) in Sweden and Odda (Hordaland) in Norway), collected in August 1974. The first two populations were situated on the border of the temperate to hemiboreal region,

the third in the boreal and the last on the border of the western pine and deciduous forest to the alpine region (cf. SJÖRS 1967).

Three seed fractions were distinguished and separately studied 1) fresh ripe seeds, 2) fresh seeds collected from the litter and 3) hibernated seeds. As fresh ripe seeds were considered seeds discharged from the capsules after drying at room temperature for 24 hours. To test germination, seeds were placed in petri dishes on filter paper moistened with tap water. Dependant on the number of seeds available 50, sometimes 75 or 100 seeds per dish, and two replicates per treatment, were used. Once a week the tests were inspected and germinated seeds counted. Seeds were considered as germinated 1) when the roottips had penetrated the testa or 2) when the seedlings had emerged from the testa. The experiments were carried out in germination chambers with a 12 hours light regime (TL 33) at various constant temperatures and continued for at least 150 days, in most tests for more than 300 days. Standard tests were performed at 10°C. When treated with gibberellic acid seeds were soaked for 24 or 48 hours at 20°C in a solution of 100 or 500 ppm GA_3.

Germination percentages are based on the total number of germinated, and viable non germinated seeds present at the end of the tests. Half time values (T_{50}), i.e. the number of days necessary to reach half the final germination or half the final number of seedlings acquired after radicle emergence, are used as a measure for the germination rate. Ability to germinate is expressed as activation value, that is as germination rate multiplied by the germination percentage ($= 1/T_{50} \times$ germination %).

To study changes in the germination response under natural conditions seeds were collected from the field, mixed with some humus, enclosed in bags of synthetic lace material and laid down again in the litter or on the soil covered by vegetation. At regular intervals samples were brought into the laboratory and tested. One experiment was done with fresh ripe seeds collected in July and during after-ripening tested in August and September at a range of temperatures, another one with hibernated seeds, collected from the litter in spring and tested at 10°C at monthly intervals.

Since vegetation analyses and field observations pointed to a preference for dense grassy sites, germination was studied separately in a number of microhabitats occurring in various populations. Germinated and non germinated seeds were counted on 25 × 25 cm^2 plots after radicle germination had stopped (November). The plots were chosen at random and assigned by eye to one of the following microhabitat types:

1. densely packed, layered leaf litter.
2. open patches with some plants and/or litter.
3. loose tufts or mats of grasses (mainly *Deschampsia flexuosa*) with some litter or mosses.
4. dense tufts or mats of *Deschampsia flexuosa*, rarely *Festuca* species.
5. mats dominated by mosses.
6. dense patches of *Vaccinium* species (*V. myrtillus* and/or *V. vitis-idaea*).

Colour (glossy, whitish to light brown) and size of the seeds permitted count-

ing them individually in the field. This study was performed in five populations: Eext (1973/74, Zeegse (1973), Appelbergen (1974/75), Annen (1974/75) and Zeijener strubben (1973 and 1975). Throughout the years of investigation a gradual shift to other populations was inevitable, since the vegetation structure became disturbed by the searching for seeds.

To obtain insight into the factors affecting the seed population in the field, numbers of seeds were studied in four selected plots of 1 m^2 in the population at Annen, less intensively in some plots at Eext and Appelbergen. Hibernated seeds were collected at the start of this experiment (end-June) and put down together in a comparable site just outside the plots. During summer (July to beginning September) fresh seeds were counted every two weeks, later on once per month (end-September to mid-December). Seedlings were counted in March and mature plants in July of the following year. To study transport, seeds and mature plants were removed from an area of 2 m around one of the plots (all together 24 m^2) by end-June. Seeds that had been carried away (by ants) from the plot to this area were counted by mid-September.

Nomenclature of phanerogams follows Rothmaler (1972).

3. RESULTS

3.1. Germination and dormancy

Like in *M. lineare* at least three stages can be distinguished in the germination process of seeds of *M. pratense*. After incubation the first phase, usually called radicle germination, ends when the radicle penetrates the seed coat. The last phase of development starts at the growth and extension of the cotyledons and is finished when the seedling emerges from the testa. Both phases are linked together by a period of epicotyl dormancy during which no visible development of the epicotyl takes place, though radicle and hypocotyl may continue to extend. To complicate the germination pattern even more, the phase of radicle germination may be preceded by one of primary or secondary dormancy. In seeds still enclosed in the capsules (fresh ripe seeds) primary or "innate" dormancy may be present, on the other hand seeds that hibernate, enter in a state of secondary or induced dormancy (see ROBERTS 1972 for the definitions of these terms). The quantity and intensity of both dormancy types vary and may have a strong influence upon the results of germination experiments.

To complete germination successfully the presence or absence of light appeared to be of no importance, this contrary to the requirements set to temperature and moisture.

3.1.1. Radicle germination

Seeds of the Drenthian populations studied proved to have essentially the same temperature range, in which radicle germination took place (*table 1*). The upper limit was at about 15 °C. High germination percentages could still be found at 2.5 °C and some germination may even be possible below 0 °C, since in an experiment in which the seeds received a low temperature treatment (–2.5 °C)

Table 1. Activation values and germination percentages (between brackets) at various low temperatures for seed samples of *M. pratense*, collected from five different populations in the Drenthian district, after 0, 1 and 2 months after-ripening under natural conditions in the field (summer 1974); replicates taken together).

		Temperatures					
		2.5°C	5°C	7.5°C	10°C	12.5°C	15°C
Appelbergen	July	0.6 (23)	2.3 (61)	**4.6** (97)	2.7 (77)	0.3 (33)	– (0)
	August	1.4 (46)	3.5 (81)	**4.2** (92)	2.6 (87)	0.5 (36)	– (0)
	Sept.	2.4 (62)	4.7 (80)	**5.3** (84)	3.6 (87)	0.5 (40)	– (0)
Eext,	July	1.6 (46)	3.3 (73)	**5.9** (83)	4.6 (83)	2.4 (81)	0.4 (4)
	August	2.4 (64)	4.1 (86)	**6.2** (86)	4.0 (91)	1.9 (88)	0 (1)
	Sept.	3.9 (71)	5.0 (75)	**5.4** (76)	4.6 (74)	2.4 (79)	0.2 (4)
Annen,	July	2.5 (76)	4.0 (93)	**6.5** (91)	5.4 (87)	2.8 (84)	0.1 (10)
	August	2.8 (89)	5.1 (91)	**7.4** (96)	4.1 (95)	2.2 (97)	0 (1)
	Sept.	4.3 (64)	5.5 (71)	**6.0** (78)	5.9 (77)	4.0 (83)	0.5 (9)
Norg,	July	0.5 (17)	2.9 (69)	4.6 (87)	**5.4** (91)	3.7 (97)	– (0)
	August	3.2 (97)	5.0 (100)	**7.1** (100)	5.8 (98)	3.3 (99)	– (0)
	Sept.	4.7 (84)	6.1 (97)	**6.3** (95)	6.0 (96)	4.1 (99)	– (0)
Amen,	July	1.6 (51)	3.8 (90)	**4.8** (91)	3.4 (88)	0.5 (52)	– (0)
	August	3.0 (89)	**5.3** (100)	5.1 (97)	3.0 (100)	1.0 (75)	– (0)
	Sept.	3.9 (94)	5.7 (97)	**6.5** (98)	3.5 (99)	1.2 (69)	– (0)

some seeds were found with an emerged radicle (which, however, developed into dwarfed seedlings). Therefore the lower limit will be about 0 °C, but actually it is more flexible and dependant than is the upper limit (see below).

Fresh ripe seeds showed an optimal germination at about 7.5 °C. Here activation value and often also germination percentage turned out to be highest. During after-ripening the optimum widened and the results changed to such an extent that only small differences remained between 5°, 7.5° and 10 °C (cf. *table 1*). Otherwise the data of *table* 1 shows that the increase in activation (and germination percentages with it) during after-ripening was more obvious at temperatures below than above 7.5 °C.

No germination was obtained at alternating temperatures of 25°/10° or 20°/10 °C (during 12 hours each), but at 15°/5 °C germination was similar to that at 10 °C.

The results of an experiment with seeds of Scandinavian lowland populations were similar to those mentioned above (*table 2*). For populations from boreal and mountainous areas (Arvika, Odda) the ranges and optima of temperatures for radicle germination were found to be slightly higher. However, since the seeds had been stored for different periods (2–4 weeks) and under different climatic conditions, the results probably also reflect differences in the degree of after-ripening.

Table 2. Activation values and germination percentages (between brackets) at various low temperatures for seed samples of some Scandinavian populations of *M. pratense* (1974, seeds collected in August and incubated on 8th September; replicates taken together).

	Temperatures					
	2.5°C	5°C	7.5°C	10°C	12.5°C	15°C
Sweden						
Karlshamn, (14-8-1974)	3.0 (87)	6.3 (95)	**6.5** (98)	5.8 (99)	3.8 (96)	0 (2)
Sandby, (16-8-1974)	1.8 (48)	3.8 (72)	5.4 (86)	**5.8** (87)	4.7 (84)	0.3 (10)
Arvika, (18-8-1974)	1.9 (57)	4.0 (85)	5.4 (92)	6.1 (97)	**6.3** (100)	0.7 (30)
Norway						
Odda, (28-8-1974)	0.4 (13)	2.2 (47)	4.2 (67)	4.7 (80)	**6.4** (89)	1.7 (57)

3.1.2. Primary and secondary dormancy

Samples of fresh ripe seeds collected at various moments in the growing season often varied with regard to the germination obtained at 10°C (or 5°C). When compared for successive years, even large fluctuations may be observed (*table 3*). Samples of seeds collected in late autumn and winter did not germinate at 5°, but slowly so at 10°C. For the radicle germination at 10°C for instance, T_{50} values were found ranging from 80 to 170 days (cf. *fig. 2*).

In both cases dormancy was involved, since up to 100% of the seeds germinated at 5° or 10°C after pre-treatment at high temperatures (seeds incubated at 20°, 25° or 30°C preferably for more than 2 weeks) (*fig. 1*). Similar or even better results were obtained, when gibberellic acid was applied to the seeds before incubation at low temperatures (*table 4*).

It is supposed that the primary dormancy occurring in fresh ripe seeds was induced in periods of warm and dry weather and even strongly so, when the parent plants were in a state of drought stress. The idea is based on field observations and is supported by a positive correlation ($r_{spearman} = 0.98$;

Table 3. Relation between percentage of primary dormant seeds present in samples fresh ripe seeds of *M. pratense* and average daily temperature.
Fresh ripe seeds from different populations collected monthly during three successive summers; average daily temperature based on measurements of the meteorological station at Eelde and calculated over 5 weeks previous to the date of sampling.

Year:	1973			1974			1975		
Seeds collected in:	July	Aug.	Sept.	July	Aug.	Sept.	July	Aug.	Sept.
Percentages of dormant seeds:									
Eext	45	75	46	17	21	28	36	51	44
Zeegse	61	79	59	–	–	–	–	–	–
Appelbergen	–	–	–	23	29	37	41	65	59
Average daily temperature in °C	16.3	17.0	16.3	14.7	15.2	15.6	15.4	16.5	16.2

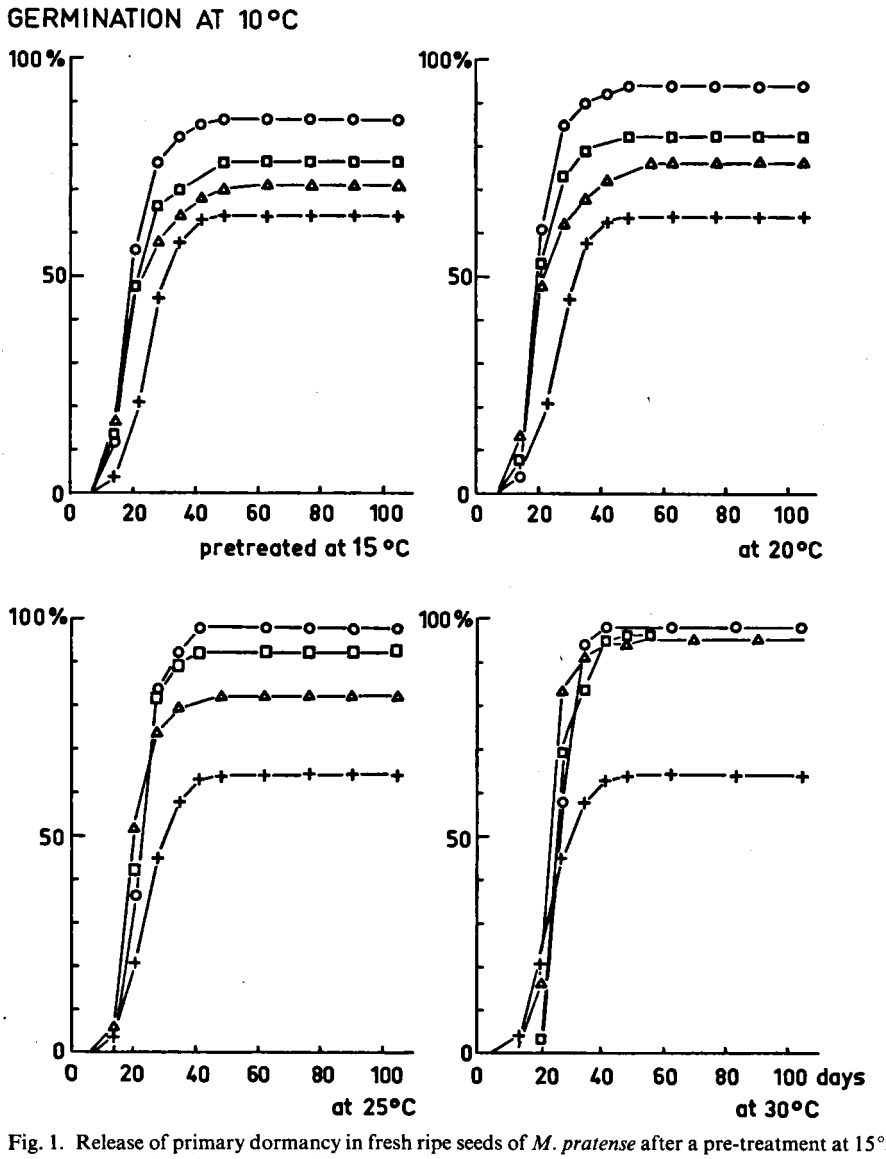

Fig. 1. Release of primary dormancy in fresh ripe seeds of *M. pratense* after a pre-treatment at 15°, 20°, 25° or 30°C during 2 (△), 4 (□) or 8 (≤) weeks; controls (+).
After pre-treatment seeds were incubated at 10°C; duration of pre-treatment excluded from the graphs.

$p < 0.01$) found to exist between percentage of non-germinating seeds at 10 °C and average daily temperature, calculated over the period during which the seeds develop (*table 3*). The importance of dryness could also be deduced from the opposite effects of high temperature upon induction (in the field) and release (in laboratory tests) of primary dormancy (cf. *fig. 1* and *table 3*).

Secondary dormancy might be induced at temperatures below those that are favourable for radicle germination. It was found to be present in seeds collected in the field in late autumn and winter after radicle germination had stopped (cf. *fig. 2*). Secondary dormancy was also found to be induced in non germinated seeds stored moist at low temperatures (5 °C or lower; unpublished data).

3.1.3. Epicotyl dormancy and seedling development

If germinating seeds in which the radicle had penetrated the testa were brought to 15 °C or higher temperatures, no further development took place. Most seeds

Table 4. Average duration of seedling development.
For some experiments in which a temperature treatment or GA_3 has been used to break epicotyl dormancy, T_{50} values are given for the radicle germination, seedling development after radicle emergence and duration of the whole germination process at 5° or 10 °C. Between brackets, germination percentages obtained in the tests.

	A half time value of radicle germination	B half time value of seedling emergence after radicle emergence	C half time value of seedling emergence (C = A + B)
Seeds that have just passed radicle germination, pretreated at 5°, and afterwards transferred to 10 °C.			
0 week at 5° (control 10°)	–	145	–
1 week at 5°	–	136	–
2 weeks at 5°	–	121	–
4 weeks at 5°	–	98	–
6 weeks at 5°	–	113	–
8 weeks at 5°	–	118	–
control at 5°	–	120	–
Partly secondary dormant seeds, pretreated with GA_3.			
at 5°, control	54 (39)	125	179
at 5°, 100 ppm GA_3	59 (93)	114	173
at 5°, 500 ppm GA_3	37 (100)	112	149
at 5°, 2 × 500 ppm GA_3	36 (100)	108	144
at 10°, control	60 (56)	132	192
at 10°, 100 ppm GA_3	43 (97)	123	166
at 10°, 500 ppm GA_3	40 (100)	106	146
at 10°, 2 × 500 ppm GA_3	39 (100)	98	137
Non dormant seeds, pretreated with GA_3.			
at 10°, control	25 (89)	138	163
at 10°, 100 ppm GA_3	22 (97)	127	149
at 10°, 500 ppm GA_3	22 (98)	107	129
at 10°, 2 × 500 ppm GA_3	21 (98)	107	128

began to rot and finally withered away. Only when such seeds were maintained at lower temperatures, seedlings finally emerged. Below 15 °C the number of days necessary to achieve half the ultimately acquired number of seedlings after radicle germination (T_{50}) was lowest between 5° and 7.5 °C.

Results of experiments also indicated that somewhat higher temperatures stimulated seedling development in the final phase of development, since T_{50} values decreased when seeds with emerging radicles were incubated for some time at 5°, followed by a transfer to 10 °C (cf. *table 4*). Because T_{50} values tended to increase after a longer treatment at 5 °C, the time necessary to break epicotyl dormancy at that temperature was about 4 weeks. At a constant temperature of 10 °C this time had already doubled (4 weeks + (138–98) or (145–98) days) (cf. *table 4*).

Table 4 also shows that the need of low temperatures necessary to break epicotyl dormancy might be replaced by applying gibberellic acid to the seeds. It did not only shorten radicle germination but also further development to seedling. For the stages after radicle germination GA_3 in a concentration of 500 ppm is as effective as a temperature treatment of 4 weeks 5°, followed by 10 °C.

3.2. Germination behaviour of seeds in the field

3.2.1. Changes with time

The germination response of seeds present on the forest soil was studied by testing samples collected at various times of the year. It was found to change with time (*fig. 2B* and *C*).

In 1973 primary dormancy of fresh seeds appeared to be maximal in the first half of August. After 250 days at 10 °C about 50% of the seeds had not yet germinated (consequently a T_{60} value is lacking in *fig. 2B*). The increase during the first part of the summer was connected with a similar trend in fresh ripe seeds (cf. *table 3*). Though in the latter primary dormancy was still considerable in September, by then a clear change had occurred in the fraction of fresh seeds. The proportion of non dormant seeds increased to about 70% of the total seed number; similarly the germination rate increased, as is demonstrated by the decrease of the T_{40} value from about 200 to 15 days. From field observations it was obvious that seeds being dried out in mid-summer gradually became turgid again afterwards, a feature brought about by some rain and probably even more so by dew fall at night. Since moisture conditions improved, the breakdown of dormancy could be performed by temperatures in late August and the first part of September, still being relatively high (*fig. 2A*).

In most years radicle germination in the field starts at the end of September i.e. the time in which the average daily temperature comes near or just below 10 °C (cf. *fig. 2A*). According to *table 1* this is about the optimal temperature. In 1973 the first seeds with extruding radicles were observed on September 26th, and by mid-November when germination had stopped about 50% of the total seed population had radicles (cf. *table 5*).

It will be clear that while germination proceeds, the composition of the

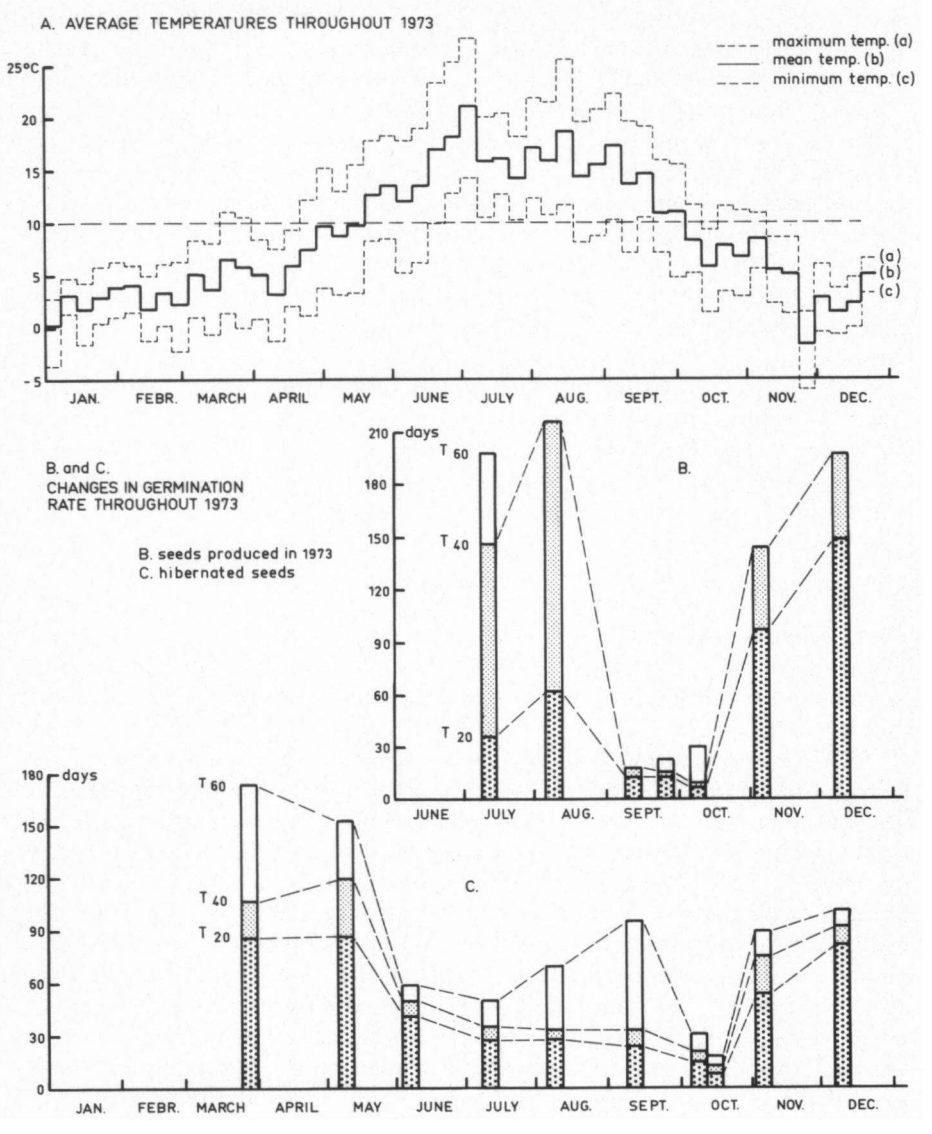

Fig. 2. Temperature and germination rate throughout 1973.
A: weekly averages of daily maximum (a), mean (b) and minimum (c) temperature (the data presented based upon measurements of the weather station at Eelde).
B and *C*: changes in germination rate of the seed population (Eext) present on the soil floor.
B: seeds produced in 1973.
C: hibernated seeds mainly produced in 1972.
Germination rate is expressed as number of days necessary to reach 20, 40 or 60% germination at 10°C.

remaining seed population is changing. Owing to the 50% loss of seeds that have germinated, a relative increase of primary dormant seeds (from about 30 to 60%) took place. As a consequence, germination did not reach 60% within 250 days in November and December samples. Similarly, the non-primary dormant, non-germinated part of the seed population in which drought prevented germination (cf. 3.2.2.) increased from about 20 to 40%. When temperatures in November and December dropped further below those favourable for germination, induction of secondary dormancy started in this part, as shown by the rapid increase of all T values after the end of October.

Similar phenomena occurred in the fraction of hibernated seeds (*fig. 2C*). In late spring when average temperatures again reached about 10°C, germination of the hibernated seeds was prevented by the presence of induced dormancy. Seeds were released from dormancy in May and June, when moisture was not limiting, but average temperatures surpassed 10°C (cf. 3.1.1.). In October about 75% of the fraction germinated. If germination was omitted once more, dormancy was induced again, and seeds might hibernate for a second time. However, as hibernated seeds reacted more slowly and germinated later than fresh seeds (cf. *fig. 2B* and *C*), it may be doubted whether these seeds will be able to germinate successfully in a third autumn.

The increase in T_{60} values occurring in August and September (*fig. 2C*) appeared to be due to drying up of part of the seeds during August, for in laboratory tests this dormancy (which was also present in some samples of fresh seeds) could easily be removed by shaking seeds with water.

3.2.2. Variation between different microhabitats

The germination percentages did not differ essentially between most microhabitats (*table 5*). However, there were two exceptions. Germination was considerably lower in layered leaf litter (microhabitat 1) and, perhaps rather un-

Table 5. Numbers of seeds and germination of *M. pratense* in 6 different microhabitats for the years 1973, 1974 and 1975. Data based on counts made in November on randomly chosen 25 × 25 cm² plots in different populations. Microhabitats are described in chapter 2.

Microhabitat:	1	2	3	4	5	6	Total
1973 (totals).							
number of seeds	255	566	750	1343	269	133	3316
average number of seeds/m²	89	105	140	358	134	67	152
% germinated seeds	22	69	67	28	77	68	49
1974 (totals).							
number of seeds	928	347	566	1210	732	–	3783
average number of seeds/m²	275	87	181	372	195	–	216
% germinated seeds	48	81	73	54	64	–	60
1975 (totals).							
number of seeds	471	332	603	1164	659	291	3520
average number of seeds/m²	199	81	210	373	211	93	188
% germinated seeds	36	65	69	32	74	70	53

expected in view of the preference of mature plants for this type, in dense tufts or mats of *Deschampsia* (4). Contrary to the low germination percentage the number of seeds per m^2 was always highest in the latter type. From the seed numbers, it appeared that the low germination in dense, grassy sites affected largely the total germination percentages in the field.

From field observations, it became clear that the low germination in microhabitats 1 and 4 was caused by the dryness which, in many of these sites, lasted till after the germination period.

3.3. The dynamics of the seed population

Each flower of *M. pratense* is able to produce four seeds at most. The average number of seeds per flower was found to range from 2.2 to 3.1 (cf. KWAK 1979), the lower values prevailing late in the growing season. One plant may produce 40–50 flowers throughout summer and therefore about 100–150 seeds. Counts revealed, however, that in most populations the number of seeds per plant was much lower, viz. 40–75 seeds, of which 20–60 may germinate, the others being viable but dormant. Hence the reproduction capacity is low (cf. SAGAR & MORTIMER 1976).

Various factors appeared to affect the seed numbers in the field (*table 6*). In samples of closed capsules, already 20–25% of the seeds were found to be attacked by either larvae of a fly (*Phytomyza sp.*; Agromyzidae) or a fungus, both of which develop on the growing seeds. Only seeds lightly attacked by *Phytomyza* were able to survive and to produce seedlings. Other infected or attacked seeds finally withered away.

After having been discharged from the capsules, a major proportion of the seeds disappeared from soil and litter. To judge from seed remnants and faeces left behind, the seeds must have been eaten by small animals. As mice (*Mus musculus* L. and *Sylvaemus sylvaticus* (L.)) have been observed several times searching the litter intensively and eating seeds, it is thought that by far most losses in the plots may be attributed to their activities. In autumn and winter seeds were also eaten. Once rooted, their disappearance could rather easily be established, as the hypocotyl was partly left behind.

Losses in the fraction of hibernated seeds (*fig. 3*) may also be attributed mainly to the predatory activity of mice. It is thought that these losses are overrepresented in the data given, because the seeds had been moved out of their original "safe" site. Normally only the most sheltered seeds will have survived predation after hibernation.

Part of the losses may also have been caused by the activity of ants (Formicidae). Observations showed that some seeds were moved outside, but others also inside the plots. Usually, however, seeds were not moved more than a few dm or not at all (small ants only sucked at the elaiosome), because the ants were hindered by vegetation, and probably also because the seeds soon lost their attraction by drying up. Their impact was evaluated somewhat more closely in an area of 24 sq. m around plot 4 from which *Melampyrum* plants and seeds had been removed. By mid-September, 14 seeds were found within a distance of 0.5

Table 6. The fate of fresh seeds of *M. pratense* in four sq.m plots during 1974–1975 in the population at Annen; *Quercus* coppice with scattered *Deschampsia flexuosa*.

	microhabitat 2/3				microhabitat 4					
	plot 1		plot 2		plot 3		plot 4		total	
	n	%	n	%	n	%	n	%	n	%
number of adult plants	24		30		18		11		83	
number of seeds produced									3411	*100*
seeds in the capsules:										
attacked by Phytomyza[1]									594	*17*
infected with fungi[1]									205	*6*
healthy seeds shed	804	*100*	944	*100*	576	*100*	288	*100*	2612	*77/100*
July – end September										
rotted off	37	*5*	31	*3*	50	*9*	22	*8*	140	*5*
disappeared[2]	484	*60*	674	*71*	283	*49*	104	*36*	1545	*59*
non-germinated	283	*35*	239	*25*	243	*42*	162	*56*	927	*36*
July – mid November										
rotted off	42	*5*	34	*4*	50	*9*	22	*8*	148	*6*
disappeared[2]	590	*73*	758	*80*	288	*50*	193	*67*	1829	*70*
non-germinated	74	*9*	63	*7*	72	*13*	24	*8*	233	*9*
germinating	98	*12*	89	*9*	166	*29*	49	*17*	402	*15*
July – mid December										
rotted off	42	*5*	34	*4*	50	*9*	22	*8*	148	*6*
disappeared[2]	608	*76*	764	*81*	316	*55*	193	*67*	1881	*72*
non-germinated	56	*7*	57	*6*	44	*8*	24	*8*	181	*7*
germinating, bitten off[2]	57	*7*	70	*7*	104	*18*	17	*6*	239	*9*
germinating, viable	41	*5*	19	*2*	62	*11*	32	*11*	154	*6*
number of seedlings, March '75	23	*3*	18	*2*	38	*7*	23	*8*	102	*4*
number of adult plants, July '75	10	*1*	15	*2*	26	*5*	18	*6*	69	*3*

[1] percentages given are those found to exist in samples of seed capsules collected in July and August near the plots.

[2] most likely eaten by mice; see text.

m, and in all 17 within a distance 2 m of plot 4. Although this kind of short range dispersal cannot be regarded as losses if the (seed) population is considered as a whole, these seeds are included under "disappeared" in *table 6*.

Out of 2612 fresh seeds discharged on the soil floor 64% was lost at the beginning of field germination, and by mid-December no less than 87%. Since comparable losses occurred in the fraction of hibernated seeds which did not possess elaiosomes, the influence of ants on the seed losses was but small. The impact of other insects and microorganisms (see *table 6*, seeds rotted off) was also too small to account for these heavy losses, so that predation by small mammals must have been the most important cause.

For the population at Annen the combined data of fresh and hibernated seeds, supplemented with information on seedlings and mature plants, allowed the construction of a life table over the period 1974/75 (see *fig. 3*).

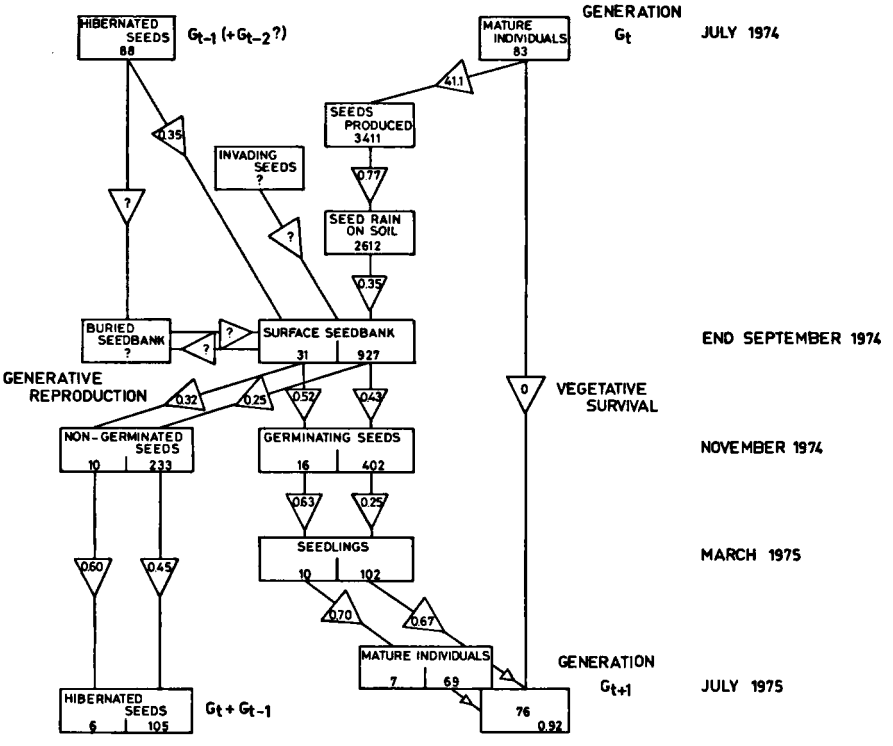

Fig. 3. Life table for *M. pratense* based on counts of fresh and hibernated seeds in four 1 m^2 plots (population Annen, 1974/75).
In squares: number of individuals, in triangles: average seed production per plant and percentages of survival between successive phases (outline derived from SAGAR & MORTIMER 1976, modified).

4. DISCUSSION

According to OESAU (1975) seeds of *M. pratense* collected in southern Germany show radicle germination at temperatures ranging from 2° to 14°C. The same range has been found in our study for seeds from the Netherlands and south-east Sweden. Hence, it may be concluded that temperature requirements for radicle germination are much the same in a wide area of western Europe.

For various other *Melampyrum* species it is reported that radicle germination takes place at low temperatures (*M. arvense*, OESAU 1973, 1975; *M. cristatum*, HORRILL 1972, OESAU 1975; *M. lineare*, ZALASKY 1962, CURTIS & CANTLON 1963, 1968; *M. nemorosum*, and *M. sylvaticum*, OESAU 1975). Besides this a prolonged need of cold or at least a long duration of the seedling development is mentioned. Since both statements point to the presence of epicotyl dormancy, temperature requirements and pattern of germination seem to be remarkably alike within this genus.

In the present study, it has been found that optimal temperatures for radicle

germination (7.5°–10°C), breakdown of epicotyl dormancy (5°C) and subsequent seedling emergence (10°–15°C) slightly differ in *M. pratense*. The duration of the whole germination process can be reduced by applying the severally optimal temperatures to a minimum of 3–4 months. These temperature demands have not been studied in other *Melampyrum* species but for the radicle germination.

CURTIS & CANTLON (1968) found, that activation and deactivation (in- or decrease in germination ability) in seeds of *M. lineare* correspond with the endogenous activity of gibberellin-like substances. In bioassays of cold stored (secondary dormant) seeds no activity could be detected, in ripe (partly primary dormant?) seeds less than in unripe seeds. Since in both species seeds can be activated or deactivated artificially in the same way, endogenous gibberellin-like substances are probably as important in determining germination ability in *M. pratense* (see 3.1.2. and 3.1.3.) as in *M. lineare*.

Seeds stored moist are activated by high and deactivated by low temperatures. It explains why in germination experiments with stored seeds misleading and contradicting results can be obtained. Radicle germination below 0°C is such an example (cf. 3.1.1.; previous to the treatment mentioned seeds were stored at 20°C). Under natural conditions germination is unlikely to occur at these temperatures, since in winter activated seeds will be absent in the field. Contrary to this, in field experiments with *M. arvense* radicle germination had been found to continue until March (OESAU 1973). However, germination in winter was obtained after monthly sowing seeds that up to the date of sowing had been stored at high temperatures, and so will have been activated.

It has been observed that under dense tufts of mats of *Deschampsia* and in layered leaf litter dryness of soil and litter may continue long after the outset of autumn. The hypothesis that dryness has been responsible for the low germination observed in these microhabitats is supported by the differences in germination percentages found over the years of observation (*table 3*). Unlike the other years, 1974 had a cool summer with high precipitation. Accordingly, germination in microhabitats 1 and 4 is higher than in 1973 or 1975.

During after-ripening a widening of the temperature range over which radicle germination occurs, has been observed (*table 1*). According to VEGIS (1963, 1964) such a phenomenon is known from various plants and thought by him to be due to the release of a partial dormancy. This partial dormancy may be identical with primary dormancy in *M. pratense*, since the release was also accompanied by an increase of germination at suboptimal temperatures. It would mean too that by the cool, wet summer of 1974 the effect of after-ripening was but small. VEGIS (1963, 1964) further states that dormancy and germination are not rigidly determined by an endogenous rhythm (cf. OESAU 1973, 1975), but depend on external factors to a high degree. The changes observed in the germination rate (3.2.1. and *fig. 2*) fully support this view.

Epicotyl dormancy has been but rarely met in other plants e.g. various species among *Liliaceae* (STOKES 1965, BARTON 1965), usually species from shaded habitats. In having both, radicle and epicotyl dormancy, *M. pratense* resembles

Convallaria majalis to a high degree. In the latter seeds are known to possess double dormancy also, but contrary to *M. pratense* the development of root and shoot is separated by at least one year, while both root and epicotyl dormancy are broken by low temperatures (e.g. STOKES 1965).

Since *M. pratense* is an annual, the presence of a prolonged germination is a remarkable feature, which might be related with the parasitic way of life. It permits the roots to form haustorial connections at a time in which the epicotyl is still resting. However, root growth before green chlorophyl bearing parts are present, is only possible when the seeds possess sufficient resources, the more so since germination occurs without a host stimulus, i.e. host roots may be at some distance. This condition obviously limits the number of seeds that might be produced.

Characteristics like an annual life cycle, a few but large seeds per flower, and a prolonged germination are generally met in *Melampyrum* spp. On the other hand in *Euphrasia*, *Odontites* and *Pedicularis palustris*, annual and biannual hemiparasites, the reproduction capacity is higher, the seeds are small, while epicotyl dormancy is lacking (e.g. YEO 1961, KWAK 1979, TER BORG pers. comm.). Hence two strategies to ensure establishment and survival seem to occur in parasitic *Scrophulariaceae*.

An intermediate position is taken by *Rhinanthus* spp., all of which are also annual hemiparasites. In *R. serotinus*, for instance, seeds have an intermediate size, the number of seeds per flower is higher than in *M. pratense* (TER BORG 1972, KWAK 1979), while roots develop during winter and become attached to host roots before cotyledons emerge. Like in *M. pratense* radicle germination has a strict need of cold, but epicotyl dormancy is absent (TER BORG 1972 and pers. comm.). Within this range the partly parasitic, partly hemiparasitic *Tozzia alpina*, another member of the Rhinanthoideae occurring in moist, often shaded habitats, seems to take a still more extreme position than *Melampyrum*. Within the capsule only one seed develops. A root system is formed long before the scale-like cotyledons emerge from the capsule, and a shoot develops subterraneously during at least one year (WEBER 1973).

It should be noted, that the risk of a prolonged germination can only be afforded in a stable environment. In this respect *M. pratense* corresponds closely for example with *Convallaria majalis* and *Polygonatum commutatum*, species also occurring in woodlands and possessing double dormancy (e.g. STOKES 1965). In *M. pratense*, another form of risk spreading may be seen in the fraction hibernating seeds, that reinforces the seed population of the next generation.

The plots at Annen in which the seed population has been studied, may be attributed to different microhabitat types. Plot 1 and 2, partly covered by litter, belonged to type 2 and 3; plots 3 and 4, covered by densely clustered tufts of *Deschampsia* to type 4. Within the population types (2 + 3) and 4 were about equally distributed, when taking the various areas occupied into account. Therefore, the data under "Total" in *table 6* present a reasonably realistic account of the processes in the total population. The overall decrease in number of mature plants over the period 1974/75 was statistically not significant. This outcome

was also supported by observations in later years, which showed that a well developed population was present in summer.

The number of plants appeared to increase in plots 3 and 4 and to decrease in plots 1 and 2. Accordingly, percentages of germinated seeds were higher in plots 3 and 4, while on the other hand percentages of disappeared seeds were lower than those in the first two plots. Therefore, the factors affecting the seed numbers did not influence the various plots in the same degree and less so in dense *Deschampsia* vegetation. Corresponding differences in the survival of seeds and consequently that of mature plants have been observed within other populations. As in case of the plots at Annen, these differences always coincided with differences in the vegetation structure. It appears right to conclude, therefore, that the different survival of seeds is connected with the density of the vegetation. Seeds in open sites will be more easily found by seed eating animals than those in dense sites (*table 5*).

Further study is needed to confirm the assumption that small mammals viz. mice are the main predators which reduce largely the seed numbers on the soil floor. From literature it is known, that seeds of *M. pratense* are eaten by birds (RIDLEY 1930, SALO 1971), but no data are available on seed eating mammals. CURTIS & CANTLON (1968) state, however, that predation by seed eating invertebrate and vertebrate animals is the most important source of losses in seed populations of *M. lineare.*

The higher survival of seeds and plants in dense, grassy sites may be counterbalanced by fluctuations in the density of seed eating animals, by the low germination that often occurs in sites with dense tufts, and also by the dispersal of seeds by ants. However, the data in *table 6* indicate that both latter processes have a quantitatively low impact. It seems justified to conclude therefore, that the observed spatial coincidence of *M. pratense* – a parasite on woody species – with tufted grasses is due to the pressure of seed eating animals on the seed population.

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