Results

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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
Arabis hirsuta	264	(22.0%)	1480	(74.0%)	98%
Linum catharticum	238	(19.8%)	629	(31.5%)	0%
Medicago lupulina	146	(12.2%)	534	(26.7%)	5%
Plantago lanceolata	217	(18.1%)	1122	(56.1%)	45%
Primula veris s.l.	-		594	(29.7%)	0%
Sanguisorba minor	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.

	Bromus			*Onobrychis*			*Salvia*		Moss cover	
	gap	edge	tuft	gap	edge	tuft	gap	edge	-	+
Arabis hirsuta										
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**
Linum catharticum										
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**
Medicago lupulina										
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**
Plantago lanceolata										
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**
Primula veris										
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)

	Bromus			*Onobrychis*			*Salvia*		Moss cover	
	gap	edge	tuft	gap	edge	tuft	gap	edge	-	+
Sanguisorba minor										
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.

	Arabis hirsuta	*Linum catharticum*	*Medicago lupulina*	*Plantago lanceolata*	*Primula veris*	*Sanguisorba minor*
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).

	Arabis hirsuta		*Linum catharticum*	*Medicago lupulina*		*Plantago lanceolata*		*Primula veris* s.l.	*Sanguisorba minor*
sowing	1986	1987	1986	1986	1987	1986	1987	1987	1987
central-plant **Bromus erectus**									
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 **Onobrychis viciifolia**									
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 **Salvia pratensis**									
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)
Arabis hirsuta	Oct.-Nov. 1986	227	22.5% (Oct. 87)	3.1% (Apr. 89)
	Aug.-Oct. 1987	1389	15.1% (Oct. 88)	8.3% (Apr. 89)
Linum catharticum	Apr.-June 1987	238	46.4% (Oct. 87)	0.4% (Jun. 88)
	Apr.-May 1988 [1]	629	0.0% (Jun. 88)	
Medicago lupulina	Apr.-June 1987	143	72.7% (Sept. 87)	57.4% (Apr. 88)
	Apr.-May 1988	515	22.5% (Sep. 88)	
Plantago lanceolata	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)	
Primula veris	Apr.-May 1988	581	28.1% (Oct. 88)	23.8% (May 89)
Sanguisorba minor	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.
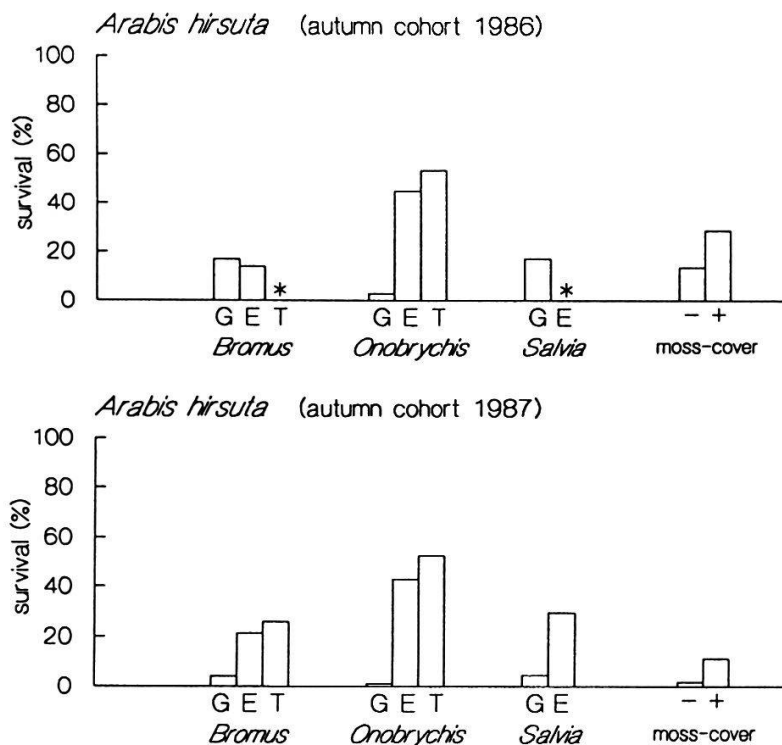
Fig. 4. Survivorship of *Arabis hirsuta* after one growth period in the different microsites. G = gap, E = edge, T = tuft, - = bare microsite, + = moss-covered microsite, * = less than 3 replicates
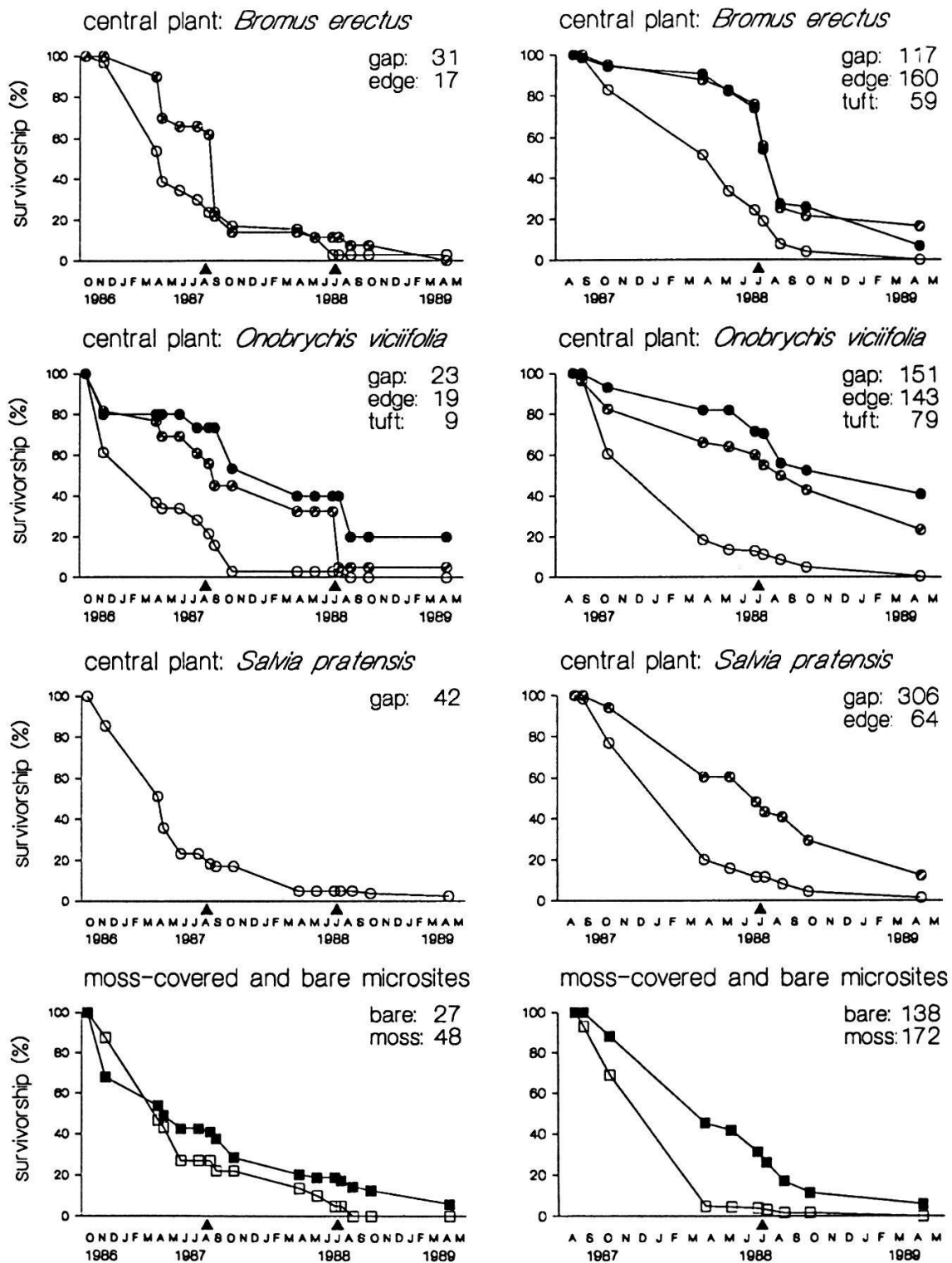
Fig. 5. Survivorship curves of *Arabis hirsuta* in different microsites. Left: Autumn cohort 1986. Right: Autumn cohort 1987. Total number of seedlings in each microsite (= 100%) in right top corner of each plot. Curves based on less than three replicates are omitted.

Microsites: o = gap, ø = 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

	Bromus erectus			*Onobrychis viciifolia*			*Salvia pratensis*			
	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).
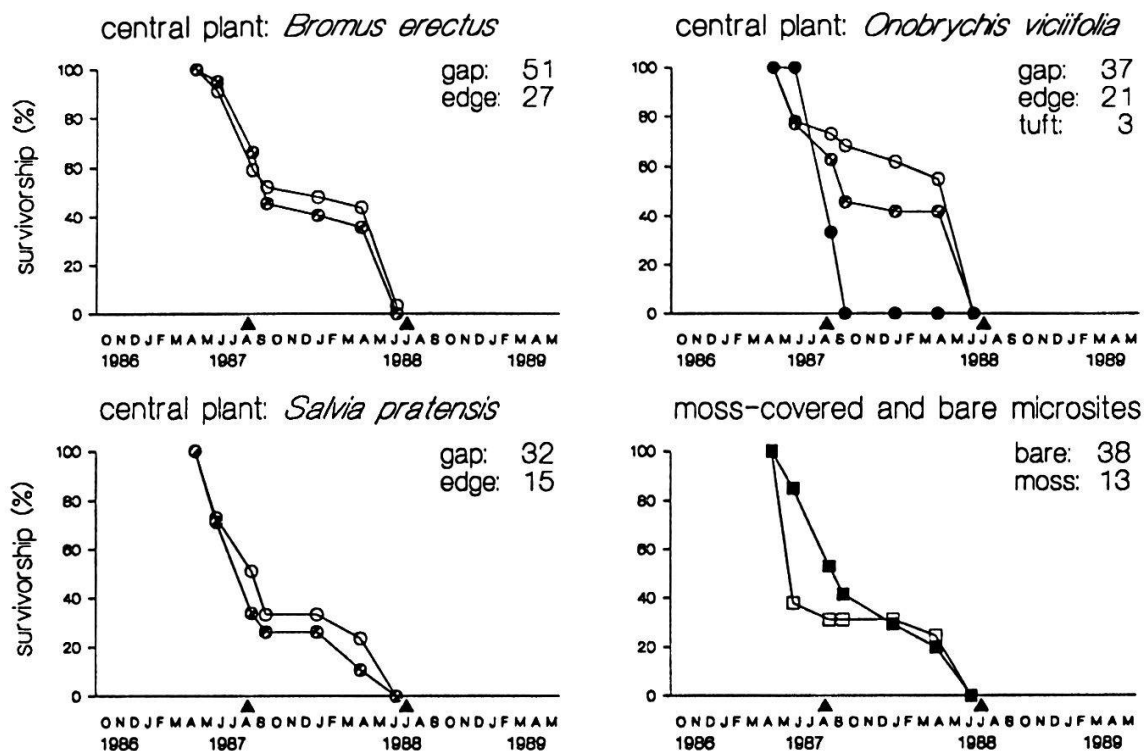
3.2.2. *Linum catharticum*

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.

Linum catharticum   (spring cohort 1987)
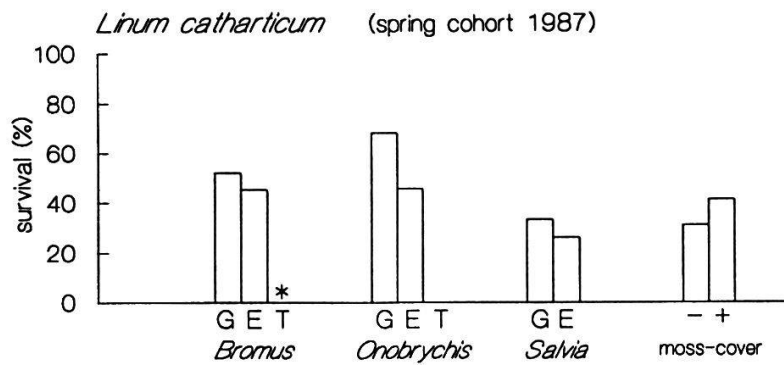
Fig. 6. Survivorship of *Linum catharticum* after one growth period in the different microsites.

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: o = gap, ⊚ = edge, ● = tuft, □ = bare, ■ = moss-covered. ▲ = time of mowing.

Table 8. Death rates of *Linum catharticum* between the recordings in different microsites (in %).
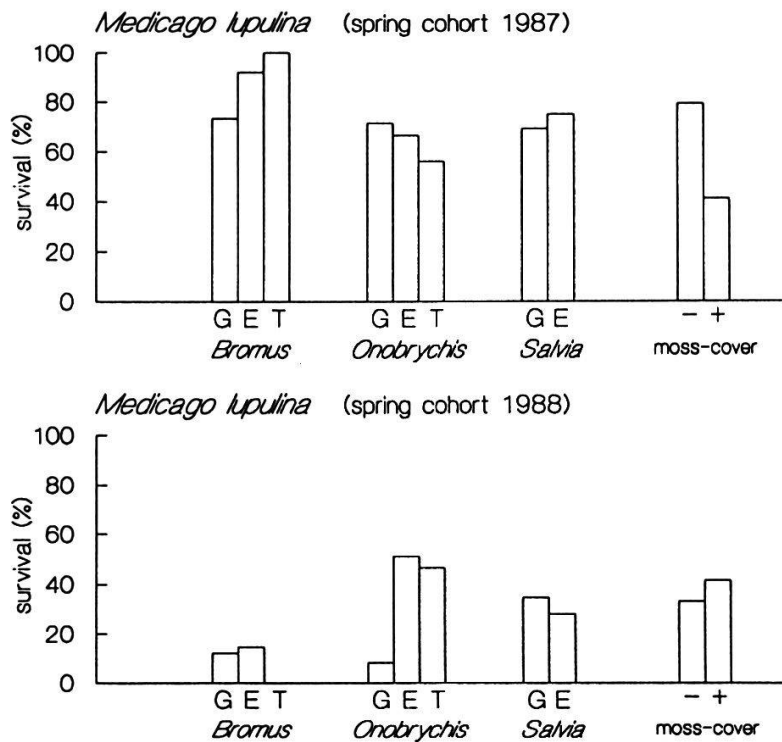- = seedlings in less than 3 replicates

	Bromus erectus			*Onobrychis viciifolia*			*Salvia pratensis*			
	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
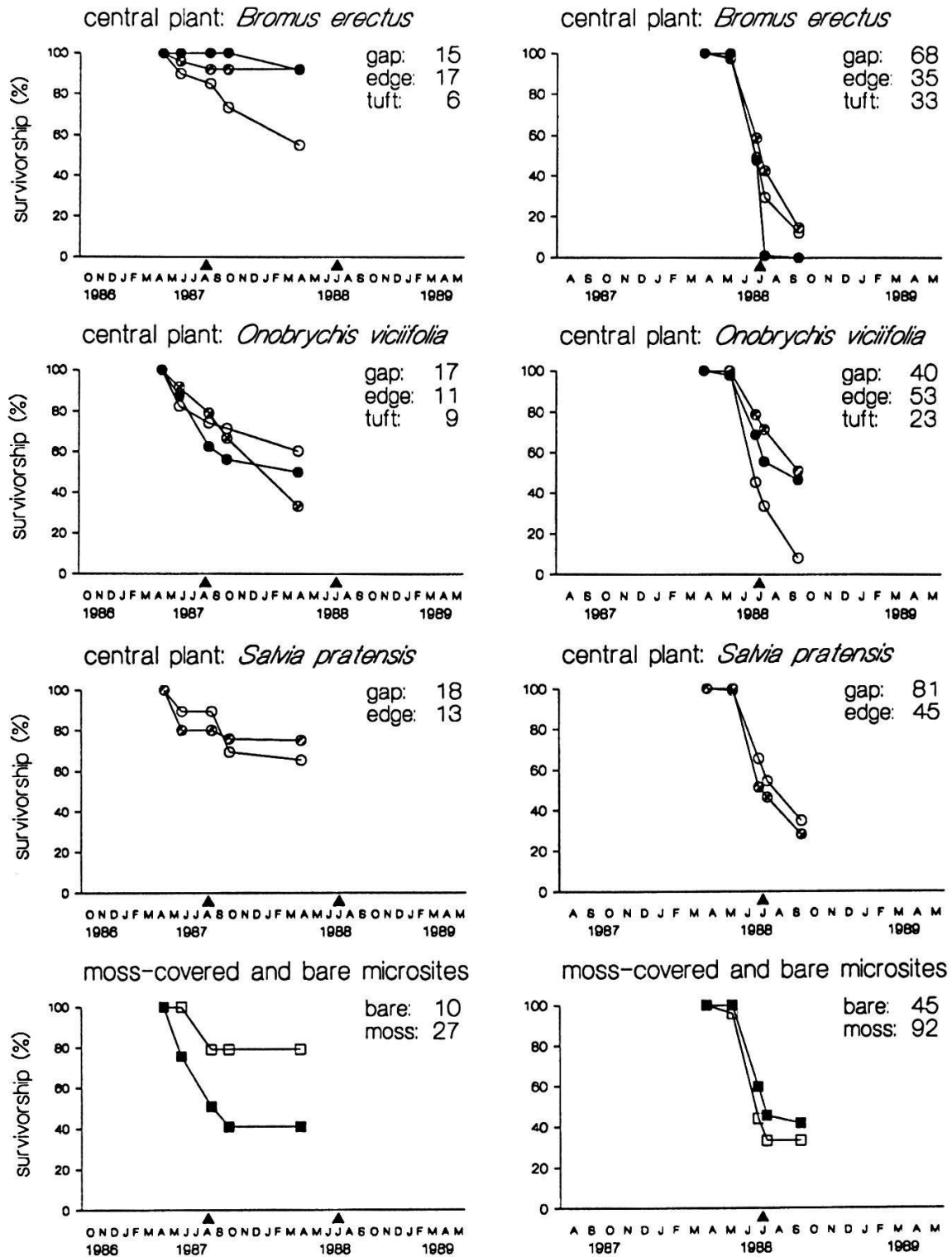
Fig. 8. Survivorship of *Medicago lupulina* after one growth period in the different micro-sites.
G = gap, E = edge, T = tuft, - = bare microsite, + = moss-covered microsite.

Table 9. Death rates of *Medicago lupulina* between the recordings in different microsites (in %).
- = seedlings in less than 3 replicates

	Bromus erectus			*Onobrychis viciifolia*			*Salvia pratensis*			
	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: o = 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.
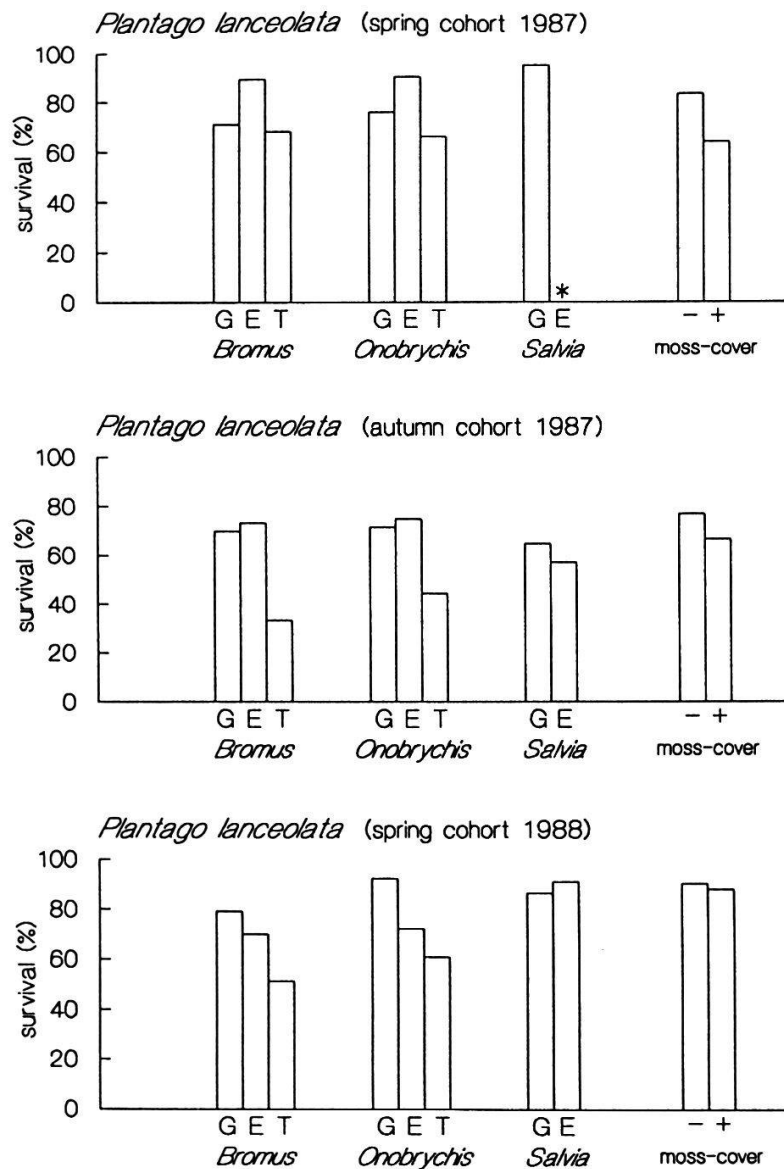
3.2.4. *Plantago lanceolata*

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

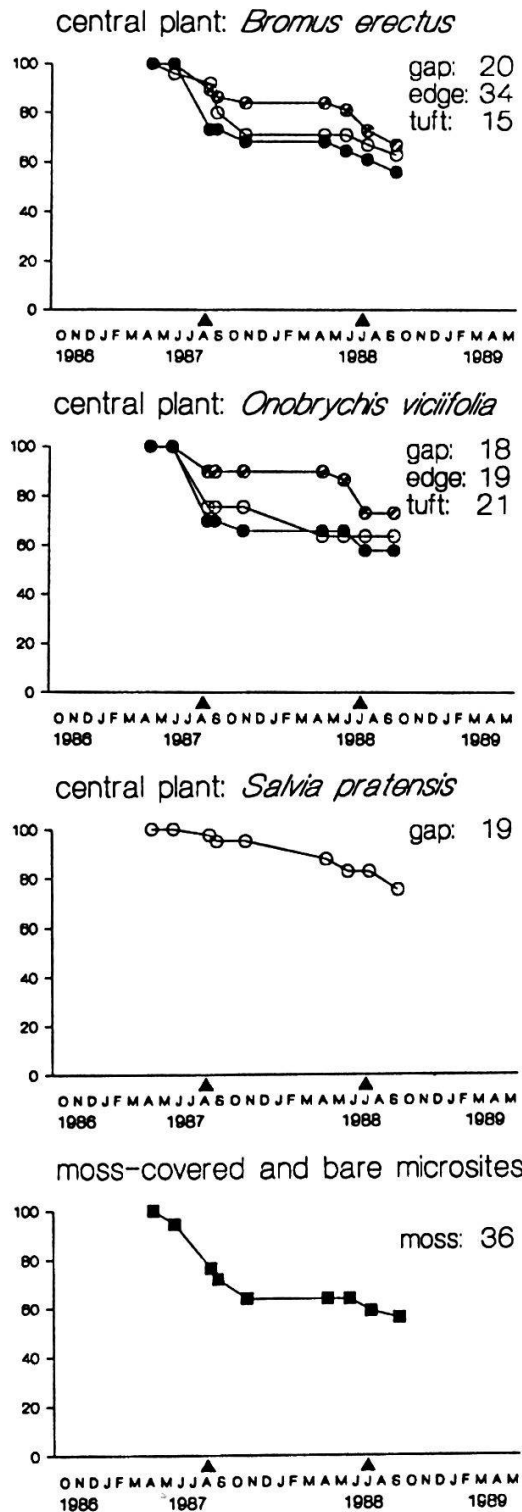**Table 10.** Death rates of *Plantago lanceolata* between the recordings in different microsites (in %).
- = seedlings in less than 3 replicates

	Bromus erectus			*Onobrychis viciifolia*			*Salvia pratensis*			
	gap	edge	tuft	gap	edge	tuft	gap	edge	bare	moss
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.

central plant: *Bromus erectus*

central plant: *Onobrychis viciifolia*

central plant: *Salvia pratensis*

moss-covered and bare microsites

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: o = gap, ⊘ = edge, ● = tuft, □ = bare, ■ = moss-covered. ▲ = time of mowing.
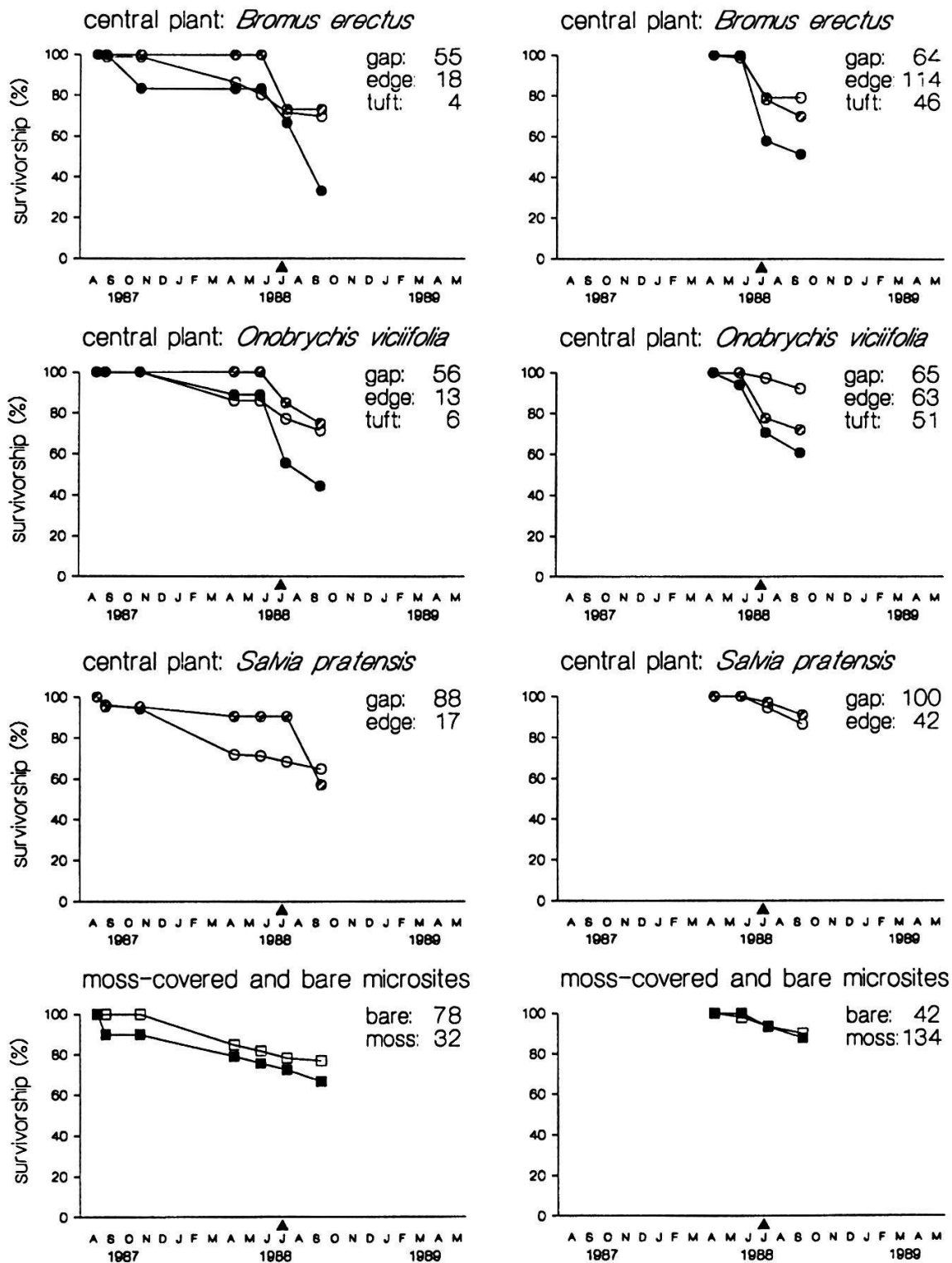
Fig. 11 (continued)
Left: Autumn cohort 1987. Right: Spring cohort 1988.

Microsites: o = 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.
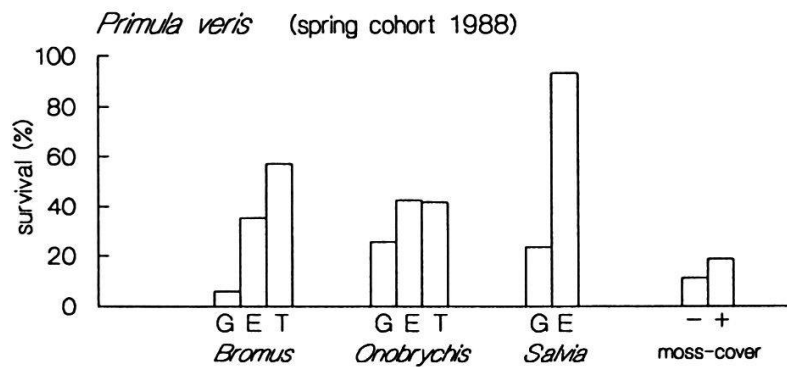
3.2.5. *Primula veris* s.l.

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). Survivorhip after one growth period

Table 11. Death rates of *Primula veris* between the recordings in different microsites (in %).
- = seedlings in less than 3 replicates

| | *Bromus erectus* | | | *Onobrychis viciifolia* | | | *Salvia pratensis* | | | |
	gap	edge	tuft	gap	edge	tuft	gap	edge	bare	moss
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.
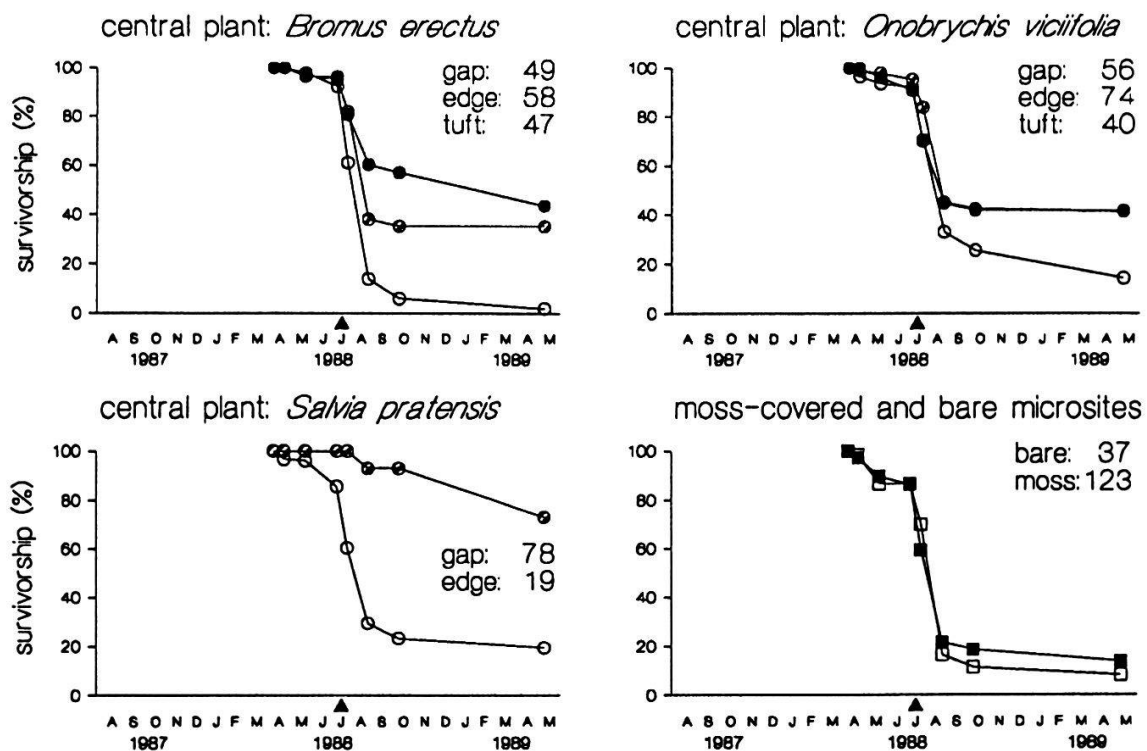
Fig. 13. Survivorship curves of *Primula veris* in different microsites. Spring cohort 1988. Total number of seedlings in each microsite (= 100%) in right top corner of each plot.

Microsites: o = gap, ø = edge, • = tuft, □ = bare, ■ = moss-covered. ▲ = time of mowing
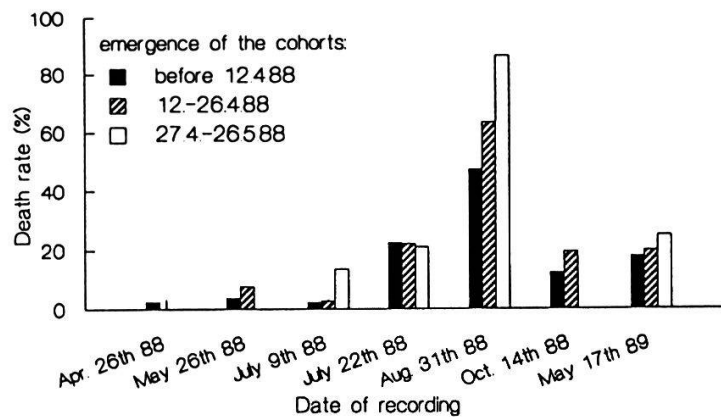
Fig. 14. Death rates of the cohorts observed at different recordings of *Primula veris* in different microsites.

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.
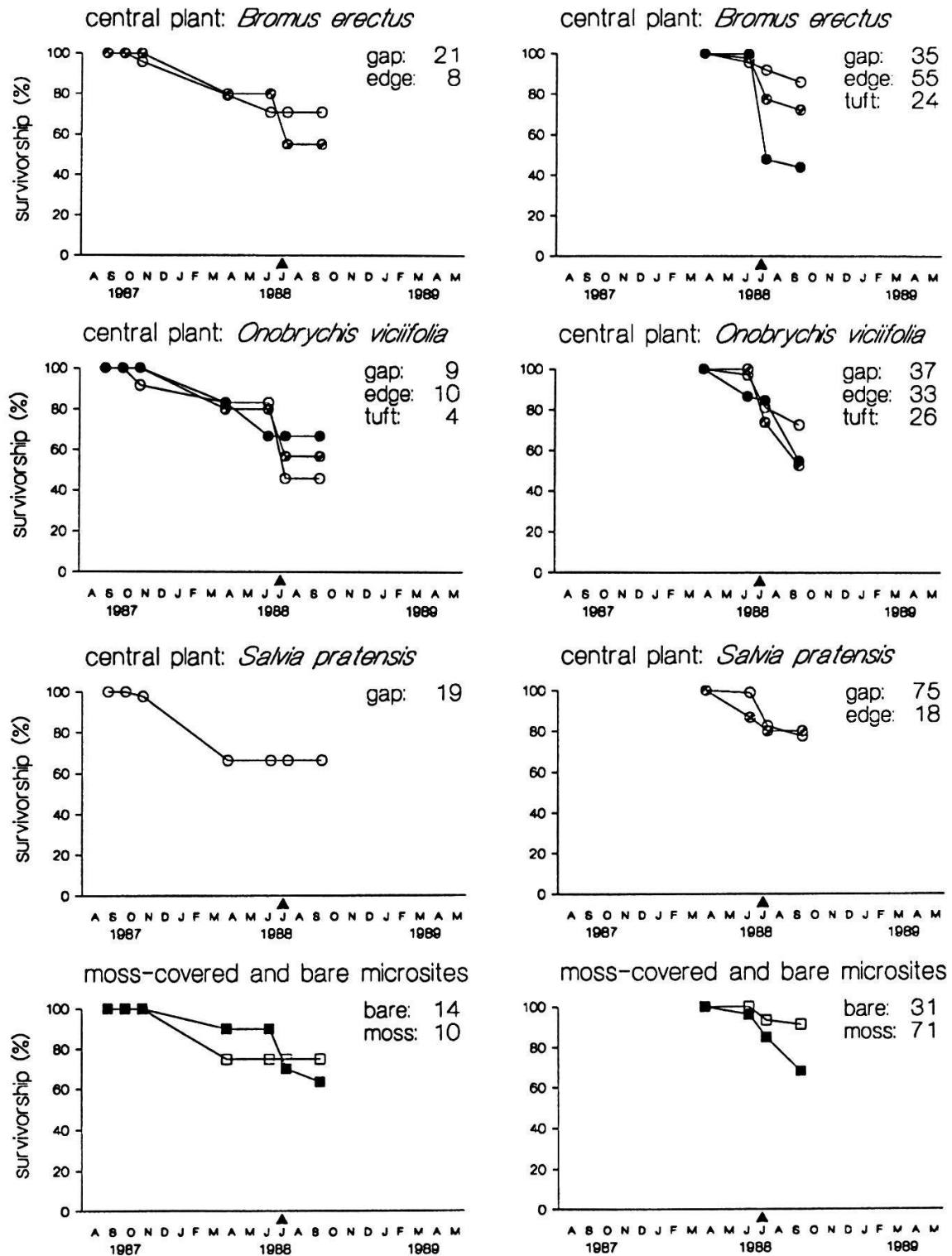
3.2.6. *Sanguisorba minor*

Sanguisorba emerged as well in autumn as in spring, but after the first sow-ing the number of seedlings was very low. Hence only the autumn and spring cohorts emerging after the second sowing were analysed. There was no sig-nificant 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% respec-tively (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 mi-crosites. 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.
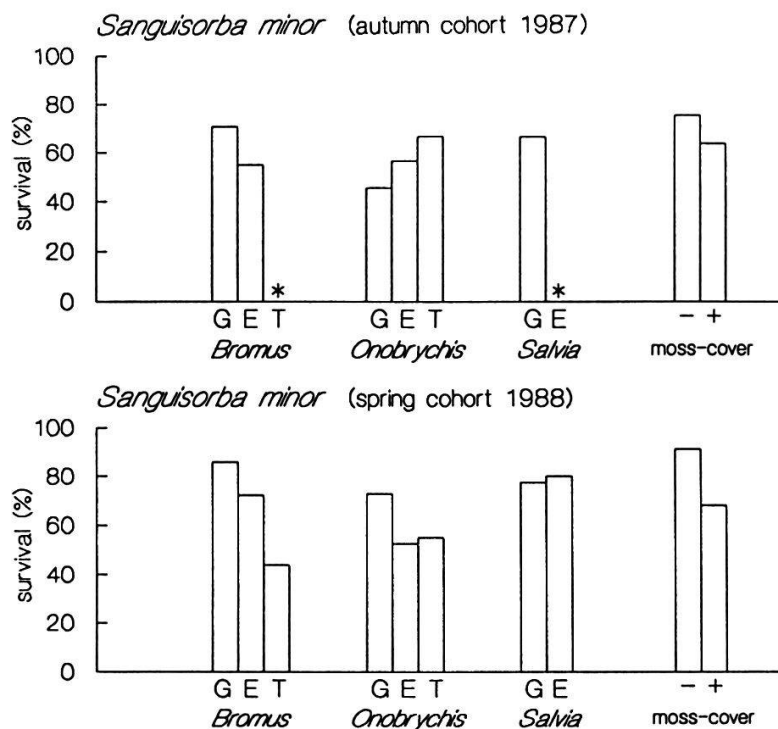
Fig. 15. Survivorship of *Sanguisorba minor* after one growth period in the different mi-crosites.
G = gap, E = edge, T = tuft, - = bare microsite, + = moss-covered microsite. * = less than 3 replicates

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: o = 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

	Bromus erectus			*Onobrychis viciifolia*			*Salvia pratensis*			
	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-
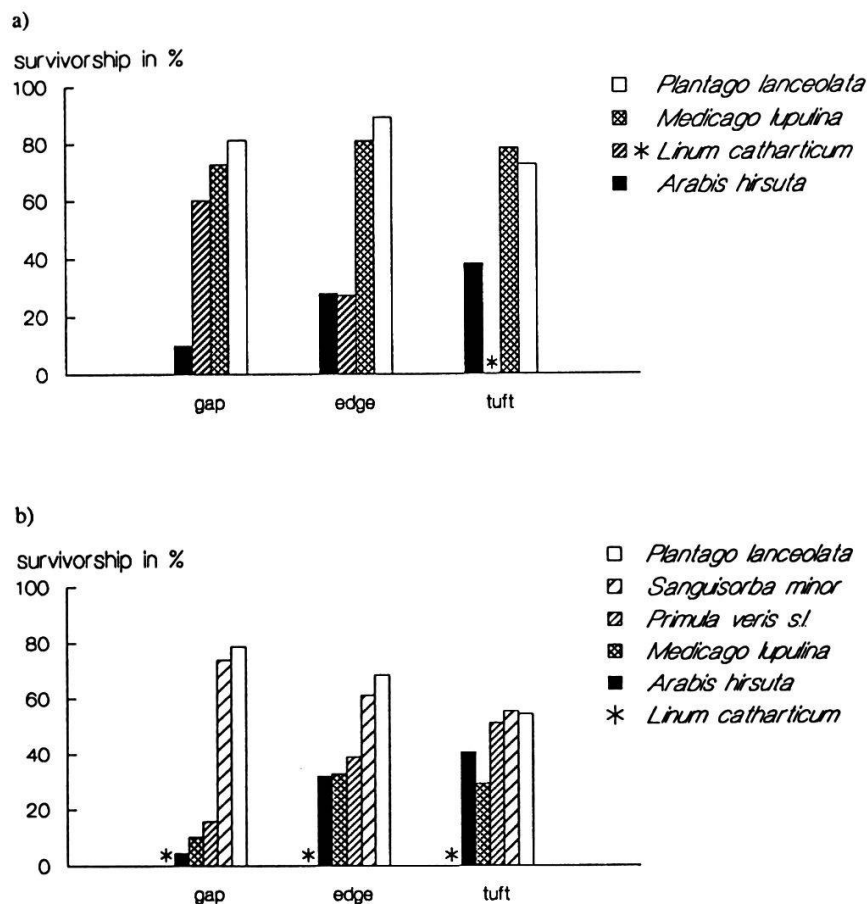
Fig. 17. Survivorship of the studied species in different microsites after one growth period. a) sowing in August 1986, b) sowing in August 1987.
The bars represent the mean values of survivorship in all *Bromus*- and *Onobrychis*-plots. Cohorts used for the analysis are listed in Table 6. The autumn- 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 *Bromus*-plots (p<0.05).
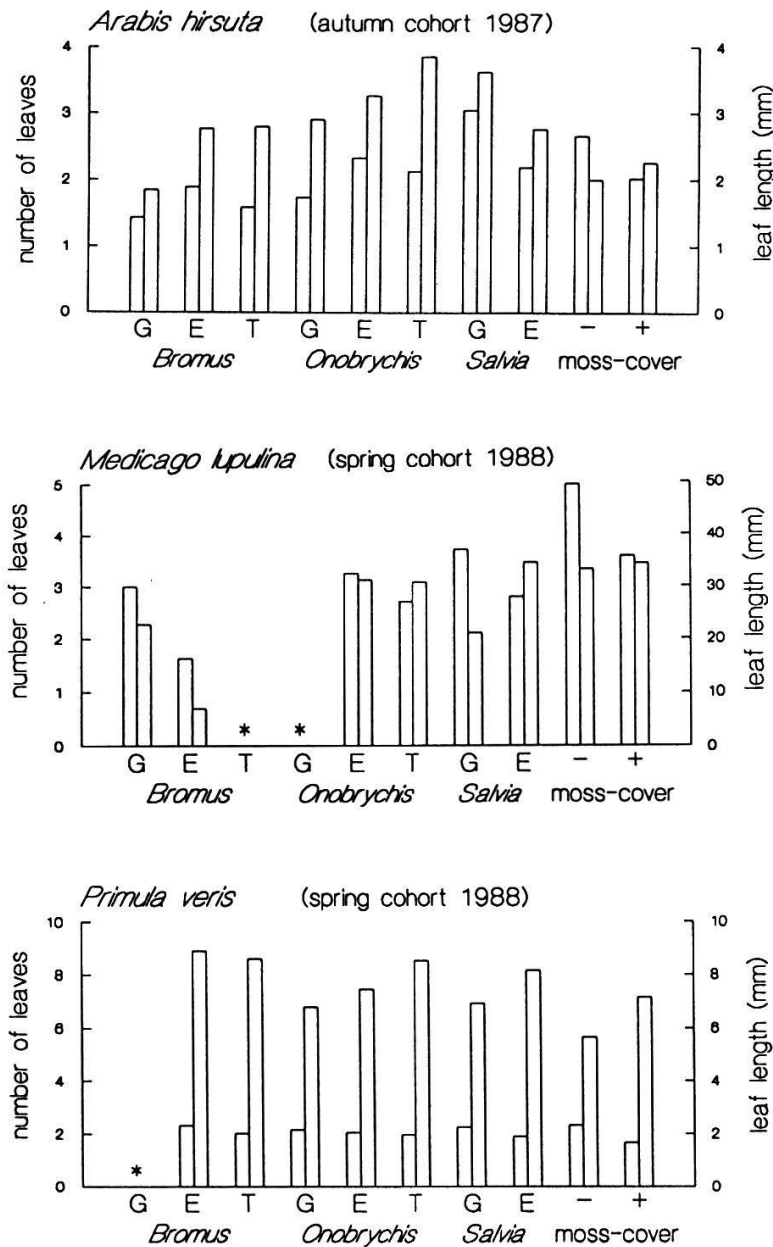
Fig. 18. Size of the surviving plants in September 1988 in the different microsites. Left column: mean number of leaves per plant. Right column: Mean length of the longest leaf. G = gap, E = edge, T = tuft, - = bare microsite, + = moss-covered microsite
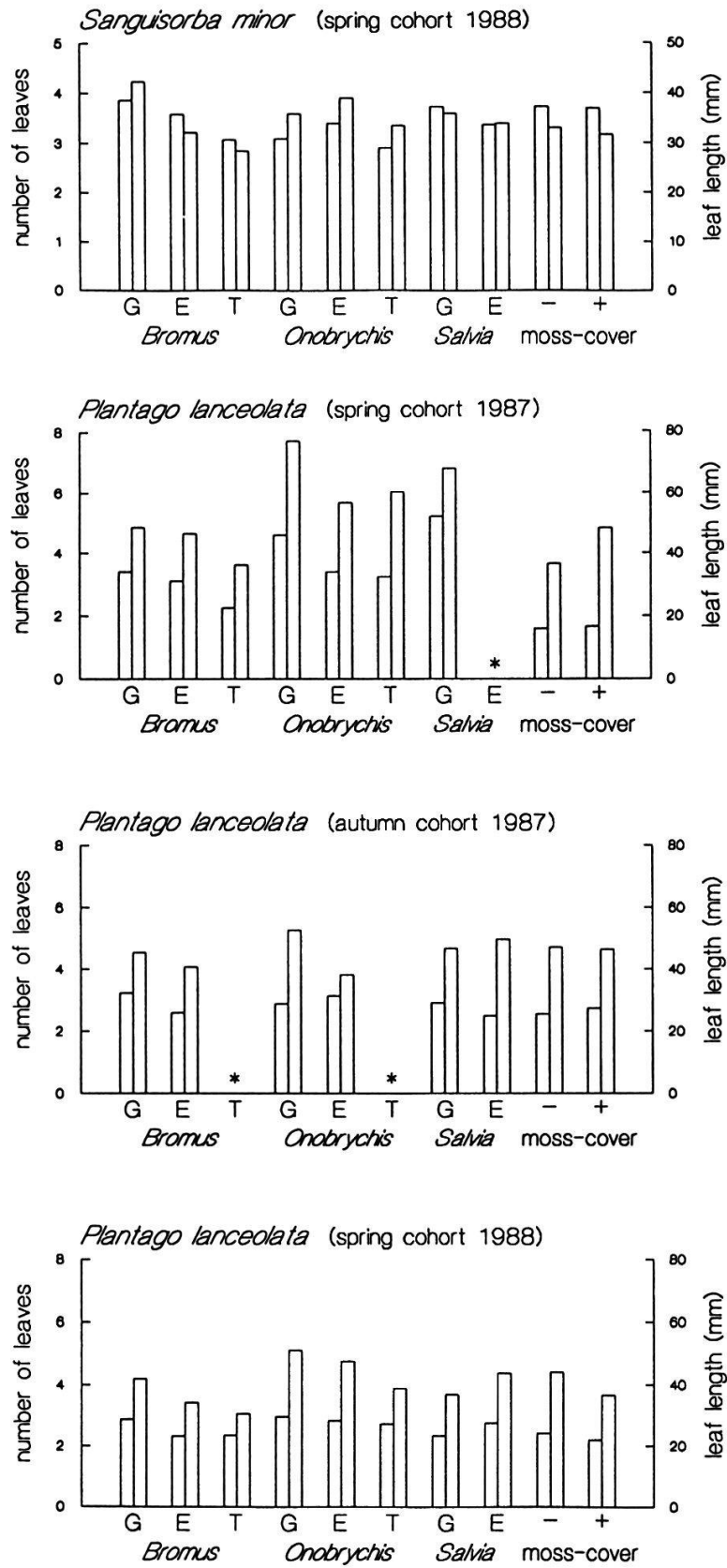* = surviving seedlings in less than three replicate microsites

Sanguisorba minor (spring cohort 1988)

Plantago lanceolata (spring cohort 1987)

Plantago lanceolata (autumn cohort 1987)

Plantago lanceolata (spring cohort 1988)

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.