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Plant species decline due to abandonment of meadows cannot easily be reversed by mowing. A case study from the southern Alps

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Abstract. We resumed mowing in two plots of ca. 100 m^2 in an abandoned meadow dominated by *Brachypodium pinnatum* on the slope of Monte Generoso (Switzerland). We monitored species composition and hay yield using point quadrats and biomass samples. Species frequencies changed little during 10 yr (1988-1997) while hay yields showed large fluctuations according to mean relative humidity in April-June. We performed a seed-addition experiment to test whether the establishment of meadow species is limited by lack of diaspores or favourable microsites for germination and recruitment from the seed bank. We sowed ca. 12 000 seeds of 12 species originating from a nearby meadow individually in plots of a 4 × 6 unbalanced Latin square with four treatments, burning, mowing, mowing and removal of a layer of decayed organic matter, and a control. We monitored the fate of seedling individuals for 24 months. Seedlings of all species were established and survived for 12 months, 10 species survived during at least 24 months, some reached a reproductive stage. Species responded to different qualities of microsites provided by the different treatments thus required different regeneration niches. Spontaneous long-distance immigration was insignificant. We conclude that the former species composition of abandoned meadows cannot easily be restored by mowing alone because many plant species of meadows do not have persistent seed banks and immigration over distances of more than 25 m and successful establishment is very unlikely.

Keywords: *Brachypodium pinnatum*; Community invasibility; Dispersal limitation; Germination; Monte Generoso; Restoration management; Seed-addition experiment; Species diversity.

Nomenclature: Lauber & Wagner (1996).

Introduction

Economical changes during the second half of the 20th century have thoroughly altered land use practices in the Alps. Abandonment of small mountain farms and migration of inhabitants to urban centres have caused a sharp decline in the extension of meadows, particularly in the southern valleys of the Swiss Alps where only ca. 400 ha of species-rich hay meadows are left. Most of these meadows have been reduced to fragments of less than 1 ha today.

It has been well documented (e.g. Willems 1983; Bakker 1989; Ryser et al. 1995; Schreiber & Schiefer 1985; Stampfli & Zeiter in press) and theoretically explained (Grime 1979; Huston 1979, 1994; Grubb 1985), that plant species diversity decreases when mowing is stopped in a meadow of high species richness, while when stronger competitors increase, weaker species are excluded. However, it is not clear whether such a process will be reversed when mowing is resumed. The dynamic equilibrium theory (Huston 1994) would predict that species diversity increases when an 'intermediate disturbance' regime, such as mowing, is resumed in abandoned grasslands. If resource levels after resumed mowing are similar to resource levels in meadows, more species should be able to coexist. Competitive dominants should more or less strongly decrease as a consequence of the mortality of modules, depending on their vulnerability to physical damage caused by mowing. Species diversity, however, can only increase if species are available in the surrounding landscape, or in terms of the species pool concept, at the next larger spatial scale (Taylor et al. 1990; Eriksson 1993; Zobel 1997; Zobel et al. 1998). If 'new' species appear after mowing an abandoned grassland they are either expected to have immigrated or recruited from the seed bank or from vegetative parts in the soil.

Since 1988 we compared the consequences of mowing in an abandoned meadow (Poma) and abandoning of a mown meadow (Pree) at two neighbouring experimental sites in an area with traditional hay making and late-summer grazing (Fig. 1). Soil properties, variation in slope and slope aspect are similar for both grasslands. We assume that the species pools of both grasslands had been similar before 1968 when abandonment started to favour *Brachypodium pinnatum* at Poma. In 1988 the two grasslands showed clear differences in species-abundance proportions and small-scale species diversity. Ca. 25 % of the species occurring in the mown meadow at Pree were no longer present at Poma.

Moreover, an abandonment experiment in the mown meadow of Pree which started in 1988 showed that, within 8 yr, *B. pinnatum* had strongly increased in cover and 18 of the 70 herbs in the experimental quadrats had

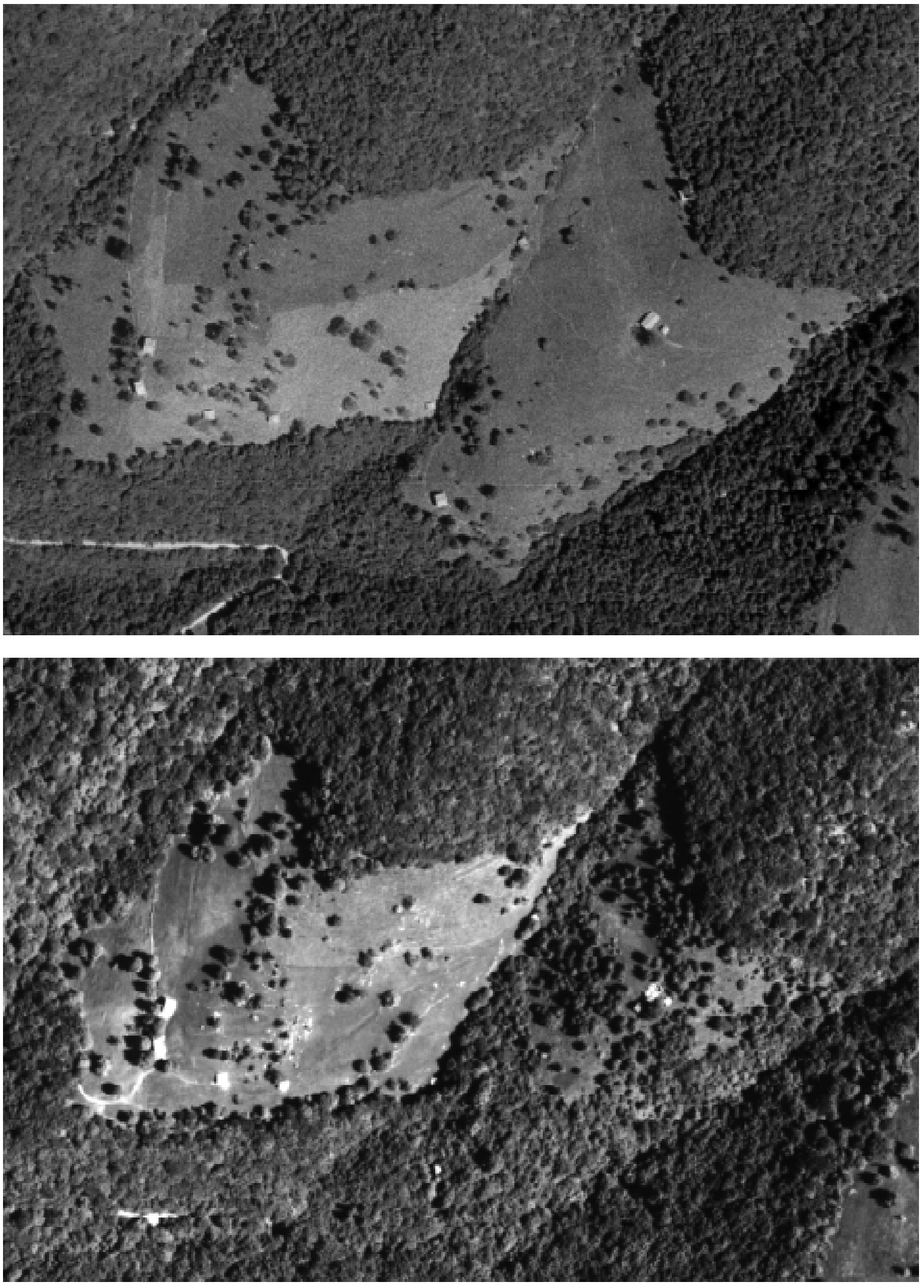

Fig. 1. Grasslands of Pree and Poma separated by a small brook and surrounded by deciduous forest at the slope of Monte Generoso on aerial photographs taken in the summer of 1967 (above) and 1989. Pree (left) is still used for hay production, Poma was abandoned in 1968 and woody species, mainly *Betula pendula* and *Corylus avellana,* have started to grow up. In 1967 both grasslands were each ca. 5 ha. On the 1989 photograph the study site is situated in the lowermost grassland patch of Poma. Northward direction is upwards, the east-west extension of the grassland area is ca. 550 m. Photographs: Swiss Federal Office of Topography.

vanished (A. Stampfli & M. Zeiter in press).

In this paper we demonstrate how species composition and hay yield changed after resumed mowing and manuring during 10 yr at a spatial scale exceeding 100 m^2. Unexpectedly the species composition responded very slowly to mowing over time and we could not satisfactorily explain the slow speed of this process. The concept of seed limitation and an experimental approach had to be integrated with our first ideas to gain new insight. We started a seed-addition experiment at a spatial scale of approximately 10 m^2. For 24 months we observed experimental plots to test whether the establishment of meadow species is limited by a lack of diaspores or favourable microsites for germination and recruitment from the seed bank. In recent experiments in grasslands, seed mixtures were sown to investigate invasibility at a plant community level (Burke & Grime 1996; Tilman 1997). By monitoring the fate of individual seedlings we estimated germination, survivorship and mortality rates with time. Such an approach does not only allow conclusions on the process of dispersal (seed limitation) but also on interactions between the sown species and their variable environment with time.

Study area

The experimental site is situated at Poma (990 m a.s.l., 45° 53' 56" N, 9° 00' 54" E), an abandoned grassland of ca. 5 ha on Monte Generoso, a calcareous peak (1701 m a.s.l.) situated in the southern Prealps on the Swiss-Italian border which is mainly covered with forests and grasslands. Poma is separated from a meadow of the same size by a small brook. It is surrounded by deciduous *Fagus sylvatica* and mixed broad-leaved forests at the slope of Monte Generoso (Fig. 1). Until the late 1950s a farmer family used to live at Poma during the summer, mainly for hay making. This land use was continued until 1968 when Poma was completely abandoned. In later years flocks of rambling goats have sporadically visited the former meadow which changed into a landscape mosaic with patches of *Corylus avellana* and *Rubus fruticosus* thicket, open *Betula pendula* stands, and species-poor *Brachypodium pinnatum*-dominated grassland with abundant geophytes, *Anemone nemorosa*, *Narcissus verbanensis*, *Anthericum liliago* and *Asphodelus alba*.

In 1988 we fenced a homogeneous *Brachypodium*-dominated patch of about rectangular shape (17 m × 18 m) with an annex of ca. 6.5 m × 9 m. This patch is on a SSW-SW slope of 15°. The soil is > 100 cm deep (organic and mineral soil layers above a mixed rock-mineral layer below 60 cm). It has a pH (H_2O) of 5.0 in the uppermost 10 cm. The climate is temperate-humid with a short cold season. Mean annual rainfall is ca. 1900 mm; long-term means of monthly rainfall in the summer exceed 100 mm. Exceptional droughts (records from the Swiss Meteorological Institute station at Stabio, at 9 km from the study site) occurred in the summers of 1990 and 1991 and the early spring of 1997. For instance, from 18 June to 11 September 1991, the rainfall was only 70 mm; 81 out of 86 days had a precipitation ≤ 1 mm. Occasionally snow covers the site in winter.

Methods

Monitoring of experimentally mown plots

Within the fenced area we permanently marked three roughly rectangular plots (A, B, C) of ca. 5.75 m × 16.5 m each with wooden pickets and allocated the following treatments in west-east direction: (A) mown (by scythe) twice, in early July and late September or early October; (B) mown once in early July; (C) not mown. Mowing started in July 1988 and followed local practice regarding dates. In November 1994, we added mature manure (2 kg/m^2) from the nearby farm at Pree to plot B to test whether such a treatment would accelerate changes in species composition. Traditionally, manure has been used as fertilizer in similar quantities at intervals of 2 - 3 yr.

We recorded species presence and cover (categories < 1 %, 1 - 5 %, 5 - 25 %, 25 - 50 %, 50 - 75 %, > 75 %) in July 1989 (plots A and B) and 1995 (A, B and C) to obtain a general impression on the effects of regular mowing on species composition at maximum standing crop. Because species performances varied seasonally, and surveying dense vegetation of large plots was impossible, such a list of species cannot be considered complete. Moreover, estimated cover values are not accurate enough to detect year-to-year changes (Stampfli 1991). Therefore we recorded the annual presence of species in plots A and B during several visits from spring to autumn from 1988-1997. We recorded annual point frequencies from 1988-1997 in each of the mown plots A and B (except for plot A in 1994 and 1996 and for plot B in 1992, 1994 and 1996) using 6 × 76 points at regular distances of 20 cm located in central strips of 1.2 m × 15.2 m. We sampled in late September/early October before cutting the aftermath in plot A to reduce working time for point-frequency sampling to two days per year. Therefore early seasonal geophytes were absent from our frequency records. The sampling effort would have been much larger in July, before cutting, when the vegetation is denser and the canopy is higher making protection from wind and rain indispensable (Stampfli 1991). We used a rigid sampling apparatus, a pin of 3 mm in diameter, a water level, guide lines and permanent marks to relocate approximately the same points in successive years. Standard errors of frequency samples repeated with time were conservatively estimated to be 0.7 - 1.2 for values between 10 - 90 % and < 0.7 for values < 10 % (Stampfli 1991).

Before mowing the plots we harvested the standing crop by cutting 10 regularly spaced strips of 9.5 cm × 100 cm, 2 - 4 cm above ground, using a small electric lawn mower. In successive years we cut strips in roughly the same areas. We separated fractions of graminoid herbs and forbs (in 1994 two × five samples were pooled), and we separated *Brachypodium pinnatum* in samples from both plots (in 1996) and in samples from plot A (in 1995 and 1997), before oven-drying of biomass at 80 °C for 24 h.

In 1989 we counted reproductive *B. pinnatum* shoots, and we measured shoot lengths of five culms selected from left to right in 10 regularly spaced areas in all of plots A - C using a frame of 33 cm × 100 cm.

Seed-addition experiment

We selected 12 species, four grasses and eight forbs, of the nearby meadow Pree, which were present neither in the annex of the fenced area in 1995 nor in plots A - C before mowing was resumed in 1988. Most of the selected

Table 1. Attributes of species selected for seed-addition experiment, conditions of second germination test, and results of both germination tests in growth chambers. S: sensitivity to abandonment (Häfelfinger et al.1995), m = more often/abundant in meadows than abandoned grasslands, . = indifferent; P: persistence of seed bank (Bakker et al. 1996; Thompson et al. 1997), t = transient, sp = short-term persistent, ? = unknown; I: I = method ISTA (Anon. 1996); Filter paper: place of seeds in growth chamber, t = on top of filter paper, p = between pleated filter paper; D: duration of test; T: temperature regime; G: germinated seeds; t^{50}: 'half time'; V = viable seeds at end of second test.

Species	Attribute		Conditions of germination test 2					Test 1		Test 2		
	S	P	I	Germination stimulating pre-treatments	Filter paper	D (d)	T (°C)	G (%)	t^{50} (d)	G (%)	V (%)	t^{50} (d)
Anthoxanthum odoratum	m	t/sp	I	chilling (10°C 7d)	t	14	20-30	88	4	49	3	7
Helictotrichon pubescens	.	t/sp	.	chilling (10°C 7d)	t	14	20-30	59	15	25	17	7
Leontodon hispidus	m	t/sp	.	chilling (10°C 7d)	p	21	20-30	93	4	63	25	7
Sanguisorba minor	m	?	I	chilling (10°C 7d)	p	21	20-30	45	22	26	25	7-14
Bromus erectus	.	?	I	chilling (10°C 7d)	t	7	15-20	93	<1	98	0	<4
Festuca tenuifolia	m	?	I	chilling (10°C 7d)	t	7	15-20	55	3	54	0	<4
Salvia pratensis	.	?	I	—	t	21	20-30	37	2	25	0	<4
Arabis ciliata	m	?	.	chilling (5°C 7d) / KNO_3	t	7	20-30	54	29	96	0	<4
Helianthemum nummularium	.	?	I	KNO_3 / interposed chill.	t	21	20-30	36	45	8	80	7-14
Ranunculus bulbosus	m	t/sp	.	gibberellic acid	t	14	15-20	80	27	68	10	<4
Scabiosa columbaria	m	t/sp	.	gibberellic acid	p	14	20-30	65	6	63	2	7
Anthyllis vulneraria	m	?	I	scarification	t	14	20	68	30	95	0	<4

species are sensitive to abandonment or have short-term persistent seed banks (Table 1). In July 1995 we collected whole plants with seeds and laid them out to air-dry. Once dry, the seeds were cleaned and stored at room temperature until sowing in October 1995.

We tested the germination ability of 100 seeds of every species under two different sets of conditions in growth chambers. In the first test all 12 species were subjected to the same standard method: 50 seeds were placed on filter paper in each of two Petri-dishes; after pre-chilling during 11 days at 5 °C in dark/moist conditions, the seeds were transferred for 107 days to a growth chamber providing light for 16 h at 25 °C and darkness for 8 h at 15 °C. In the second test the ISTA-method (Anon. 1996) was applied: this included species-specific germination stimulating pre-treatments and growth-chamber conditions (Table 1).

In early October 1995 we established our experimental site in the annex of the fenced area. We applied three treatments representing management techniques used by farmers: (1) mowing, for which we cut the vegetation with a small electric lawn mower at ca. 5 cm above ground and removed the mown plants and the 'above-ground litter', a loose layer (ca. 20 cm thick) of mainly dead grass leaves accumulated in the preceding year; (2) burning, where we covered the plots during a rainy day and subsequently set fire to them after adding a splash of alcohol to the above-ground litter: the plants, the 'above-ground litter' and a part of the 'top-soil litter', a dense layer (ca. 5 cm thick) of decayed organic matter on top of the mineral soil, were burnt; (3) mowing as in (1) but with complete removal of the 'top-soil litter' by hand. We included a fourth treatment, a 'control' on artificial soil, to serve as a safe site for germination (no seed predation, no competition with established plants): two plastic trays (each 49 cm × 32 cm × 6 cm, bottoms with perforations) were filled with a mixture of sterile potting soil and sand and enclosed with a meshed cloth (0.2-mm mesh width) to prevent predation and seed input.

We combined sowing with these four treatments in a 6 × 6 Latin square (distance between plots: 0.4 m) in which only 24 (four × six) of the 0.6 m × 0.6 m plots were used. In the 'control' plots (trays) the sowing density was 13 % higher due to the size of the trays, but we assume that this had no effect on proportions germinating. In the remaining 12 (two × six) plots of the Latin square we applied treatments (1) or (2) without sowing in order to estimate the potential contribution of seedlings from the seed bank.

The vegetation removed from the experimental site in October 1995 consisted of 405 ± 59 g/m^2 (n = 18 out of 24) mown plants, 602 ± 149 g/m^2 (n = 18 out of 24) 'above-ground litter' and 882 ± 265 g/m^2 (n = 9 out of 12) 'top-soil litter' (dry weight, mean ± SD, uncompleted set of samples from n 0.36-m^2 plots of the Latin square deliberately selected to include a balanced number of rows and columns). In the years following the setup (1996/1997) all plots were mown twice, in July and in September/October. Burning was not continued because it is not practicable without accumulated litter. The control was removed after twelve months.

We sowed all 12 species in every plot, three species in each quarter (Fig. 2). Per species and plot we sowed 45 seeds individually, five seeds per species at regular distances in lines which were randomly repeated in the nine 10 cm × 10 cm subquadrats within a quarter of each plot (Fig. 2). The densities of sown seeds did not exceed the annual per-species rain of seed in dry meadows (Poschlod & Jackel 1993). The experimental design was unbalanced because seeds of some species were not collected in sufficient quantities: in the burnt plots *Sanguisorba* was sown in reduced numbers (18 instead of 45 seeds per plot) and *Anthyllis, Salvia, Festuca* were not sown.

Over 24 months we recorded seedling emergence and subsequent survival at intervals of ca. 10 days during the main germination period in spring/summer 1995 and at intervals of 1 or 2 months during the remaining time except for the winter of 1996/97 when the interval was 5 months. We choose these intervals to minimise the number of seedlings germinating and dying between the two censuses. We marked every seedling with a coloured ringlet, and mapped its position on a grid, so that those seedlings which had germinated since the previous census could be reliably identified. In some cases it was not possible to determine a species during the first census but then it was determined in one of the following censuses after its germination. A few seedlings died before identification. Later the complete history of each seedling was compiled from the maps.

The data analysis was complicated by the fact that the experimental design was an unbalanced partial Latin square (needing to be analysed with a regression approach which can have only one error term) with a split-plot arrangement (having two error terms). The design had two strata: (a) subplot level $n = 24$, six plots × four treatments; (b) species × subplot level, $n = 12$, with species nested within each subplot. Using the four treatment set ($n = 270$ instead of 288) we ran an unbalanced ANOVA routine in GENSTAT 5.3 (1993) fitting treatment, column, row and species. This assumed a completely factorial model with one (within-subplot) error term. To build the split-plot design we ran the analysis again with subplots as units and one error term. From these results we reconstructed the ANOVA table with two error terms, and then all factors could be tested. To overcome the non-normality of counts data we square-root transformed the number of germinants. From this first ANOVA we found that row (F = 2.4; d.f. = 5, 10; $p > 0.05$) and column (F = 0.2; d.f. = 5, 10; $p > 0.05$) factors were insignificant. These and their interactions could safely be pooled within the first error term and we could proceed by taking the subplots as simply six replicates of each treatment. We omitted the three species (*Anthyllis, Festuca, Salvia*) that were not sown into the burnt plots because if they had been included it would have led to a treatment imbalance and no solution to the ANOVA. We multiplied the number of *Sanguisorba* germinants in the burnt plots by 2.5 so that all data were counts out of 45 as only balanced designs reliably provide the interaction, the means and the standard errors with which to compare means in a straightforward way. We also ran the analysis with *Sanguisorba* eliminated.

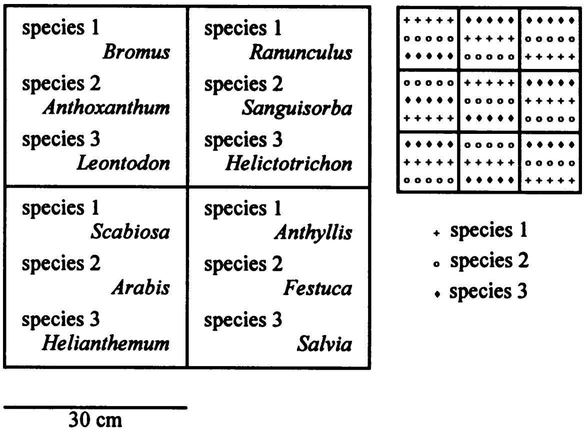

Fig. 2. Seed-addition design at the experimental plots at Poma.

The final analysis thus had four treatments, six subplots and nine species.

We recorded spontaneous emergence and survival of seedlings from the seed bank in all the 30 plots on natural soil. Moreover, we determined the minimal potential immigration distance of the naturally germinating species that were not present within the experimental plots as the distance of the nearest established individual outside the experimental plots.

Results

10-yr changes of hay yield and species composition

Annual biomass produced on the mown plots A and B was clearly dependent on the extent to which growth was limited by summer droughts in the current year. The bulk of it normally developed before July. During 10 yr the first harvest in plot A varied between 74 % and 93 % of the total annual yield. Mean July yields of plots A and B did not show a significant trend with time during 10 years after mowing was resumed but there were strong fluctuations which were well explained by the mean relative humidity during the growth period April-June (Fig. 3).

Although forb and gramineous-herb fractions of the July yields did not show significant trends during 10 yr, the forb biomass tended to increase with time, when the 1997-value from a growth period affected by exceptionally dry weather was excluded (i.e. considering a 9-yr period after resumed mowing) the increase of July forb biomass in plot A with time was significant (linear regression; log-transformed values; $t = 2.56$; d.f. = 6; $p < 0.05$). *Brachypodium pinnatum* biomass, in 1988 estimated

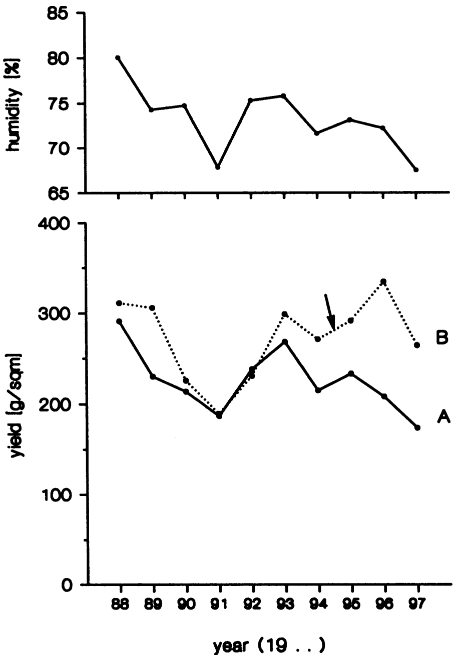

Fig. 3. Mean yield in July in plots A and B at Poma. Differences between plots were significant in 1989, 1996 and 1997 (*t*-test; $p < 0.01$; log-transformed values; no test for 1994). The arrow shows the time of manuring in plot B. Mean relative humidity during the growth period (1 April - 30 June) measured at the Swiss Meteorological Institute station Stabio. Variation in relative humidity explains 88 % of yield variation in plot A (linear regression).

to make up 70 % of the July yield in plot A and B (> 200 g/m^2), dropped to 44 - 51 % of the July yields in plot A in 1995-1997.

As long as no manure was added to plot B (period 1988-1994) mean July yields of both plots showed significantly correlated variation with time ($r = 0.79$, $t = 2.92$, d.f. = 5, $p < 0.05$). July yield clearly increased in the second year (1996) after manuring of plot B. *B. pinnatum* biomass was almost twice as large (175 ± 68 g/m^2, mean ± SD; 55 % of July yield) and showed a larger proportion than in plot A (89 ± 28 g/m^2, mean ± SD; 44 % of July yield). Density measurements of reproductive *B. pinnatum* shoots in mown ($n = 20$) and unmown plots ($n = 10$) made in 1989 indicated a positive short-term effect of mowing (56 vs. 26 shoots/m^2; log-transformed values; separated variances; $t = 2.79$; d.f. = 16.9; $p < 0.05$). In the same year reproductive shoots showed a stepwise reduction in length from plot C (98 cm, $n = 8$) to plot B (85 cm, $n = 10$) to plot A (69 cm, $n = 10$) in 1989 (ANOVA of medians from five measurements in 3 × 10 sampled areas with 10 measurements missing in plot C; F = 24.0; d.f. = 2, 25; $p < 0.00001$; post-hoc Bonferroni-corrected pairwise comparisons indicate significant differences between plots, A-B: $p < 0.01$, B-C: $p < 0.05$).

July relevés did not indicate large abundance shifts of herbaceous species during a period of 7 yr after mowing was resumed (1989-1995), however, regularly mown plots showed a distinctly larger number of herbaceous species and differed from the unmown plot in a lack of woody species which covered ca. 15 % in 1995 (App. 1). Ranks among the two most abundant species *Brachypodium pinnatum* and *Potentilla erecta* had not changed following 10 yr of regular mowing in plot A and B. *B. pinnatum* maintained a dense cover of shoots; it was present in 83 - 93 % of the vegetation cover and only decreased from 89 - 78 % towards the end of the decade in plot A. *B. pinnatum* frequency fluctuated, as with hay yield, consistently with relative humidity (Figs. 3 and 4). The summed frequencies of all the other species remained comparably low during the first 6 yr and increased strongly during the last 4 yr. Trends in frequencies with time of 15 herbs were all positive either in plot A, B or in both plots. The number of established herbaceous species observed in both plots together (190 m^2) increased from 46 (in 1988 or 1989) to 68 (in 1996 or 1997), the cumulative number of herbaceous species was 71. We considered species which were first recorded after 1989, 25 in plot A, 23 in plot B, 'newly established' (App. 1). The proportion of newly established species before/after November 1994 significantly differed between plot A and B ($\chi^2 = 6.52$; d.f. = 1; $p < 0.02$) and was larger in B.

Spontaneous germination

In the 2 × 6 plots without seed addition, no seedlings of the 12 sown species emerged, except two *Helianthemum* seedlings. It is possible that the two *Helianthemum* seedlings originated from sown seed which had been dispersed over a short distance. However, we cannot exclude the alternative that some *Helianthemum* seedlings emerged from the seed bank. Apart from the 1258 seedlings which recruited from imported seeds during the 2 yr, 3895 seedlings of herbaceous species emerged spontaneously in the 30 plots (Table 2). Most seedlings (93 %) originated from established species of the experimental plots; the dominant *Brachypodium pinnatum* only contributed four seedlings. Most of the 'new' herbaceous species had already been established within a short distance (5 m) from the experimental plots (6 % of all herbaceous seedlings), and only two of them showed potential immigration distances of up to 25 m (*Viola hirta, Trifolium campestre*). Two species, *Trifolium repens* and *Polygonum aviculare,* which occurred in the pathways between experimental plots, showed immigration distances of more than 25 m: they were probably imported during the censuses.

Table 2. Spontaneously germinated species in 5 × 6 plots on natural soil (10.8 m^2) or in pathways between plots (x, no counts). Frequency (120 quarters of plots) or minimal immigration distance (in 1995/96), respectively; E_1: sum of emerged seedlings of first 1-yr period 1995/1996; $L_1(12)$: surviving seedlings of first 1-yr period in September 1996; $S_1(24)$: surviving individuals of the first 1-yr period after 24 months in September 1997; E_2: sum of emerged seedlings in second 1-yr period 1996/1997; $L_2(12)$: surviving seedlings of second 1-yr period in September 1997. Unidentified seedlings died before identification or could not reliably be identified at last census in September 1997.

	Frequency / distance(m)	E_1	L_1 (12)	S_1 (24)	E_2	L_2 (12)
Herbs	Frequency					
Brachypodium pinnatum	120	1	0	0	3	0
Anemone nemorosa	86	x	x	.	.	.
Potentilla erecta	38	2972	976	537	527	131
Asphodelus albus	32	56	11?	9?	8	0?
Festuca rubra s.l.	10	1	0	0	.	.
Anthericum liliago	9	.	.	.	.	.
Narcissus verbanensis	9	8	0?	0?	.	.
Carex montana	5	4	1	0	33	21
Peucedanum oreoselinum	5	.	.	.	.	.
Colchicum autumnale	3	.	.	.	.	.
Crocus albiflorus	3	.	.	.	.	.
Betonica officinalis	2	.	.	.	.	.
Cruciata glabra	1	28	11	6	.	.
Galium rubrum	1	.	.	.	.	.
Lathyrus heterophyllus	1	3	3	3	.	.
Luzula campestris	1	.	.	.	.	.
	Distance					
Dianthus seguieri	< 5	3	2	2	.	.
Helianthemum nummularium	< 5	2	0	0	.	.
Lotus corniculatus s.l.	< 5	61	31	22	11	7
Phyteuma betonicifolium	< 5	41	15	9	8	2
Rubus idaeus	< 5	11	1	0	.	.
Scorzonera humilis	< 5	x	x	x	.	.
Rumex acetosa	< 5	60	53	21	23	18
Silene nutans	< 5	1	1	1	.	.
Solidago virgaurea	< 5	3	1	0	.	.
Stellaria graminea	< 5	11	4	3	.	.
Trifolium pratense	< 5	3	3	1	2	1
Ajuga reptans	5 - 25	x	x	x	.	.
Hypericum perforatum	5 - 25	x	x	x	.	.
Hypochaeris radicata	5 - 25	x	x	x	.	.
Trifolium campestre	5 - 25	7	7	0	8	3
Veronica officinalis	5 - 25	x	x	x	.	.
Viola hirta	5 - 25	1	1	1	1	1
Trifolium repens	25 - 100	x	x	.	.	.
Polygonum aviculare agg.	?	x	x	.	.	.
Trees, shrubs, lianas						
Acer pseudoplatanus	25 - 100	3	0	0	.	.
Betula pendula	5 - 25	144	19	1	401	37
Carpinus betulus	5 - 25	1	1	0	2	0
Castanea sativa	5 - 25	6	6	4	.	.
Clematis vitalba	5 - 25	10	0	0	.	.
Cytisus scoparius	5 - 25	.	.	.	x	.
Laburnum sp.	?	x	x	.	1	0
Unidentified		11?	0	0	12	6

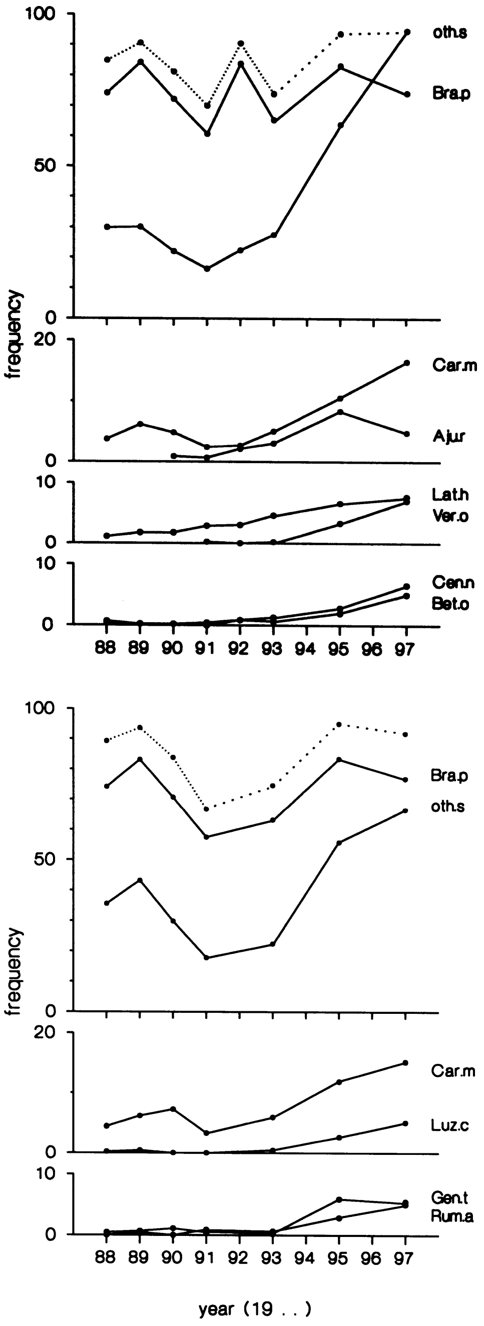

Fig. 4 a. Frequency of *Brachypodium pinnatum* and the summed frequencies of other species in plot A at Poma over 10 yr after mowing had been resumed. Increasing species making up at least 5 % in 1997 are presented separately: *Carex montana, Ajuga reptans, Lathyrus heterophyllus, Veronica officinalis, Centaurea nigrescens* and *Betonica officinalis.* Frequency of total vegetation and area of open gaps, its complement, are shown by a dotted line. **b.** Frequency of *B. pinnatum* and the summed frequencies of other species in plot B at Poma over 10 years after mowing had been resumed. Increasing species making up at least 5 % in 1997 are presented separately: *C. montana, L. campestris, Genista tinctoria* and *Rumex acetosa.* Frequency of total vegetation is shown by a dotted line.

Germination success of sown species

In growth chambers seeds of *Bromus erectus, Leontodon hispidus, Anthoxanthum odoratum* and *Ranunculus bulbosus* showed high viability (80 - 98 % germinated), *Salvia pratensis, Sanguisorba minor, Helictotrichon pubescens, Festuca tenuifolia* and *Scabiosa columbaria* reduced viability (25 - 60 % germinated seeds, 35 - 75 % dead seeds). The seeds of *Anthyllis vulneraria, Arabis ciliata* and *Helianthemum nummularium* were also highly germinable or they had a large proportion of living seeds, but a reduced seedling emergence was to be expected in the field due to missing dormancy-breaking or germination-stimulating factors.

In the field all treatments provided safe sites for germination for all of the sown species. The majority of species germinated in spring 1996 (Fig. 5). Germination of *Bromus, Anthoxanthum* and *Festuca* started in winter 1996 and proceeded continuously during the first half of 1996. *Leontodon, Helictotrichon, Sanguisorba, Scabiosa* and *Salvia*, mainly germinated in May 1996 after a rainy period in late April. *Arabis* and *Helianthemum* germinated in spring and in autumn 1996 and *Ranunculus* germinated mainly in autumn 1996. *Anthyllis* germinated in May 1996 and in spring 1997. Except for *Salvia* and *Scabiosa* germination also continued in the second year but the number of emerged seedlings in three × six plots on natural soil was lower compared with the first year: 64 % (*Anthyllis*), less than 25 % (*Festuca*, *Bromus)* or less than 10 % (all other species) germinated in the second year. Two years after sowing, the total number of emerged seedlings in three × six plots on natural soil varied between eight (*Helianthemum*, 1 % of the sown seeds) and 374 (*Leontodon*, 46 % of the sown seeds, density 231 seedlings/m^2).

Treatment ($F = 18.1$; d.f. = 3, 20; $p < 0.001$), species ($F = 73.9$; d.f. = 8, 160; $p < 0.001$) and species × treatment interaction ($F = 3.8$; d.f. = 24, 160; $p < 0.001$) had a significant influence on seedling emergence in the first growing season. The number of all seedlings of all species was significantly the highest in the trays ($p < 0.01$). The number of seedlings decreased from mown plots with litter removal to mown plots and burnt plots, but among treated plots on natural soil only burnt and mown plots with litter removal differed significantly ($p < 0.05$) if *Sanguisorba* was not eliminated from the analysis (Table 3).

Leontodon showed the highest seedling emergence in the field ($p < 0.01$), followed by *Helictotrichon, Anthoxanthum* and *Bromus* (Table 3). The latter three species showed significantly higher germination abilities than *Scabiosa, Sanguisorba, Arabis* ($p < 0.05$), *Anthyllis, Festuca* and *Salvia* (not analysed because of the unbalanced design). The germination ability of *Ranunculus* was significantly lower ($p < 0.05$), and *Helianthemum* showed the lowest germination ability in the field ($p < 0.01$). Treatments influenced seedling emergence of different species differently (Table 3).

Table 3. Mean number of emerging seedlings (maximum of 45) in differently treated plots ($n = 6$) 1 yr after sowing. **a.** species with analysable data; superscripts $^{a\text{-}c}$ show significantly different means in rows, superscripts $^{v\text{-}z}$ show significantly different means in the last column ($p < 0.05$); values in [ ] influenced by the multiplication by 2.5. **b.** species with unanalyzable data due to an unbalanced design.

	Mown, litter removed	Mown	Burnt	Trays	Mean
a.					
Anthoxanthum odoratum	13.5^{a}	6.3^{b}	6.3^{b}	16.3^{a}	10.6^{w}
Arabis ciliata	3.2^{a}	1.0^{a}	3.3^{a}	21.0^{b}	7.1^{x}
Helictotrichon pubescens	6.8	7.2	8.8	11.3	8.5^{w}
Bromus erectus	8.5^{a}	8.2^{a}	8.2^{a}	17.8^{b}	10.7^{w}
Helianthemum nummularium	0.8	0.0	0.0	1.2	0.5^{z}
Leontodon hispidus	24.0^{a}	20.0^{a}	17.0^{a}	35.3^{b}	24.1^{v}
Ranunculus bulbosus	2.0^{a}	2.5^{a}	1.0^{a}	13.0^{b}	4.6^{y}
Sanguisorba minor	8.3^{a}	5.7^{a}	[1.3^{b}]	7.3^{a}	[5.7^{x}]
Scabiosa columbaria	5.0^{a}	4.3^{a}	4.3^{a}	9.8^{b}	5.9^{x}
Mean	8.0^{a}	$6.1^{a,b}$	[5.6^{b}]	14.8^{c}	
b.					
Anthyllis vulneraria	6.3	3.0	-	7.8	5.2
Salvia pratensis	2.3	1.6	-	11.2	5.6
Festuca tenuifolia	3.3	0.8	-	12.7	5.0

Mortality, survival and growth of seedlings

For the majority of species the main period of seedling mortality in the first 1-yr period was June to July (*Sanguisorba*) or June to September (*Anthoxanthum, Anthyllis, Helictotrichon, Bromus, Festuca, Helianthemum, Leontodon, Scabiosa*, Fig. 5). Seedlings of *Arabis* and *Salvia* mainly died soon after germination, in early spring or May 1996, respectively. However, seedlings of all the sown species survived for at least 12 months. *Leontodon*, the most successful of the sown species in all treatments after 12 months, showed the highest rate of established seedlings (30 %) in mown plots with litter removal.

Sown individuals of 10 species survived for at least 24 months; six species showed at least 12 surviving individuals. By September 1997 survivorship rates of the four grasses were highest (27-36 % of germinated seeds) followed by *Anthyllis* (26 %) and *Leontodon* (25 %). Six or less individuals of *Scabiosa, Helianthemum, Sanguisorba* and *Arabis*, and no seedlings of *Ranunculus* and *Salvia* survived. Seedling populations of the latter two and *Arabis* were almost entirely killed during the long drought of mid January to April 1997.

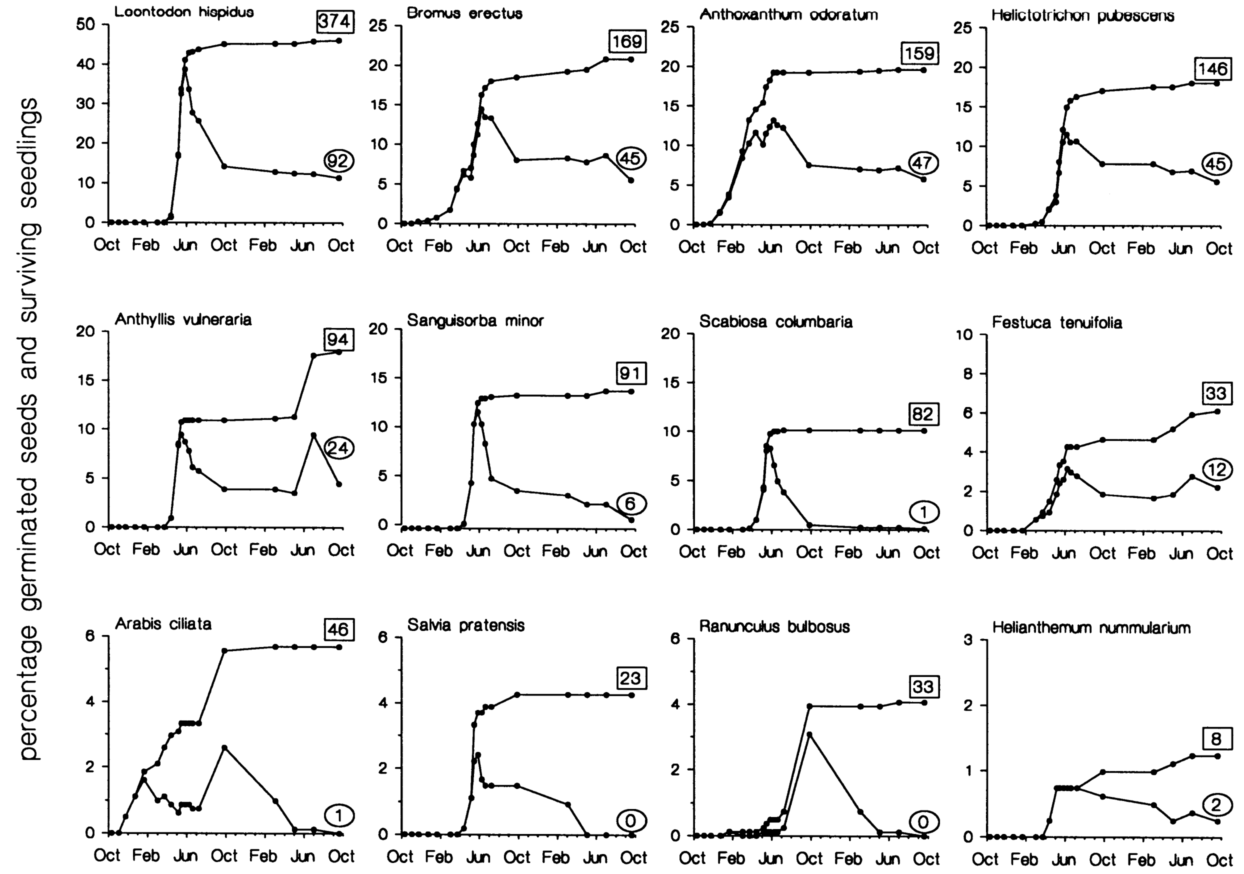

Fig. 5. Cumulative number of germinated seeds (open symbols) and surviving individuals (closed symbols) of sown species in three × six plots on natural soil of a seed-addition experiment at Poma over a period of 24 months (percentage of $n = 810$ sown seeds, except for *Sanguisorba:* $n = 648$; *Anthyllis, Festuca, Salvia*: $n = 540$). Total numbers of emerged seedlings/surviving individuals by 24 September 1997 are indicated in boxes/ovals.

Growth of seedlings was relatively slow for the majority of species. After 24 months of sowing less than 45 % of the surviving germinated individuals had grown beyond seedling stage or taller than 5 cm. However, many individuals of the fastest growing species, *Anthoxanthum* (81 %) and *Leontodon* (74 %) were taller than 5 cm. Individuals of some grasses, *Anthoxanthum* (30), *Helictotrichon* (11), *Festuca* (5), showed clonal growth and a few of them formed dense tufts. Six *Anthoxanthum* individuals flowered in July 1997. At the same time *Leontodon* had reached the highest cover values of up to 5 % in mown plots with litter removal (61 individuals/m^2), with 11 individuals flowering in September 1997.

Discussion

Species diversity response to mowing and manuring

Our results show a slow response of species composition to resumed mowing in *Brachypodium*-dominated grassland. Originally, such a result was not expected because *Brachypodium pinnatum* is considered to be vulnerable to mowing (Briemle & Ellenberg 1994). This view is supported by field experiments in northwestern Europe (e.g. Dierschke 1985; Bobbink & Willems 1991).

B. pinnatum is well-known for its ability to fill open space by rhizome expansion and formation of tall shoots which overtop other species. This ability is based on a large viable bud bank and an efficient mechanism of withdrawal of nutrients from senescent shoots, translocation to the rhizome system and remobilization of the reserves in the following spring (de Kroon & Bobbink 1997). Midsummer cutting should prevent *B. pinnatum* from effectively overtopping other species (Bobbink et al. 1987, 1989; Bobbink & Willems 1991) and limit the formation of new shoots from rhizome buds when starch and nitrogen become limiting (de Kroon & Bobbink 1997). However, long-term experiments with *Pteridium aquilinum*, another possible dominant in abandoned grasslands, showed that extensive rhizomes persisted even after 12 yr of cutting twice yearly (e.g. Marrs et al. 1993).

In our experiment mowing did not cause increased shoot mortality of the dominant. *B. pinnatum* maintained a dense vital network of rhizomes and shoot complexes for 10 yr. Although biomass was reduced and nutrients were removed from its clones by mowing, its space-filling ability was maintained. After the first year, when large amounts of accumulated litter had been removed and gaps had been created by mowing, horizontal growth was stimulated, resulting in a higher culm density in the second year and the highest frequency (> 90 %) in the second-year aftermath. Of course, continued horizontal expansion after nutrient deprivation of clones causes a reduction in length of vertical shoots.

The competitive disadvantage of reduced shoot length was not relevant for *B. pinnatum* for several years, because potential competitors were either absent or suffered from the dry summers from 1989 to 1991. After this period, in which drought-induced vegetation gaps had reached a maximum area of 30 %, *B. pinnatum* recovered more vigorously than other species. It took 6 yr of regular mowing (without manuring) before other species started to increase. The most successful species (*Ajuga reptans, Carex montana, Genista tinctoria, Lathyrus montanus, Veronica officinalis*) increased through clonal growth. They expanded from populations which had already been established before mowing was resumed. *A. reptans* and *V. officinalis* probably initially recruited from a persistent soil seed bank. *A. reptans* seeds were frequently found in the upper soil level (10 cm) of the abandoned plot C where it was absent from the established vegetation (320 seeds/m^2, in 60 samples of totally 12 dm^3, A. Stampfli & M. Zeiter unpubl.).

Although reproducing populations of species depending on seed dispersal *(Centaurea nigrescens, Betonica officinalis, Luzula campestris, Rumex acetosa*) were present before mowing was resumed, these species did not increase during the first 6 yr. Most of the *Euphorbia verrucosa* seedlings, observed in large numbers in the 1989 aftermath, died. Thus recruitment from seeds did not play an important role after mowing was resumed. From monitoring large plots on a yearly basis it is not clear whether seedlings did not appear because seeds were not available or whether they could not establish because of unfavourable weather and/or unsuccessful competition with *B. pinnatum* clones.

As 'new' species were mostly present at short distances from the experimental plots and several abundant species of the nearby meadow at Pree (e.g. *Arrhenatherum elatius, Helictotrichon pubescens, Festuca ovina, Leontodon hispidus, Trisetum flavescens*) appeared for the first time only after manuring in 1994, a factor which may have acted as a seed source, we conclude that limitation of seeds of meadow species was probably a major reason for the slow shifts in species composition observed during 10 yr.

Seed limitation

In the seed-addition plots dispersal limitation was indicated by the fact that virtually no species emerged which had not already been present in the established vegetation in, or around, the plots. 11 out of 12 species of the sowing experiment germinated in plots in which seeds had been added, but did not appear in plots where no seeds had been added. Once seed limitation was overcome by seeds added in quantities which did not exceed the annual per-species seed rain in dry meadows (Poschlod & Jackel 1993), species germinated, survived and some of them even reproduced within 24 months.

Our data stress the importance of dispersal limitation in grasslands. This concept was put forward by Primack & Miao (1992) and tested in other recent studies (Burke & Grime 1996; Tilman 1997). Indeed, many grassland species are unable to disperse to unoccupied sites which otherwise would be suitable for new populations. Verkaar et al. (1983) found seed dispersal distances of only 0.3 - 3.5 m. Furthermore, recruitment is limited because a majority of meadow species have only transient or short-term persistent (< 5-yr) soil seed banks (Poschlod et al. 1995; Thompson et al. 1997). Therefore the speed of a restoration process often depends on the distance between the target area and seed sources in its surroundings (e.g. Zobel et al. 1998; Willems & Bik 1998; Dzwonko & Loster 1998).

Microsite limitation

The lack of seeds was not the only reason why a rapid increase of species diversity was prevented after resumed mowing. The establishment success of 'new' species was also reduced by microsite quality (microsite limitation, Eriksson & Ehrlén 1992). Seed predation, competition with established plants and top-soil litter were the main factors provided by our treatments which differentiate the quality of microsites for germination. Seed predation and/or competition with established plants were effective in all treatments except trays; top-soil litter was present in mown and partly also in burnt plots, but not in trays and in mown plots with litter removal. Significant species × treatment interactions indicate negative effects by litter and/or predation and competition on the single species: Seedling emergence of *Helictotrichon*, *Helianthemum*, and probably of *Anthyllis* (data not analysed), was equivalent in all four treatments, and therefore it was neither influenced by top-soil litter nor by predation and competition with established plants. In the case of *Helictotrichon* this can be explained by hygroscopic awns which enable the seeds to move on the soil surface and to reach more suitable microsites for germination and establishment (Peart 1984). Potential effects of top-soil litter, seed predation and competition with established plants on germination of *Helianthemum* were not realized because its hard coat prolonged dormancy and this led to a very low seedling emergence in the field. Seedling emergence of *Arabis*, *Bromus*, *Leontodon*, *Ranunculus*, *Scabiosa* and probably also of *Salvia* and *Festuca* (not analysed) were negatively affected by seed predation and competition with established plants, but not by the top-soil litter. Seedling emergence of a single species, *Anthoxanthum*, was clearly reduced by top-soil litter. The reduced germination of *Sanguisorba* in the burnt plots was not firmly established statistically.

Even if it is difficult to show this statistically, the data suggest that mortality of young seedlings of *Leontodon* and *Helictotrichon* was higher when top-soil litter was not removed. Litter has been shown to inhibit seedling emergence (e.g. Goldberg & Werner 1983; Rusch & Fernández-Palacios 1995; Bakker et al. 1996; Kitajima & Tilman 1996) and to reduce seedling survival (Fowler 1988; Bergelson 1990). A litter layer of a few cm causes light reduction and mechanical impediment (Goldberg & Werner 1983; Bergelson 1990). In our experiment, however, seeds were sown on the surface of a dense layer of top-soil litter and some may have entered this layer in the course of time. The higher mortality of seedlings in plots without litter removal can be explained by the fact that seedlings which germinated on top-soil litter are often killed by desiccation before their roots reach the mineral soil below (Grubb 1977).

Germination success of most species was reduced by the combined effect of seed predation and competition with established plants. Many herbaceous species require an opening in the vegetation for successful recruitment, and competition with established plants is detrimental to growth and survival of seedlings (Fenner 1978; Gross & Werner 1982; Goldberg & Werner 1983; Fenner 1985; Rusch 1988; Křenová & Lepš 1996). However, in moisture-limited habitats, seedlings may also be facilitated by established plants (Ryser 1993). Reader (1993) showed that control of seedling emergence by seed predation is directly related to seed size while control by ground cover is inversely related to seed size. This author concluded that under natural conditions, the combined effects of ground cover and seed predation may reduce seedling emergence equally for species with small seeds and those with large seeds.

Between-species differences in total seedling emergence during the first 1-yr period can partly be explained by the quality of the sown seeds (many dead seeds of *Festuca, Salvia, Sanguisorba* and *Scabiosa*), dormancy (*Ranunculus*), lack of germination-stimulating factors in case of hard-coat dormancy (*Helianthemum* and *Anthyllis*) or by positive effects of a hygroscopically active awn (*Helictotrichon*). The 12 sown species not only differed in germination rate but also in germination time. Timing of germination in the field is a combined effect of changes in environmental conditions and changes in the state of dormancy. Germination is stimulated by favourable weather conditions in favourable seasons. In unfavourable seasons it may be prevented by dormancy in spite of favourable weather conditions (Vleeshouwers et al. 1995). In our experiment, the timing of germination of most species was mainly determined by weather conditions: germination of most species started or increased in May 1996 after a period of rain in late April, and 50 % of all observed individuals germinated during this period. Dormancy prevented germination of *Ranunculus* in spring but not in autumn 1996. Dry storage (equivalent to summer drought) has been shown to increase the germination rate of *Ranunculus* (Harper 1957). Hard-seed dormancy, caused by a water-impermeable seed coat which can be broken by scarification in germination tests (Baskin & Baskin 1989), delayed germination of a part of the *Anthyllis* seeds and resulted in another, large, population of seedlings in the second spring after sowing.

Not only germination, but also mortality of the seedlings strongly depended upon the weather conditions, especially on moisture availability: in the first year mortality was highest during the relatively dry summer; most seedlings of *Arabis*, *Ranunculus* and *Salvia* did not survive the early spring drought in 1997. A high susceptibility of *Ranunculus* seedlings to drought was also deduced from its particular phenology (Grime et al. 1988). Desiccation appeared to be a main cause of death in seedlings of herbaceous species in calcareous grasslands (Ryser 1993). Due to the stochastic nature of extreme weather events, germination and establishment success can vary from year to year. Mortality rates of seedlings are generally high in dry grasslands (e.g. Silvertown & Dickie 1980; Ryser 1993) and the relative importance of different causes of death can vary from place to place and from year to year (Fenner 1987). Under the particular conditions in the two years of our experiment, all grasses and two herbaceous species showed maximal establishment success. Herbivory was not a major cause of seedling mortality. Differences in seed dormancy, germination rate and time, survivorship of the seedlings and in their responses to the qualities of different microsites (shown by the sown species of our experiment) support Grubb's (1977) idea that regeneration from seeds plays a central role in explaining species diversity and its maintenance in plant communities: coexistence of many species is possible because plants have different regeneration requirements (regeneration niches) which are at least occasionally fulfilled.

Conclusions

The poor establishment success of meadow species in abandoned meadows after restoration was not due to unfavourable microsite conditions, but to limited seed availability. If seeds are available, germination and establishment may be restricted by litter, seed predation, seedling herbivory and competition with established plants. Successful regeneration in dry meadows strongly depends upon favourable weather conditions.

More experimental studies will be necessary for a better understanding of the sensitivity of seeds (which may vary according to their origin) and seedlings to stochastic weather events in a variable micro-environment influenced by many interacting factors. There are still many herbaceous plant species occurring in the grasslands of the southern Prealps which are unknown in terms of their regenerative strategies.

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References

Anon. 1993. *Genstat 5.3. Reference manual*. Genstat 5 Committee. Clarendon Press, Oxford.

Anon. 1996. International rules for seed testing. Vol. 24, Suppl. ISTA, Zürich.

Bakker, J.P. 1989. *Nature management by grazing and cutting*. Kluwer, Dordrecht.

Bakker, J.P., Bakker, E.S., Rosén, E., Verweij, G.L. & Bekker, R.M. 1996. Soil seed bank composition along a gradient from dry alvar grassland to *Juniperus* shrubland. *J. Veg. Sci.* 7: 165-176.

Baskin, J.M. & Baskin, C.C. 1989. Physiology of dormancy and germination in relation to seed bank ecology. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (eds.*) Ecology of soil seed banks*, pp. 53-66. Academic Press, San Diego, CA.

Bergelson, J. 1990. Life after death: site pre-emption by the remains of *Poa annua*. *Ecology* 71: 2157-2165.

Bobbink, R. & Willems, J.H. 1991. Impact of different cutting regimes on the performance of *Brachypodium pinnatum* in Dutch chalk grassland. *Biol. Conserv.* 56: 1-21.

Bobbink, R., den Dubbelden, K. & Willems, J.H. 1989. Seasonal dynamics of phytomass and nutrients in chalk grassland. *Oikos* 55: 216-224.

Bobbink, R., During, H.J., Schreurs, J., Willems, J.H. & Zielman, R. 1987. Effects of selective clipping and different mowing time on species diversity in chalk grassland. *Folia Geobot. Phytotax.* 22: 363-376.

Briemle, G. & Ellenberg, H. 1994. The mowing compatibility of grassland plants. *Natur Landsch.* 69: 139-147.

Burke, M.J.W. & Grime, J.P. 1996. An experimental study of plant community invasibility. *Ecology* 77: 776-790.

de Kroon, H. & Bobbink, R. 1997. Clonal plant dominance under elevated nitrogen deposition, with special reference to *Brachypodium pinnatum* in chalk grassland. In: de Kroon, H. & van Groenendael, J. (eds.) *The ecology and evolution of clonal plants*, pp. 359-379. Backhuys, Leiden.

Dierschke, H. 1985. Experimentelle Untersuchung zur Bestandesdynamik von Kalkmagerrasen (Mesobromion) in Südniedersachsen, I Vegetationsentwicklung auf Dauerflächen 1972-1984. In: Schreiber, K.-F. (ed.) *Sukzession auf Grünlandbrachen, Münst. Geograph. Arb.* 20: 35-44.

Dzwonko, Z. & Loster, S. 1998. Dynamics of species richness and composition in a limestone grassland restored after tree cutting. *J. Veg. Sci*. 9: 387-394.

Eriksson, O. 1993. The species-pool hypothesis and plant community diversity. *Oikos* 68: 371-374.

Eriksson, O. & Ehrlén, J. 1992. Seed and microsite limitation of recruitment in plant populations. *Oecologia* (*Berl.*) 91: 360-364.

Fenner, M. 1978. A comparison of the abilities of colonizers and close turf species to establish from seed in artificial swards. *J. Ecol*. 66: 953-963.

Fenner, M. 1985. *Seed ecology*. Chapman & Hall, London.

Fenner, M. 1987. Seedlings. *New Phytol*. 106 (Suppl.): 35-47.

Fowler, N.L. 1988. What is a safe site?: neighbor, litter, germination date, and patch effects. *Ecology* 69: 947-961.

Goldberg, D.A. & Werner, P.A. 1983. The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (*Solidago* sp.). *Oecologia* (*Berl.*) 60: 149-155.

Grime, J.P. 1979. *Plant strategies and vegetation processes.* J. Wiley & Sons, Chichester.

Grime, J.P., Hodgson, J.G. & Hunt, R. 1988. *Comparative plant ecology*. Unwin Hyman, London.

Gross, K.L. & 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.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev*. 52: 107-145.

Grubb, P.J. 1985. Plant populations and vegetation in relation to habitat, disturbance and competition: problems of generalization. In: White, J. (ed.) *The population structure of vegetation. Handbook of vegetation science 3*, pp. 595-621. Junk, Dordrecht.

Häfelfinger, S., Lörtscher, M., Guggisberg, F. & Studer-Ehrensberger, K. 1995. Prati magri e abbandonati della fascia montana del Ticino, una panoramica geobotanica e zoologica. In: Antognoli, C., Guggisberg, F., Lörtscher, M., Häfelfinger, S. & Stampfli, A. (eds.) *Prati magri ticinesi tra passato e futuro*, pp. 27-55. Poncioni, Losone.

Harper, J.L. 1957. Biological Flora of the British Isles: *Ranunculus bulbosus* L. *J. Ecol.* 45: 325-342.

Huston, M.A. 1979. A general hypothesis of species diversity. *Am. Nat.* 113: 81-101.

Huston, M.A. 1994. *Biological diversity*. University Press, Cambridge.

Kitajima, K. & Tilman, D. 1996. Seed banks and seedling establishment on an experimental productivity gradient. *Oikos* 76: 381-391.

Křenová, Z. & Lepš, J. 1996. Regeneration of a *Gentiana pneumonanthe* population in an oligotrophic wet meadow. *J. Veg. Sci.* 7: 107-112.

Lauber, K. & Wagner, G. 1996. *Flora Helvetica*. Haupt, Bern.

Marrs, R.H., Pakeman, R.J. & Lowday, J.E. 1993. Control of bracken and the restoration of heathland. V. Effects of bracken control treatments on the rhizome and its relationship with frond performance. *J. Appl. Ecol.* 30: 107-118.

Peart, M.H. 1984. The effects of morphology, orientation and position of grass diaspores on seedling survival. *J. Ecol*. 72: 437-453.

Poschlod, P. & Jackel, A.-K. 1993. Untersuchungen zur Dynamik von generativen Diasporenbanken von Samenpflanzen in Kalkmagerrasen. I. Jahreszeitliche Dynamik des Diasporenregens und der Diasporenbank auf zwei Kalkmagerrasenstandorten der Schwäbischen Alb. *Flora* 188: 49-71.

Poschlod, P., Kiefer, S. & Fischer, S. 1995. Die potentielle Gefährdung von Pflanzenpopulationen in Kalkmagerrasen auf der Mittleren Schwäbischen Alb durch Sukzession (Brache) und Aufforstung - ein Beispiel für eine Gefährdungsanalyse von Pflanzenpopulationen. *Beih. Veröff. Naturschutz Landschaftspflege Bad.-Württ.* 83: 199-277.

Primack, R.B. & Miao, S.L. 1992. Dispersal can limit local plant distribution. *Conserv. Biol.* 6: 513-519.

Reader, R.J. 1993. Control of seedling emergence by ground cover and seed predation in relation to seed size for some old-field species. *J. Ecol*. 81: 169-175.

Rusch, G. 1988. Reproductive regeneration in grazed and ungrazed limestone grassland communities on Öland. Preliminary results. *Acta Phytogeogr. Suec.* 76: 113-124.

Rusch, G. & Fernández-Palacios, J.M. 1995. The influence of spatial heterogeneity on regeneration by seed in a limestone grassland. *J. Veg. Sci*. 6: 417-426.

Ryser, P. 1993. Influences of neighbouring plants on seedling establishment in limestone grassland. *J. Veg. Sci.* 4: 195-200.

Ryser, P., Langenauer, R. & Gigon, A. 1995. Species richness and vegetation structure in a limestone grassland after 15 years management with six biomass removal regimes. *Folia Geobot. Phytotax.* 30: 157-167.

Schreiber, K.-F. & Schiefer, J. 1985. Vegetations- und Stoffdynamik in Grünlandbrachen – 10 Jahre Bracheversuche in Baden-Württemberg. In: Schreiber, K.-F. (ed.) Sukzession auf Grünlandbrachen. *Münst. Geograph. Arb.* 20: 111-153.

Silvertown, J.W. & Dickie, J.B. 1980. Seedling survivorship in natural populations of nine perennial chalk grassland plants. *New Phytol.* 88: 555-558.

Stampfli, A. 1991. Accurate determination of vegetational change in meadows by successive point quadrat analysis. *Vegetatio* 96: 185-194.

Stampfli, A. & Zeiter, M. In press. Species responses to climatic variation and change in management in grasslands of southern Switzerland. In: Burga, C.A. & Kratochwil, A. (eds.) *Biomonitoring. General and applied aspects in regional and global scales*. Kluwer, Dordrecht.

Taylor, D.R., Aarssen, L.W. & Loehle, C. 1990. On the relationship between r/K selection and environmental carrying capacity: a new habitat templet for plant life history strategies. *Oikos* 58: 239-250.

Thompson, K., Bakker, J.P. & Bekker, R.M. 1997. *The soil seed banks of North West Europe: methodology, density and longevity*. University Press, Cambridge.

Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78: 81-92.

Verkaar, H.J., Schenkeveld, A.J. & van de Klashorst, M.P. 1983. The ecology of short-lived forbs in chalk grassland: dispersal of seeds. *New Phytol*. 95: 335-344.

Vleeshouwer, L.M., Bouwmeester, H.J. & Karssen, C.M. 1995. Redefining seed dormancy: an attempt to integrate physiology and ecology. *J. Ecol*. 83: 1031-1037.

Willems, J.H. 1983. Species composition and above ground phytomass in chalk grassland with different management. *Vegetatio* 52: 171-180.

Willems, J.H. & Bik, L.P.M. 1998. Restoration of high species density in calcareous grassland: the role of seed rain and soil seed bank. *Appl. Veg. Sci.* 1: 91-100.

Zobel, M. 1997. The relative role of species pools in determining plant species richness: an alternative explanation of species coexistence? *Trends Ecol. Evol.* 12: 266-269.

Zobel, M., van der Maarel, E. & Dupré, C. 1998. The species pool: the concept, its determination and significance for community restoration. *Appl. Veg. Sci*. 1: 55-66.

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App. 1: see next page

App. 1. Changes in species composition in permanent plots at Poma, Switzerland. Established species in plot A (mown 2 × / yr) and/ or B (mown 1 × / yr and manured in November 1994); 10-yr trends (+/–, $p < 0.05$) calculated as linear regressions of arcsin square-rooted frequency values on time (for species, present at least in 3 yr, which show non-zero frequency at least in 1 yr); cover values (%) of species observed in July 1989 (mown plots A, B) and 1995 (mown plots A, B and abandoned plot C); year of first observation of newly established species in plots A, B before (<) and after (>) November 1994.

Species	1988/89	10-yr trend		Cover July '89		Cover July '95			New in A		New in B	
	A/B	A	B	A	B	A	B	C[*]	<	>	<	>
High frequency, stable												
Brachypodium pinnatum	x	n.s.	n.s.	> 75	> 75	50-75	50-75	> 75	.	.	.	.
Potentilla erecta	x	n.s.	n.s.	5 - 25	5 - 25	1 - 5	1 - 5	5 - 25	.	.	.	.
Abundant early seasonal geophytes												
Anemone nemorosa	x	.	.	.	.	.	.	.	.	.	.	.
Anthericum liliago	x	n.s.	.	1 - 5	1 - 5	1 - 5	1 - 5	< 1	.	.	.	.
Asphodelus albus	x	.	.	5 - 25	5 - 25	5 - 25	5 - 25	5 - 25	.	.	.	.
Narcissus verbanensis	x	.	.	< 1	< 1	< 1	< 1	< 1	.	.	.	.
Low frequency 1988/1989, increasing												
Betonica officinalis	x	+	+	< 1	< 1	1 - 5	1 - 5	< 1	.	.	.	.
Carex montana	x	+	+	.	< 1	1 - 5	1 - 5	< 1	.	.	.	.
Centaurea nigrescens	x	+	+	< 1	.	1 - 5	< 1	.	.	.	.	.
Festuca rubra s.l.	x	+	n.s.	.	< 1	1 - 5	1 - 5	< 1	.	.	.	.
Genista tinctoria	x	n.s.	+	< 1	< 1	< 1	1 - 5	< 1	.	.	.	.
Lathyrus heterophyllus	x	+	.	< 1	< 1	1 - 5	< 1	< 1	.	.	.	.
Luzula campestris	x	n.s.	+	.	< 1	< 1	1 - 5	.	91	.	.	.
Phyteuma betonicifolium	x	+	+	< 1	< 1	1 - 5	1 - 5	.	.	.	.	.
Rumex acetosa	x	+	+	< 1	< 1	1 - 5	1 - 5	< 1	.	.	.	.
Low frequency since 1988/1989												
Achillea millefolium s.l.	x	.	.	.	.	< 1	.	.	.	.	.	.
Agrostis capillaris	x	n.s.	.	< 1	.	< 1	< 1	.	.	.	90	.
Anthoxanthum odoratum	x	.	n.s.	.	.	.	.	.	93	.	.	.
Arnica montana	x	.	.	< 1	.	< 1	.	.	.	.	.	.
Astrantia major	x	.	.	< 1	.	< 1	.	.	.	.	.	.
Carex pallescens	x	+	.	< 1	.	< 1	< 1	< 1	.	.	.	95
Carlina acaulis	x	.	n.s.	.	< 1	.	1-5	.	.	.	.	.
Centaurea scabiosa	x	.	.	< 1	.	< 1	.	.	.	.	.	.
Chaerophyllum villarsii	x	n.s.	.	< 1	.	< 1	.	.	.	.	.	.
Colchicum autumnale	x	.	.	.	.	.	.	< 1	.	.	.	.
Cruciata glabra	x	n.s.	n.s.	< 1	< 1	< 1	1 - 5	< 1	.	.	.	.
Dactylis glomerata	x	n.s	n.s.	< 1	< 1	.	< 1	.	.	.	.	.
Dianthus carthusianorum	x	.	.	.	< 1	.	< 1	.	.	.	.	.
Euphorbia verrucosa	x	n.s.	n.s.	1 - 5	< 1	1 - 5	< 1	< 1	.	.	.	.
Galium rubrum	x	.	n.s.	< 1	< 1	< 1	< 1	< 1	.	.	.	.
Galium verum	x	n.s.	.	< 1	.	< 1	.	.	.	.	.	.
Geranium sylvaticum	x	n.s.	+	< 1	< 1	< 1	< 1	< 1	.	.	.	.
Gymnadenia conopsea	x	.	.	.	< 1	< 1	< 1	.	90	.	.	.
Laserpitium gaudinii	x	.	.	< 1	< 1	< 1	< 1	.	.	.	.	.
Lathyrus linifolius	x	.	.	< 1	.	< 1	.	.	.	.	.	.
Lilium croceum	x	.	.	.	< 1	.	< 1	.	.	.	.	.
Peucedanum oreoselinum	x	n.s.	n.s.	< 1	.	1 - 5	1 - 5	< 1	.	.	.	.
Phyteuma ovatum	x	.	.	.	.	< 1	< 1	.	90	.	.	.
Scorzonera humilis	x	.	n.s.	.	< 1	.	< 1	< 1	.	96	.	.
Silene nutans	x	n.s.	.	< 1	.	< 1	< 1	.	.	.	.	95
Silene vulgaris	x	n.s.	.	.	.	1 - 5	.	.	.	.	.	96
Solidago virgaurea	x	n.s.	.	< 1	< 1	< 1	< 1	.	.	.	.	.
Stellaria graminea	x	.	n.s.	< 1	< 1	< 1	1 - 5	< 1	.	.	.	.
Thesium bavarum	x	.	.	.	< 1	.	< 1	< 1	.	96	.	.
Thymus pulegioides	x	.	.	.	< 1	< 1	< 1	.	.	95	.	.
Urtica dioica	x	.	.	.	< 1	.	.	.	.	.	.	.
Established after 1989												
Bromus erectus s.l.	.	.	.	.	.	.	.	.	90	.	90	.
Dianthus seguieri	.	.	.	.	.	.	.	< 1	.	96	.	96
Established after 1989, first in plot A												
Ajuga reptans	.	+	.	.	.	< 1	.	.	90	.	.	96
Cirsium erisithales	.	n.s.	.	.	.	< 1	.	.	91	.	.	.
Crocus albiflorus	.	.	.	.	.	.	.	.	.	96	.	.
Helianthemum nummularium	.	n.s.	.	.	.	< 1	.	.	90	.	.	.
Hypericum perforatum	.	.	.	.	.	< 1	.	.	.	95	.	.
Leucanthemum vulgare agg.	.	.	.	.	.	< 1	.	.	.	95	.	96
Lotus corniculatus s.l.	.	n.s.	.	.	.	< 1	< 1	.	91	.	.	95
Phyteuma orbiculare	.	n.s.	.	.	.	< 1	.	.	93	.	.	.
Polygala pedemontana	.	.	.	.	.	.	.	.	.	96	.	.
Rubus fruticosus agg.	.	.	.	.	.	< 1	.	.	.	95	.	96
Trifolium pratense	.	.	.	.	.	.	.	.	.	96	.	97
Veronica officinalis	.	+	.	.	.	< 1	< 1	.	91	.	.	95
Viola hirta	.	+	.	.	.	.	.	.	91	.	.	95
Established after 1989, first in plot B												
Helictotrichon pubescens	.	.	.	.	.	.	.	.	.	.	.	95
Arrhenatherum elatius	.	.	.	.	.	.	.	.	.	.	.	96
Danthonia decumbens	.	+	+	.	.	< 1	< 1	.	93	.	90	.
Dactylorhiza sambucina	.	.	.	.	.	.	.	.	.	96	.	95
Festuca ovina s.l.	.	.	.	.	.	.	.	.	.	.	.	96
Festuca tenuifolia	.	.	.	.	.	.	< 1	.	.	96	.	95
Holcus lanatus	.	.	.	.	.	.	< 1	.	.	.	.	95
Hypochaeris radicata	.	.	.	.	.	.	.	.	.	.	.	96
Leontodon hispidus	.	.	.	.	.	.	.	.	.	.	.	97
Trisetum flavescens	.	.	.	.	.	.	.	.	.	.	.	96
Total number of herbaceous species	46	11	9	29	29	46	39	24	13	12	3	20

[*] Eight species, seven of them woody, established in plot C; *Acer pseudoplatanus, Castanea sativa, Prunus avium, Tilia cordata, Vincetoxicum hirundinaria* (cover of < 1 %); *Rubus idaeus, Sorbus aria* (1 -5 %); *Corylus avellana* (5 - 25 %).