

Influence of gaps and neighbouring plants on seedling establishment in limestone grassland : experimental field studies in northern Switzerland = Einfluss von Kahlstellen und benachbarten Pflanzen auf die Keimlingsentwicklung in Trespen-Halbtrockenrasen...

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**Influence of gaps and neighbouring plants on seedling
establishment in limestone grassland**

Experimental field studies in northern Switzerland

**Einfluss von Kahlstellen und benachbarten Pflanzen auf die
Keimlingsentwicklung in Trespen-Halbtrockenrasen.**

Experimentelle Felduntersuchungen in der Nordschweiz

Peter RYSER

1990

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1. INTRODUCTION

The influence of plants on each other is usually considered to be negative, and competition is supposed to be the most important interaction between them. Species-rich habitats thus intrigue ecologists, as the ability of numerous species to coexist in a small scale seems to contradict the importance of competition.

Several theories have been formulated to explain this contradiction. Coexistence is explained by the avoidance of competition by niche differentiation or, by absence of competitive equilibrium. The differing habitat requirements obviously cannot sufficiently explain high numbers of coexisting plant species, and elaborated models of the niche have been developed to increase the possibilities for variation. GRUBB (1977) divides a plant's niche into habitat-, life form-, phenology- and regeneration niche, emphasizing especially the significance of the last one. TILMAN (1982, 1988) suggests that various competitive abilities at different ratios of available nutrients and light together with spatial heterogeneity of these factors enable coexistence. Selection towards equal competitive abilities of the species is proposed by AARSEN (1983) as a mechanism of coexistence.

Natural communities are subject to continuous changes and environmental fluctuations. Already HUTCHINSON (1941, 1961) questioned the significance of the exclusion of inferior competitors at competitive equilibrium, but only during the last two decades have a number of theories explaining coexistence in non-equilibrium systems been formulated (for a review see CHESSON and CASE 1986). Equilibrium may be prevented by disturbance (CONNELL 1978, WHITE 1979, PICKETT 1980, SOUSA 1984), which leads to a mosaic-like patchy structure of non-equilibrium communities with increased species richness (LEVIN 1974, WHITTAKER and LEVIN 1977). The character of a patch is determined by random initial events such as colonization pattern. The dynamics of patches of different successional stages allows the reproduction or growth of different species (PICKETT 1980), but also patchiness per se increases the species diversity. Plants themselves may increase the spatial heterogeneity by microsite differentiation; thus homogeneous environments may become heterogeneous and heterogeneous environments even more so (LEVIN 1974, GIGON 1981).

The combined effects of disturbance and low productivity most effectively limit competitive dominance, and the highest species densities may be achieved at low levels of productivity and intermediate levels of disturbance (GRIME

1979, HUSTON 1979). Spatial and temporal mass effects by immigration of propagules from neighbouring communities or by yearly fluctuation of environmental conditions may further increase species density (SHMIDA and ELLNER 1984).

In central Europe limestone grasslands are among the most species-rich plant communities. Infertility and regular management either by grazing or mowing are important factors for the maintenance of their high species density (DURING and WILLEMS 1984). Considering the theories reviewed above, regeneration of the species is likely to be an important aspect of the maintenance of species richness. Many species occurring in limestone grasslands are dependent on a regular regeneration by seed. They must have safe sites for germination and favourable microsites for establishment to be able to survive in the community. As the influence of vegetation is usually considered as being detrimental to seedling establishment, attention has been focused on the role of gaps as such safe sites (GRUBB 1976, RUSCH 1988, SILVERTOWN 1981). They seem to be important for the regeneration of short lived species, but considering the very high species density in small scale, which is possible in calcareous grasslands - up to 10 species per dm² on average (VAN DER MAAREL 1988 and pers. obs.) - it is difficult to imagine gaps as the only possibility for seedling establishment.

The aim of the present work was to assess the influence of neighbouring plants on seedling establishment in a species-rich infertile limestone grassland. The following aspects were regarded:

- Does competition by the established vegetation limit the establishment of new seedlings or are they able to survive also in a closed canopy?
- Do different species influence seedling establishment in their neighbourhood differently?
- Special interest was paid on the possible existence of positive influences (GIGON and RYSER 1986) of vegetation on establishment, as indicated by the works of HILLIER (1984) and SCHENKEVELD and VERKAAR (1984).

For that purpose seeds of six dicotyledonous species were sown in microsites with a different degree of influence of three different species of neighbouring plants. The survival of the emerged seedlings in the different microsites was recorded during two years. Further, the influence of moss cover on establishment was studied on separate plots.

Seedling establishment is often defined as the stage when seedlings become independent of seed reserves and are able to live with their own photosynthetic activity (e.g. HARPER 1977). As the distinction is difficult to make in the

field and the growth of the seedlings is very slow in a nutrient poor limestone grassland, in the present work seedlings surviving the first growth period are regarded as established.

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2. STUDY SITE AND METHODS

2.1. SITE DESCRIPTION

The study site is located in northern Switzerland in Merishausen, 7.5 km north of Schaffhausen. It lies on the Gräte, a hill at the northeastern end of the Jurassic mountains, the Randen, at 710 m a.s.l. (47°45'50"N and 8°36'58"E, National Grid Reference 688230/290950) (Fig. 1).

The vegetation is a nutrient poor grassland of the type *Mesobrometum erecti*, subassociation with *Medicago falcata* (ZOLLER 1954a). The site was used as an arable field until about one hundred years ago. The actual management consists of a yearly mowing in Mid-July, and there is no fertilizer treatment. Natural grazing by roes (*Capreolus capreolus*) and smaller animals occurs. The dominating grass is *Bromus erectus*, other common graminoids are *Bri-za media*, *Festuca ovina*, *Carex caryophyllea* and *Carex flacca*. The most common dicots are *Salvia pratensis*, *Sanguisorba minor*, *Onobrychis viciifolia* and *Leucanthemum vulgare*. The meadow is species-rich, having about 40 species of vascular plants and several mosses per square meter. Species density is high even in small-scale, the mean being 11 species per 100 cm². The maximum standing crop is about 300 g/m² dry matter (measured in mid-July 1987); 90% of this above-ground biomass is below the height of 25 cm.

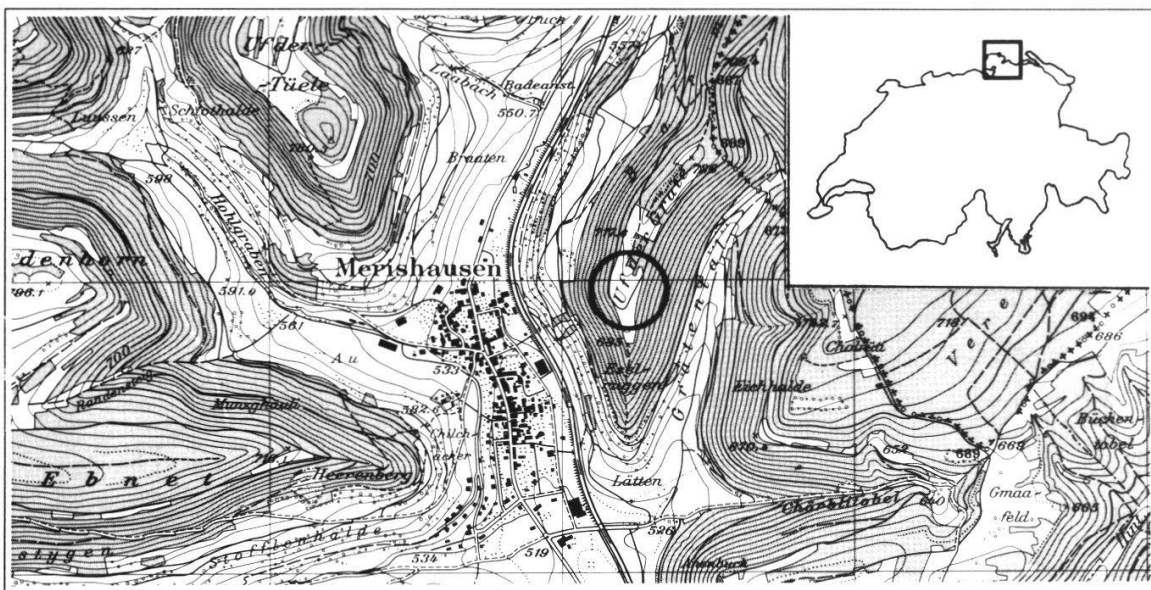


Fig. 1. Location of the study site.

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The soil is a nutrient poor marly rendzina on γ -marl limestone with a skeleton-free top layer of 10-15 cm. The pH (CaCl_2) varies between 7.1 and 7.4.

2.2. CLIMATIC CONDITIONS

All the climatic data presented here were collected by the Swiss Meteorological Institute, and also the phenological description is based on their data. The precipitation is measured in Merishausen (572 m a.s.l.) 1.5 km north of the study site. The temperature measurements were made at the weather station in Schaffhausen (437 m a.s.l.) 8 km south of the study site. Description of the snow-cover is based on data of the weather station in Hallau (435 m a.s.l.), 13 km to the south-west of the study site.

The yearly course of the long-term average monthly precipitation and mean temperature are presented in Fig. 2. The average yearly precipitation in Merishausen is 910 mm, the highest values in summer (June 100.6 mm) and lowest in late winter (February 57.8 mm). The average mean temperature of the year in Schaffhausen is 8.0°C, with maximum in July, 17.1°C, and minimum in January, -1.7°C. As the study site lies about 300 m higher than the weather station of Schaffhausen, the mean temperature there is probably 1-2°C colder. A short summary of the climatic conditions during the study period is presented here with an emphasis on the data relevant for the interpretation of the results. The course of monthly precipitation and mean temperature can be seen in Fig. 2.

1986. The precipitation and temperature in summer were above average, so that after a late spring the year was phenologically normal from May onwards. The end of August was fairly wet, but after the sowing of the seeds on the 29th and 30th of August the autumn was very dry, with periods of 13 and 29 days without any precipitation until mid-October. The last third of October was rainy, November again dry. The mean temperatures in autumn were above long-term average. During the last third of December there was some snow.

1987. Snow covered the ground during the major part of January, the last third of February and the beginning of March. April was warm and dry with only 45 mm precipitation. After the cold, wet May and June the whole phenological development was late during the summer. Because of the rainy weather the study site could not be mown until the 13th of August. The day of mowing was followed by 4 dry days with high temperatures (max. 30.1°C).

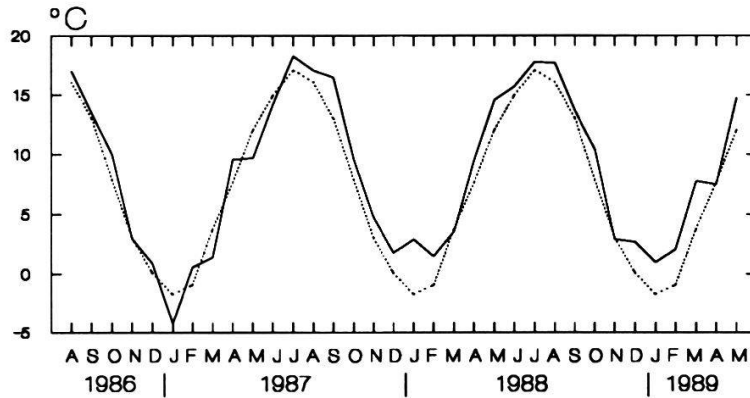


Fig. 2a. Mean monthly temperature in Schaffhausen, 437 m a.s.l.

..... Average of 1901 to 1960
—— Values for the study period August 1986 to May 1989

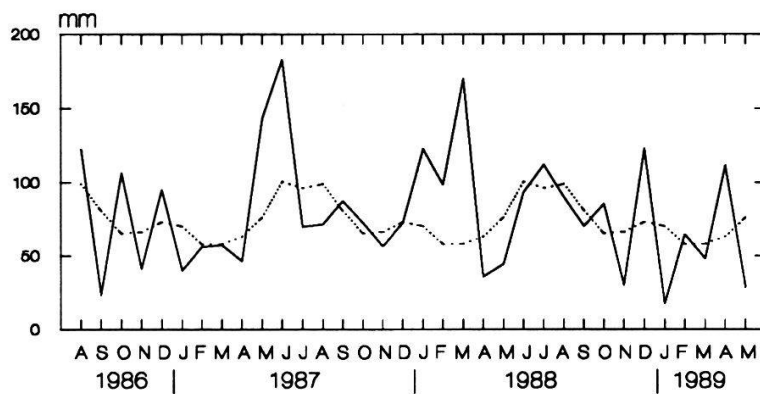


Fig. 2b. Monthly precipitation in Merishausen, 572 m a.s.l.

..... Average of 1901 to 1960
—— Values for the study period August 1986 to May 1989

After the sowing on 19th-20th of August there were several rainy days and during the whole autumn the intervals without precipitation were not longer than 2-5 days, except once in mid-September 11 days. The whole autumn was warm, especially September with a mean temperature of 16.5°C, 3.5°C above average.

1988. The winter was warm and, except for a few days with some snow-fall, there was no snow before the end of February. The snow-cover of a couple of centimeters lasted only a short time, until the beginning of March. The rainy and cool March was followed by very dry warm April and May. Summer was warmer than average with phenological development 1-2 weeks ahead. The day of the mowing (20th of July) and the following 4 days were without pre-

precipitation and temperatures were high (max. 33.2°C). The drying out of the soil was facilitated also by a breeze. The fairly dry and warm autumn was followed by a cold November with some snow during a couple of days.

1989. The winter was again exceptionally warm. It snowed only on 3 days and a lasting snow-cover was missing. March was warm, 4°C above average, April cool and rainy.

2.3. EXPERIMENTAL DESIGN

Germination, establishment of the seedlings and the subsequent survival as well as growth of the juvenile plants were studied in microsites, which were differently influenced by the neighbouring adult plants. For that purpose plots were created, each plot consisting of an area of 15x30 cm where all the aboveground vegetation including mosses and litter was removed, except one mature plant in the middle, further called the central plant. Seeds were sown in a line through the central plant and the adjacent gaps. The fate of the emerged seedlings in the different microsites was recorded.

The plots were orientated in north-south direction. Consequently one plot consisted of a central plant and gaps of 100-200 cm² on the north side as well as on the south side of the central plant (Fig. 3). As central plants three species common in the meadow were chosen: *Bromus erectus*, *Onobrychis viciifolia* and *Salvia pratensis* (description in Chapter 2.4).

For analysis the plots were divided into three different microsites depending on the degree of influence of the central plant (Fig. 3):

Tuft-microsite. Seedlings growing in the dense vegetation of the tussocks of *Bromus erectus* or *Onobrychis viciifolia* were assigned to that microsite. The seedlings were rooted between the tillers or stems of the central plant. On plots with *Salvia pratensis* as central-plant no tuft-microsite was separated, because of the rosette growth of *Salvia*.

Edge-microsite. Seedlings at the edge of the central plants not clearly growing in the tuft or in the gap were assigned to this approximately 2 cm wide microsite.

Gap-microsite. Seedlings growing at a distance of about 1 cm or more to the central-plant were assigned to the gap-microsite. Seedlings growing nearer than 2 cm to the surrounding vegetation were not included in the study and were pulled out.

In relation to the height of the vegetation in June-July the gaps were rather

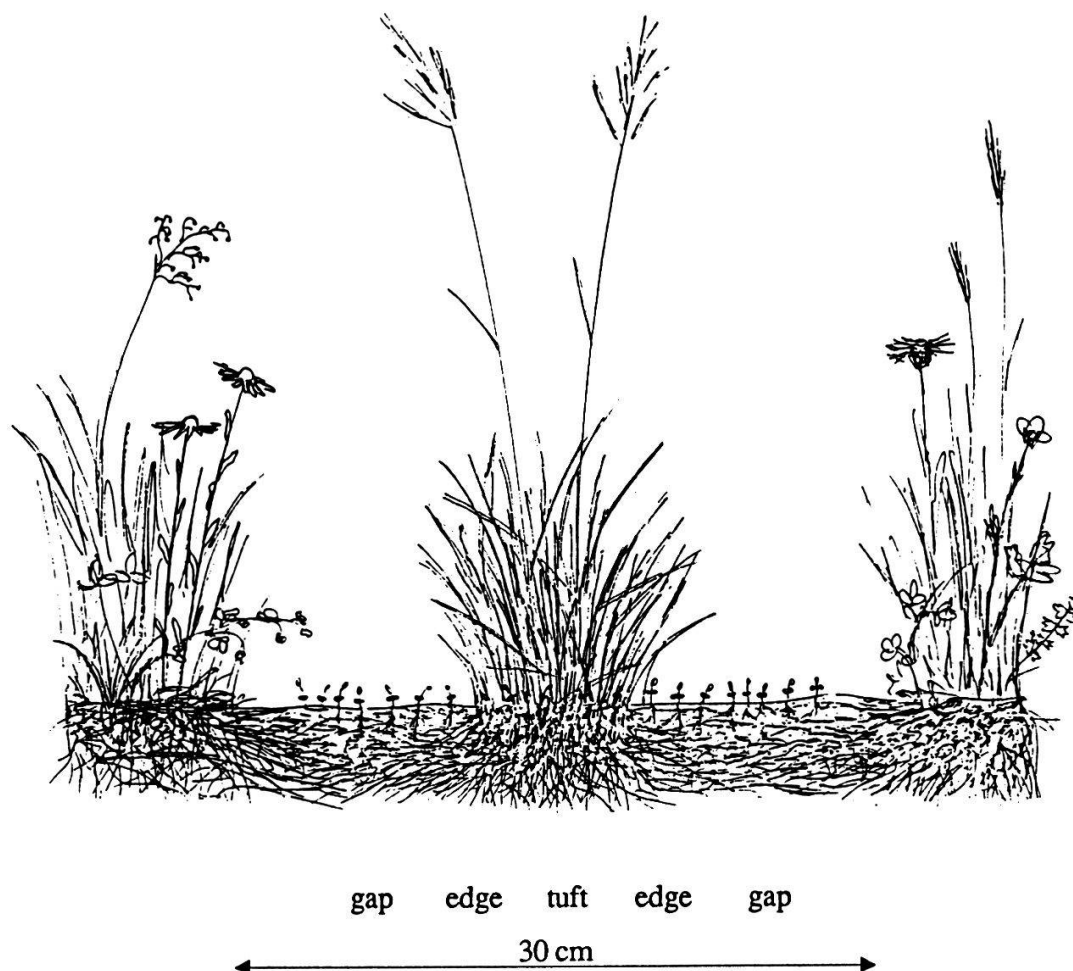


Fig. 3. Schematic view of a plot with *Bromus erectus* as central plant and the different microsites.

small and their environmental conditions were strongly influenced by the surrounding vegetation and the central plant. Besides the above-ground effects there was also a strong below-ground influence by the roots.

Salvia-rosettes had a smaller diameter at the ground-level than the tussocks of *Bromus* and *Onobrychis*, which resulted in a larger gap size in *Salvia*-plots (ca. 13x15 cm) than in the other plots (ca. 8x15 cm).

Further, the influence of the mosses on the establishment was studied. For that purpose separate plots were created, each consisting of two gaps of 15x15 cm close to each other, where all phanerogamic vegetation was removed. One of the gaps had a moss cover and the other was bare. The distance between these two gaps was 5-30 cm.

The microsites concerning the influence of moss cover are called here:

Moss-covered microsite. The moss cover consisted of a loose, 1-1.5 cm thick layer of pleurocarpic species, mainly *Homalothecium lutescens*, *Abietinella abietina* and *Thuidium delicatulum*. (Nomenclature of the mosses follows FRAHM and FREY 1983).

Bare microsite. The bare microsites were similar to gaps around central-plants, but slightly larger.

The vegetation was removed by cutting the plants with a knife as deep as possible without disturbing the topsoil too much. Easily removable rhizomes were pulled out. After their removal the soil surface was smoothed. The gaps were preferably created on sites with natural gaps or sparse vegetation. All the plots were distributed on an area of about 10x10 m with a slight slope towards the east.

Species sown on the plots were *Arabis hirsuta*, *Linum catharticum*, *Medicago lupulina*, *Plantago lanceolata*, *Primula veris* s.l. and *Sanguisorba minor*. The species are described in chapter 2.4. Seeds of each species were sown on 5 replicate plots of each of the 4 types of plots. These seeds were collected around the experimental plots during the first half of July just before the mowing and sown on the plots in August after the mowing.

The plots were prepared in August 1986. Seeds were sown on the 27th-30th August 1986 and again on 19th-20th August 1987. In the first year 60 seeds were sown on each plot (45 seeds of *Sanguisorba minor*), in the second year 100 seeds on the same plots. The plots were inspected at intervals of 2-8 weeks during the growth season, from April to November. Emerged seedlings and their position were recorded. The survival of previously recorded seedlings was controlled. If a previously recorded seedling or young plant was not found in a given position or very close to it, it was regarded as dead. In some cases seedlings having disappeared above-ground had still viable roots and reemerged. These plants could be distinguished from new seedlings, as they had no cotyledons. Seedlings of other species than the sown one, and shoots and stolons from the neighbouring vegetation sprouting in the gaps were removed at recordings.

The position of the seedlings was determined by two or more fixed points on the plot and a 1 cm grid scratched on plexiglass. The plexiglass was positioned with the help of fixed points and the coordinates could be read by looking through the grid. To avoid parallax, the 1 cm thick glass had the grid on both sides. If seedlings were growing close to each other, they were thinned until the distances between the seedlings were not less than about half a centimeter to make identification with the coordinates possible. As an addi-

tional help for the identification of seedlings of different age growing close to each other, plastic rings cut from straws were used to mark them. During the winter some seedlings moved around as a consequence of soil movement, but with some exceptions it was still possible to recognize them individually.

The fate of the seedlings was followed from emergence until September 1988 or for *Arabis hirsuta* and *Primula veris* until April and May 1989 respectively.

Further information about the performance of the seedlings in different microsites was gained by measuring the size of the surviving seedlings in August-September 1988. As a non-destructive and rapid estimation of their above-ground biomass, the number of living leaves and the length of the longest leaf was measured.

2.4. ANALYSIS OF THE DATA

Germination behaviour is characterized by the time of emergence, by the total emergence and by comparisons of the number of emerged seedlings in different microsites. The number of emerged seedlings however can be compared exactly only in the moss-covered and bare microsites, as the number of seeds in the microsites around and in the central-plants is unknown because of the variable size of these microsites (see also Chapter 3.1.2).

The establishment of seedlings is characterized by two parameters: survivorship and death rate. Survivorship is the percentage of the total number of seedlings in one cohort still alive at a given date. Death rate is the percentage of seedlings having disappeared since the preceding recording. Intervals between the recordings varied, hence the death rates at different dates do not refer to equal periods.

Beside the number of leaves and the length of the longest leaf, the size of the seedlings in different microsites is compared by the product of these two measurements as a parameter to characterize the above-ground biomass.

For statistical analysis of the data nonparametric tests of SYSTAT software-package were used (WILKINSON 1987). Differences in germination and seedling behaviour between the microsites were tested with Wilcoxon signed ranks test (paired samples). Seedling performance in the plots with different central-plant species as well as the behaviour of the different species sown was compared using the Mann-Whitney test (ZAR 1984).

The number of replicates of each species-combination of sown seed and cen-

tral-plant was five. As the *Bromus*- and *Onobrychis*-plots were similar, separate tests were made for their pooled data. In these cases the number of replicates was 10. In some microsites species with poor emergence and/or high mortality had a lower number of replicates. Data based on less than three replicates is not presented.

As the number of true replicates was low, significance levels up to $p < 0.10$ are reported with the results. This gives the reader an impression of the strength of the evidence. The interpretations are not based on individual tests but on consistent trends in different tests.

2.5. SPECIES USED IN THE EXPERIMENT

2.5.1. Description of the species

Six dicotyledonous species common in the local limestone grasslands were chosen to study the early life stages. The following brief description of the species is based mainly on GRIME et al. (1988), HEGI (1908 ff.), HESS et al. (1976-1980), LANDOLT (1977) and ZOLLER (1954b). The given seed weight is that of the seeds weighed in groups of 100, before sowing.

Arabis hirsuta (L.) Scop. is a short-lived perennial hemicryptophyte forming a semi-rosette, relatively small in size. Its habitats are infertile meadows and road-verges. The CSR-strategy (GRIME 1979) of *Arabis* is intermediate between stress-tolerator and stress-tolerant ruderal. Its seeds are the smallest of the studied species, 0.13 mg.

Linum catharticum L. is a small biennial with erect stems, which occurs in open grassland on calcareous, nutrient-poor soils. The CSR-strategy of *Linum* is a stress-tolerant ruderal. Seeds are small, 0.18 mg.

Medicago lupulina L. is a short-lived perennial of a small stature with ascending or procumbent shoots. It is common on dry open habitats, meadows and verges. The CSR-strategy of *Medicago* is characterised as an intermediate between stress-tolerant ruderal and ruderal. Seeds are fairly large, 2.04 mg.

Plantago lanceolata L. is a long-lived perennial polycarpic hemicryptophyte forming a rosette with erect, lanceolate leaves. It occurs in a wide range of habitats, mostly in meadows and road-verges, and is able to tolerate dry and nutrient-poor conditions. The CSR-strategy of *Plantago* is intermediate between competitor, stress-tolerator and ruderal. Seeds are relatively large, 1.96 mg.

***Primula veris* L. s.l.** is a long-lived perennial polycarpic hemicryptophyte. The leaves form a basal rosette. WITTWER (1983) describes the subspecies growing at the study site as *Primula veris* L. em. Hudson ssp. *suaveolens* (Bertol.) Gutermann et Ehrend. (= *Primula columnae* Ten.). This subspecies is usually found in shadier habitats, such as light woods, and its occurrence in an open meadow as on the Gräte is rather uncommon. It is able to tolerate dry conditions better, but requires somewhat more nutrients than the subspecies *veris*, which is a typical plant of nutrient-poor meadows.

The population on the Gräte shows great variation. It occurs in the meadow as well as in the adjacent wood, individuals growing in the shade being markedly larger than those in open sites. Because of this variation and the diffuse systematics of the subspecies of *Primula veris* with many transitional plants occurring (TUTIN et al. 1964) the taxa studied here is subsequently referred to as *Primula veris* s.l.

The seed size of *Primula* is intermediate (1.07 mg) among the studied species. In contrast to the other species *Primula* was sown only in 1987.

***Sanguisorba minor* Scop.** is a long-lived perennial polycarpic hemicryptophyte with a semi-rosette and an erect stem. It is a typical plant of dry grasslands in the region, occurring also in other open habitats such as road-verges. Its CSR-strategy is stress-tolerant. Seeds are the largest ones of the studied species, 4.86 mg.

The early life stages of the six above-mentioned species were studied in the neighbourhood of common large-growing perennials. Three species with different growth-forms were chosen as such central-plants:

***Bromus erectus* Hudson** is a perennial tussock-forming grass being characteristic for the unfertilized limestone grasslands and dominating the vegetation of the meadow.

***Onobrychis viciifolia* Scop.** is a densely tufted herb occurring on dry nutrient-poor meadows and is common at the study site. As a *Fabaceae* it is able to fix symbiotically atmospheric nitrogen.

***Salvia pratensis* L.** forms large rosettes, which at the study site completely die above-ground during the winter. It is a typical plant in the limestone grasslands.

Bromus forms a dense rooting system around the tussock, whereas *Onobrychis* and *Salvia* have a large tap root and the fine roots near the surface are not so well developed.

The species are subsequently referred to by their genus name. Nomenclature of the vascular plant species follows BINZ and HEITZ (1986).

2.5.2. Population characteristics of the species at the study site

Some characteristics of the species were assessed at the study site. The frequency of the species was measured in July 1987 on 33 samples of 0.25 m² arranged along three stripes beside the experimental plots. In 1986 the occurrence of the species was recorded in an area of 50x355 cm with a grid of 5 cm giving the frequency in samples of 25 cm². Natural regeneration by seed was recorded on the same, slightly extended (8.625 m²) stripes from September 1986 to June 1987. In September 1987 the survival of these seedlings was recorded in one third of that area. The data of the seed bank at the study site is from RYSER (1984).

The viability of the seeds sown was tested in autumn 1986 (*Primula*: autumn 1987) in growth chamber (Table 2). One hundred seeds of each species were sown on Petri-dishes with wet blotting-paper and their germination was recorded during 50 days. The temperature regime in the climatic chamber was 20°C (day, 16 hrs.) and 10°C (night, 8 hrs.).

All the species were frequent at the study site (Table 1). In samples of the size of 0.25 m² *Arabis* was the only one with a frequency below 90% (61%). With the sample size of 25 cm² *Arabis* and *Primula* were the only ones with a frequency less than 10% (3.5% and 8.7% respectively).

All the species were observed also in the seed bank as well as seedlings in the natural vegetation. *Plantago* and *Linum* had the largest seed bank. *Linum* germinated in the natural vegetation in very large numbers but had also a high mortality of seedlings.

Tab. 1. Some attributes of the studied species at the study site.

	Percentage frequency with sampling unit size of		seedlings per m ² (emerged Sept. 86-June 87)	survivorship of these seedlings in Sept. 1987 (No. of assessed seedlings in parenthesis)	seed weight	seed bank in the topmost 2.5 cm seeds/m ²
	0.25 m ²	25 cm ²				
<i>Arabis hirsuta</i>	61%	3.5%	12	44% (52)	0.13 mg	19
<i>Linum catharticum</i>	100%	40.6%	246	38% (491)	0.18 mg	64
<i>Medicago lupulina</i>	91%	18.0%	36	48% (79)	2.04 mg	13
<i>Plantago lanceolata</i>	100%	23.1%	24	78% (37)	1.96 mg	122
<i>Primula veris</i>	91%	8.7%	7	57% (7)	1.07 mg	13
<i>Sanguisorba minor</i>	100%	15.5%	17	61% (49)	4.86 mg	26

3. RESULTS

3.1. EMERGENCE OF THE SEEDLINGS

3.1.1. Time and extent of emergence

Seedling emergence was very different in the two years of the study (Table 2). After the first sowing in August 1986 only 42 to 264 seedlings emerged, 5% to 22% of the 1200 seeds sown per species (*Sanguisorba*: 900 seeds sown). The number of emerged seedlings after the second sowing in August 1987 varied from 519 to 1480 corresponding to an emergence of 26% to 74% of the sown 2000 seeds per species.

The poor emergence after the first sowing resulted probably from the unfavourable climatic conditions. The long dry periods in autumn 1986 obviously inhibited the germination and possibly caused a high pre-emergence mortality. The first seedlings (*Arabis*) did not emerge until the end of September, one month after the sowing, while in 1987 the first seedlings (*Arabis* and *Plantago*) had already emerged 10 days after the sowing.

The viability of seeds was better than the emergence in the field indicates, as the germination test in climatic chamber shows (Table 2). Species with dormancy mechanisms failed to germinate under laboratory conditions. The used test does not give any information about the viability of the seeds of these species. Seeds of *Linum* and *Primula* require chilling to break their dormancy and those of *Medicago* show a hard-coat dormancy (GRIME et al. 1988).

Table 2. The number of emerged seedlings in the experimental plots and their percentage of the sown seeds. Also the germination percentage in growth chamber after 50 days is given, tested in autumn 1986 (*Primula*: autumn 1987) (for conditions in growth chamber see Chapter 2.5.2).

	Emergence August 1986 - July 1987		Emergence after August 1987		Germination in growth chamber
<i>Arabis hirsuta</i>	264	(22.0%)	1480	(74.0%)	98%
<i>Linum catharticum</i>	238	(19.8%)	629	(31.5%)	0%
<i>Medicago lupulina</i>	146	(12.2%)	534	(26.7%)	5%
<i>Plantago lanceolata</i>	217	(18.1%)	1122	(56.1%)	45%
<i>Primula veris</i> s.l.	-		594	(29.7%)	0%
<i>Sanguisorba minor</i>	42	(5.3%)	519	(26.0%)	43%

The germination percentages can only be approximated. Pre-emergence mortality is unknown, and also the emerged seedlings might have been dying before they were recorded. This results in an underestimation of the germination. On the other hand, a part of the emerged seedlings possibly originated from the natural seed bank resulting in an overestimation of germination. *Plantago* and *Linum* especially form a considerable seed bank in the top-soil at the study site (RYSER 1984, see also Chapter 2.4), which is indicated also by the high number of seedlings of these species in the natural vegetation. As the two sowings were made on the same plots, some seeds sown in 1986 might have germinated after the sowing in 1987.

A major part of the seedlings emerged in spring. Only *Arabis* had mainly autumn germination. In the first year 86% of the observed *Arabis*-seedlings emerged in autumn, in the second year this value was 96%. One third (33%) of the seedlings of *Plantago*, emerging after the second sowing, appeared in autumn, most of them already 10 days after the sowing. After this initial flush only a few *Plantago*-seedlings emerged until the next flush in following spring. *Sanguisorba* had 17% and 19% autumn germination in the two sowings and for *Medicago* these figures were 2% and 3%. *Linum* and *Primula* germinated exclusively in spring.

The ranking of the species in relation to the extent of their emergence was in both years about the same, *Arabis* having the highest numbers of emerged seedlings and *Sanguisorba* the lowest.

3.1.2. Influence of the microsite on emergence

All the species emerged in all microsites (Table 3). The number of emerged seedlings was somewhat lower in tufts, which is caused to a large extent by the smaller size of these microsites. As the seeds were sown in constant density in a line across the plots, lower number of seeds reached the smaller microsites. The density of the emerged seedlings was often even higher in tufts than in the gaps.

Moderate cover enhanced the germination of all species. In moss-covered microsites emerged seedlings were more numerous than in bare plots (Table 4), and the number of seedlings in edges was higher than the size of these microsites would lead one to expect. The germination was enhanced probably by a favourable microclimate under the partial vegetation cover.

Several authors describe moss cover inhibiting germination (JOHNSON and THOMAS 1978, VAN TOOREN et al. 1985). The contrasting evidence of the

Table 3. Numbers of newly observed seedlings at the different recordings in different microsites.

	<i>Bromus</i>			<i>Onobrychis</i>			<i>Salvia</i>		Moss cover	
	gap	edge	tuft	gap	edge	tuft	gap	edge	-	+
<i>Arabis hirsuta</i>										
October 1986	27	13	3	21	18	8	34	4	23	40
November 1986	4	4	4	2	1	1	8	0	4	8
April 1987	3	3	7	1	3	3	9	1	1	6
total first sowing	34	20	14	24	22	12	51	5	28	54
August 1987	80	76	14	111	108	35	181	45	104	74
September 1987	31	66	23	39	28	36	117	16	30	65
October 1987	10	26	22	2	7	18	17	5	5	33
April 1988	2	13	18	0	9	7	0	0	0	7
total second sowing	123	181	77	152	152	96	315	66	139	179
<i>Linum catharticum</i>										
April 1987	37	20	1	28	18	0	22	13	13	25
June 1987	13	7	1	9	3	3	10	2	0	13
total first sowing	50	27	2	37	21	3	32	15	13	38
April 1988/ total second sowing	100	49	25	75	28	30	119	43	70	90
<i>Medicago lupulina</i>										
October 1986	0	0	0	0	0	0	2	1	0	0
April 1987	11	14	4	16	11	8	16	11	3	24
June 1987	4	3	2	1	0	1	2	2	7	3
total first sowing	15	17	6	17	11	9	20	14	10	27
September 1987	3	0	0	0	0	0	1	0	0	0
November 1987	0	0	1	4	0	0	4	0	1	1
April 1988	33	21	21	30	36	12	54	35	34	62
May 1988	35	14	12	10	17	11	27	10	11	30
July 1988	0	1	0	0	0	0	1	0	0	2
total second sowing	71	36	34	44	53	23	87	45	46	95
<i>Plantago lanceolata</i>										
October 1986	2	2	1	2	0	0	3	0	3	3
April 1987	10	24	12	16	18	16	17	0	3	23
June 1987	10	10	3	2	1	5	2	1	1	13
August 1987	0	2	3	0	2	0	0	0	0	7
total first sowing	22	38	19	20	21	21	22	1	7	46
August 1987	54	9	1	53	9	5	77	15	73	26
September 1987	0	1	2	2	4	1	7	2	5	3
November 1987	1	8	1	1	0	0	4	0	2	3
April 1988	41	51	25	47	61	44	65	32	37	109
June 1988	23	64	18	19	6	11	36	13	5	28
July 1988	3	1	4	3	3	0	3	0	1	0
total second sowing	122	134	51	125	83	61	192	62	123	169
<i>Primula veris</i>										
April 1988 (1)	37	39	34	44	57	34	63	18	31	98
April 1988 (2)	5	14	9	10	16	5	12	0	5	14
Mai 1988	7	7	4	4	4	3	4	1	1	12
July 1988	0	1	0	0	0	0	0	1	0	0
total	49	61	47	58	77	42	79	20	37	124

Table 3 (continued)

	<i>Bromus</i>			<i>Onobrychis</i>			<i>Salvia</i>		Moss cover	
	gap	edge	tuft	gap	edge	tuft	gap	edge	-	+
<i>Sanguisorba minor</i>										
October 1986	0	0	0	0	0	0	5	0	2	0
April 1987	4	0	1	8	3	0	6	1	1	5
June 1987	0	0	0	2	0	0	3	0	0	1
total first sowing	4	0	1	10	3	0	14	1	3	6
September 1987	5		0	0	4	4	0	0	0	0
October 1987	13	5	1	5	5	4	16	2	8	6
November 1987	3	3	0	0	1	0	3	0	6	4
April 1988	9	12	0	8	10	7	19	6	10	31
June 1988	27	43	26	29	23	19	56	12	26	40
July 1988	0	0	2	0	0	1	0	0	0	5
total second sowing	57	63	29	46	43	31	94	20	50	86

present study might be explained by the relative sparseness of the moss cover, letting enough light pass but still keeping the microclimate more humid than in bare microsites.

The time of germination of several species was delayed by vegetation cover. All species (except *Medicago* sown in 1986) emerged later in moss-covered microsites compared to the bare ones (Table 5). The germination of *Arabis*, *Plantago* and *Sanguisorba* was significantly delayed by the central plants, emergence being earliest in gaps and latest in tufts. Most of the few *Arabis*-seedlings emerging in spring were in tufts, and the autumn-cohort of *Plantago* emerged almost exclusively in the gaps.

The delay under vegetation cover might have been caused by different light quality and reduced temperature fluctuations. Problems of contact with the soil might have been of importance, as a part of the seeds sown in the vegetation did not reach the soil surface immediately after sowing but remained on the leaves and litter.

Table 4. Significance levels of the differences in number of emerged seedlings between moss-covered and bare microsites (Wilcoxon).

** = $p < 0.01$, * = $p < 0.05$, + = $p < 0.10$, - = not significant.

	<i>Arabis hirsuta</i>	<i>Linum catharticum</i>	<i>Medicago lupulina</i>	<i>Plantago lanceolata</i>	<i>Primula veris</i>	<i>Sanguisorba minor</i>
first sowing	*	-	*	*		-
second sowing	*	-	-	+	*	*
both sowings	**	*	*	**	*	*

Table 5. Duration from sowing until emergence in months (mean for all emerged seedlings).

The significance level of the difference between the different microsites: + = $p < 0.10$, * = $p < 0.05$, ** = $p < 0.01$ (Wilcoxon signed ranks test, data of both sowings pooled). The position of the symbols showing the significance level in case of three microsites per plot refer to the following comparisons: (1): gap - edge, (2): gap - tuft, (3): edge - tuft (indicated in the example of *Arabis* seedlings in plots with *Bromus* as central-plant).

	<i>Arabis hirsuta</i>		<i>Linum catharticum</i>	<i>Medicago lupulina</i>		<i>Plantago lanceolata</i>		<i>Primula veris s.l.</i>	<i>Sanguisorba minor</i>
sowing	1986	1987	1986	1986	1987	1986	1987	1987	1987
central-plant <i>Bromus erectus</i>									
gap	2.7	0.9 *(1)	8.9	8.9	8.4	8.6	5.3 *	8.3	6.9 *
edge	3.2	1.5 *(2)	8.9	8.8	8.7	8.8	8.3 *	8.3	9.0 *
tuft	5.4	3.0 *(3)	9.2	9.0	8.4	9.0	8.7	8.2	10.3
central-plant <i>Onobrychis viciifolia</i>									
gap	2.4	0.7 *	8.9	8.6	7.9	8.0	5.2 *	8.2	8.3
edge	2.9	1.1 *	8.7	8.5	8.5 +	9.0	7.5 **	8.2	7.9
tuft	3.6	1.6	10.0	8.7	8.7	8.9	8.0	8.2	8.9
central-plant <i>Salvia pratensis</i>									
gap	3.3	0.8	9.0	8.0	8.2	7.8	5.2	8.2	8.3
edge	3.2	0.8	8.7	8.3	8.3	10.0	6.6	8.2	8.9
influence of moss cover									
bare	2.4	0.7	8.5	9.6	8.3	5.9	3.4	8.2	7.7
moss-covered	2.9	1.3 *	9.0	8.7	8.5	9.1	7.3 **	8.2	8.7 *

3.2. SEEDLING ESTABLISHMENT AND SUBSEQUENT SURVIVAL

To distinguish the effects of the microsite on the establishment from those of the date of emergence, establishment in different microsites was analysed separately for the different cohorts. To provide a sufficient sample size for statistical tests, only autumn and spring cohorts were formed. Odd seedlings emerging much earlier or later than the majority were not included in the analysis. The formed cohorts are listed in Table 6 with the total survivorship after one growth period, and at the last recording.

The significance levels of the differences in survivorship and death rates are given in the appendix.

Table 6. Cohorts formed for the analysis and their total survivorship after one growth period and at the last recording. Month of the recording is given in parentheses.

- 1) Establishment was not analysed because all seedlings died shortly after germination due to a fungal disease.
- 2) No analysis of the influence of microsites on establishment because of the low number of seedlings.

species	emergence period	number of seedlings	survivorship after one growth period	survivorship at the last recording (if not the same)
<i>Arabis hirsuta</i>	Oct.-Nov. 1986	227	22.5% (Oct. 87)	3.1% (Apr. 89)
	Aug.-Oct. 1987	1389	15.1% (Oct. 88)	8.3% (Apr. 89)
<i>Linum catharticum</i>	Apr.-June 1987	238	46.4% (Oct. 87)	0.4% (Jun. 88)
	Apr.-May 1988 ¹⁾	629	0.0% (Jun. 88)	
<i>Medicago lupulina</i>	Apr.-June 1987	143	72.7% (Sept. 87)	57.4% (Apr. 88)
	Apr.-May 1988	515	22.5% (Sep. 88)	
<i>Plantago lanceolata</i>	Apr.-June 1986	187	74.3% (Nov. 87)	59.9% (Sep.88)
	Aug.-Nov. 1987	367	67.9% (Sep. 88)	
	Apr.-June 1988	718	80.8% (Sep. 88)	
<i>Primula veris</i>	Apr.-May 1988	581	28.1% (Oct. 88)	23.8% (May 89)
<i>Sanguisorba minor</i>	Apr.-June 1987 ²⁾	35	82.9% (Oct. 87)	80.0% (Sep. 88)
	Sep.-Nov. 1987	98	68.4% (Sep. 88)	
	Apr.-June 1988	405	72.8% (Sep. 88)	

3.2.1. *Arabis hirsuta*

Total mortality of *Arabis* was high. Only 23% and 15% of the seedlings emerging in autumn 1986 and 1987 respectively survived the first year (Table 6). During the summer, spring-cohorts had higher death rates than autumn-cohorts, but the difference was not significant. The number of seedlings emerging in spring was low, and hence only the autumn cohorts are used for further analysis of the establishment. Both of these cohorts behaved similarly, but because of the relatively low number of seedlings in the cohort emerging in 1986 the quantitative description is based mainly on the data of the autumn cohort 1987.

Vegetation cover clearly reduced the mortality of *Arabis*. After one growth period the survivorship of autumn cohort 1987 was significantly higher in edges and tufts than in gaps in all types of plots (Fig. 4). In moss-covered microsites the survivorship was higher than in bare microsites. Autumn-cohort 1986 behaved similarly, but after one growth period too few seedlings were alive for any significant differences between the microsites to be detected.

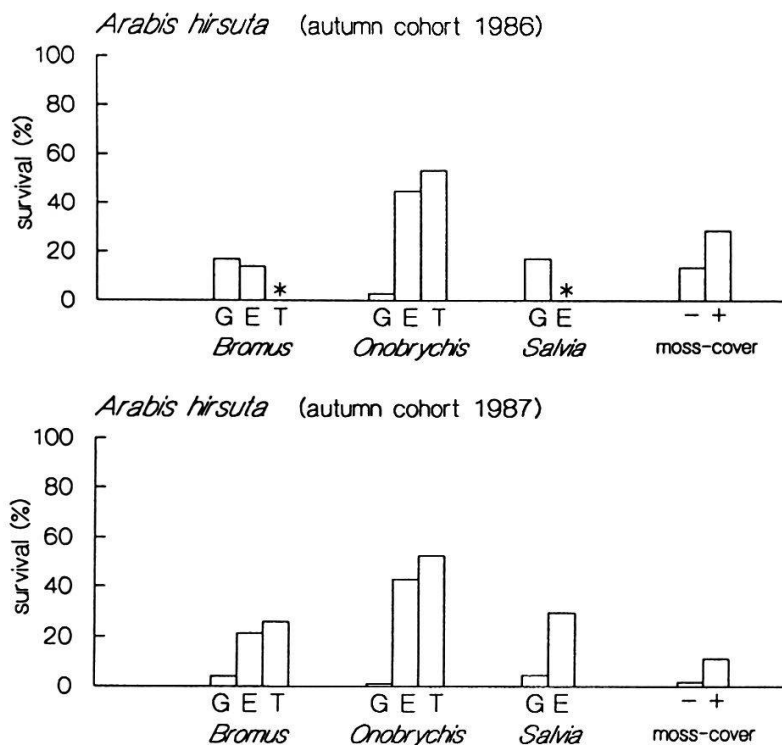


Fig. 4. Survivorship of *Arabis hirsuta* after one growth period in the different microsites. G = gap, E = edge, T = tuft, - = bare microsite, + = moss-covered microsite, * = less than 3 replicates

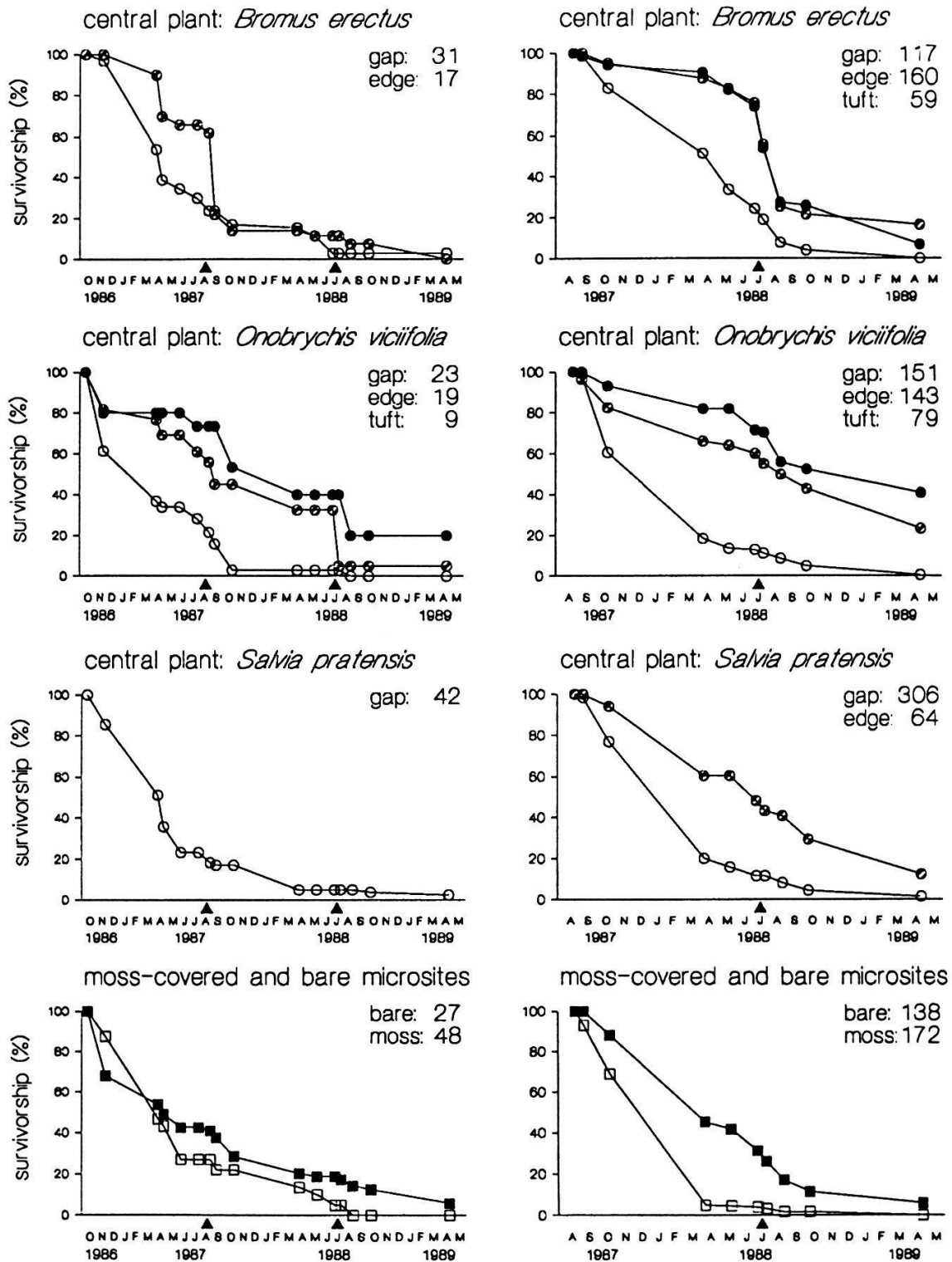


Fig. 5. Survivorship curves of *Arabis hirsuta* in different microsites. Left: Autumn cohort 1986. Right: Autumn cohort 1987. Total number of seedlings in each microsite (= 100%) in right top corner of each plot. Curves based on less than three replicates are omitted.

Microsites: ○ = gap, ◐ = edge, ● = tuft, □ = bare, ■ = moss-covered. ▲ = time of mowing.

Table 7. Death rates of *Arabis hirsuta* between the recordings in different microsites (in %).

- = seedlings in less than 3 replicates

	<i>Bromus erectus</i>			<i>Onobrychis viciifolia</i>			<i>Salvia pratensis</i>			
	gap	edge	tuft	gap	edge	tuft	gap	edge	bare	moss
cohort:										
autumn 1986										
Okt. 86 - Nov. 86	3.1	0.0	-	38.6	18.3	20.0	14.5	-	12.5	32.0
Nov. 86 - Apr. 87	43.3	10.0	-	37.8	5.0	0.0	43.3	-	40.7	19.5
Apr. 87 - Apr. 87	27.5	30.0	-	6.2	12.5	0.0	34.5	-	8.3	8.2
Apr. 87 - June 87	9.3	5.0	-	0.0	0.0	0.0	41.1	-	44.4	10.2
June 87 - July 87	12.5	0.0	-	16.7	12.5	8.3	0.0	-	-	0.0
July 87 - Aug 87	26.7	0.0	-	25.0	6.2	0.0	33.3	-	-	2.9
Aug. 87 - Sep. 87	0.0	6.2	-	44.4	33.3	0.0	-	-	-	8.0
Sep. 87 - Oct. 87	23.3	-	-	-	0.0	25.0	-	-	-	25.0
Oct. 87 - Apr. 88	33.3	-	-	-	38.9	33.3	-	-	-	20.0
cohort:										
autumn 1987										
Aug. 87 - Sept. 87	1.1	0.0	1.9	1.5	3.6	0.0	1.8	0.0	7.6	0.0
Sept. 87 - Oct. 87	16.1	4.9	4.2	38.9	14.6	6.9	21.8	6.0	25.8	11.9
Oct. 87 - Apr. 88	39.0	8.0	4.1	74.1	21.7	12.1	74.2	35.3	92.8	50.0
Apr. 88 - May 88	28.7	5.8	10.0	31.2	4.3	0.0	23.6	0.0	8.3	12.7
May 88 - July 88	26.7	8.4	13.1	2.1	6.3	11.4	28.2	20.3	12.5	31.4
July 88 - July 88	22.9	26.4	22.3	9.5	11.5	2.0	0.0	11.7	8.3	16.9
July 88 - Aug. 88	68.9	55.4	49.3	21.5	15.4	18.9	38.2	8.5	37.5	46.4
Aug. 88 - Oct. 88	36.7	11.8	6.2	42.7	13.7	6.7	51.5	37.2	0.0	37.0
Oct. 88 - Apr. 89	100.0	27.3	66.7	83.3	30.6	22.4	72.2	65.3	100.0	41.4

Already in autumn death rates in gaps were the highest of all microsites. This was more pronounced during the winter, when a major part of the seedlings in gaps died (Table 7). Winter mortality in gaps of central-plant plots varied between 39% and 74%, while in edge- and tuft-microsites it was significantly lower, 8-35% and 0-12%, respectively. The highest winter mortality occurred in bare microsites (93%), which had the largest gap size. In moss-covered microsites mortality was significantly lower (50%), but still higher than in edge- and tuft-microsites.

The reason for the high winter mortality in gaps was frost heave. Soil movement uprooted the *Arabis*-seedlings, which then desiccated during the dry and sunny April. Most seedlings died shortly before the recording in April. Central-plants reduced the harshness of the climate and their roots stabilized the soil in the edge- and tuft-microsites reducing the effects of frost heave,

and thus enhancing survival during the winter.

After the mowing, high mortality occurred in all microsites. The highest death rates were not observed in the recording three days after the mowing but between this date and the recording after one month. This indicates that the cause of mortality was desiccation of the seedlings due to the severe microclimate in the low vegetation, rather than the mowing itself. The seedlings in edges and tufts of *Bromus* suffered a high mortality, but death rates were still lower than in gaps. In *Onobrychis*-plots the effect of mowing was less severe.

The number of seedlings of the autumn cohort 1986 surviving longer than one year was too low for a proper assessment of the survival in the different microsites during the second growth period. However, the total mortality was also high then (Fig. 5).

The establishment in northern and southern edges did not differ significantly. The species of the central-plant influenced the establishment of *Arabis* (Fig. 5). Winter mortality was higher in the gaps around *Onobrychis* and *Salvia* than around *Bromus*. After mowing, the mortality was higher in all microsites of *Bromus*-plots than in *Onobrychis*- and *Salvia*-plots. Survivorship in October was highest in tufts and edges of *Onobrychis* plots.

The different effects might be explained by the root morphology of these species. *Bromus* has a broad and dense system of fine roots in the topsoil around the tussock, while *Onobrychis* and *Salvia* have a deep taproot. This does not influence the neighbouring top soil much, leaving it vulnerable to frost heave, but also having less competitive effect. Dead leaves of *Bromus* decompose more slowly than those of *Onobrychis*, which might also contribute to the better sheltering effect of *Bromus* during the winter. The symbiosis between rhizobia and *Onobrychis* might also influence the availability of nitrogen in its neighbourhood (see also Chapter 3.3).

3.2.2. *Linum catharticum*

In May-June 1988 a fungal disease extinguished the *Linum*-populations in the experimental plots and also in the surrounding vegetation. All plants died in a short time regardless of their age and the microsite where they were growing. Therefore the survival could be followed only in case of the small cohort having emerged in spring 1987, and only during one year. The sample size is small, especially in tuft-microsites where only 5 seedlings of that cohort emerged.

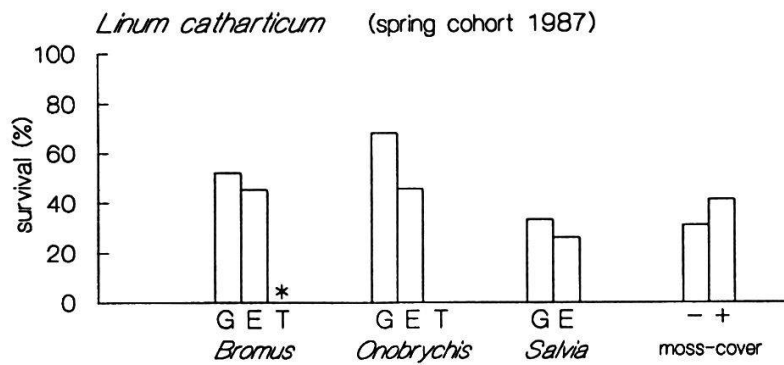


Fig. 6. Survivorship of *Linum catharticum* after one growth period in the different microsites. G = gap, E = edge, T = tuft, - = bare microsite, + = moss-covered microsite, * = less than 3 replicates

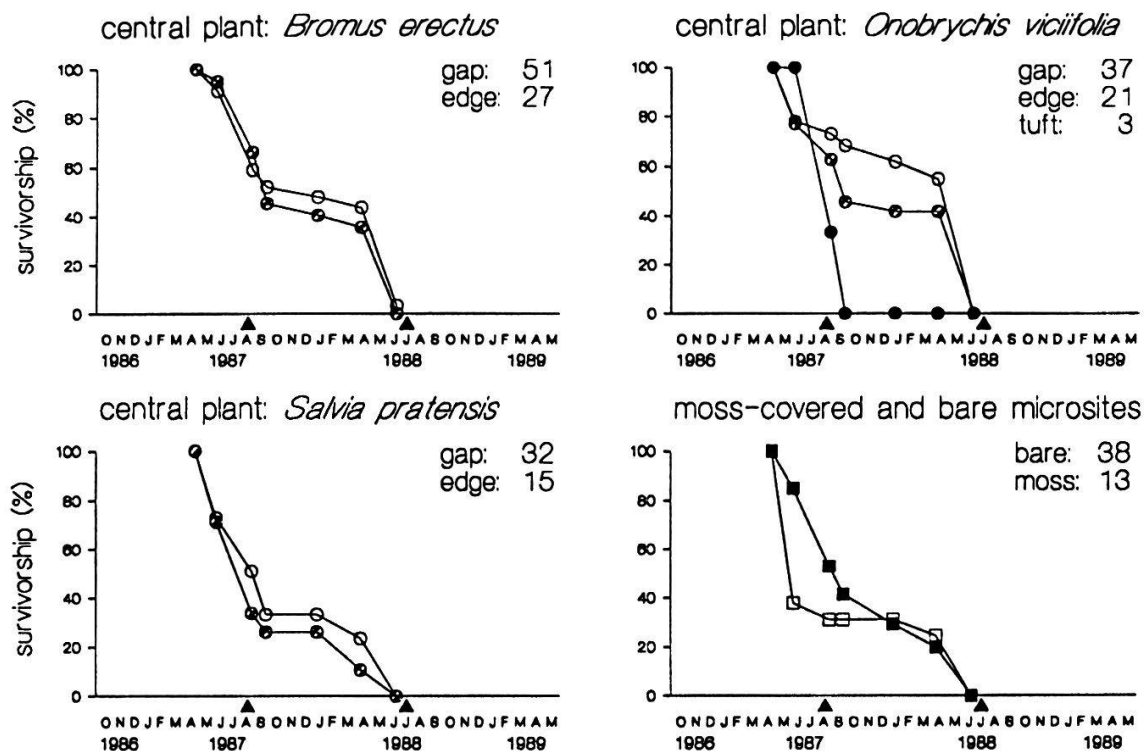


Fig. 7. Survivorship curves of *Linum catharticum* in different microsites. Spring cohort 1987. Total number of seedlings in each microsite (= 100%) in right top corner of each plot. Curves based on less than three replicates are omitted.

Microsites: ○ = gap, ◐ = edge, ● = tuft, □ = bare, ■ = moss-covered. ▲ = time of mowing.

Table 8. Death rates of *Linum catharticum* between the recordings in different microsites (in %).

- = seedlings in less than 3 replicates

	<i>Bromus erectus</i>			<i>Onobrychis viciifolia</i>			<i>Salvia pratensis</i>			
	gap	edge	tuft	gap	edge	tuft	gap	edge	bare	moss
cohort: spring 1987										
Apr. 87- June 87	8.9	5.0	-	21.9	22.9	0.0	26.8	28.6	62.2	15.1
June 87 - Aug. 87	36.4	30.6	-	5.6	15.0	66.7	22.6	50.0	11.1	36.7
Aug. 87 - Sep. 87	12.5	39.0	-	5.8	23.3	-	31.7	25.0	0.0	24.0
Sep. 87 - Jan. 88	8.7	10.0	-	8.0	10.0		0.0	0.0	0.0	43.3
Jan. 88 - Apr. 88	9.4	6.2	-	10.0	0.0		26.7	70.0	16.7	37.5
Apr. 88 - June 88	95.0	100.0	-	100.0	100.0		100.0	100.0	100.0	100.0

During the first spring and summer the mortality of *Linum* was fairly high, but decreased during the autumn and winter before the total extinction in the following spring (Fig. 7, Table 8). After one growth period the highest survivorship was in the gaps of *Bromus*- and *Onobrychis*-plots, 52% and 68% respectively. In edges the survivorship was less (33% and 26%) and in tufts none of the 5 emerged seedlings survived until September (Fig. 6). As all the 5 seedlings were in different replicate plots, the mortality in tufts was significantly higher than in gaps and edges ($p < 0.05$), despite of the low number of seedlings. In the larger gaps in *Salvia*-plots and moss-plots (15x15 cm) *Linum* suffered a higher mortality than in the smaller gaps in *Bromus*- and *Onobrychis*-plots (7x15 cm). This suggests, that open microsites with some degree of sheltering are the most favourable for the establishment of *Linum*. The influence of moss cover on its establishment was not significant.

Most *Linum*-plants, that had germinated in 1987 and survived until spring 1988, were beginning to flower before succumbing the disease.

3.2.3. *Medicago lupulina*

Establishment of *Medicago* was very different in the two years studied. In 1987 73% of the seedlings having emerged in spring survived until September, while in 1988 the mortality was higher, with only 23% survivorship in September (Table 6). In 1987 *Medicago* was growing vigorously and the surviving plants were removed in April 1988 to prevent their influence on the new seedlings germinating on the same plots. Establishment was fairly high

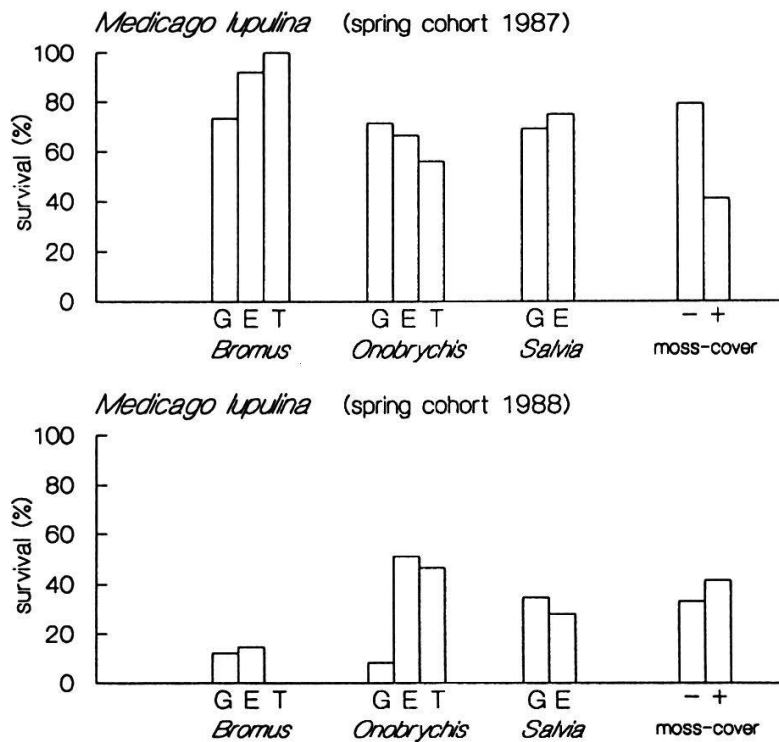


Fig. 8. Survivorship of *Medicago lupulina* after one growth period in the different microsites.

G = gap, E = edge, T = tuft, - = bare microsite, + = moss-covered microsite.

Table 9. Death rates of *Medicago lupulina* between the recordings in different microsites (in %).

- = seedlings in less than 3 replicates

	<i>Bromus erectus</i>			<i>Onobrychis viciifolia</i>			<i>Salvia pratensis</i>			
	gap	edge	tuft	gap	edge	tuft	gap	edge	bare	moss
cohort: spring 1987										
Apr. 87 - June 87	10.0	4.0	0.0	17.4	8.3	12.5	10.7	20.0	24.2	0.0
June 87 - Aug. 87	6.7	5.0	0.0	9.4	12.5	25.0	0.0	0.0	26.7	20.8
Aug. 87 - Oct. 87	16.7	0.0	0.0	5.0	12.5	8.3	20.0	6.2	16.7	0.0
Oct. 87 - Apr. 88	20.0	0.0	8.3	18.8	62.5	11.1	5.0	0.0	0.0	0.0
cohort: spring 1988										
Apr. 88 - May 88	2.7	2.0	0.0	0.0	0.0	2.2	10.0	0.0	0.0	4.2
May 88 - July 88	49.0	39.6	52.1	54.6	21.1	30.0	33.7	48.7	40.3	56.0
July 88 - July 88	54.6	17.5	88.9	30.6	11.7	27.1	25.1	6.7	27.2	44.4
July 88 - Sep. 88	68.2	57.0	-	85.7	26.4	11.2	0.0	58.3	4.6	-

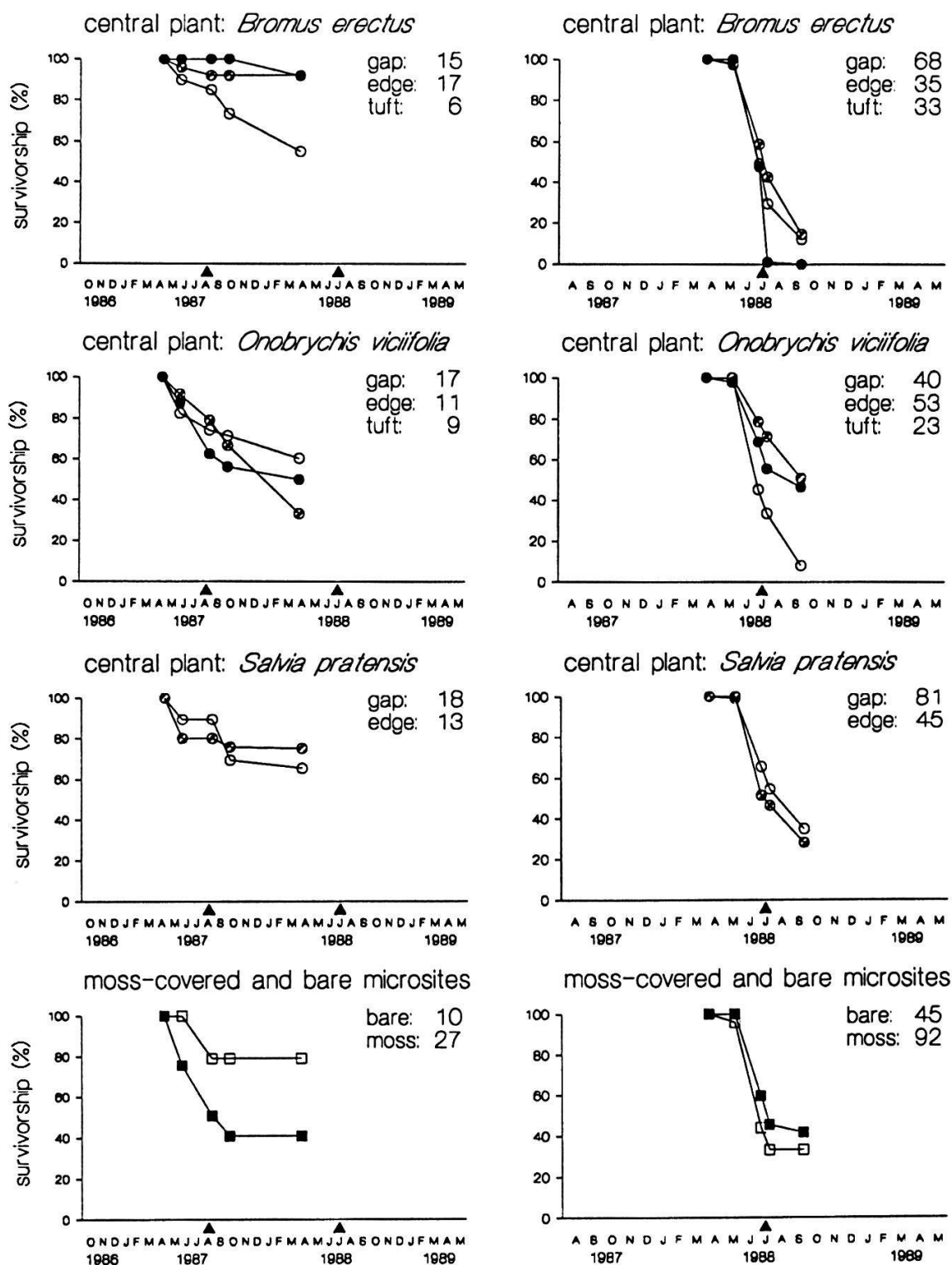


Fig. 9. Survivorship curves of *Medicago lupulina* in different microsites. Left: Spring cohort 1987. Right: Spring cohort 1988. Total number of seedlings in each microsite (= 100%) in right top corner of each plot.

Microsites: ○ = gap, ◐ = edge, ● = tuft, □ = bare, ■ = moss-covered. ▲ = time of mowing.

in all microsites and no significant differences were found between them (Fig. 8).

The cohort emerging in spring 1988 had high death rates in all microsites already in early summer (Fig. 9, Table 9). The surviving plants appeared sickly. The central-plant had a slight positive effect on establishment in *Onobrychis*-plots, where the survivorship in edges and tufts was higher than in gaps (Fig. 8). Survivorship in edges and tufts of *Onobrychis*-plots was higher than in *Bromus*-plots.

3.2.4. *Plantago lanceolata*

The mortality of *Plantago* was low. After one growth period 82% and 87%

Table 10. Death rates of *Plantago lanceolata* between the recordings in different microsites (in %).

- = seedlings in less than 3 replicates

	<i>Bromus erectus</i>			<i>Onobrychis viciifolia</i>			<i>Salvia pratensis</i>		bare moss	
	gap	edge	tuft	gap	edge	tuft	gap	edge		
cohort: spring 1987										
Apr. 87 - June 87	4.0	0.0	0.0	0.0	0.0	0.0	0.0	-	0.0	5.4
June 87 - Aug. 87	4.0	10.7	26.8	24.3	10.0	30.0	2.5	-	16.7	19.7
Aug. 87 - Sep. 87	13.0	4.0	0.0	0.0	0.0	0.0	2.9	-	0.0	6.9
Sep. 87 - Nov. 87	11.7	2.9	5.0	15.0	0.0	0.0	8.3	-	0.0	0.0
Nov. 87 - Apr. 88	0.0	0.0	0.0	15.5	0.0	0.0	8.3	-	0.0	0.0
Apr. 88 - June 88	0.0	5.0	8.3	0.0	6.7	0.0	6.7	-	0.0	0.0
June 88 - July 88	10.0	10.0	12.5	0.0	13.3	12.5	0.0	-	0.0	6.7
July 88 - Sep. 88	5.0	9.0	6.2	0.0	0.0	0.0	14.0	-	0.0	5.0
cohort: autumn 1987										
Aug. 87 - Sep. 87	1.3	0.0	0.0	0.0	0.0	0.0	4.0	4.8	0.0	10.0
Sep. 87 - Nov. 87	0.0	0.0	16.7	0.0	0.0	0.0	1.8	0.0	0.0	0.0
Nov. 87 - Apr. 88	12.7	0.0	0.0	14.0	0.0	11.1	23.5	5.6	15.0	10.8
Apr. 88 - June 88	6.5	0.0	0.0	0.0	0.0	0.0	1.0	0.0	3.1	4.0
June 88 - July 88	11.9	26.7	33.3	10.6	15.0	33.3	6.0	0.0	4.3	5.0
July 88 - Sep. 88	2.9	0.0	-	6.7	10.0	-	5.4	33.3	1.8	9.2
cohort: spring 1988										
Apr. 88 - June 88	1.3	0.0	0.0	0.0	0.0	5.8	0.0	0.0	2.0	0.0
June 88 - July 88	19.7	21.8	42.2	2.5	22.1	27.2	5.5	2.9	4.7	6.7
July 88 - Sep. 88	0.0	9.9	10.8	5.5	23.6	30.8	8.8	6.7	3.3	5.7

(sowings of 1986 and 1987 respectively) of all the emerged seedlings were still alive, after 2 growth periods 63% (sowing of 1986) (Table 6). After the first sowing *Plantago* germinated mainly in spring, hence only the spring cohort was analysed. After the second sowing both autumn and spring cohorts had sufficient seedlings for the analysis of establishment. There were no significant differences in mortality rates between autumn and spring cohorts.

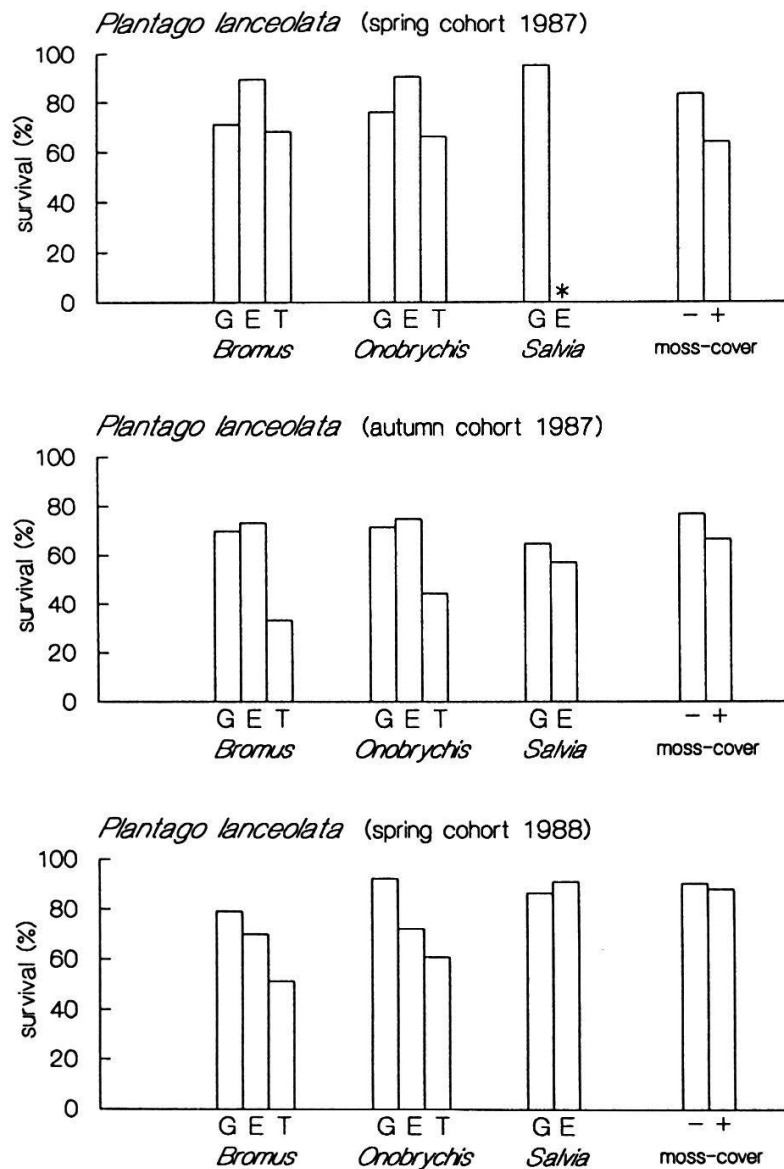


Fig. 10. Survivorship of *Plantago lanceolata* after one growth period in the different microsites. G=gap, E=edge, T=tuft, - =bare microsite, + = moss-covered microsite. * = less than 3 replicates.

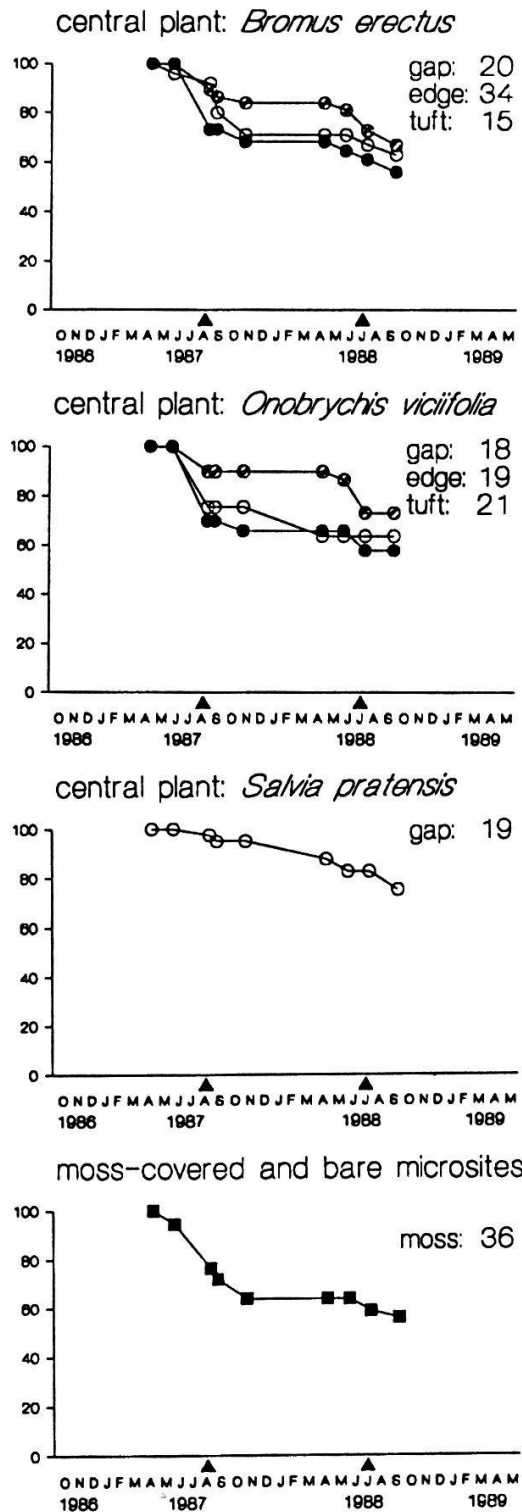


Fig. 11. Survivorship curves of *Plantago lanceolata* in different microsites. Spring cohort 1987. Total number of seedlings in each microsite (= 100%) in right top corner of each plot. Curves based on less than three replicates are omitted.

Microsites: ○ = gap, ◐ = edge, ● = tuft, □ = bare, ■ = moss-covered. ▲ = time of mowing.

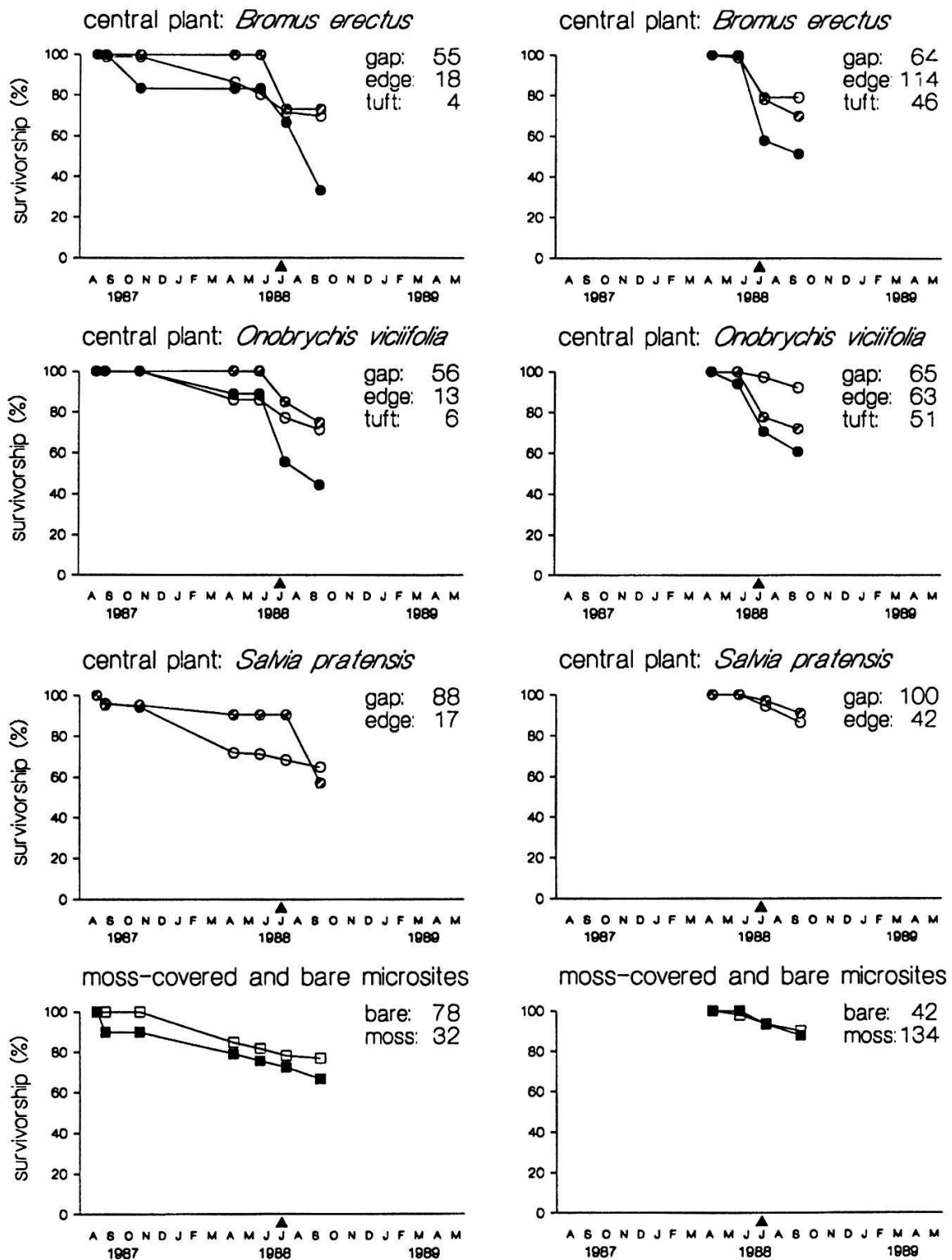


Fig. 11 (continued)

Left: Autumn cohort 1987. Right: Spring cohort 1988.

Microsites: ○ = gap, ◐ = edge, ● = tuft, □ = bare, ■ = moss-covered. ▲ = time of mowing.

Seedlings having emerged in autumn 1987 had between November and April significantly higher death rates in gaps than in edges (Table 10). In summer their mortality was higher in edges and tufts. The influence of the central-plants was thus positive in winter and negative in summer. In winter it probably reduced the effects of frost heave, while in summer competitive effects were influential. In September 1988, after one growth period, there were no differences in survivorship between gaps and edges, but in tufts mortality was higher (Fig. 10).

Spring-cohorts had the highest mortality in tufts, but also in these microsites more than 50% of the emerged seedlings became established. The lowest mortality was 1987 in edges, 1988 in gaps.

Mortality during the second growth period was low and survivorship after two years was in all microsites more than 50% (Fig. 11).

Moss cover had no influence on the establishment of *Plantago*. Survivorship differed only marginally in the plots with different central-plant species.

3.2.5. *Primula veris* s.l.

In spring and early summer the mortality of *Primula* was low in all microsites, but increased after the mowing, leaving only 28% of surviving seedlings in October 1988. In May 1989, one year after emergence, 24% of the seedlings were still alive (Table 6).

Death rates after mowing were highest in microsites, where shelter by the central-plant was missing (Table 11). Survivorship after one growth period

Table 11. Death rates of *Primula veris* between the recordings in different microsites (in %).

- = seedlings in less than 3 replicates

	<i>Bromus erectus</i>			<i>Onobrychis viciifolia</i>			<i>Salvia pratensis</i>		bare moss	
	gap	edge	tuft	gap	edge	tuft	gap	edge		
cohort: spring 1988										
Apr. 88 - Apr. 88	0.0	0.0	0.0	4.0	1.2	0.0	3.3	0.0	1.5	2.7
Apr. 88 - May 88	2.0	3.1	3.5	3.1	1.0	4.0	0.7	0.0	11.7	8.4
May 88 - July 88	5.9	1.5	0.0	1.8	2.8	5.6	10.6	0.0	0.0	3.4
July 88 - July 88	32.7	14.1	16.5	24.8	12.6	23.7	30.5	0.0	18.3	30.8
July 88 - Aug. 88	84.0	60.4	33.1	59.8	46.6	42.9	46.6	6.9	73.2	66.7
Aug. 88 - Oct. 88	-	5.1	4.2	26.7	4.1	5.0	17.0	0.0	44.4	11.1
Oct. 88 - May. 89	-	0.0	18.3	50.0	5.0	0.0	14.0	20.0	33.3	30.4

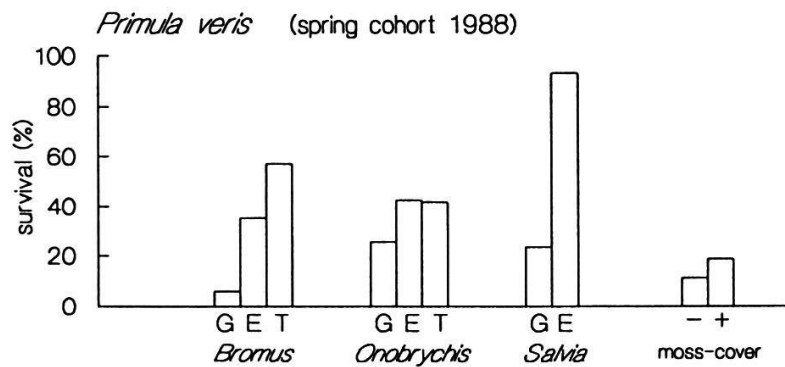


Fig. 12. Survivorship of *Primula veris* after one growth period in the different microsites. G=gap, E=edge, T=tuft, - =bare microsite, + = moss-covered microsite.

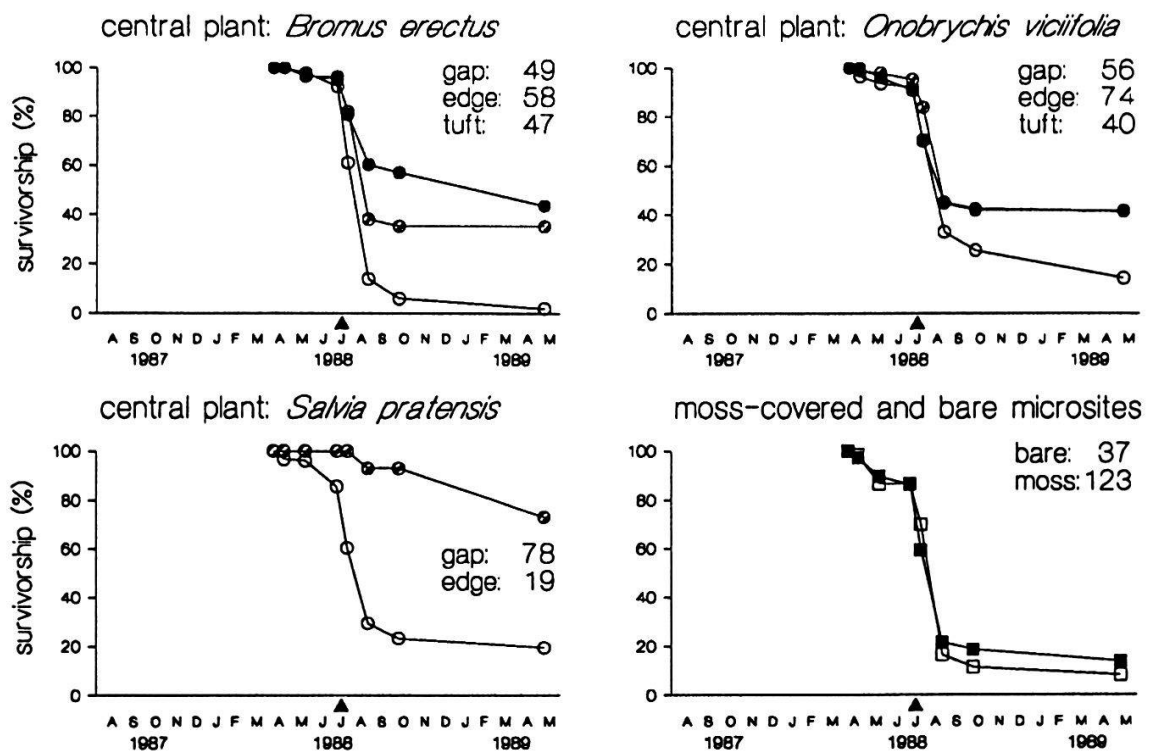


Fig. 13. Survivorship curves of *Primula veris* in different microsites. Spring cohort 1988. Total number of seedlings in each microsite (= 100%) in right top corner of each plot.

Microsites: ○ = gap, ◐ = edge, ● = tuft, □ = bare, ■ = moss-covered. ▲ = time of mowing

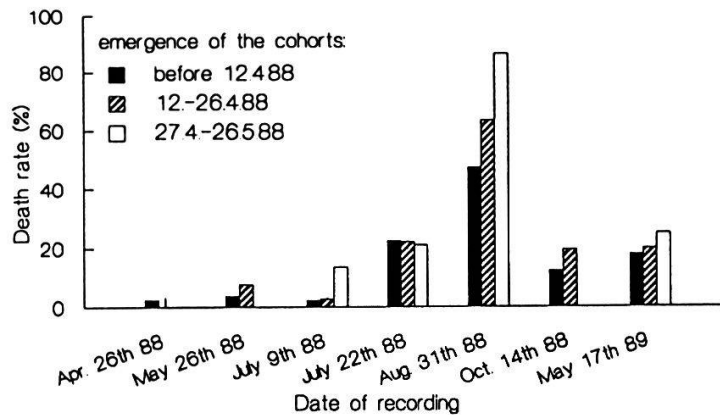


Fig. 14. Death rates of the cohorts observed at different recordings of *Primula veris* in different microsites.

was lowest in gaps, varying between 6% and 26%. In edges and tufts more seedlings survived; 35-93% of the emerged seedlings were still alive in October 1988. In bare as well as in moss-covered microsites survival was low, 11% and 18%, respectively (Figs. 12 and 13).

Desiccation was the main cause of mortality. The vulnerability of *Primula*-seedlings to drying out was probably due to their small roots. Late emerged seedlings had significantly higher death rates than the earlier emerged ones. (Fig. 14). This was pronounced especially between the end of July and the end of August, when the total mortality was highest. Then the death rates for the cohorts observed in the beginning of April, end of April and end of May were 40%, 64% and 86%, respectively, and the difference highly significant ($p < 0.001$, Kruskal-Wallis test). The roots of the younger seedlings were probably not developed enough to withstand the desiccation of the topsoil. Survivorship in the shadier northern edges was slightly higher than in the southern edges, but the difference was not significant.

Between plots with different central-plant species there were no large differences in establishment. Only the edges of *Salvia*-plots stood out with their low mortality ($p < 0.01$). The growth-form of *Salvia* might explain this: It has a sparse root system in the top-soil with less competitive effects, and its leaves appeared soon after the mowing thus protecting the seedlings.

3.2.6. *Sanguisorba minor*

Sanguisorba emerged as well in autumn as in spring, but after the first sowing the number of seedlings was very low. Hence only the autumn and spring cohorts emerging after the second sowing were analysed. There was no significant difference between the death rates of these two cohorts until autumn, when between July and September 1988 the death rate of the autumn cohort was significantly lower than that of the spring-cohort ($p < 0.05$). Survivorship of both cohorts was about the same in September 1988, 68% and 72% respectively (Table 6).

Sanguisorba established fairly well in all microsites (Figs. 15 and 16). In *Bromus*-plots the central-plant appeared to have a slightly negative effect on survivorship, but the survivorship did not differ significantly between the microsites. The spring cohort had in moss-covered microsites a higher mortality than in bare microsites. The highest death rates occurred between the end of June and the end of July (Table 12). Whether the mortality occurred during the weeks before mowing, when the vegetation was at its highest or at the mowing is not visible from the data.

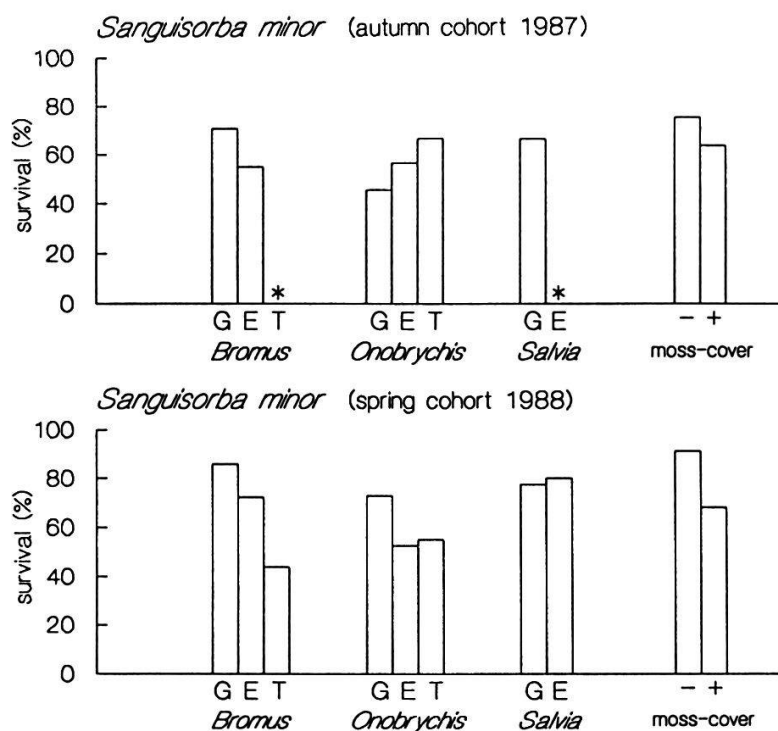


Fig. 15. Survivorship of *Sanguisorba minor* after one growth period in the different microsites.

G = gap, E = edge, T = tuft, - = bare microsite, + = moss-covered microsite. * = less than 3 replicates

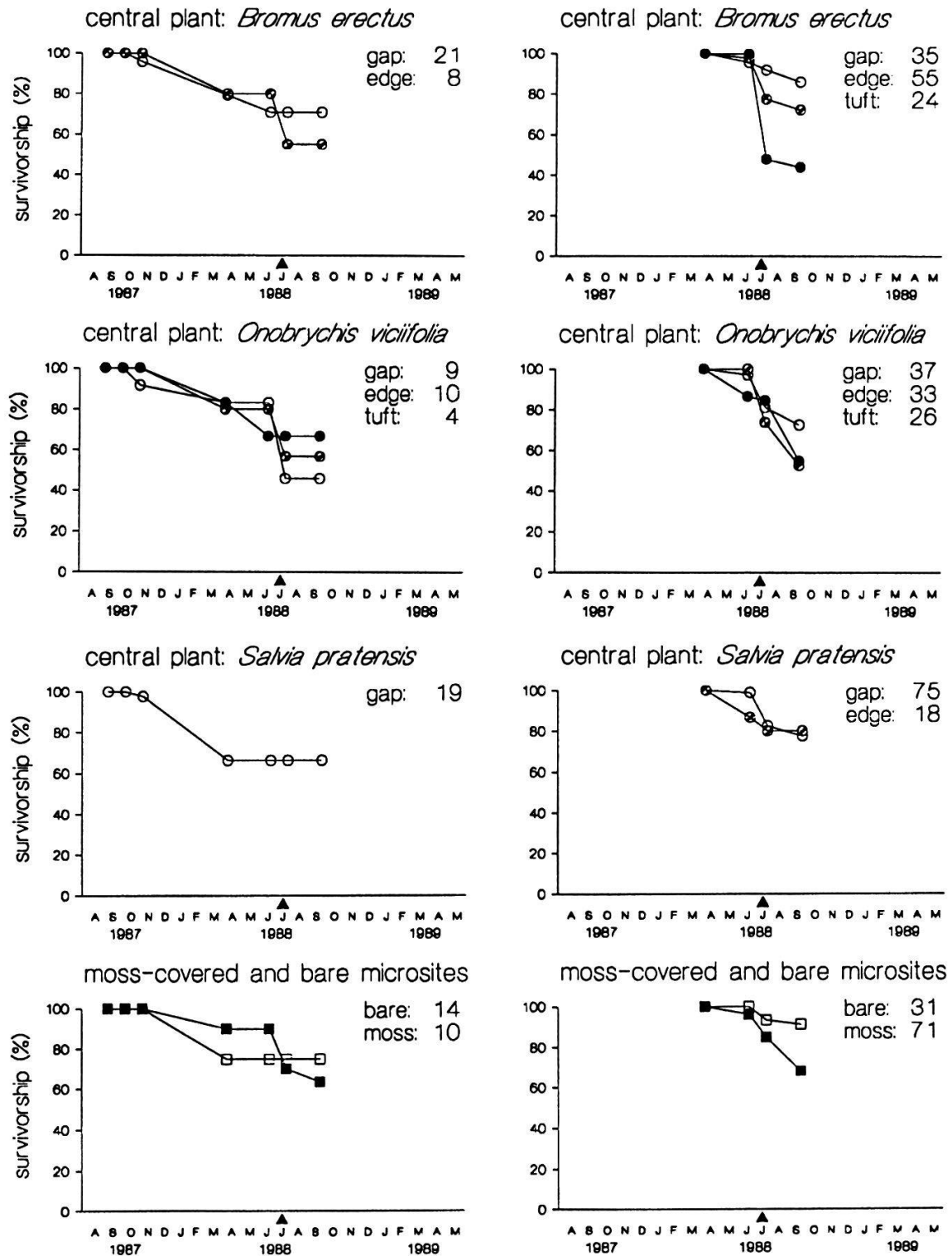


Fig. 16. Survivorship curves of *Sanguisorba minor* in different microsites. Left: Autumn cohort 1987. Right: Spring cohort 1988. Total number of seedlings in each microsite (= 100%) in right top corner of each plot. Curves based on less than three replicates are omitted.

Microsites: ○ = gap, ◐ = edge, ● = tuft, □ = bare, ■ = moss-covered. ▲ = time of mowing

Table 12. Death rates of *Sanguisorba minor* between the recordings in different microsites (in %).

- = seedlings in less than 3 replicates

	<i>Bromus erectus</i>			<i>Onobrychis viciifolia</i>			<i>Salvia pratensis</i>			
	gap	edge	tuft	gap	edge	tuft	gap	edge	bare	moss
cohort: autum 1987										
Sep. 87 - Okt 87	0.0			0.0	0.0					
Okt. 87 -Nov. 87	4.2	0.0	-	8.3	0.0	0.0	0.0	-	0.0	0.0
Nov. 87 - Apr. 88	17.5	20.0	-	12.5	20.0	16.7	31.7	-	25.0	10.0
Apr. 88 -June 88	8.3	0.0	-	0.0	0.0	33.3	0.0	-	0.0	0.0
June 88 - July 88	0.0	31.2	-	37.5	29.2	-	0.0	-	0.0	20.0
July 88 - Sep. 88	0.0	0.0	-	0.0	0.0	-	0.0	-	0.0	8.3
cohort: spring 1988										
Apr. 88 -June 88	4.2	2.2	0.0	2.9	0.0	13.3	1.1	13.3	0.0	3.8
June 88 - July 88	3.8	21.6	52.0	16.3	26.0	1.8	17.1	6.7	6.7	11.8
July 88 - Sep. 88	7.3	14.8	12.5	10.7	34.8	30.0	5.6	0.0	2.0	19.4

3.2.7. Comparison of the different species regarding their establishment

The influence of the central-plant was the most marked on *Bromus*- and *Onobrychis*-plots and a comparison of the survivorship of the different species in the different microsites has been done using the data from these plots. The studied species varied widely in their establishmentary behaviour (Fig. 17).

Especially the ability to establish in gaps showed pronounced differences. *Arabis* and *Primula* with less than 16% survivorship after one growth period could establish only very poorly in those microsites, while *Sanguisorba* and *Plantago* had a survivorship of over 70%. Behaviour of *Medicago* varied between the two years of study. In 1987 it was among the good survivors with 73% survivorship in October, but in September 1988 only 10% of the seedlings having germinated in the previous spring were still alive in gaps. *Linum* survived fairly well in gaps (60%), but significantly worse than *Plantago* with the highest survivorship ($p < 0.05$). The difference between the species with a high survivorship (over 50%) and the species with a lower one was always highly significant ($p < 0.001$).

The same division of the species into good and bad survivors could be ob-

served also in the edges, where *Arabis* and *Primula* had a poor establishment compared to *Sanguisorba* and *Plantago*. The survivorship of the bad survivors was here not quite as bad as in gaps, while the good survivors had similar survivorship in both microsites. *Medicago* showed also here two kinds of behaviour depending on the year. In 1988, when its survivorship was poor, *Medicago* established better in the edges than in gaps, but in 1987 with a high total survivorship, there was no difference in survivorship between the microsites. *Linum* was the only species, which did not fit into this division of good and bad survivors, being in gaps a good survivor and in the edges a bad one. Again the difference between the good and bad survivors was significant, $p < 0.01$ for the seedlings from the first sowing and $p < 0.05$ for the seed-

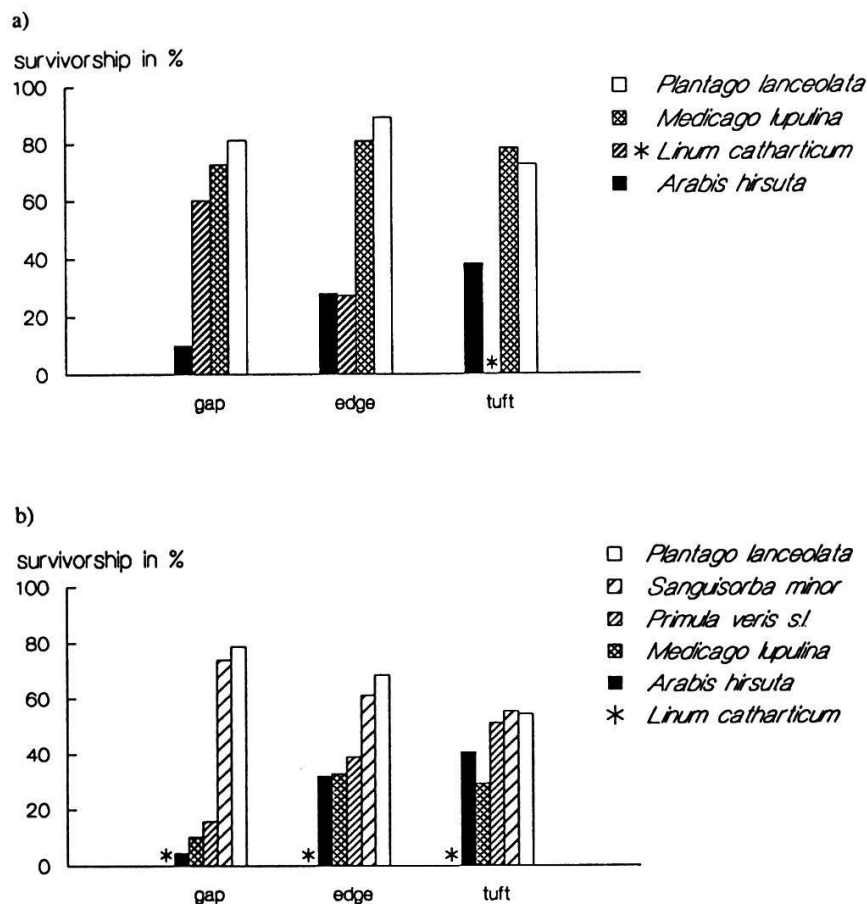


Fig. 17. Survivorship of the studied species in different microsites after one growth period. a) sowing in August 1986, b) sowing in August 1987. The bars represent the mean values of survivorship in all *Bromus*- and *Onobrychis*-plots. Cohorts used for the analysis are listed in Table 6. The autumn- and spring-cohorts for *Sanguisorba* and *Plantago* are pooled in b).

lings from the second. Differences of *Sanguisorba* from *Medicago* and *Primula* were significant only at the level $p < 0.10$.

Also in the tuft-microsites the good survivors in gaps and edges survived slightly better than the bad ones. It is however remarkable, that the differences in survivorship between the species were not significant, with the exception of *Linum*. Failing completely to establish in the tufts, its behaviour was also here distinct from that of the other species and had a significantly lower survivorship than *Plantago* and *Medicago*. *Linum* was also the only species which managed to flower during the study period, but it could not set seed because of the complete mortality in early summer of 1988.

3.3. INFLUENCE OF THE MICROSITE ON GROWTH OF THE ESTABLISHED SEEDLINGS

The mean number of living leaves per plant and the mean length of the longest leaf of the seedlings in autumn 1988 are presented in Fig. 18.

***Arabis hirsuta*.** The surviving seedlings were small to tiny, most of them having 1-3 leaves of only 1-4 mm length. The largest individuals had leaves of 10 mm length. In *Bromus*- and *Onobrychis*-plots the survivors growing in tufts were larger than those in gaps ($p < 0.05$, Wilcoxon), which were just about to die. In the gaps of the *Salvia*-plots the plants were larger. Plants in the *Onobrychis*-plots were larger than in *Bromus*-plots ($p < 0.10$, Mann-Whitney). The few survivors of the autumn-cohort 1986 were about the same size as those having emerged in autumn 1987. The growth of *Arabis* was extremely slow and somewhat less hampered in the shelter of neighbouring plants. Obviously physical hazards, especially drought, were more important than competition for the determination of the size of the plants.

***Linum catharticum*.** No plants survived until autumn 1988.

***Medicago lupulina*.** The few surviving seedlings varied greatly in size and no significant size-differences between the plants in the different microsites could be found. Average length of the longest leaf was 20-40 mm, the largest individuals had leaves of 60 mm.

***Plantago lanceolata*.** Central-plants reduced the growth of *Plantago*. In all

cohorts the plants in gaps were larger than those in edges ($p < 0.01$, Wilcoxon) or in tufts ($p < 0.05$). In *Onobrychis*-plots the plants were larger than in *Brumus*-plots ($p < 0.05$).

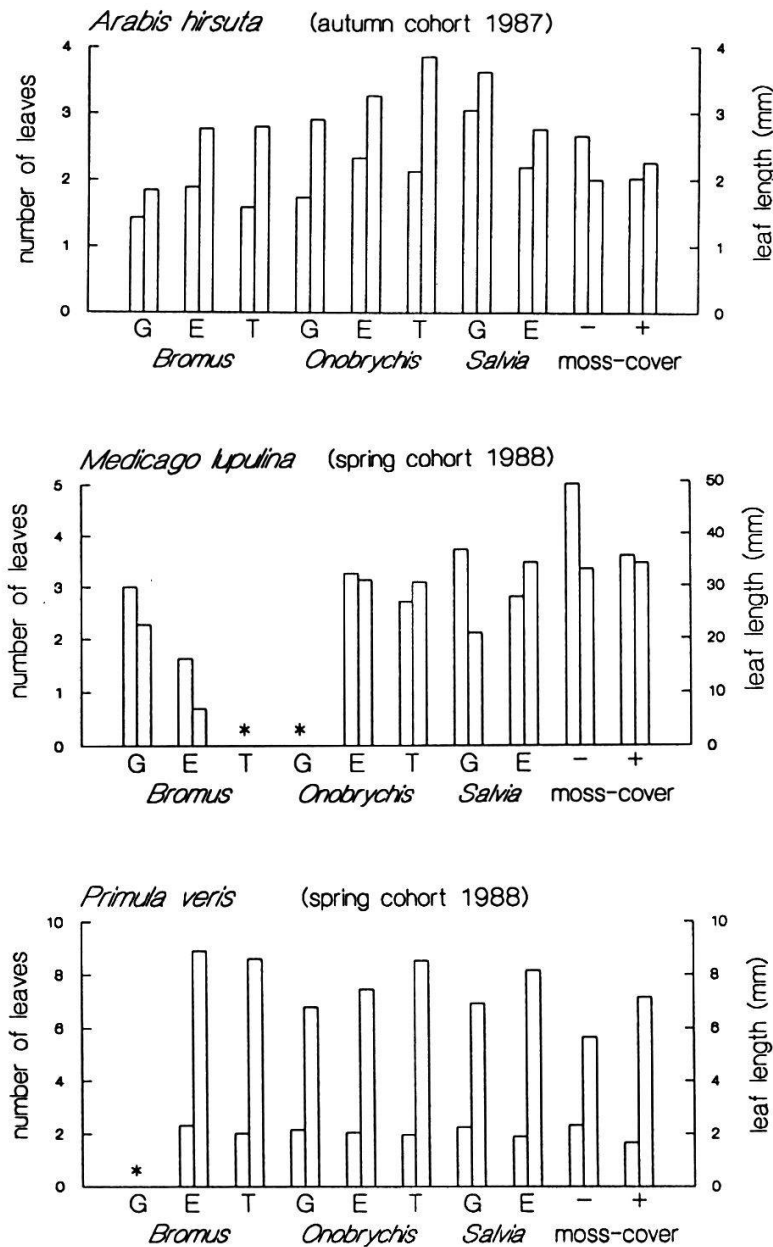


Fig. 18. Size of the surviving plants in September 1988 in the different microsites. Left column: mean number of leaves per plant. Right column: Mean length of the longest leaf. G = gap, E = edge, T = tuft, - = bare microsite, + = moss-covered microsite
* = surviving seedlings in less than three replicate microsites

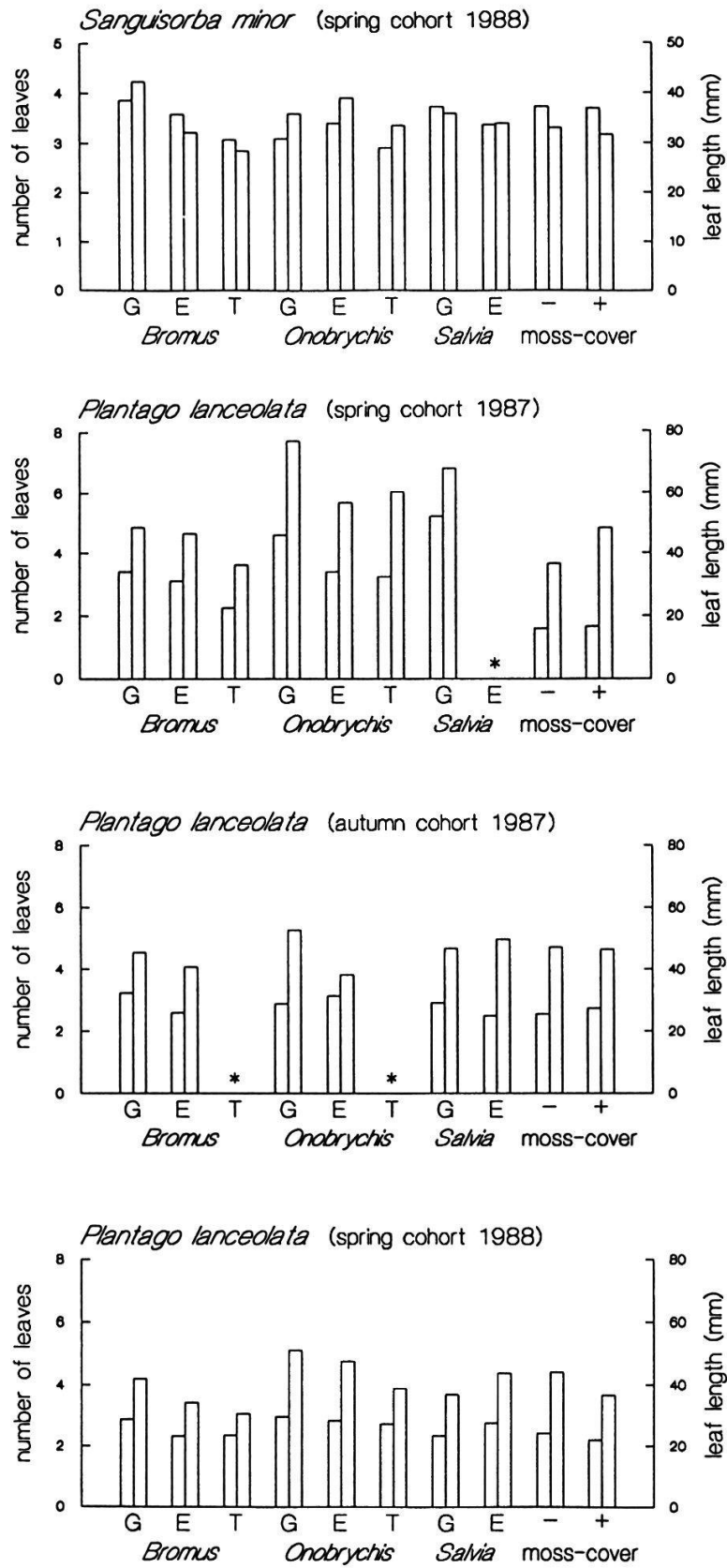


Fig. 18 (continued)

The length of the leaves was in average 40-80 mm for the spring cohort 1987, 40-55 mm for the autumn cohort 1987 and 35-55 mm for the spring cohort 1988. Leaf length of the largest individuals of the spring cohort 1987 was 120 mm, of the others 100 mm.

Primula veris. The growth of *Primula* did not differ significantly between the different micro-sites. The mean length of the longest leaf was about 6-8 mm in all microsites, the number of leaves per plant was about two. Leaves of the largest individuals were 15-19 mm long.

4. DISCUSSION

4.1. NEIGHBOURHOOD EFFECTS ON GERMINATION

Germination is obviously not limited by the availability of open microsites in the grassland of the Gräte. Sowing of seeds resulted in higher seedling densities in all microsites than were observed in the natural vegetation, regardless of their cover. Moderate vegetation cover even enhanced the emergence resulting in a high number of seedlings in edges and moss-covered microsites. Limiting factors for the emergence of all species seem thus to be rather the availability of seeds and climatic conditions including soil water availability. The delayed emergence under the vegetation cover had no influence on the number of seedlings and their establishment. The only species with an age-dependent mortality was *Primula*, whose time of emergence was not influenced by the vegetation cover.

It is plausible that vegetation cover did not inhibit recruitment, as the canopy is short in autumn and spring, i.e. at the time when germination occurs. As drought is frequent at that time, moderate vegetation cover may even enhance germination by preventing a rapid desiccation of the topsoil.

4.2. PATTERNS OF ESTABLISHMENT

Based on survival during the first growth period, three major patterns of establishment in relation to the influence of neighbouring plants could be distinguished among the six species studied.

- Low mortality in all microsites. The establishment of the seedlings was either slightly hampered by neighbouring plants or no clear effect could be detected (*Plantago lanceolata* and *Sanguisorba minor*).
- Low mortality in gaps, reduced survival under vegetation cover (*Linum catharticum*).
- High mortality in open microsites because of the harsh abiotic conditions. Survival was clearly improved in the shelter of the vegetation (*Arabis hirsuta* and *Primula veris* s.l.).

The pattern of establishmentary behaviour that a species shows, is influenced by the environmental conditions. The possible variation of this pattern from year to year could be seen in the establishment of *Medicago lupulina*. It had

a high total survival in 1987, while in 1988 it suffered high mortality with slightly better survival under cover of *Onobrychis*.

4.2.1. Low mortality in all microsites

The species with a low mortality, *Plantago* and *Sanguisorba*, as well as *Medicago* in 1987, established well in all microsites. They were not much affected by the harsh climatic conditions in the open microsites, and competition by established vegetation did only slightly reduce their survival. Their growth was somewhat inhibited in tufts, but also here the plants appeared healthy. The good survival was not limited just to the first growth period, but was pronounced in the second year as well. These best surviving species were also the best growing ones among the species studied, and among the most abundant ones in the meadow.

Large seeds enable these species to expand their roots and leaves quickly. With their deep root system they can escape the dry conditions of the topsoil and the erect leaves obtain light also in closed vegetation. Large seeds and quick initial growth even in shade are important characteristics for establishment in closed turf (GRIME and JEFFREY 1965, GROSS 1984).

Causes of death were not easy to detect, as the seedlings mostly just vanished. Mortality occurred mainly during the growth period and was slightly higher in tufts, which indicates a reduced survival of the plants because of competition. Despite the smaller size most plants grew well in tufts, and competition itself may not prevent establishment. It rather increased the vulnerability of the seedlings to other factors such as desiccation, pathogens and herbivory. If the growth of the roots is inhibited by competition, drying out of the plants may be more likely. Plants growing in shady conditions are often susceptible to fungal diseases (GRIME 1965, GRIME and JEFFREY 1965). Microsites influenced the activity of animals, e.g. aphids were often observed in *Onobrychis* tufts and the holes of crickets (*Gryllus campestris*) only in gap-microsites. Worm heaps occurred also in tufts. Young plants of *Plantago* and *Sanguisorba* were however rather resistant towards burrowing because of their erect growth-form.

4.2.2. Low mortality in gaps, reduced survival under vegetation cover

Dense vegetation inhibited the establishment of *Linum*. On the other hand, mortality was higher in large gaps than in those of an intermediate size. This

is partly in accordance with previous studies on *Linum*, which found the best establishment of this species at intermediate vegetation densities (HILLIER 1984, SCHENKEVELD and VERKAAR 1984, KELLY 1989). However, the present work suggests that establishment is best in gaps of intermediate size rather than in sparse vegetation, as in the cited studies.

Seeds of *Linum* are small and form a large seed bank. Seedlings occur very abundantly in natural vegetation but have a rather high mortality. Fungal diseases seem to be an important cause of death for *Linum*. VAN TOOREN (1990) also reports this as an important mortality factor. A large number of seedlings with a high mortality together with the preference for rather open microsites fits well in the described character of *Linum* as stress-tolerant ruderal (GRIME et al. 1988) or spender (DURING et al. 1985).

4.2.3. High mortality in open microsites, improved establishment in vegetation

Arabis hirsuta and *Primula veris* s.l. could hardly establish at all in open microsites. In the shelter of vegetation they survived markedly better, although not quite as well as *Sanguisorba* and *Plantago*.

The main cause of mortality for *Arabis* and *Primula* was desiccation. Highest death rates of seedlings occurred after mowing when the vegetation was low and the topsoil dried up. *Arabis* suffered high mortality also in spring, when the seedlings in gap-microsites desiccated after uprooting by frost. The shelter of vegetation reduced the impact of climate thus enhancing establishment. Even a sparse moss cover improved the survival of *Arabis*.

Though *Arabis* is less abundant in the natural vegetation than the other species, it cannot be regarded as rare. Therefore its poor survival was rather surprising, especially the total failure to establish in gaps. This species is often described as a ruderal with a preference for open habitats. As the environmental conditions are so crucial for the establishment of *Arabis* it is likely to vary from year to year. Favourable years may be decisive for its existence on the Gräte. The study period was obviously unfavourable for this species. There was little snow in either winter, which increased the impact of frost-heave. Drought periods in spring and after mowing enhanced desiccation.

Microsites with higher nutrient levels might be important especially for the performance of *Arabis*, as it is one of the few plants in limestone grasslands without mycorrhiza (HARLEY and HARLEY 1986). Such microsites are e.g. colonies of voles with faecal deposits, in which the abundance of *Arabis* is in-

creased compared to vegetation without the influence of voles (LEUTERT 1983).

The vulnerability of the seedlings of *Primula* in open microsites may explain its habitat requirements. The subspecies *suaveolens*, to which the studied plants belong, is usually found in shady habitats such as open woodlands and its occurrence in an open meadow, as on the study site, is rather uncommon. In a meadow favourable microsites for its establishment are likely to be scarce. This is however influenced by the time of mowing, as the hardness of the seedlings against desiccation increases with their age. Mowing in June every or every other year is harmful for *Primula* compared to a later or a less frequent mowing (KRÜSI 1981, MERZ 1986). In meadows near the study site mown end of June, *Primula* is almost extinguished (MERZ 1986). The meadow of the present study is mown in mid-July, and the occurrence of *Primula* here shows, that this difference of 2-3 weeks in the time of mowing is already decisive for establishment. Older seedlings are better able to withstand desiccation after the mowing and are more likely to find favourable microsites. Variation in phenological development may cause similar differences in establishment between the years.

Such subtleties may be important for the existence of a species in a community and should be considered when choosing management practices in nature conservation.

The behaviour of *Medicago* and *Linum* shows, that establishment of a species may greatly vary between the years and short-term studies give only an incomplete picture about the regeneration of a species. The variation in environmental conditions and occurrence of favourable years may be more limiting for the existence of these species than favourable microsites.

4.3. NEIGHBOURHOOD EFFECTS ON ESTABLISHMENT AND SUBSEQUENT SURVIVAL

4.3.1. Significance of competition

On the whole, competition by the established vegetation did not prevent the establishment of seedlings of most species on the study site. It reduced growth and may have caused a higher mortality risk, but survival of the seedlings was fairly high even in densely vegetated tuft-microsites. After one growth period, survival of emerged seedlings was mostly over 50% in these

microsites. Lower survival in tufts occurred only when the mortality cause was drought or fungal disease, and in these cases vegetation cover either improved the survival or had no influence. Gaps may be important for the regeneration of short-lived species, as the behaviour of *Linum* indicates.

In small gaps, like the ones used in the present study, mainly the above-ground competition is reduced. Below-ground competition occurs also in these microsites because of the lateral growth of the roots of the neighbouring vegetation. The significance of microsites with no competition at all (e.g. large gaps) is however likely to be small in the community studied, as such microsites do not occur frequently.

This unimportance of competition for establishment results obviously from the low growth-rates of the whole vegetation in these nutrient poor habitats, and the yearly mowing. As above-ground productivity is low and growth after the mowing poor, competition for light is likely to be intense only during a short time of the year. Further, the mowing keeps the ground fairly open by removing the above-ground biomass periodically and preventing the accumulation of litter. The rather early mowing removes nutrients with the phytomass preventing the dominance of species, which would be able to accumulate the nutrients. Below-ground competition reduces the growth of the seedlings. Nevertheless they obtain enough nutrients to survive.

The results conflict with a common opinion, that regards competition as the main hazard for seedlings (e.g. FENNER 1985, WATKINSON 1986). That opinion is based on a vast number of studies under nutrient rich conditions, where the detrimental effects of competition by established vegetation on seedling establishment is clearly shown (CARUSO 1970, FOSTER 1964, GOLDBERG and WERNER 1983, GROSS 1980, GROSS and WERNER 1982, MCCONNAUGHAY and BAZZAZ 1987, NEWELL et al. 1981, PUTWAIN and HARPER 1970, ROBOCKER et al. 1953, ROSS and HARPER 1972, SHAW and ANTONOVICS 1986, SILVERTOWN and TREMLETT 1989, STERGIOS 1976, TURKINGTON et al. 1979). It is however often neglected, that these effects depend on the productivity of the habitat. The impact of competition on plant growth decreases with decreasing nutrient levels and increasing disturbance (CAMPBELL and GRIME *subm.*). The present work indicates this to be the case also for seedling establishment, and there is also supporting evidence in the literature. Fertilizer treatment often results in a poorer establishment of seedlings (FOSTER 1964, HOWE and SNAYDON 1986, KEDDY 1981, KELLY 1989, PEMADASA and LOWELL 1974, but see MILES 1973b, 1974). In nutrient-poor habitats gaps are not the most favourable microsites for establishment, although germination is often improved in them (SCHENKE-

VELD and VERKAAR 1984, SILVERTOWN 1981, SILVERTOWN and WILKIN 1983). The habitat-dependent variation of the significance of gaps on seedling establishment has been shown by HILLIER (1984) in chalk grasslands in Derbyshire. The regeneration by seed was strongly gap-dependent in north-facing slopes while in south-facing slopes the emergence of seedlings did not increase in gaps and survival was even enhanced by the presence of established vegetation. The north-facing slopes had a more luxuriant vegetation, where gaps were the only possibility for many species to escape competition in contrast to the more open south-facing slopes where drought was a more important factor. Also SHARITZ and MCCORMICK (1973) observed in case of two annuals in communities on granite outcrops in the southeastern United States, that with increasing environmental harshness the importance of competitive interactions between species decreases.

The effect of vegetation may be negative also on infertile soils, but the mechanism is not necessarily competition. MILES (1972, 1973a, 1974) found an improved establishment on experimentally bared soil in a southern English heath and in different sites in Scotland, mostly in rather species-poor *Callunetum* communities on podsollic or peaty soils. He produced the gaps by stripping the vegetation with a sharp spade disturbing also the litter on the soil surface and the other top-layers. The exposed mineral soil might thus have been responsible for the improved establishment rather than the reduced competition, as the physical properties of *Calluna* raw humus are unfavourable for seedling establishment (ELLENBERG 1986). MILES (1972) mentions drought as the main cause of mortality. It is also possible that the vegetation structure of a *Callunetum* might be unfavourable for seedlings. In winter however the mortality in vegetation was less than in bare plots, due to reduced frost heave (MILES 1973a).

The effect of established vegetation on seedlings consists of different mechanisms, e.g. above- and belowground competition, sheltering or influence on other organisms like herbivores or mycorrhiza. The relative importance of these mechanisms and the outcome of interaction depends on the environmental conditions. Considering the results of the present study and the evidence gained from the literature, one can say that competition by established vegetation surely reduces the growth of seedlings and may prevent their establishment, but in less productive habitats other factors gain in importance and may overweigh the effects of competition.

4.3.2. Shelter against adverse climate

Climatic factors, such as frost heave and drought, cause the high mortality of *Arabis* and *Primula*. The small size of their roots does not give enough support in the moving soil and does not allow water uptake in a dry top soil. The establishment is enhanced under vegetation cover, as the roots of neighbouring plants stabilize the soil and the canopy protects the topsoil effectively against desiccation. The sheltering effect of vegetation on micro-climate can be very pronounced, as the measurements of CERLETTI (1988) on the Gräte have shown. He measured the influence of vegetation on water-regime in topsoil. During sunny summer weather the topsoil dried fast in gaps of the size of 30x35 cm, and its wilting point was reached already two days after the last precipitation. After seven days the soil was completely dried out up to a depth of 3-4 cm. In sheltered microsites the topsoil never dried below the wilting-point, even not after the mowing, when the vegetation was very low. The exposure had a significant effect. South-facing edges of the vegetated patches dried out rapidly while the northern edge had a more favourable water-regime. Vegetation has a similar effect on the relative humidity of the air and on the soil surface temperature (VON GUNTEN 1987).

At the study site, gaps are created mainly by small mammals, voles and moles. Nutrient levels in the upheaved soil are lower than those in the topsoil under undisturbed vegetation (SCHÄPPI 1989), and the loose soil in the fairly large gaps desiccates quickly. All this reduces the significance of gaps for seedling recruitment. Seedlings are rarely observed in them and the slow recolonization occurs vegetatively from the surroundings (pers.obs.). The increase of some short-lived species, also *Arabis*, due to vole-activity in fertilized and unfertilized meadows, as observed by LEUTERT (1983) in same area as the present study, might be explained by the different importance of gaps in different habitats and in different years. Also the influence of enhanced nutrient levels by voles are important for many species, as already discussed in Chapter 4.3.1. LEUTERT (1983) did not establish, whether the increase of the short-lived species, as compared to the closed vegetation, occurs in the centre of the vole-gaps or in the more protected edges.

The significance of gaps on regeneration by seed is often emphasized, but sheltering effects are mostly considered to restrict themselves to habitats with extremely severe climatic conditions. The necessity of sheltering nurse-plants for seedling establishment is known e.g. in the Sonoran Desert (FRANCO and NOBEL 1988, 1989, NIERING et al. 1963, TURNER et al. 1966) and in subalpine

herb communities in Utah (ELLISON 1949). In these habitats seedlings are not able to survive on bare soil, as the temperature, desiccation, frost-heave or herbivory are too severe. Besides that, the soil nitrogen levels are higher under nurse-plants. Competition reduces the growth of the seedlings in patches of vegetation, but the overall effect is still positive for the seedlings. Slight differences in their position in the vegetation patches strongly influence the outcome of the interaction (FRANCO and NOBEL 1988, 1989).

Shelter plays a role in establishment also in more mesic habitats, if not always so obviously. Often the effects of competition are just outweighed. Apart from the work of HILLIER (1984, see Chapter 4.3.1), there is further evidence for sheltering effects in the literature. SCHENKEVELD and VERKAAR (1984) observed that in Dutch chalk grasslands the early survival of many short-lived species was better in dense than in open vegetation or in bare sites. In summer, when the vegetation cover was closing, this was however partly reversed. In a southern-English chalk grassland the emergence was enhanced in microsites with reduced cover (SILVERTOWN 1981, SILVERTOWN and WILKIN 1983), but there was no relationship between mortality and the cover of microsites. In a year of drought, seedling mortality was even lower in microsites with more cover (SILVERTOWN 1979). In a midsuccessional oldfield studied by GOLDBERG (1987) establishment in gaps and vegetated microsites differed only marginally as the positive effect of reduced competition in the gaps was outweighed by the desiccation of the topsoil.

In a dry Texas grassland FOWLER (1988) observed a better establishment of seedlings of the grasses *Aristida longiseta* and *Bouteloa rigidiseta* with neighbouring plants of the same species than without neighbours. She considered this phenomenon mainly as aggregation of seedlings on favourable microsites, perhaps also as some facilitation due to shading. In the greenhouse the establishment of these species was enhanced in microsites sheltered by litter or rocks, where the topsoil desiccated less (FOWLER 1986).

The positive effect of shelter, as observed in the present study, are thus more abundant than generally assumed. Apart from extreme habitats, where their significance is obvious, they are important also in more mesic habitats, especially during extreme years and for species, which are at the limit of their tolerance. Whether this positive influence of vegetation on establishment has a lasting effect on growth and reproduction may still be questioned. The two years of observation in the present study were too short a time to answer this because of the slow growth of the plants. The requirements of juvenile and adult plants may be different from those of seedlings (MORRIS and WOOD

1989, PARRISH and BAZZAZ 1985). In habitats with low production, vulnerability to climatic hazards seems to be more decisive than competitive ability in the early life stages such as germination and establishment. Positive effects of neighbours such as sheltering may thus be important. In later stages competitive effects may become more significant and determine the relative abundance of the species, as the work by MITCHLEY and GRUBB (1986) and MARTI (in prep.) suggests.

4.3.3. Effect of different species as neighbours

Species differ in their influence on the establishment and growth of seedlings in their neighbourhood. In the present study the performance of the seedlings was often better near *Onobrychis* than near *Bromus*. This results probably from the different growth form of the species, particularly from the different root morphology and also from differences in decomposition rates of their leaves (see also Chapter 3.2.1). Levels of available nutrients below the different species may also differ, particularly that of nitrogen, as *Onobrychis* has a symbiotic association with nitrogen-fixing organisms. There is a small-scale variation in the levels of nitrogen, phosphate or potassium in the soil of the study site (SCHÄPPI 1989), but no clear correlation with the vegetation cover, specially with *Onobrychis*, could be found. The importance of the effect of individual species on a microsite in natural vegetation might be too diffuse to be measured, as the individuals are tightly interwoven. Thus their effect on the establishment of seedlings may be less pronounced than in the monospecific patches in the experimental plots of the present work.

There was no combination of central plant and seedlings of the same species, and there is thus no information about possible differences in the intra- and interspecific interactions between seedlings and established vegetation. This is frequently observed in forests, where many tree species are able to regenerate better in the neighbourhood of other species than their own (FORCIER 1975, FOX 1977, SIMAK 1951, WOODS 1984).

4.4. FURTHER PERFORMANCE OF THE PLANTS AND CONSEQUENCES FOR SPECIES-RICHNESS

In the studied grassland many plants are able to survive for years as tiny plantlets. CHIPPINDALE (1948) and FENNER (1978) have previously observed

this kind of arrested growth of seedlings during several months, but under nutrient-poor conditions seedlings are obviously able to remain in this state much longer. Whether their development to adulthood requires favourable years, some incidental events in the neighbourhood such as the excrements of animals or the dying of neighbouring plants, or just time, remains unanswered. For the regeneration of forest trees such dormant juvenile plants are important (HIBBS and FISCHER 1979, MAYER 1980, SERNANDER 1936, UHL et al. 1988), but in grasslands their significance is unknown. Mycorrhizal infection can be very important for the survival of such seedlings (GRIME et al. 1987). This might be the effect of assimilates exported from dominant species to seedlings over the mycorrhizal network (READ et al. 1985).

The observed slow growth and the ability of juvenile plants to survive for a long time in vegetation allow a high species density in a small scale. This confirms the significance of the low nutrient levels and mowing for the maintenance of the species richness and supports the models of GRIME (1979) and HUSTON (1979). They suggest, that high species densities are possible in high or intermediate levels of stress and disturbance, as the expression of competitive dominance is limited. In too extreme habitats the number of species declines, as only a few specialists are able to survive.

Because of slow growth and good survival, immigrated propagules and occasional favourable years for seed production or establishment also have long-lasting effects on species composition (SHMIDA and ELLNER 1984). Such effects may be particularly important for short-lived species, as gaps (GRUBB 1976, KELLY 1989, RUSCH 1988) and dry years momentarily reducing the cover of perennial species (LÜDI and ZOLLER 1949) are important for their regeneration even in nutrient poor habitats.

In the study site the annual species were rare even in open microsites. It is interesting, that the exceptions were *Rhinanthus alectorolophus*, *Rh. minor* and *Trifolium dubium*, species which are able to gain nutrients from other organisms either hemi-parasitically or symbiotically. Other interactions than competition might be decisive also for the establishment of annual species in this habitat.

SUMMARY

The influence of vegetation on the establishment of new seedlings was studied experimentally in a limestone grassland (*Mesobrometum*) in northern Switzerland. Seeds of six dicotyledonous species (*Arabis hirsuta*, *Linum catharticum*, *Medicago lupulina*, *Plantago lanceolata*, *Primula veris* s.l. and *Sanguisorba minor*) were collected at the study site and sown in artificially created microsites, which were differentially influenced by adult plants of three species common in the meadow (*Bromus erectus*, *Onobrychis viciifolia* and *Salvia pratensis*). The microsites were tufts of the adult plants, the edges around them and gaps beside them. The influence of moss cover on the establishment was studied on separate plots. Seeds were sown in August of 1986 and 1987. Emergence, fate of emerged seedlings and their growth was followed during one or two years. As the emergence after the first sowing was poor, the quantitative data presented in the summary is based on results of the second sowing.

1. Germination occurred in all microsites. Moderate vegetation cover increased the number of seedlings of all species, although it often delayed the emergence. Most seedlings emerged in spring. The only species with mainly autumn germination was *Arabis*.
2. Three major patterns of establishment in relation to the influence of neighbouring plants could be distinguished:
 - *Plantago* and *Sanguisorba* established well in all microsites. Their mortality was slightly higher in dense vegetation than in gaps, but in all microsites 50-90% of the emerged seedlings survived the first growth period.
 - *Linum* was extinguished by a fungal disease in spring 1988 regardless of the microsite. Thus the analysis of establishment is based only on the small number of seedlings, whose fate could be followed during 1987. The results indicate a good establishment in gaps and a detrimental effect of dense vegetation cover.
 - *Arabis* and *Primula* were hardly at all able to establish in gaps. They suffered a high mortality because of abiotic factors such as frost heave in winter (*Arabis*) and desiccation after the mowing of the meadow. The vegetation enhanced the establishment by stabilizing the soil and preventing the desiccation. Less than 5% of the *Arabis*-seedlings survived one year in the gaps, while the survival was 21-43% in edges and 25-52% in tufts. Moss cover enhanced the establishment of *Arabis* significantly. *Primula* survived to less than 25% in gaps, the figures for edges and tufts being 35-93% and 42-57%, respectively. Late emerging *Primula*-seedlings had a significantly higher mortality in summer than the early emerging ones.

Medicago differed in its establishment in the two years of study. Survival in 1987 was high, 56-100% in the different microsites after one growth period. In 1988 survival was low. It was better in the shelter of *Onobrychis* (47-51%) than in the other microsites (0-42%).
3. The growth of the seedlings was very slow, and the seedlings remained small until the end of the study. Species with the best survival, *Plantago* and *Sanguisorba*, had the largest plants in autumn 1988. The growth of these species was reduced by vegetation cover.
4. The species of the neighbouring plant influenced the establishment and growth of *Arabis*, *Medicago* and *Plantago*. Seedlings of these species established better and were larger in *Onobrychis*-plots than in *Bromus*-plots.
5. Vegetation cover did not prevent the establishment of seedlings. Climatic factors were more decisive for their survival than competition. Neighbouring plants had a positive effect on establishment of species vulnerable to climatic hazards. On the whole, species differed more in their ability to establish in gaps than in dense vegetation. The observed slow growth and the survival of the seedlings over long periods in undisturbed turf are important factors for the maintenance of the high species density in nutrient-poor limestone grasslands.

ZUSAMMENFASSUNG

Der Einfluss der Vegetation auf die Etablierung neuer Keimlinge wurde experimentell in einem Trespen-Halbtrockenrasen (*Mesobrometum*) in der Nord-Schweiz untersucht. Samen von sechs dicotylen Arten (*Arabis hirsuta*, *Linum catharticum*, *Medicago lupulina*, *Plantago lanceolata*, *Primula veris* s.l. und *Sanguisorba minor*) wurden in der Nähe der Untersuchungsflächen gesammelt und in künstlich erzeugte Mikrostandorte eingesät. Die Mikrostandorte wurden durch adulte Pflanzen von drei in der Wiese häufigen Arten (*Bromus erectus*, *Onobrychis viciifolia* und *Salvia pratensis*) unterschiedlich beeinflusst: die Horste der adulten Pflanzen, ihre Randzonen und die Lücken neben ihnen. Der Einfluss der Moosbedeckung wurde an separaten Mikrostandorten untersucht. Die Samen wurden im August 1986 und 1987 gesät. Das Aufkommen von Keimlingen, ihr Schicksal und Wachstum wurde während eines bzw. zwei Jahren registriert. Weil nach der ersten Saat nur eine geringe Anzahl Keimlinge aufkam, basieren die Zahlenangaben der Zusammenfassung auf den Daten der zweiten Saat.

1. Keimlinge kamen an allen Mikrostandorten auf, grösstenteils im Frühling. Nur *Arabis* zeigte vor allem Herbstkeimung. Eine leichte Vegetationsbedeckung erhöhte die Anzahl der Keimlinge, obwohl die Keimung verzögert wurde.
2. Es konnten drei verschiedene Etablierungsmuster bezüglich des Einflusses der benachbarten Pflanzen unterschieden werden:

- *Plantago* und *Sanguisorba* etablierten sich gut an allen Mikrostandorten. Ihre Sterblichkeit war etwas höher in dichter Vegetation, aber 50-90% aller Keimlinge überlebten die erste Vegetationsperiode an den verschiedenen Mikrostandorten.
- *Linum* wurde im Frühling 1988 vollständig durch eine Pilzkrankheit ausgelöscht, unabhängig vom Mikrostandort. Die wenigen bereits 1987 erhaltenen Resultate deuten darauf hin, dass die Etablierung in den Lücken gut ist und die Vegetationsbedeckung sich nachteilig auswirkt.
- *Arabis* und *Primula* konnten sich kaum in den Lücken etablieren. Abiotische Faktoren, wie Frosthebung im Winter (*Arabis*) und Austrocknung nach der Mahd, verursachten eine hohe Sterblichkeit. Der Schutz durch die Vegetation begünstigte die Etablierung, indem der Boden stabilisiert und die Austrocknung verhindert wurde. Weniger als 5% der *Arabis*-Keimlinge überlebte ein Jahr in den Lücken. In den Randzonen und Horsten war die Überlebensrate 21-43% bzw. 25-52%. Moosbedeckung begünstigte die Etablierung von *Arabis* deutlich. In den Lücken überlebten knapp 25% der *Primula*-Keimlinge. Die entsprechenden Zahlen für Randzonen und Horste waren 35-93% und 42-57%. Spät gekeimte Pflanzen hatten eine höhere Sterblichkeit im Sommer als früh gekeimte.

Die Etablierung von *Medicago* war in den zwei Untersuchungsjahren verschieden. 1987 war die Sterblichkeit gering: 56-100% der Keimlinge überlebten die erste Vegetationsperiode in den verschiedenen Standorten. 1988 war die Sterblichkeit hoch. Im Schutz von *Onobrychis* überlebten 47-51% der Keimlinge, an den anderen Mikrostandorten nur 0-42%.

3. Die Keimlinge wuchsen langsam und blieben bis zum Untersuchungsabschluss klein. Die Keimlinge der Arten mit den höchsten Überlebensraten, *Plantago* und *Sanguisorba*, waren die grössten. Das Wachstum dieser Arten wurde durch die Vegetation gehemmt.
4. Die Etablierung von *Arabis*, *Medicago* und *Plantago* wurde durch die Spezies der benachbarten Pflanzen beeinflusst. Die Keimlinge der genannten Arten etablierten sich besser und waren zugleich grösser in den *Onobrychis*-Flächen als in den *Bromus*-Flächen.
5. Die Vegetation verhinderte die Keimlingsetablierung nicht. Klimatische Faktoren waren für das Überleben der Keimlinge entscheidender als Konkurrenz. Die Vegetation

hatte einen positiven Einfluss auf die Etablierung der Arten, die empfindlich auf die klimatischen Faktoren reagierten. Insgesamt unterschieden sich die Arten mehr in ihrer Fähigkeit sich in den Lücken als in der Vegetation zu etablieren. Das beobachtete langsame Wachstum und die Fähigkeit der Pflanzen, lange Zeitperioden in der Vegetation zu überleben, sind wichtige Faktoren für die Erhaltung des Artenreichtums in nährstoffarmen Grünlandgesellschaften.

REFERENCES

- AARSSSEN L.W., 1983: Ecological combining ability and competitive combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. *Am.Nat.* 122, 707-731.
- BINZ A. and HEITZ C., 1986: Schul- und Exkursionsflora für die Schweiz mit Berücksichtigung der Grenzgebiete. Schwabe, Basel. 624 pp.
- CAMPBELL B.D. and GRIME J.P. (submitted 1990): An experimental test of plant strategy theory.
- CARUSO J., 1970: Early seedling survival of *Melilotus* in bluegrass sod. *Ecology* 51, 553-554.
- CERLETTI G., 1988: Experimentelle Untersuchungen zum Bodenwasserhaushalt in Trespen-Halbtrockenrasen (bei Merishausen). Diplomarbeit. Geobot. Inst. ETH, Stiftung Rübel, Zürich. 84 pp. (unpubl.).
- CHESSON P.L. and CASE T.J., 1986: Overview: Nonequilibrium community theories: Chance, variability, history, and coexistence. In: DIAMOND J. and CASE T.J. (eds.), *Community ecology*. Harper & Row, New York. 229-239.
- CHIPPINDALE H.G., 1948: Resistance to inanition in grass seedlings. *Nature* 161, 65.
- CONNELL J.H., 1978: Diversity in tropical rain forests and coral reefs. *Science* 199, 1302-1310.
- DURING H.J., SCHENKEVELD A.J., VERKAAR H.J. and WILLEMS J.H., 1985: Demography of short-lived forbs in chalk grassland in relation to vegetation structure. In: WHITE J. (ed.), *The population structure of vegetation*. Junk, Dordrecht. 341-370.
- DURING H.J. and WILLEMS J.H., 1984: Diversity models applied to a chalk grassland. *Veg-etatio* 57, 103-114.
- ELLENBERG H., 1986: *Vegetation Mitteleuropas mit den Alpen*. (4th ed.). Ulmer, Stuttgart. 989 pp.
- ELLISON L., 1949: Establishment of vegetation on depleted subalpine range as influenced by microenvironment. *Ecological Monographs* 19, 97-121.
- FENNER M., 1978: A comparison of the abilities of colonizers and closed-turf species to establish from seed in artificial swards. *J.Ecol.* 66, 953-963.
- FENNER M., 1985: *Seed ecology*. Chapman & Hall, London, New York. 151 pp.
- FORCIER L.K., 1975: Reproductive strategies and the co-occurrence of climax tree species. *Science* 189, 808-810.
- FOWLER N., 1986: Microsite requirements for germination and establishment of three grass species. *Amer.Midland Naturalist* 115, 131-145.
- FOWLER N., 1988: What is safe site?: neighbor, litter, germination date and patch effects. *Ecology* 69, 947-961.
- FOX J.F., 1977: Alternation and coexistence of three species. *Am. Nat.* 111, 69-89.
- FRAHM J.-P. and FREY W., 1983: *Moosflora*. Ulmer, Stuttgart. 522 pp.
- FRANCO A.C. and NOBEL P.S., 1988: Interactions between seedlings of *Agave deserti* and the nurse plant *Hilaria rigida*. *Ecology* 69, 1731-1740.

- FRANCO A.C. and NOBEL P.S., 1989: Effect of nurse plants on the microhabitat and growth of cacti. *J.Ecol.* 77, 870-886.
- GIGON A., 1981: Koexistenz von Pflanzenarten, dargelegt am Beispiel alpiner Rasen. *Verh. Ges. Ökologie* 9, 165-172.
- GIGON A. and RYSER P., 1986: Positive Interaktionen zwischen Pflanzenarten. *Veröff.Gebot.Inst.ETH, Stiftung Rübel, Zürich* 87, 372-387.
- GOLDBERG D., 1987: Seedling colonization of experimental gaps in two old-field communities. *Bull.Torr.Bot.Club* 114, 139-148.
- GOLDBERG D. and WERNER P.A., 1983: The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (*Solidago* spp.). *Oecologia* 60, 149-155.
- GRIME J.P., 1965: Shade tolerance in flowering plants. *Nature* 208, 161-163.
- GRIME J.P., 1979: Plant strategies and vegetation processes. Wiley, Chichester. 222 pp.
- GRIME J.P., HODGSON J.G. and HUNT R., 1988: Comparative plant ecology. A functional approach to common British species. Unwin Hyman, London. 742 pp.
- GRIME J.P. and JEFFREY D.W., 1965: Seedling establishment in vertical gradients of sunlight. *J.Ecol.* 53, 621-642.
- GRIME J.P., MACKEY J.M.C., HILLIER S.H. and READ D.J., 1987: Floristic diversity in a model system using experimental microcosms. *Nature* 323, 420-422.
- GROSS K.L., 1980: Colonization by *Verbascum thapsus* (Mullein) of an old-field in Michigan: Experiments on the effects of vegetation. *J.Ecol.* 68, 919-927.
- GROSS K.L., 1984: Effects of seed and growth form on seedling establishment of six monocarpic perennial plants. *J.Ecol.* 72, 369-387.
- GROSS K.L. and WERNER P.A., 1982: Colonizing abilities of 'biennial' plant species in relation to ground cover: implications for their distributions in a successional sere. *Ecology* 63, 921-931.
- GRUBB P., 1977: The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol.Rev.* 52, 107-145.
- GRUBB P.J., 1976: A theoretical background to the conservation of ecologically distinct groups of annuals and biennials in the chalk grassland ecosystem. *Biol.Conserv.* 10, 53-76.
- HARLEY J.L. and HARLEY E.L., 1986: A checklist of mycorrhizas in the British Flora. *New Phytol.* 105 (suppl), 1-102.
- HARPER J.L., 1977: Plant population dynamics. Acad.Press, London. 892 pp.
- HEGI G., 1908 ff.: Flora von Mitteleuropa. München. 7 vols.
- HESS H.E., LANDOLT E. and HIRZEL R., 1976-1980. Flora der Schweiz und angrenzender Gebiete. (2nd ed.). Birkhäuser, Basel. 3 vols. 2690 p.
- HIBBS D.E. and FISCHER B.C., 1979: Sexual and vegetative reproduction of striped maple (*Acer pennsylvanicum* L.). *Bull.Torr.Bot.Club* 106, 222-227.
- HILLIER S.H., 1984: A quantitative study of gap recolonization in two contrasted limestone grasslands. Ph.D. Thesis, Univ. Sheffield, UK. 138 pp.
- HOWE C.D. and SNAYDON R.W., 1986: Factors affecting the performance of seedlings and ramets of invading grasses in an established ryegrass sward. *J.Appl.Ecol.* 23, 139-146.
- HUSTON M., 1979: A general hypothesis of species diversity. *Am.Nat.* 113, 81-101.
- HUTCHINSON G.E., 1941: Ecological aspects of successions in natural populations. *Am.Nat.* 65, 406-418.
- HUTCHINSON G.E., 1961: The paradox of the plankton. *Am.Nat.* 95, 137-145.
- JOHNSON C.D. and THOMAS A.G., 1978: Recruitment and survival of seedlings of a perennial *Hieracium* species in a patchy environment. *Can.J.Bot.* 56, 572-580.
- KEDDY P.A., 1981: Experimental demography of the sand-dune annual, *Cakile edentula*, growing along an environmental gradient in Nova Scotia. *J.Ecol.* 69, 615-630.
- KELLY D., 1989: Demography of short-lived plants in chalk grassland. II. Control of mortality and fecundity. *J.Ecol.* 77, 770-784.

- KRÜSI B., 1981: Phenological methods in permanent plot research. The indicator value of phenological phenomena - A study in limestone grassland in northern Switzerland. Veröff. Geobot. Inst. ETH, Stiftung Rübel, Zürich 75, 115 pp.
- LANDOLT E., 1977: Ökologische Zeigerwerte zur Schweizer Flora. Veröff. Geobot. Inst. ETH, Stiftung Rübel, Zürich 64, 208 pp.
- LEUTERT A., 1983: Einfluss der Feldmaus, *Microtus arvalis* (Pall.), auf die floristische Zusammensetzung von Wiesen-Ökosystemen. Veröff. Geobot. Inst. ETH, Stiftung Rübel, Zürich 79, 126 pp.
- LEVIN S.A., 1974: Dispersion and population interactions. Am. Nat. 108, 207-228.
- LÜDI W. and ZOLLER H., 1949: Einige Beobachtungen über die Dürreschäden des Sommers 1947 in der Nordschweiz und am schweizerischen Jurarand. Ber. Geobot. Inst. Rübel, Zürich 20, 69-85.
- MARTI R., (in prep.): Experimentelle Untersuchungen zur Koexistenz von seltenen mit häufigen mehrjährigen Pflanzenarten in Trespen-Halbtrockenrasen (Mesobrometen) bei Schaffhausen.
- MAYER H., 1980: Waldbau auf soziologisch-ökologischer Grundlage. (2nd ed.). Fischer, Stuttgart. 483 p.
- MCCONNAUGHAY K.D.M. and BAZZAZ F.A., 1987: The relationship between gap size and performance of several colonizing annuals. Ecology 68, 411-416.
- MERZ B., 1986: Vegetationszusammensetzung von Trespen-Halbtrockenrasen nach 10-jähriger Brache, Mahd- und Brandbewirtschaftung bei Merishausen (Kt. Schaffhausen). Diplomarbeit. Geobot. Inst. ETH, Stiftung Rübel, Zürich. 114 pp. (polycopy)
- MILES J., 1972: Experimental establishment of seedlings on a southern English heath. J. Ecol. 60, 225-234.
- MILES J., 1973a: Early mortality and survival of self-sown seedlings in Glenfeshie, Inverness-shire. J. Ecol. 61, 93-98.
- MILES J., 1973b: Natural recolonization of experimentally bared soil in Callunetum in north-east Scotland. J. Ecol. 61, 399-412.
- MILES J., 1974: Effects of experimental interference with stand structure on establishment of seedlings in *Callunetum*. J. Ecol. 62, 675-687.
- MITCHLEY J. and GRUBB P.J., 1986: Control of relative abundance of perennials in chalk grassland in southern England. J. Ecol. 74, 1139-1166.
- MORRIS W.F. and WOOD D.M., 1989: The role of lupine in succession on Mount St. Helens: facilitation or inhibition. Ecology 70, 697-703.
- NEWELL S.J., SOLBRIG O.T. and KINCAID D.T., 1981: Studies on the population of the genus *Viola*. III. The demography of *Viola blanda* and *Viola pallens*. J. Ecol. 69, 997-1016.
- NIERING W.A., WHITTAKER R.H. and LOWE C.H., 1963: The saguaro: a population in relation to environment. Science 142, 15-23.
- PARRISH J.A.D. and BAZZAZ F.A., 1985: Ontogenic shifts in old-field annuals. Ecology 66, 1296-1302.
- PEMADASA M.A. and LOVELL P.H., 1974: Interference in populations of some dune annuals. J. Ecol. 62, 855-868.
- PICKETT S.T.A., 1980: Non-equilibrium coexistence of plants. Bull. Torr. Bot. Club 107, 238-248.
- PUTWAIN P.D. and HARPER J.L., 1970: Studies in the dynamics of plant populations. III. The influence of associated species on populations of *Rumex acetosa* and *Rumex acetosella* in grassland. J. Ecol. 58, 251-262.
- READ D.J., FRANCIS R. and FINLAY R.D., 1985: Mycorrhizal mycelia and nutrient cycling in plant communities. In: FITTER A., ATKINSON D., READ D.J. and USHER M.B. (eds.), Ecological interactions in soil. Blackwell, Oxford. 193-217.
- ROBOCKER W.C., CURTIS J.C. and AHLGREN H.L., 1953: Some factors affecting emergence

- and establishment of native grass seedlings in Wisconsin. *Ecology* 34, 194-198.
- ROSS M.A. and HARPER J.L., 1972: Occupation of biological space during seedling establishment. *J.Ecol.* 60, 77-88.
- RUSCH G., 1988: reproductive regeneration in grazed and ungrazed limestone grassland communities on Öland. Preliminary results. *Acta phytogeogr. suec.* 76, 113-124.
- RYSER P., 1984: Samenvorrat im Boden und Mikrostandorte für das Aufwachsen neuer Pflanzen in Wiesen des Randens bei Merishausen. Diplomarbeit. Geobot.Inst.ETH,Stiftung Rübel,Zürich . 79 pp. (polycopy)
- SCHÄPPI B., 1989: Kleinräumiger Bodenchemismus und die Verteilung ausgewählter Pflanzenarten in Trespen-Halbtrockenrasen. Diplomarbeit. Geobot.Inst.ETH,Stiftung Rübel,Zürich. 77 pp. (polycopy)
- SCHENKEVELD A.J. and VERKAAR H.J., 1984: On the ecology of short-lived forbs in chalk grasslands. Ph.D Thesis, RU Utrecht. 180 pp.
- SERNANDER R., 1936: Granskär och Fiby urskog. En studie över stormluckornas och Marbuskarnas betydelse i den Svenska granskogens regeneration. *Acta phytogeogr. suec* 8, 232 pp.
- SHARITZ R.R. and MCCORMICK J.F., 1973: Population dynamics of two competing annual species. *Ecology* 54, 723-740.
- SHAW R.G. and ANTONOVICS J., 1986: Density-dependence in *Salvia lyrata*, a herbaceous perennial: the effects of experimental alteration of seed densities. *J.Ecol.* 74, 797-813.
- SHMIDA S. and ELLNER S.P., 1984: Coexistence of plant species with similar niches. *Vegetatio* 58, 29-55.
- SILVERTOWN J., 1981: Micro-spatial heterogeneity and seedling demography in species rich grassland. *New Phytol.* 88, 117-128.
- SILVERTOWN J. and TREMLETT M., 1989: Interactive effects of disturbance and shade upon colonization of grassland: an experiment with *Anthriscus silvestris* (L.) Hoffm., *Conium maculatum* L., *Daucus carota* L. and *Heracleum sphondylium* L. *Functional Ecology* 3, 229-235.
- SILVERTOWN J.W. and WILKIN F.R., 1983: An experimental test of the role of micro-spatial heterogeneity in the co-existence of congeneric plants. *Biol.J.Linn.Soc.* 19, 1-8.
- SIMAK M., 1951: Untersuchungen über den natürlichen Baumartenwechsel in schweizerischen Plenterwälder. *Mitt.schweiz.Anst.forstl.Vers.wes.* 27, 406-468.
- SOUSA W.P., 1984: The role of disturbance in natural communities. *A. Rev.Ecol.Syst.* 15, 353-391.
- STERGIOS B.G., 1976: Achene production, dispersal, seed germination, and seedling establishment of *Hieracium aurantiacum* in an abandoned field community. *Can.J.Bot.* 54, 1189-1197.
- TILMAN D., 1982: Resource competition and community structure. Univ.Press, Princeton. 296 pp.
- TILMAN D., 1988: Plant strategies and the dynamics and structure of plant communities. Univ. Press, Princeton. 360 pp.
- TURKINGTON R., CAHN A., VARDY A. and HARPER J.L., 1979: The growth, distribution, and neighbour relationships of *Trifolium repens* in a permanent pasture. III. The establishment and growth of *Trifolium repens* in natural and perturbed sites. *J.Ecol.* 67, 231-243.
- TURNER R.M., ALCORN S.M., OLIN G. and BOOTH J.A., 1966: The influence of shade, soil and water on saguaro establishment. *Bot.Gazette* 127, 95-102.
- TUTIN T.G., HEYWOOD V.H., BURGESS N.A., MOORE D.M., VALENTINE D.H., WALTERS S.M. and WEBB D.A., 1964: *Flora Europaea*. Univ.Press, Cambridge. 5 volumes + index.
- UHL C., CLARK K. and MAQUIRINO P., 1988: Vegetation dynamics in Amazonian treefall gaps. *Ecology* 69, 751-763.
- VAN DER MAAREL E., 1988: Species diversity in plant communities in relation to structure

- and dynamics. In: DURING H.J., WERGER M.J.A. and WILLEMS J.H. (eds.), Diversity and pattern in plant communities. SPB Acad.Publishing, The Hague. 1-14.
- VAN TOOREN B.F., 1990: Recruitment and establishment of short-lived flowering plant species in dutch chalk grasslands. In: HILLIER S.H., WALTON D.W.H. and WELLS D.A. (eds.), Calcareous grasslands - ecology and management. Bluntisham books, Bluntisham. 100-105.
- VAN TOOREN B.F., DURING H.J. and LENSINK M.J.G., 1985: The influence of the bryophyte layer on the microclimate in chalk grasslands. *Abstr.Bot.* 9 (suppl. 2), 219-230.
- VON GUNTEN B., 1987: Experimentelle Untersuchungen zu Mikroklima und Keimlingsentwicklung in Trespen-Halbtrockenrasen (bei Merishausen). Diplomarbeit. Geobot.Inst. ETH, Stiftung Rübel, Zürich. 97 pp. (polycopy)
- WATKINSON A.R., 1986: Plant population dynamics. In: CRAWLEY M. (ed.), Plant Ecology. Blackwell, Oxford. 137-184.
- WHITE P., 1979: Pattern, process, and natural disturbance in vegetation. *Bot.Review* 45, 229-299.
- WHITTAKER R.H. and LEVIN S.A., 1977: The role of mosaic phenomena in natural communities. *Theoretical population biology* 12, 117-139.
- WILKINSON L., 1987: SYSTAT. The System for statistics. Evanston IL. SYSTAT, Inc.
- WITTEWER F., 1983: Untersuchungen der Wuchsform verschiedener Pflanzenarten in Abhängigkeit von der Bewirtschaftung. Diplomarbeit. Geobot.Inst.ETH,Stiftung Rübel, Zürich. 86 pp. (polycopy)
- WOODS K.D., 1984: Pattern of tree replacement: canopy effects on understory pattern in hemlock-northern hardwood forests. *Vegetatio* 56, 87-107.
- ZAR J.H., 1984: Biostatistical analysis. (2nd ed.) Prentice Hall, Englewood Cliffs, N.J. 718 pp.
- ZOLLER H., 1954a: Die Typen der *Bromus erectus*-Wiesen des Schweizer Juras. *Beitr. Geobot. Landesaufn.Schweiz* 33, 309 pp.
- ZOLLER H., 1954b: Die Arten der *Bromus erectus*-Wiesen des Schweizer Juras. *Veröff. Geobot.Inst.Rübel,Zürich* 28, 283 pp.

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APPENDIX

Tables 18 to 29:

Significance levels of differences in survivorship and in death rates between the microsites.

Table 18. Significance levels of differences between survivorship of *Arabis hirsuta* in different microsites.

** = $p < 0.01$, * = $p < 0.05$, + = $p < 0.10$, - = non-significant, *Bro* = *Bromus*, *Ono* = *Onobrychis*, *Sal* = *Salvia*

	<div> <div>gap/edge</div> <div>gap/tuft</div> <div>edge/tuft</div> </div> <div><i>Bromus</i></div>			<div> <div>gap/edge</div> <div>gap/tuft</div> <div>edge/tuft</div> </div> <div><i>Ono</i></div>			<div> <div>gap/edge</div> <div>gap/tuft</div> <div>edge/tuft</div> </div> <div><i>Bromus</i> + <i>Ono</i></div>			Salvia	gap/edge	moss covered / bare	<i>Bro</i> gap / <i>Ono</i> gap	<i>Bro</i> edge / <i>Ono</i> edge	<i>Bro</i> tuft / <i>Ono</i> tuft	<i>Bro</i> gap / <i>Sal</i> gap	<i>Bro</i> edge / <i>Sal</i> edge	<i>Ono</i> gap / <i>Sal</i> gap	<i>Ono</i> edge / <i>Sal</i> edge	<i>Bromus</i> gap / bare	<i>Ono</i> gap / bare	<i>Salvia</i> gap / bare	<i>Bromus</i> edge / moss	<i>Ono</i> edge / moss	<i>Salvia</i> edge / moss	<i>Bromus</i> tuft / moss	<i>Ono</i> tuft / moss
emergence: autumn 1986																											
Nov. 86	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	**	-	-	-	-	-	+
Apr. 87 (1)	*	-	-	+	+	-	**	*	-	-	-	-	-	-	-	*	-	-	+	-	*	-	-	+	-	-	+
Apr. 87 (2)	*	-	-	+	+	-	*	*	-	-	-	-	-	-	-	-	+	-	+	-	-	-	-	-	-	-	+
June 87	+	-	-	+	+	-	*	*	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	-	-	-	+
July 87	+	-	-	+	+	-	*	*	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	-	-	-	+
Aug. 87	+	-	-	+	+	-	*	*	-	-	-	-	-	-	-	-	-	+	-	-	+	-	-	-	-	-	+
Sep. 87	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+
Oct. 87	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+
Apr. 88	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+
May 88	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+
July 88 (1)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+
July 88 (2)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	+
emergence: autumn 1987																											
Oct. 87	*	-	-	*	*	+	***	-	-	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Apr. 88	*	-	-	*	*	-	***	-	-	*	*	*	-	-	-	*	-	-	-	-	**	**	**	-	-	*	*
May 88	*	+	-	*	*	-	****	-	-	*	*	*	-	-	-	+	-	-	-	-	**	*	**	-	-	+	*
July 88 (1)	*	+	-	*	*	+	****	-	-	*	*	-	-	-	-	+	+	-	-	-	**	*	**	-	-	+	*
July 88 (2)	*	+	-	*	*	+	****	-	-	*	*	-	-	-	-	-	-	-	-	-	**	*	**	-	-	+	**
Aug. 88	*	+	-	*	*	-	****	-	-	*	+	-	-	*	-	-	-	-	-	-	-	+	-	-	-	-	**
Oct. 88	*	+	-	*	*	-	****	-	-	+	+	-	-	*	-	-	-	-	-	-	-	-	+	+	-	-	**
Apr. 89	**	-	-	*	*	-	****	-	-	-	+	-	-	*	-	-	-	-	-	-	-	-	+	*	-	-	**

Table 19. Significance levels of differences between death rates of *Arabis hirsuta* in different microsites.

** = $p < 0.01$, * = $p < 0.05$, + = $p < 0.10$, - = non-significant, *Bro* = *Bromus*, *Ono* = *Onobrychis*, *Sal* = *Salvia*

	<i>Bromus</i> gap/edge gap/tuft edge/tuft	<i>Ono</i> gap/edge gap/tuft edge/tuft	<i>Bromus</i> + <i>Ono</i> gap/edge gap/tuft edge/tuft	<i>Salvia</i> gap/edge	moss covered / bare	<i>Bro gap / Ono gap</i> <i>Bro edge / Ono edge</i> <i>Bro tuft / Ono tuft</i>	<i>Bro gap / Sal gap</i> <i>Bro edge / Sal edge</i>	<i>Ono gap / Sal gap</i> <i>Ono edge / Sal edge</i>	<i>Bromus gap / bare</i> <i>Ono gap / bare</i> <i>Salvia gap / bare</i>	<i>Bromus edge / moss</i> <i>Ono edge / moss</i> <i>Salvia edge / moss</i>	<i>Bromus tuft / moss</i> <i>Ono tuft / moss</i>
emergence: autumn 1986											
Okt. 86 - Nov. 86	-	-	-	-	-	-	+	-	-	-	-
Nov. 86 - Apr. 87	*	-	-	-	-	-	-	-	-	**	-
Apr 87 - June 87	-	-	-	-	-	+	-	-	-	-	-
emergence: autumn 1987											
Aug. 87 - Sep. 87	-	-	-	-	-	-	+	-	+	+	-
Sep. 87 - Oct. 87	*	-	* *	*	-	-	-	-	-	-	-
Oct. 87 - Apr. 88	* +	* *	** **	*	*	*	-	*	**	** *	*
Apr. 88 - May 88	+ +	-	* *	+	-	-	-	-	+	-	-
May 88 - July 88	* +	-	-	-	+	*	+	*	-	*	-
July 88 - July 88	-	-	-	-	-	-	*	+	-	-	-
July 88 - Aug. 88	-	-	-	+	-	*	*	+	-	+	*
Aug. 88 - Oct. 88	-	-	-	-	-	-	-	-	+	*	*
Oct. 88 - Apr. 89	-	-	-	*	+	-	-	-	-	-	-

Table 22. Significance levels of differences between survivorship of *Medicago lupulina* in different microsites.

** = $p < 0.01$, * = $p < 0.05$, + = $p < 0.10$, - = non-significant, *Bro* = *Bromus*, *Ono* = *Onobrychis*, *Sal* = *Salvia*

	<div> <div>gap/edge</div> <div>gap/tuft</div> <div>edge/tuft</div> </div> <div><i>Bromus</i></div>			<div> <div>gap/edge</div> <div>gap/tuft</div> <div>edge/tuft</div> </div> <div><i>Ono</i></div>			<div> <div>gap/edge</div> <div>gap/tuft</div> <div>edge/tuft</div> </div> <div><i>Bromus</i> + <i>Ono</i></div>			<div>gap/edge</div> <div><i>Salvia</i></div>	<div>gap/edge</div> <div>moss covered / bare</div>	<div>gap/edge</div> <div><i>Bro</i> gap / <i>Ono</i> gap</div>	<div>gap/edge</div> <div><i>Bro</i> edge / <i>Ono</i> edge</div>	<div>gap/edge</div> <div><i>Bro</i> tuft / <i>Ono</i> tuft</div>	<div>gap/edge</div> <div><i>Bro</i> gap / <i>Sal</i> gap</div>	<div>gap/edge</div> <div><i>Bro</i> edge / <i>Sal</i> edge</div>	<div>gap/edge</div> <div><i>Ono</i> gap / <i>Sal</i> gap</div>	<div>gap/edge</div> <div><i>Ono</i> edge / <i>Sal</i> edge</div>	<div>gap/edge</div> <div><i>Bromus</i> gap / bare</div>	<div>gap/edge</div> <div><i>Ono</i> gap / bare</div>	<div>gap/edge</div> <div><i>Salvia</i> gap / bare</div>	<div>gap/edge</div> <div><i>Bromus</i> edge / moss</div>	<div>gap/edge</div> <div><i>Ono</i> edge / moss</div>	<div>gap/edge</div> <div><i>Salvia</i> edge / moss</div>	<div>gap/edge</div> <div><i>Bromus</i> tuft / moss</div>	<div>gap/edge</div> <div><i>Ono</i> tuft / moss</div>
emergence: spring 1987																										
June 87	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	+	-	*	-
Aug. 87	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	*	-
Sep. 87	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	*	-
Nov. 87	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	*	-
Apr. 88	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	*	-	*	-
emergence: spring 1988																										
July 88 (1)	-	-	-	+	-	-	*	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
July 88 (2)	-	-	-	*	-	-	*	-	-	-	-	-	-	+	-	-	-	-	-	-	-	-	-	-	*	-
Sep. 88	-	-	-	*	+	-	*	+	-	-	-	-	*	+	-	-	-	-	-	-	-	-	-	-	*	-

Table 23. Significance levels of differences between death rates of *Medicago lupulina* in different microsites.

** = $p < 0.01$, * = $p < 0.05$, + = $p < 0.10$, - = non-significant, *Bro* = *Bromus*, *Ono* = *Onobrychis*, *Sal* = *Salvia*

	<div><div><div>gap/edge</div><div>gap/tuft</div><div>edge/tuft</div></div><div><i>Bromus</i></div></div>			<div><div><div>gap/edge</div><div>gap/tuft</div><div>edge/tuft</div></div><div><i>Ono</i></div></div>			<div><div><div>gap/edge</div><div>gap/tuft</div><div>edge/tuft</div></div><div><i>Bromus</i> + <i>Ono</i></div></div>			<div><div>gap/edge</div><div><i>Salvia</i></div></div>	<div>moss covered / bare</div>	<div><i>Bro</i> gap / <i>Ono</i> gap</div>	<div><i>Bro</i> edge / <i>Ono</i> edge</div>	<div><i>Bro</i> tuft / <i>Ono</i> tuft</div>	<div><i>Bro</i> gap / <i>Sal</i> gap</div>	<div><i>Bro</i> edge / <i>Sal</i> edge</div>	<div><i>Ono</i> gap / <i>Sal</i> gap</div>	<div><i>Ono</i> edge / <i>Sal</i> edge</div>	<div><i>Bromus</i> gap / bare</div>	<div><i>Ono</i> gap / bare</div>	<div><i>Salvia</i> gap / bare</div>	<div><i>Bromus</i> edge / moss</div>	<div><i>Ono</i> edge / moss</div>	<div><i>Salvia</i> edge / moss</div>	<div><i>Bromus</i> tuft / moss</div>	<div><i>Ono</i> tuft / moss</div>
emergence: spring 1987																										
Apr. 87 - June 87	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	-	+	-	*	-		
June 87 - Aug 87	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	+	-	-		
Oct. 87 - Apr. 88	-	-	-	-	-	-	-	-	-	-	-	*	-	-	-	-	+	-	-	*	-	-	*	-		
emergence: spring 1988																										
May 88 - July 88	-	-	-	+	-	-	*	+	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-		
July 88 - July 88	-	-	-	-	-	-	*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	*	-	-		
July 88 - Sep. 88	-	-	-	+	-	-	+	-	-	-	-	-	-	-	*	+	-	-	*	-	*	-	-	-		

Table 24. Significance levels of differences between survivorship of *Plantago lanceolata* in different microsites.

** = $p < 0.01$, * = $p < 0.05$, + = $p < 0.10$, - = non-significant, *Bro* = *Bromus*, *Ono* = *Onobrychis*, *Sal* = *Salvia*

	<i>Bromus</i> gap/edge gap/tuft edge/tuft	<i>Ono</i> gap/edge gap/tuft edge/tuft	<i>Bromus</i> + <i>Ono</i> gap/edge gap/tuft edge/tuft	<i>Salvia</i> gap/edge	moss covered / bare	<i>Bro</i> gap / <i>Ono</i> gap <i>Bro</i> edge / <i>Ono</i> edge <i>Bro</i> tuft / <i>Ono</i> tuft	<i>Bro</i> gap / <i>Sal</i> gap <i>Bro</i> edge / <i>Sal</i> edge	<i>Ono</i> gap / <i>Sal</i> gap <i>Ono</i> edge / <i>Sal</i> edge	<i>Bromus</i> gap / bare <i>Ono</i> gap / bare <i>Salvia</i> gap / bare	<i>Bromus</i> edge / moss <i>Ono</i> edge / moss <i>Salvia</i> edge / moss	<i>Bromus</i> tuft / moss <i>Ono</i> tuft / moss
emergence: spring 1986											
Aug. 87	-	-	-	-	-	+	-	-	-	-	-
Nov. 87	-	-	-	-	-	-	+	-	-	+	-
Apr. 88	-	-	-	-	-	-	-	-	-	+	-
emergence: autumn 1987											
Nov. 87	-	-	-	-	-	-	-	-	-	+	-
Apr. 88	+	-	+	*	-	-	-	-	-	+	-
June 88	+	-	+	*	-	-	-	-	-	+	-
Sep. 88	-	-	-	+	-	-	-	-	-	-	-
emergence: spring 1988											
July 88	-	-	+	-	-	*	-	-	+	-	-
Sep. 88	-	-	+	*	-	+	-	-	-	-	-

Table 25. Significance levels of differences between death rates of *Plantago lanceolata* in different microsites.

** = $p < 0.01$, * = $p < 0.05$, + = $p < 0.10$, - = non-significant, *Bro* = *Bromus*, *Ono* = *Onobrychis*, *Sal* = *Salvia*

	<i>Bromus</i> gap/edge gap/tuft edge/tuft	<i>Ono</i> gap/edge gap/tuft edge/tuft	<i>Bromus</i> + <i>Ono</i> gap/edge gap/tuft edge/tuft	<i>Salvia</i> gap/edge	moss covered / bare	<i>Bro</i> gap / <i>Ono</i> gap <i>Bro</i> edge / <i>Ono</i> edge <i>Bro</i> tuft / <i>Ono</i> tuft	<i>Bro</i> gap / <i>Sal</i> gap <i>Bro</i> edge / <i>Sal</i> edge	<i>Ono</i> gap / <i>Sal</i> gap <i>Ono</i> edge / <i>Sal</i> edge	<i>Bromus</i> gap / bare <i>Ono</i> gap / bare <i>Salvia</i> gap / bare	<i>Bromus</i> edge / moss <i>Ono</i> edge / moss <i>Salvia</i> edge / moss	<i>Bromus</i> tuft / moss <i>Ono</i> tuft / moss
emergence: spring 1987											
June 87 - Aug. 87	-	-	-	-	-	+	-	+	-	-	-
Nov. 87 - Apr. 88	-	-	-	-	-	+	-	-	-	-	-
emergence: autumn 1987											
Nov. 87 - Apr. 88	+	-	+	*	-	-	-	-	-	-	-
emergence: spring 1988											
June 88 - July 88	-	-	-	-	-	*	+	-	*	-	-
July 88 - Sep. 88	-	-	+	+	-	+	+	-	-	-	-

Table 26. Significance levels of differences between survivorship of *Primula veris* in different microsites.

** = $p < 0.01$, * = $p < 0.05$, + = $p < 0.10$, - = non-significant, *Bro* = *Bromus*, *Ono* = *Onobrychis*, *Sal* = *Salvia*

	<i>Bromus</i> gap/edge gap/tuft edge/tuft	<i>Ono</i> gap/edge gap/tuft edge/tuft	<i>Bromus</i> + <i>Ono</i> gap/edge gap/tuft edge/tuft	<i>Salvia</i> gap/edge	moss covered / bare	<i>Bro</i> gap / <i>Ono</i> gap	<i>Bro</i> edge / <i>Ono</i> edge	<i>Bro</i> tuft / <i>Ono</i> tuft	<i>Bro</i> gap / <i>Sal</i> gap	<i>Bro</i> edge / <i>Sal</i> edge	<i>Ono</i> gap / <i>Sal</i> gap	<i>Ono</i> edge / <i>Sal</i> edge	<i>Bromus</i> gap / bare	<i>Ono</i> gap / bare	<i>Salvia</i> gap / bare	<i>Bromus</i> edge / moss	<i>Ono</i> edge / moss	<i>Salvia</i> edge / moss	<i>Bromus</i> tuft / moss	<i>Ono</i> tuft / moss
emergence: spring 1988																				
July 88 (1)	-	-	-	-	+	-	-	-	-	-	-	+	-	-	-	-	-	*	-	-
July 88 (2)	+	+	-	-	*	-	-	-	-	+	-	*	-	-	-	-	-	**	-	-
Aug. 88	-	+	-	-	+	*	*	-	*	*	-	*	-	-	-	-	+	**	-	-
Oct. 88	-	+	-	-	*	*	*	-	*	**	-	**	-	-	-	-	*	**	-	-
May 89	-	+	-	*	+	*	*	-	*	+	-	-	-	-	-	-	*	+	+	+

Table 27. Significance levels of differences between death rates of *Primula veris* in different microsites.

** = $p < 0.01$, * = $p < 0.05$, + = $p < 0.10$, - = non-significant, *Bro* = *Bromus*, *Ono* = *Onobrychis*, *Sal* = *Salvia*

	<i>Bromus</i> gap/edge gap/tuft edge/tuft	<i>Ono</i> gap/edge gap/tuft edge/tuft	<i>Bromus</i> + <i>Ono</i> gap/edge gap/tuft edge/tuft	<i>Salvia</i> gap/edge	moss covered / bare	<i>Bro</i> gap / <i>Ono</i> gap	<i>Bro</i> edge / <i>Ono</i> edge	<i>Bro</i> tuft / <i>Ono</i> tuft	<i>Bro</i> gap / <i>Sal</i> gap	<i>Bro</i> edge / <i>Sal</i> edge	<i>Ono</i> gap / <i>Sal</i> gap	<i>Ono</i> edge / <i>Sal</i> edge	<i>Bromus</i> gap / bare	<i>Ono</i> gap / bare	<i>Salvia</i> gap / bare	<i>Bromus</i> edge / moss	<i>Ono</i> edge / moss	<i>Salvia</i> edge / moss	<i>Bromus</i> tuft / moss	<i>Ono</i> tuft / moss
emergence: spring 1988																				
May 88 - July 88	-	-	-	-	+	-	-	-	-	-	-	-	-	-	*	-	-	-	-	-
July 88 - July 88	-	-	-	-	+	-	-	-	-	+	-	*	-	-	-	-	-	**	-	-
July 88 - Aug. 88	-	+	-	-	+	*	*	-	-	*	-	*	-	-	-	-	-	*	-	-
Oct. 88 - May 89	-	-	-	-	+	+	-	-	-	-	-	-	-	-	-	+	-	*	-	-

Table 28. Significance levels of differences between survivorship of *Sanguisorba minor* in different microsites.

** = $p < 0.01$, * = $p < 0.05$, + = $p < 0.10$, - = non-significant, *Bro* = *Bromus*, *Ono* = *Onobrychis*, *Sal* = *Salvia*

	<i>Bromus</i> gap/edge gap/tuft edge/tuft	<i>Ono</i> gap/edge gap/tuft edge/tuft	<i>Bromus</i> + <i>Ono</i> gap/edge gap/tuft edge/tuft	<i>Salvia</i> gap/edge moss covered / bare	<i>Bro</i> gap / <i>Ono</i> gap <i>Bro</i> edge / <i>Ono</i> edge <i>Bro</i> tuft / <i>Ono</i> tuft	<i>Bro</i> gap / <i>Sal</i> gap <i>Bro</i> edge / <i>Sal</i> edge	<i>Ono</i> gap / <i>Sal</i> gap <i>Ono</i> edge / <i>Sal</i> edge	<i>Bromus</i> gap / bare <i>Ono</i> gap / bare <i>Salvia</i> gap / bare	<i>Bromus</i> edge / moss <i>Ono</i> edge / moss <i>Salvia</i> edge / moss	<i>Bromus</i> tuft / moss <i>Ono</i> tuft / moss
emergence: spring 1987 Sep. 88	-	-	-	-	+	-	-	-	+	-

Tab. 29. Significance levels of differences between death rates of *Sanguisorba minor* in different microsites.

** = $p < 0.01$, * = $p < 0.05$, + = $p < 0.10$, - = non-significant, *Bro* = *Bromus*, *Ono* = *Onobrychis*, *Sal* = *Salvia*

	<i>Bromus</i> gap/edge gap/tuft edge/tuft	<i>Ono</i> gap/edge gap/tuft edge/tuft	<i>Bromus</i> + <i>Ono</i> gap/edge gap/tuft edge/tuft	<i>Salvia</i> gap/edge moss covered / bare	<i>Bro</i> gap / <i>Ono</i> gap <i>Bro</i> edge / <i>Ono</i> edge <i>Bro</i> tuft / <i>Ono</i> tuft	<i>Bro</i> gap / <i>Sal</i> gap <i>Bro</i> edge / <i>Sal</i> edge	<i>Ono</i> gap / <i>Sal</i> gap <i>Ono</i> edge / <i>Sal</i> edge	<i>Bromus</i> gap / bare <i>Ono</i> gap / bare <i>Salvia</i> gap / bare	<i>Bromus</i> edge / moss <i>Ono</i> edge / moss <i>Salvia</i> edge / moss	<i>Bromus</i> tuft / moss <i>Ono</i> tuft / moss
emergence: autumn 1987 Apr. 88 - June 88	-	-	-	-	-	-	-	*	-	-
emergence: spring 1988 June 88 - July 88	-	-	-	-	-	-	+	-	-	*
July 88 - Sep. 88	-	+	-	-	*	-	**	-	**	-