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DISPERSAL AND MICROSITE LIMITATION IN AN ABANDONED CALCAREOUS GRASSLAND OF THE SOUTHERN PREALPS

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Abstract: Dispersal limitation is often involved when the species composition of a dry abandoned grassland shows a slow response to resumed regular mowing. A seed-addition experiment, using 32 species which do not belong to the local species pool, was performed on Monte San Giorgio (southern Switzerland) to test whether the low recruitment success was due to dispersal limitation or due to unfavourable microsite conditions. In October 1997, 20 species were individually sown in six 3 × 4 m blocks of a 2 × 2 factorial "partial" split-plot design with treatments of abandonment vs. mowing and undisturbed vs. root-removed soil, this last being applied in small naturally-degradable pots. Moreover, 12 species were sown only in the treatments on undisturbed soil. Seedlings of sown and spontaneously germinating seeds were observed on 16 occasions over one 12-month period.

Seeds of 31 out of the 32 species germinated. Twenty-four species showed germination rates higher than 5% and different seasonal germination patterns. Established vegetation, especially the tussocks of *Molinia arundinacea*, reduced the quality of microsites for germination. Whereas a few species germinated better under the litter of *Molinia arundinacea*, many more germinated better under the more variable microsite conditions of a mown grassland.

Only a few seedlings of 25 species out of the 31 germinated species survived until October 1998. Seedling survival was negatively affected by litter, unfavourable weather conditions (frost and dry periods followed by heavy rains) and herbivory (slugs and grasshoppers). Tussocks of *Molinia arundinacea*, however, tended to protect seedlings.

The poor establishment success of "new" species observed in abandoned meadows on Monte San Giorgio after resumed mowing is due to dispersal and microsite limitations.

INTRODUCTION

It has been well documented that species richness in a grassland declines when mowing is stopped (WILLEMS 1983, SCHREIBER & SCHIEFER 1985, BAKKER 1989, RYSER et al. 1995, STAMPFLI & ZEITER, in press). Often competitively strong grasses exclude weaker species. Because of the sensitivity of the germination process on various microsite factors, limitations to germination may be partly responsible for such a decline in species (TILMAN 1993, ŠPAČKOVÁ et al. 1998). Litter and competition with the established vegetation, for example, have been shown to reduce germination success and seedling survival (GOLDBERG & WERNER 1983, RUSCH & FERNANDEZ-PALACIOS 1995, ŠPAČKOVÁ et al. 1998, STAMPFLI & ZEITER 1999).

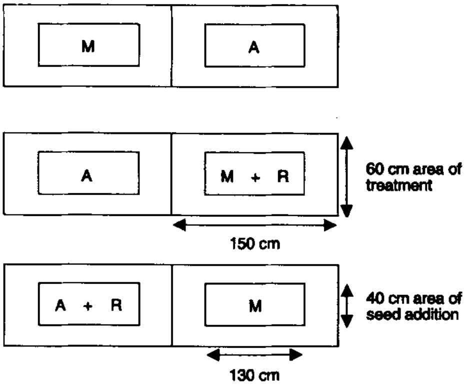

Fig. 1. Design of one out of six blocks, containing six plots, which were mown (M) or abandoned (A). Twenty small pots with root-removed soil (R) were added to one mown and one abandoned plot per block. Allocation of the treatment was randomized independently within each block.

Seedling survival can also be reduced by root competition or increased because of protection by the established plants (AGUIAR et al. 1992, RYSER 1993). Requirements for regeneration, however, are unknown for many common species in the grasslands of the southern Prealps.

If mowing is resumed in an abandoned grassland, microsite conditions and limitations to germination change. Species diversity, however, can only increase to former high levels if seeds of new species can invade from populations of surrounding areas or if species can recruit from the seed bank. In 1988 an experiment was started on Monte San Giorgio to restore a meadow by regularly mowing an abandoned grassland (STAMPFLI 1992). During 10 years of regular mowing, the yield of the dominant grass *Molinia arundinacea*, the total standing crop and the number of species declined (STAMPFLI et al. 1994, A. STAMPFLI, unpubl. data). Only a few species, which were all established in the close neighbourhood, newly colonized the experimental plots (A. STAMPFLI, unpubl. data). Several species which occurred at distances of less than 50 m have not invaded the experimental plots. As in another recent study in an abandoned grassland on the nearby Monte Generoso (STAMPFLI & ZEITER 1999) we hypothesize that this result could be a consequence of dispersal limitation.

Some taxa which are potentially able to grow in grassland habitats such as those on Monte San Giorgio (e.g. *Bromus erectus* subsp. *condensatus*, *Thalictrum minus*, *Stachys alopecuros*, *Silene otites* and *Trinia glauca*) are not present on the mountain, although they are frequent at similar sites on nearby mountains, e.g. on Monte Barro at a distance of ca. 30 km.

We performed a seed-addition experiment to test whether the low recruitment success found in the grassland on Monte San Giorgio was due to dispersal limitation or due to unfavourable microsite conditions. Taking into account that results of seed-addition experiments depend much on the species choice and the origin of seeds (ZOBEL 1997), we used 32 different species from Monte San Giorgio and from similar grasslands in the region (Monte Generoso, Monte Barro). By monitoring the individual fate of the sown and spontaneously germinated seeds, we estimated microsite dependent rates of germination, survival and mortality for each species. In this article we discuss the effects of treatments and different structures of vegetation on the sown species after a 12-month period.

Nomenclature: LAUBER & WAGNER (1996) and PIGNATTI (1982), the latter for taxa not occurring in Switzerland.

STUDY AREA

The study was performed in a patch of ca. 500 m^2 of calcareous grassland situated at an elevation of 900 m on the south-facing ridge of Monte San Giorgio in the southern Prealps of Switzerland (45°54'31"N, 8°56'58"E). This slightly inclined (10°) and easterly facing meadow is surrounded by a deciduous oak forest with beech (*Quercus pubescens*, *Sorbus aria*, *Fagus sylvatica*, *Acer pseudoplatanus*). Hay-making and probably also grazing had been a common practice until abandonment in the 1950s (STAMPFLI et al. 1994). There is no exact information about the floristic composition of the former meadow. Contemporary botanists, however, reported observations of floristically rich meadows (KOCH 1943, LÜDI 1949). Monte San Giorgio was included in the inventory of Swiss Landscapes and Natural Monuments of National Importance (BLN 1977). In autumn 1995 and 1996 the study area was mowed as part of a cantonal plan for conservation management.

In September 1997 a fence was built to protect the study site (5 × 20 m) from human trampling and dogs. The vegetation was dominated by the tussock-grass *Molinia arundinacea*. *Carex humilis*, *C. montana* and *C. tomentosa* were locally frequent, 18 other herbaceous species showed low abundance and mosses were very sparse. The standing crop was 320.5 g m^{-2} ± 56.1 g m^{-2} (mean ± s.d., n = 12, yields of 0.4 × 1.3 m plots, two mown plots were selected in each of the six blocks, Fig. 1).

Mean annual precipitation is ca. 1,900 mm. The monthly rainfall from the spring to the autumn of 1998 exceeded 100 mm. Dry periods of 1–3 weeks were followed by heavy rains or thunderstorms. Snow covered the site in December 1997, at the end of January, at the end of March and in the mid April 1998.

Soil depth varied between 55–70 cm (measured with a pointed iron rod). Whereas bare soil at the soil surface showed a neutral reaction (pH = 7, measured with HELLIGE Indicator), the soil in the surroundings of *Molinia arundinacea* tussocks was moderately acidic (pH = 5). The upper stratum (above 15–25 cm), an organic layer, was decarbonated and considerably acidic (pH = 4). Below it was a mineral layer with calcareous rock (pH = 7).

METHODS

Choice of species and seed collection

We selected species which were not established in the study site nor within the surrounding area. Some of them (*Ranunculus bulbosus*, *Ononis spinosa*, *Astragalus glycyphyllos*, *Phyteuma betonicifolium*, *Agrostis capillaris* and *Danthonia decumbens*), however, grew in a nearby meadow separated by a few trees. By selecting 32 species we intended to include a broad range of the southern Prealp grassland species with different seed weights, dispersal strategies (HODGSON et al. 1995) and tolerances to mowing (BRIEMLE & ELLENBERG 1994).

In June and July 1997 whole plants with mature seeds were collected from meadows on Monte San Giorgio and from calcareous grasslands at a distance of 5 km (Monte Generoso, Switzerland) and 30 km (Monte Barro, northern Italy). The reproductive parts were laid out to dry at room temperature. Once dry, the seeds were stored in small paper bags. Seed weight was measured by taking the mean dispersule weight of 100 seeds.

Germination tests under controlled conditions

The germination ability of 100 to 400 seeds of all species was tested in growth chambers, starting in early October 1997, under a day – night (16 h – 8 h) light regime and the different sets of conditions shown in Tab. 1. In the first test seeds were placed on filter-paper or pleated paper for 14 to 87 days. Germination-stimulating treatments of ISTA (1996) were set for all species specified in ISTA (1996). In the second germination test seeds were not stimulated

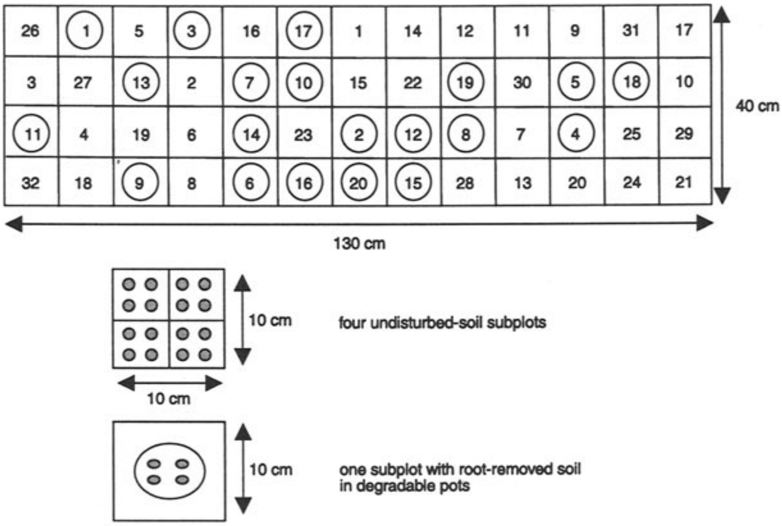

Fig. 2. Design of one plot containing 148 subplots: 4 x 32 subplots with undisturbed soil and 20 subplots with small degradable pots filled with root-removed soil. Numbers represent the 32 selected species; species 1–20 were sown in undisturbed and root-removed soil, species 21–32 were only sown in undisturbed soil. Four seeds of one species were added per subplot. Positions of the subplots were separately chosen at random in all 36 plots.

and sown to pots filled with commercial potting soil (i.e. forestry compost soil without peat), which were stored at room temperature and watered at 14-day intervals over 12 months.

Seed-addition experiment in the field

At the beginning of October 1997, during one week, ca. 20,000 seeds from the 32 species were individually sown. The beginning of October was selected as the sowing period because it was undesirable to store seeds longer than 1–3 months and chilling should be able under field conditions.

Twenty species were sown in six 3 x 4 m blocks of a 2 x 2 factorial "partial" split-plot design with the treatments of abandonment vs. mowing and undisturbed vs. root-removed soil, this last being applied in small (6 cm in diameter) naturally-degradable pots (made of wood fibre and peat) (Figs. 1 and 2). Twelve species originating from Monte Barro (all except *Daucus carota*) were sown only in the undisturbed soil. For the root-removal treatment small holes (6 cm in diameter) were dug and the excavated soil was freed of all visible roots and shoots. This root-removed soil was then filled into the pots and placed back into the holes. In each little pot four seeds of the same species were sown, and on undisturbed soil 4 x 4 seeds were added to an area of 10 cm^2 (Fig. 2). The 4 x 4 seeds per species were sown to keep four seeds as the subplot total and to obtain an area equal to the space used with the pots (Fig. 2). With this arrangement the achieved seed density on undisturbed soil was 1,600 seeds per m^2. This does not exceed the order of magnitude of natural annual seed rain in mown grasslands (Poschlod & Jackel 1993). The subplots with undisturbed or root-removed soil were allocated randomly within the mown and abandoned plots (Fig. 2). Furthermore, the mowing treatment was applied to an area greater than the mown plots to minimize edge effects (Fig. 1).

Table 1. Species selected for the seed-addition experiment, characteristics of seed samples, conditions and results of germination ability tests. W – weight measured after drying 100 dispersules at room temperature; dispersules – seeds (s), achenes (a) or other indehiscent germinules (d); O – origin of seeds: (A) Monte San Giorgio, (B) Monte Generoso or (C) Monte Barro; S – duration of storage prior to setting test conditions; Stimulation treatment: (^{ISTA}) according to method ISTA (1996). FP – filter paper; (TP) on top of paper, (PP) between pleated paper; D – duration of test (d); T – temperature regime (night – day); G – germinated seeds (%): (*) values obtained by second germination ability test at room temperature were higher ($P < 0.01$); H – hard seeds (%); V– viable seeds (%); M – dead seeds (%).

Species (subspecies)	Seed sample			Conditions of germination test				Test results (%)			
	W (mg)	O	S (d)	Stimulation treatments	FP	D (d)	T (°C)	G*	H	V	N
Agrostis capillaris	0.058 a	A	40	chilling (7d 10 °C) + KNO_3 ^{ISTA}	TP	21	20–30	98	.	.	2
Anthoxanthum odoratum	0.691 a	B	90	. ^{ISTA}	TP	35	20–30	80	.	.	20
Bromus erectus subsp. *condensatus*	1.921 a	C	91	chilling (7d 5 °C) ^{ISTA}	TP	28	15–25	91	.	.	9
Danthonia decumbens	2.222 a	A	76	chilling (7d 10 °C)	TP	65	15–25	20*	.	71	9
Festuca paniculata	5.485 s	B	73	chilling (7d 10 °C)	TP	63	15–25	53	.	13	34
Holcus lanatus	0.494 a	B	74	chilling (7d 10 °C) ^{ISTA}	TP	35	20–30	84	.	.	16
Carex austroalpina	1.547 s	C	91	chilling (28d 5 °C) + KNO_3	TP	84	20	11*	.	31	58
Carex baldensis	2.597 s	C	91	chilling (28d 5 °C) + KNO_3	TP		20	2	.	29	69
Achillea millefolium s.l.	0.084 s	A	71	. ^{ISTA}	TP	14	20–30	98	.	.	2
Arabis hirsuta	0.152 s	B	74	chilling (7d 10 °C) ^{ISTA}	TP	28	20–30	93	.	.	7
Astragalus glycyphyllos	4.867 s	A	70	chilling (7d 10 °C, 7d 5 °C)	TP	42	15–25	11	.	.	89
Centaurea nigrescens	2.611 s	B	70	.	TP	28	15–25	59	.	26	15
Coronilla vaginalis	6.335 s	C	39	interposed chilling (7d 10 °C)	PP	35	20	0*	95	.	5
Cytisus sessilifolius	13.665 s	C	71	scarification after 35d	PP	55	20	2*	.	.	98
Daucus carota	0.823 d	C	39	gibberellic acid ^{ISTA}	TP	35	20–30	66	.	2	32
Dictamnus albus	13.151 s	C	40	interposed chilling (7d 10 °C)	PP	35	20	5	79	.	16
Laserpitium nitidum	6.284 d	C	39	chilling (7d 5 °C) + KNO_3	PP	35	20	0	.	84	16
Lomelosia graminifolia	4.783 d	C	71	.	PP	35	15–25	18	.	.	82
Medicago lupulina	1.535 s	B	74	scarification after 21d ^{ISTA}	TP	35	20	76	1	.	23
Ononis spinosa s. str.	2.411 s	A	38	.	TP	56	15–25	5*	67	.	28
Phyteuma betonicifolium	0.038 s	B	90	chilling (7d 5 °C) + KNO_3	TP	56	15–25	64	.	.	36
Plantago lanceolata	1.022 s	B	89	chilling (7d 10 °C, 7d 5 °C) ^{ISTA}	TP	63	20–30	63	.	15	22
Ranunculus bulbosus	2.566 d	B	74	chilling (6 week 5 °C) + gibberellic acid	TP	87	15–25	29*	.	56	15
Rumex acetosa	1.505 d	B	75	chilling (7d 10 °C) ^{ISTA}	TP	63	20–30	54	.	17	29
Silene nutans s. str.	0.398 s	B	90	.	TP	28	15–25	87	.	.	13
Silene otites	0.390 s	C	71	.	TP	28	15–25	90	.	.	10
Silene vulgaris s. str.	0.606 s	A	70	.	TP	35	15–25	92	.	.	8
Stachys alopecuros	0.970 s	C	91	interposed chilling (7d 10 °C, 7d 5 °C)	TP	56	20	0*	.	10	90
Stachys recta	1.022 s	B	74	chilling (7d 10 °C, 7d 5 °C)	TP	56	20	47	.	33	20
Thalictrum minus s. str.	2.078 d	C	39	chilling (7d 5 °C) + gibberellic acid	TP	63	15–25	53	.	5	42
Trifolium campestre	0.457 s	B	75	. ^{ISTA}	TP	25	20	2	93	.	5
Trinia glauca	1.587 d	C	71	chilling (7d 5 °C) + KNO_3	TP	63	20	21*	.	31	48

During one year the position of all germinated seeds was recorded once or twice every month on a grid map and the seedlings were individually marked with coloured ringlets, so that their survival could be followed individually.

The vegetation of the subplots was recorded to distinguish between the following four structures: tussocks of *Molinia arundinacea*, edges of tussocks, vegetation composed of other species and bare soil.

Data analysis

The data analysis for testing microsite effects was complicated by the fact that the experimental design was an unbalanced "partial" split-plot design with counts. The ability to germinate and survive was rather low for most of the 32 investigated species resulting in many zero-values at the subplot level. Taking these zero-values and the several sources of

Table 2. Effects of the mowing and root-removing treatments on the germination and survival of the 24 most frequent species (> 5%), tested using REML ($P < 0.01$) and GLMM: positive (+), indifferent (.), negative (-) or not investigated (blank). Indices showing divergent test results: a – GLMM not significant, b – REML not significant.

Species (subspecies)	Effect of treatment			
	mowing		root-removing	
	germination	survival	germination	survival
Bromus erectus subsp. *condensatus*	-[b]	.		
Thalictrum minus s. str.	-	.		
Danthonia decumbens	-	.	.	.
Daucus carota	-	.	.	.
Laserpitium nitidum	-[a]	.		
Ononis spinosa s. str.	.	.	.	.
Trifolium campestre	.	.	.	.
Stachys alopecuros	.	.		
Plantago lanceolata	.	+[a]	+	.
Rumex acetosa	.	.	+[b]	.
Festuca paniculata	.	.	+	.
Medicago lupulina	.	.	+	.
Arabis hirsuta	+	+	+	.
Anthoxanthum odoratum	+[b]	.	+[b]	.
Holcus lanatus	+	.	+	.
Silene nutans s. str.	+	.	+	.
Achillea millefolium s.l.	+	.	+	.
Agrostis capillaris	+	.	+	.
Phyteuma betonicifolium	+[a]	.	+	.
Centaurea nigrescens	+[b]	.	.	.
Silene vulgaris s. str.	+	.	.	.
Silene otites	+	.		
Trinia glauca	+	+[a]		
Ranunculus bulbosus	+[a]	+[a]	.	.

variation into account, the subplot data were analyzed for each species separately using the following three models in GENSTAT 5.3 (1993):

(a) GLM (Generalized linear model) was used with the binomial error distribution, fitting block, mowing, block-plot interaction, root--removing, vegetation and block-plot-subplot interaction. As regression in GLM uses only one error term (GENSTAT 5 COMMITTEE 1993), other error terms were eliminated by treating the block and block-plot factors as other treatment factors. Significance was tested by comparing the change in deviance.

(b) REML (Residual maximal likelihood method) was used, fitting mowing, root-removal and vegetation as fixed effects and blocks as a random factor. (The block-plot-subplot interactions were left out because they did not affect the estimated means.) Unlike GLM, REML can account for more than one source of variation in the data, but it is constructed for normally distributed errors and the results for binomial data are therefore an approximation. Significance was tested with Wald's test.

(c) GLMM (Generalized linear mixed model) was used with binomial distribution and with the same fixed and random effects as REML. In this study, the null hypothesis was rejected when the standard error of differences had a smaller value than the difference in the absolute means between treatments.

The three approaches (a, b, c) showed similar results when effects of microsite quality for germination and survival were compared. Methods (a) and (b) differed only for *Anthoxanthum odoratum*. Using GLM (a), mowing and root-removing had an effect on the seedling emergence of *Anthoxanthum odoratum* (change in deviance = 4.32 and 10.81, respectively, d.f. = 1, $P < 0.05$), but not when using REML (Wald's statistic = 3.0 and 3.6, respectively, d.f. = 1). Results of the REML (b) and GLMM (c) approaches are shown in Tab. 2 and Fig. 4. REML tended to reject the null hypothesis more often than GLMM when the frequencies were small and when the variability within treatments was large (e.g. in the cases of *Laserpitium nitidum*, *Phyteuma betonicifolium* and *Ranunculus bulbosus*). GLMM, however, showed significance in cases where the differences between means of treatments were quite small (e.g. in the cases of *Anthoxanthum odoratum*, *Bromus erectus* subsp. *condensatus* and *Centaurea nigrescens*).

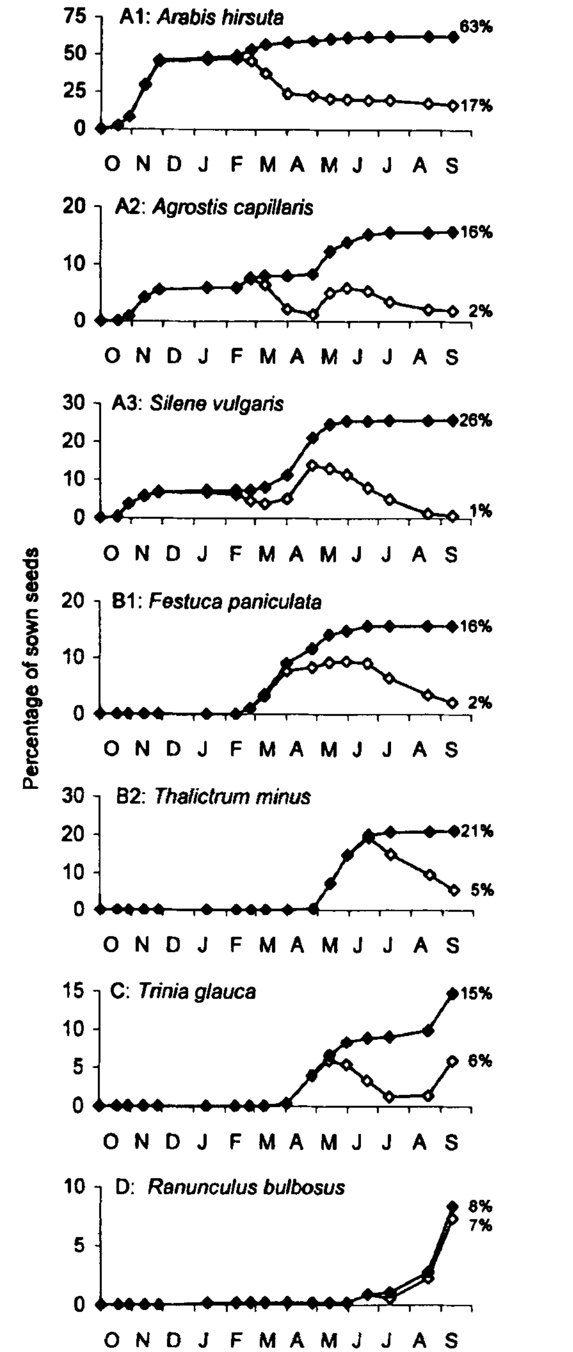

Fig. 3. Representatives of seven groups of species (A1, A2, A3, B1, B2, C and D) classified according to differences in seasonal germination patterns. Percentage germinated seeds (closed symbols) and surviving seedlings (open symbols) out of sown seeds on undisturbed soil (n = 576 seeds) over a period of 12 months (October 1997 – September 1998).

Differences between the treatments on root-removed soil (pots in abandoned and mown plots) were tested by a Mann-Whitney U-test (GENSTAT 5.3). Effects of seed size were also estimated using a Mann-Whitney U-test.

RESULTS

Germination

Germination ability under controlled conditions

Under laboratory conditions (Tab. 1) nine species showed high germination ability (> 80%), most species had reduced seed viability and three species did not germinate at all. For some species dormancy-breaking treatments or germination-stimulating factors were probably not optimal, or the duration of the test was not long enough, as higher germination rates were observed in the second germination test. The high proportion of dead seeds of *Cytisus sessilifolius* (98%) might have been due to damage from scarification. The poor germination success of other legumes *(Coronilla vaginalis, Ononis spinosa* and *Trifolium campestre)* may have been because of their hard seeds which were not scarified. High percentages of dead seeds were caused by seed--parasitism (in the case of *Astragalus glycyphyllos* which was affected by an insect of the family *Chalcidoidea*) and empty seeds (in the case of *Stachys alopecuros*). Germination ability under laboratory conditions was not used to correct the numbers of sown seeds in the field, but we shall include this aspect in the discussion of the field experiment.

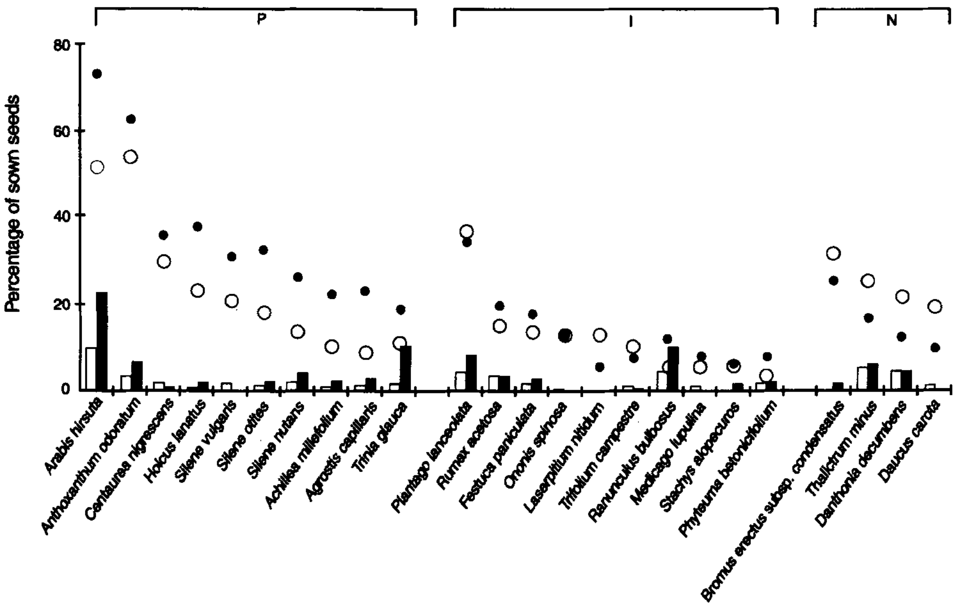

Fig. 4. Germination (circles) and survival (bars) of the 24 most frequent species and subspecies (> 5%) in abandoned (open symbols) and mown (closed symbols) plots of the seed-addition experiment between October 1997 and September 1998. Groups of taxa positively (P), indifferently (I) or negatively (N) affected by mowing (tested using GLMM). Within groups the taxa are shown in descending rank order of the cumulative number of germinated seeds.

Spontaneous germination in the field

Between October 1997 and September 1998, 39 species, 31 herbs, two lianas and six trees, germinated spontaneously in treatment subplots on undisturbed soil. All species showed established populations within a distance of less than 80 m of the study site. Most of these seedlings originated from the established species of the experimental plots, such as *Molinia arundinacea*, *Carex montana* and *Potentilla erecta*. In a subsequent article we will focus on the influence of mowing on spontaneous recruitment.

Germination of sown seeds in the field

Seedlings of the sown species were only observed in subplots where seeds were sown, except for a few seedlings which appeared in neighbouring subplots and pathways below the plots, after having been flooded as seeds or marked seedlings during thunderstorms in spring 1998. All species were affected irrespective of their dispersule weight or seed shape. Some marked seedlings were transported by water flow up to 30 cm from their place of germination. Seeds which did not germinate at their place of sowing, but in water gullies below the sowing location, were only included in the analysis if their place of sowing could reliably be reconstructed.

In the first year after sowing the species showed differences in germination rates. Seeds of 31 out of the 32 investigated species germinated (Appendix 1). *Arabis hirsuta* showed the highest germination success with more than 60% of seeds germinating on undisturbed soils (Fig. 3). Low germination rates (< 5% or < 30 emerging seedlings) were observed for the following eight species: *Astragalus glycyphyllos*, *Carex austroalpina*, *Carex baldensis*, *Coronilla vaginalis*, *Cytisus sessilifolius*, *Dictamnus albus*, *Lomelosia graminifolia* and

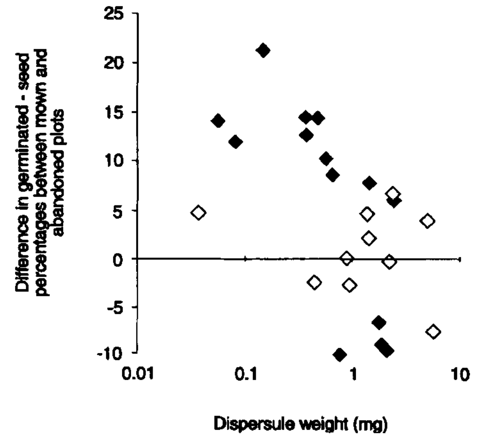

Fig. 5. Differences in germinated-seed percentages between mown and abandoned plots on undisturbed soil against the dispersule weight of the 24 most frequent species. Significantly different germination values of mown and abandoned plots (see Fig. 4; P and N) are shown with closed symbols.

Stachys recta. *Dictamnus albus* was the only species which did not germinate at all during the observation period. As the results for species showing low numbers of germinated seeds may have been strongly affected by chance, these species were excluded from a classification of seasonal germination patterns and from an analysis of microsite effects.

Seasonal patterns in germination of sown seeds

The 24 most frequent species showed differences in their seasonal germination patterns. As these patterns did not differ between the differently treated plots or the four structures of vegetation, the following groups of species could be classified (Fig. 3):

(A) Sixteen taxa started to germinate in the first 2 months after sowing. Taxa of group A1 (*Achillea millefolium*, *Anthoxanthum odoratum*, *Arabis hirsuta*, *Bromus erectus* subsp. *condensatus* and *Holcus lanatus*) mainly arose shortly after sowing in October and November 1997. A few seeds also germinated during the winter months, despite snow cover in December and at the end of January. A fairly warm period in February with temperatures up to 20 °C caused a renewed germination increase. Species of group A2 (*Agrostis capillaris*, *Medicago lupulina*, *Phyteuma betonicifolium*, *Rumex acetosa* and *Trifolium campestre*) showed similar germination success in the autumn/winter of 1997/98 and in the spring of 1998. Species of group A3 (*Centaurea nigrescens*, *Daucus carota*, *Plantago lanceolata*, *Silene nutans*, *Silene otites* and *Silene vulgaris*) had very low germination rates in the autumn of 1998. They did not germinate during the winter months and mostly arose after the melting of the last snow in the mid April 1998.

(B) Seedlings of six species emerged after the cold winter period in the spring of 1998. Species of group B1 (*Festuca paniculata* and *Ononis spinosa*) already started to germinate in February and continued until June. Species of group B2 (*Danthonia decumbens*, *Laserpitium nitidum*, *Stachys alopecuros* and *Thalictrum minus*) did not germinate before the end of April or May.

(C) Seedlings of *Trinia glauca* arose in April, May and again in September 1998.

(D) *Ranunculus bulbosus* first germinated in late summer and more frequently in autumn 1998.

Effects of treatments on germination

The seedling emergence of all species was higher in the mown than in the abandoned plots (Appendix 1, REML, Wald's statistic = 21.2, d.f. = 1, $P < 0.01$). However, mowing did not consistently affect germination of the 24 most frequent species (Fig. 4). Almost half of the species germinated better in the mown than in the abandoned plots, about one third behaved indifferently and for a small number of species germination was even negatively affected by

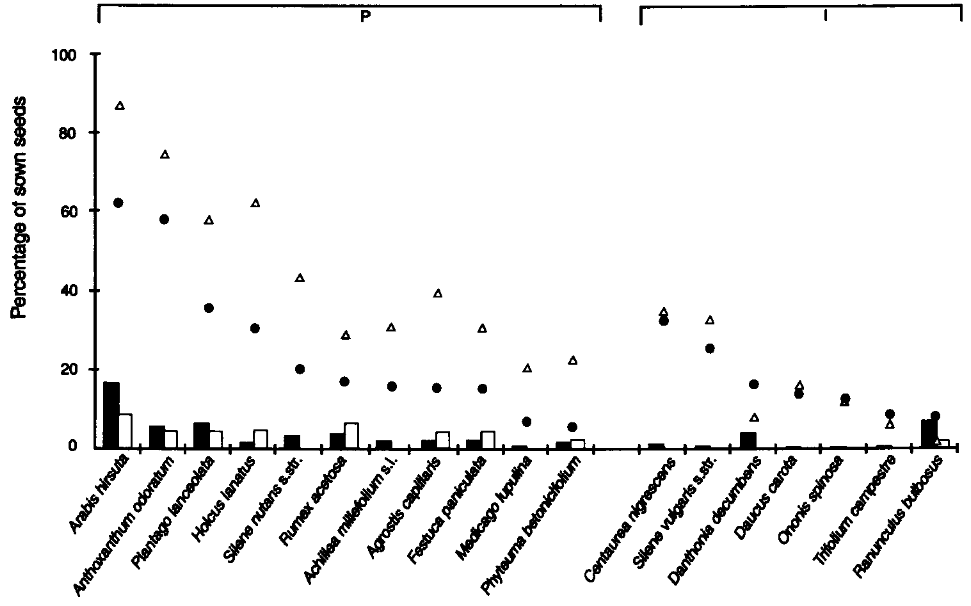

Fig. 6. Germination (circles) and survival (bars) of the 18 most frequent species (> 5%) in undisturbed-soil (closed symbols) and in root-removed-soil subplots (open symbols). Groups of species positively (P) or indifferently (I) affected by root-removing (tested using GLMM) with respect to germination between October 1997 and September 1998. Within groups the species are shown in descending rank order of the cumulative number of germinated seeds.

mowing. We found a tendency for the small seeds (dispersule weight < 1 mg) to germinate better in the mown than in the abandoned plots (Fig. 5, Mann-Whitney test for differences in germinated-seed percentages, U = 86, $n_{small} = 12$, $n_{large} = 12$, $P < 0.01$).

For all species the number of germinated seedlings over all species was higher on root-removed soil than on undisturbed soil (Appendix 1, Wald's statistic = 45.1, d.f. = 1, $P < 0.01$). The germination of more than half of the investigated species was favoured and no species showed significantly lower germination success on root-removed than on undisturbed soil (Fig. 6, Tab. 2). No difference in germination was found between pots in mown and pots in abandoned plots (Appendix 1, Mann-Whitney test, U = 6650, $n_1 = n_2 = 120$, $P = 0.31$).

Effects of vegetation structure on germination

For all species the number of germinated seedlings was lower on tussocks of *Molinia arundinacea* than at the edge of tussocks, on bare soil or in vegetation composed of other species (Appendix 1, Wald's statistic = 14.5, d.f. = 3, $P < 0.01$). The impact of established vegetation on seedling emergence was, however, not the same for all species. The germination of three grasses (*Agrostis capillaris, Anthoxanthum odoratum* and *Bromus erectus* subsp. *condensatus*) and three herbs (*Achillea millefolium, Arabis hirsuta* and *Centaurea nigrescens*) was positively affected by gaps (bare soil) and negatively affected by tussocks ($P < 0.01$). The difference between mown and abandoned plots was higher on bare soil than on tussocks (interaction mowing × vegetation, Wald's statistic = 12.1, d.f. = 3, $P < 0.01$), especially for *Thalictrum minus, Danthonia decumbens* and *Holcus lanatus* ($P < 0.01$). In abandoned plots

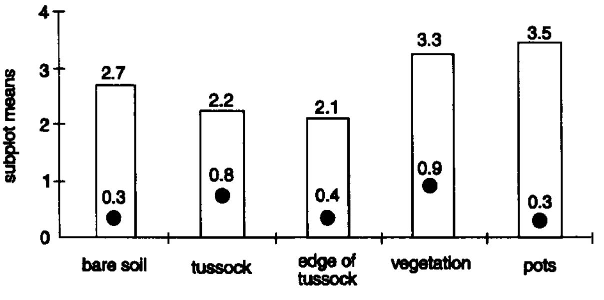

Fig. 7. Mean number of germinated seeds (open bars) and surviving seedlings (closed circles) of *Arabis hirsuta* in four types of vegetation cover on undisturbed and on root-removed soil in degradable pots.

Daucus carota germinated better on tussocks than on bare soil or in other vegetation, but in the reverse order on mown plots (Appendix 1, Wald's statistic for vegetation = 10.1 and the interaction of mowing × vegetation = 9.7, d.f. = 3, $P < 0.01$). All the other species were not influenced by the structure of vegetation.

Mortality and survival

Survival of sown seeds

Until the autumn of 1998 few seedlings of all 24 frequent species survived, apart from those of *Laserpitium nitidum* (Appendix 1). *Arabis hirsuta*, the species which germinated best, also showed the highest establishment of seedlings on undisturbed soil (16.5%). The highest survival ratios (i.e. surviving seedlings as a percentage of germinated seeds) were found for species which germinated mostly in the autumn of 1998, *Ranunculus bulbosus* (87.5%) and *Trinia glauca* (40%).

Seasonal patterns in seedling mortality

The main periods of seedling mortality were March, April and the summer of 1998 (Fig. 3). A few seedlings of group A already died in November and December 1997. The observed causes of mortality changed with season. During the late autumn and winter months seedlings died because of low temperatures. In the spring and summer of 1998 seedlings were killed by dry periods of 1–3 weeks, heavy rains or herbivory by slugs and grasshoppers.

Effects of treatments on survival

The seedlings of a few species benefited from mowing (Fig. 4, Appendix 1). Mowing had a positive effect on *Plantago lanceolata*, because it died mainly in abandoned plots (Tab. 2, Wald's statistic = 4.1, d.f. = 1, $P < 0.05$). *Arabis hirsuta, Ranunculus bulbosus* and *Trinia glauca* were the only species which germinated and also survived better in mown plots (Tab. 2, Wald's statistic = 12.8, 7.5 and 18.3, respectively, d.f. = 1, $P < 0.01$).

In the decomposing pots seedling mortality was generally very high. No species survived significantly better in pots than on undisturbed soil (Fig. 6, Tab. 2). No difference in survival was found between pots in mown and abandoned plots (Appendix 1, Mann-Whitney test, U = 7023, $n_1 = n_2 = 120$, $P = 0.74$).

Effects of vegetation structure on survival

The number of seedlings which survived until September 1998 was generally not lower on tussocks of *Molinia arundinacea* than on bare soil (Appendix 1). This was also the case for species which showed lower germination on tussocks than on bare soil. *Arabis hirsuta* even survived best when protected by established plants (Fig. 7, Wald's statistic = 8.8, d.f. = 3, $P < 0.05$).

DISCUSSION

Effects of treatments on germination

Effects of mowing on germination

Differences between the treatments in germination success among the species can be interpreted as different microsite preferences for these species. Between the treatments of mowing and abandonment the following factors may have mainly affected microsite quality at the soil surface: (i) light, (ii) variation of temperature, (iii) soil moisture and (iv) susceptibility of the soil to erosion caused by floods which follow heavy rainstorms. Light availability was increased in mown plots, due to the prevention of the accumulation of a dense layer of *Molinia arundinacea* litter in the autumn. The litter prevented the soil surface in abandoned plots from being desiccated during the short dry periods in 1998.

Whereas a few species germinated better under the litter of *Molinia arundinacea*, many more germinated better under the more variable environmental conditions of the mown grassland. Most of the investigated species with small seeds belong to this second group. This result is in accordance with BURKE & GRIME (1996) who found that small-seeded species were more dependent on disturbance (gap creation) than large-seeded ones.

The species-specific timing of germination was not influenced by the altered environmental conditions after mowing. According to MURDOCH & ELLIS (1992) dormancy-breaking factors depend upon seasonally variable environmental and weather conditions. We suppose therefore that these conditions are more important than the microsite conditions for the timing of germination. Nevertheless, the microsite conditions determined the frequency of germination of the investigated species.

Effects of root-removing on germination

For germination, the greatest differences in microsite quality between undisturbed and root-removed soil (of the small pots) may be the following: (i) soil looseness, (ii) soil chemistry (pH in the soil surrounding *Molinia arundinacea* tussocks and in the pots was lower than in bare surface-soil, measured with HELLIGE Indicator, results not shown) and (iii) the lack of established plants, especially the roots of *Molinia arundinacea*. The impact of the root-removal treatment on the canopy structure can be neglected because of the small size and the low density of the pots. The water-content of the soil in the pots was similar to that of bare soil with respect to soil-surface structure.

As most species showed higher germination in pots than on bare soil and the germination success was often equal on bare soil and within vegetation other than *Molinia arundinacea*, we conclude that the soil structure was very important for germination.

Effects of vegetation structure on germination and seedling survival

Large gaps between *Molinia* tussocks (bare soil) and small gaps between *Carex* stalks created "safe sites" for germination (HARPER et al. 1961) for most of the investigated species. However, "safe sites" were not implicitly the same for germination and survival. In our experiment low germination success, but high survival ratios in tussocks of *Molinia arundinacea* were observed, especially for *Arabis hirsuta*. Within tussocks the light availability might have limited germination, but seeds which germinated, may have been protected by *Molinia* from being uprooted by frost heaving, from being washed away after thunderstorms and from herbivory by slugs and grasshoppers. RYSER (1993) described how tussocks of

Bromus erectus and tufts of *Onobrychis viciifolia* had a soil stabilizing effect which positively affected the survival of the *Arabis hirsuta* seedlings.

Mortality and survival

Mortality was generally very high. Several of the sown species even disappeared from the experimental plots after one year, despite their relatively high numbers of germinated seeds. Most of these seedlings died because of unfavourable weather conditions, unsuitable microsite qualities and seedling herbivory. The pressure of herbivores was especially high in spring and summer and has probably been avoided or minimized by species germinating in autumn (e.g. *Arabis hirsuta*) or by a lower palatability of some species (e.g. *Plantago lanceolata).* This result is in accordance with other authors, who pointed out the importance of seasonally varying seedling herbivory (MILES 1973, GRUBB 1977, HANLEY 1998).

During the observed 12-month period the survival of many characteristic meadow species was not affected by mowing (e.g. *Anthoxanthum odoratum* and *Danthonia decumbens*). We assume that mowing generally has a positive influence on their survival, but this could not be detected during our observation period, because of the high overall mortality rates.

Influence of origin of seeds

Three species which did not occur in grasslands on Monte San Giorgio, but on neighbouring mountains (*Silene otites*, *Thalictrum minus* and *Trinia glauca*), were potentially able to grow at the experimental site. Most of the species originating from Monte Barro, however, showed great difficulties in germinating or surviving. The germination was low because of rather low seed quality (e.g. *Carex austroalpina*, *Carex baldensis*, *Lomelosia graminifolia* and *Stachys alopecuros*) or due to a lack of factors which are necessary to break dormancy or which stimulate germination (e.g. *Coronilla vaginalis*, *Cytisus sessilifolius* and *Dictamnus albus*).

Species from similar environmental sites are therefore supposed to be able to grow on Monte San Giorgio provided that the quality of the added seeds is high.

CONCLUSION

Recruitment limitation was indicated by the fact that no species emerged which was not present in the surrounding established vegetation. Thirty-one out of the 32 investigated species germinated only in plots in which seeds had been added but did not appear elsewhere at the study site. This result is in accordance with other recent studies which have pointed out the importance of dispersal limitation (PRIMACK & MIAO 1992, BURKE & GRIME 1996, TILMAN 1997, STAMPFLI & ZEITER 1999).

Microsite limitation was shown for at least six sown species, which had germinated when seeds were added but which did not survive one year, and for seven species which survived only in one of the treatments. The distinction between dispersal and microsite limitation in field experiments may not always be simple. Occasional immigration with unsuccessful survival can only be detected with short control intervals as in our seed-addition experiment.

In addition, no evidence of gap dependence for seedling establishment could be found in this study. Weather conditions, unsuitable microsite qualities and herbivory mainly controlled seedling emergence and survival. We conclude that dispersal limitation, microsite and weather conditions play an important role for the restoration of species-rich meadows on Monte San Giorgio.

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REFERENCES

AGUIAR M.R., SORIANO A. & SALA O.E. (1992): Competition and facilitation in the recruitment of seedlings in Patagonian steppe. *Funct. Ecol.* 6: 66–70.

BAKKER J.P. (1989): *Nature management by grazing and cutting*. Kluwer, Dordrecht.

BLN (1977): *Bundesinventar der Landschaften und Naturdenkmähler von nationaler Bedeutung*. Eidgenössisches Departement des Innern, Bern.

BRIEMLE G. & ELLENBERG H. (1994): Zur Mahdverträglichkeit von Grünlandpflanzen, Möglichkeiten der praktischen Anwendung von Zeigerwerten. *Natur & Landschaft* 69: 139–147.

BURKE M.J.W. & GRIME J.P. (1996): An experimental study of plant community invasibility. *Ecology* 77: 776–790.

GENSTAT 5 COMMITTEE (1993): *GENSTAT 5.3. Reference manual.* Clarendon Press, Oxford.

GOLDBERG D.A. & WERNER P.A. (1983): The effects of size of opening in vegetation and litter cover on seedling establishment of goldenrods (*Solidago* spp.). *Oecologia* 60: 149–155.

GRUBB P.J. (1977): The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* 52: 107–145.

HANLEY M.E. (1998): Seedling herbivory, community composition and plant life history traits. *Perspect. Pl. Ecol. Evol. Syst.* 2: 191–205.

HARPER J.L., CLATWORTHY J.N., MCNAUGHTON I.H. & SAGER G.R. (1961): The evolution and ecology of closely related species living in the same area. *Evolution* 15: 209–227.

HODGSON J.G., GRIME J.P., HUNT R. & THOMPSON K. (1995): *The electronic comparative plant ecology*. Chapman & Hall, London.

ISTA (1996): *International rules for seed testing 24, Supplement.* ISTA, Zürich.

KOCH W. (1943): Das *Andropogonetum Grylli insubricum*, eine Trockenwiesen Assoziation des Südtessin. *Ber. Schweiz. Bot. Ges.* 53: 579–594.

LAUBER K. & WAGNER G. (1996): *Flora Helvetica.* Haupt, Bern.

LÜDI W. (1949): Bericht über den 6. Kurs in Alpenbotanik. *Ber. Geobot. Forschungsinst. Rübel Zürich* 1948: 12–50.

MILES J. (1973): Early mortality and survival of self-sown seedlings in Glenfeshie, Inverness-shire. *J. Ecol.* 61: 93–98.

MURDOCH A.J. & ELLIS R.H. (1992): Longevity, viability and dormancy. In: FENNER M. (ed.), *Seeds – the ecology of regeneration in plant communities*, CAB International, Wallingford, pp. 193–222.

PIGNATTI S. (1982): *Flora d'Italia.* Edagricole, Bologna.

POSCHLOD P. & JACKEL A.-K. (1993): Untersuchungen zur Dynamik von generativen Diasporenbanken von Samenpflanzen in Kalkmagerrasen. 1. Jahreszeitliche Dynamik des Diasporenregens und der Diasporenbank auf zwei Kalkmagerrasenstandorten der Schwäbischen Alb. *Flora* 188: 49–71.

PRIMACK R.B. & MIAO S.L. (1992): Dispersal can limit local plant distribution. *Conservation Biol.* 6: 513–519.

RUSCH G. & FERNANDEZ-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: 195–202.

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, *Münstersche Geogr. Arbeiten* 20: 111–153.

ŠPAČKOVÁ I., KOTOROVÁ I. & LEPŠ J. (1998): Sensitivity of seedling recruitment to moss, litter and dominant removal in an oligotrophic wet meadow. *Folia Geobot.* 33: 17–30.

STAMPFLI A. (1992): Effects of mowing and removing litter on reproductive shoot modules of some plant species in abandoned meadows of Monte San Giorgio. *Bot. Helv.* 102: 85–92.

STAMPFLI A., GUGGISBERG F., BERLI S. & PESTALOZZI H. (1994): The abandoned *Danthonia alpina*-grasslands on Monte San Giorgio: evidence of floristic changes and suggested management practices. *Diss. Bot.* 234: 59–78.

STAMPFLI A. & ZEITER M. (1999): Plant species decline due to abandonment of meadows cannot easily be reversed by mowing. A case study from the southern Alps. *J. Veg. Sci.* 10: 151–164.

STAMPFLI A. & ZEITER M. (in press): Species responses to climatic variation and land-use change in grasslands of southern Switzerland. In: BURGA C.A. & KRATOCHWIL A. (eds.), *Biomonitoring*, Kluwer, Dordrecht.

TILMAN D. (1993): Species richness of experimental productivity gradients: how important is colonisation limitation? *Ecology* 74: 2179–2191.

TILMAN D. (1997): Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78: 81–92.

WILLEMS J.H. (1983): Species composition and above ground phytomass in chalk grassland with different management. *Vegetatio* 52: 171–180.

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.

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APPENDIX

Germination and survival success of the 32 sown species in differently treated plots and in four structures of vegetation. Percentage of germinated (G) and surviving (S) individuals and number of sown seeds (N). A dot indicates that a species was not sown at this treatment. A dash indicates that the vegetation structure did not occur.

Species (subspecies)	Treatments root-removing				Treatments undisturbed soil				Vegetation structure bare soil					
	abandoned		mown		abandoned		mown		abandoned			mown		
	G	S	G	S	G	S	G	S	G	S	*n*	G	S	*n*
	(*n* = 24)		(*n* = 24)		(*n* = 288)		(*n* = 288)							
Agrostis capillaris	25.0	4.2	54.2	4.2	8.7	1.0	22.9	2.8	13.4	0.9	112	31.3	6.3	112
Anthoxanthum odoratum	75.0	4.2	75.0	4.2	54.2	3.5	62.8	6.9	57.3	2.6	192	76.3	6.3	80
Bromus erectus subsp. *condensatus*	.	.	.	.	31.6	0.0	25.3	1.0	31.9	0.0	144	30.2	0.0	96
Danthonia decumbens	4.2	0.0	12.5	0.0	21.5	4.2	12.5	4.2	29.0	5.1	176	8.3	0.0	48
Festuca paniculata	33.3	0.0	29.2	8.3	13.5	1.4	17.7	2.8	8.9	0.0	112	19.6	3.6	112
Holcus lanatus	58.3	0.0	66.7	8.3	23.3	0.7	37.8	1.7	12.5	0.0	80	51.6	3.1	64
Carex austroalpina	.	.	.	.	3.1	1.4	5.6	2.4	0.9	0.0	112	5.0	2.5	80
Carex baldensis	.	.	.	.	1.4	0.0	0.7	0.0	1.3	0.0	80	0.0	0.0	80
Achillea millefolium s.l.	29.2	0.0	33.3	0.0	10.1	0.7	22.2	2.4	9.7	0.7	144	30.2	2.1	96
Arabis hirsuta	87.5	8.3	87.5	8.3	51.7	10.1	73.3	22.9	54.2	6.3	48	81.3	11.0	64
Astragalus glycyphyllos	8.3	0.0	4.2	0.0	1.4	0.0	0.0	0.0	2.1	0.0	96	0.0	0.0	96
Centaurea nigrescens	33.3	0.0	37.5	0.0	29.9	1.7	36.1	0.7	35.7	0.9	112	35.7	0.0	112
Coronilla vaginalis	.	.	.	.	0.3	0.0	1.0	0.0	0.6	0.0	176	1.8	0.0	112
Cytisus sessilifolius	.	.	.	.	1.0	0.0	2.4	0.3	1.0	0.0	96	6.3	1.6	64
Daucus carota	20.8	0.0	12.5	0.0	19.4	0.7	9.7	0.0	12.5	0.0	96	15.6	0.0	64
Dictamnus albus	.	.	.	.	0.0	0.0	0.0	0.0	0.0	0.0	176	0.0	0.0	96
Laserpitium nitidum	.	.	.	.	12.8	0.0	5.6	0.0	10.7	0.0	112	0.0	0.0	64
Lomelosia graminifolia	.	.	.	.	2.4	0.0	2.4	0.0	2.5	0.0	160	1.6	0.0	64
Medicago lupulina	25.0	0.0	16.7	0.0	5.6	0.7	8.0	0.0	6.8	1.1	176	12.5	0.0	48
Ononis spinosa s. str.	8.3	0.0	16.7	0.0	12.8	0.3	12.8	0.0	17.4	0.7	144	11.6	0.0	112
Phyteuma betonicifolium	12.5	0.0	33.3	4.2	3.1	1.4	8.0	1.7	2.5	0.6	160	7.5	0.0	80
Plantago lanceolata	70.8	0.0	45.8	8.3	36.8	3.8	34.4	8.3	46.5	5.6	144	25.0	6.3	64
Ranunculus bulbosus	4.2	4.2	0.0	0.0	4.9	4.2	11.8	10.4	12.5	10.4	96	8.3	8.3	48
Rumex acetosa	29.2	12.5	29.2	0.0	14.9	3.5	19.8	3.5	18.8	2.5	80	18.8	4.2	48
Silene nutans s. str.	33.3	0.0	54.2	0.0	13.5	1.7	26.4	4.2	14.8	2.3	128	35.9	3.1	64
Silene otites	.	.	.	.	18.1	1.0	32.6	2.4	13.9	0.7	144	41.3	1.3	80
Silene vulgaris s. str.	25.0	0.0	41.7	0.0	20.5	1.4	30.9	0.3	20.8	0.7	144	43.8	0.8	128
Stachys alopecuros	.	.	.	.	5.6	0.0	5.9	1.0	4.7	0.0	128	8.3	0.0	96
Stachys recta	0.0	0.0	0.0	0.0	1.0	0.0	0.7	0.0	0.7	0.0	144	0.0	0.0	160
Thalictrum minus s. str.	.	.	.	.	25.3	5.2	16.7	5.9	28.1	4.2	96	10.9	1.6	64
Trifolium campestre	4.2	0.0	8.3	0.0	10.1	0.7	7.6	0.3	0.0	0.0	16	11.3	1.3	80
Trinia glauca	.	.	.	.	10.8	1.4	18.8	10.4	6.9	1.3	160	21.3	11.3	160

Vegetation structure *Molinia* tussock						Vegetation structure edge of tussock						Vegetation structure other vegetation					
abandoned			mown			abandoned			mown			abandoned			mown		
G	S	*n*	G	S	*n*	G	S	*n*	G	S	*n*	G	S	*n*	G	S	*n*
10.9	3.1	64	0.0	0.0	32	4.7	0.0	64	37.5	0.0	16	0.0	0.0	48	19.5	0.8	128
46.3	6.3	80	37.5	1.0	96	-	-	0	75.0	10.0	80	56.3	0.0	16	75.0	18.8	32
22.5	0.0	80	14.6	2.1	48	31.3	0.0	32	33.3	0.0	48	53.1	0.0	32	21.9	2.1	96
7.8	0.0	64	17.2	4.7	128	6.3	6.3	16	16.7	12.5	48	15.6	6.3	32	3.1	0.0	64
20.3	4.7	64	13.8	3.8	80	18.8	3.1	32	25.0	2.1	48	12.5	0.0	80	12.5	0.0	48
20.3	0.0	64	32.8	3.1	64	56.3	6.3	16	20.3	0.0	64	27.3	0.8	128	43.8	1.0	96
2.1	0.0	48	3.1	0.0	32	4.2	0.0	48	6.3	3.1	64	6.3	5.0	80	6.3	2.7	112
0.9	0.0	112	0.0	0.0	112	0.0	0.0	48	1.6	0.0	64	4.2	0.0	48	3.1	0.0	32
4.7	1.6	64	18.8	3.1	96	15.6	0.0	32	0.0	0.0	16	14.6	0.0	48	21.3	2.5	80
39.1	8.5	128	72.2	29.3	144	43.8	0.0	16	62.5	18.8	64	68.8	15.8	96	93.8	31.3	16
1.0	0.0	96	0.0	0.0	64	0.0	0.0	32	0.0	0.0	32	1.6	0.0	64	0.0	0.0	96
22.7	2.3	128	26.0	2.1	96	37.5	6.3	16	50.0	0.0	32	34.4	0.0	32	47.9	0.0	48
0.0	0.0	96	1.3	0.0	80	-	-	0	0.0	0.0	48	0.0	0.0	16	0.0	0.0	48
0.0	0.0	64	0.8	0.0	128	0.0	0.0	32	4.2	0.0	48	2.1	0.0	96	0.0	0.0	48
27.1	2.1	96	5.0	0.0	80	37.5	0.0	32	14.1	0.0	64	9.4	0.0	64	6.3	0.0	80
0.0	0.0	96	0.0	0.0	96	0.0	0.0	96	0.0	0.0	16	-	-	0	-	-	0
10.0	0.0	80	8.6	0.0	128	18.8	0.0	16	0.0	0.0	16	17.5	0.0	80	6.3	0.0	80
3.1	0.0	64	2.1	0.0	144	0.0	0.0	16	2.1	0.0	48	2.1	0.0	48	6.3	0.0	32
5.0	0.0	80	7.5	0.0	80	-	-	0	5.0	0.0	80	0.0	0.0	32	8.8	0.0	80
8.3	0.0	48	10.9	0.0	64	16.7	0.0	48	31.3	0.0	16	0.0	0.0	48	12.5	0.0	96
10.4	6.3	48	3.1	1.0	96	0.0	0.0	16	3.1	3.1	32	0.0	0.0	64	16.3	3.8	80
16.7	0.0	48	26.0	6.3	96	56.3	0.0	16	46.9	12.5	96	27.5	3.8	80	40.6	6.3	32
2.5	2.5	80	12.5	10.7	112	0.0	0.0	32	6.3	6.3	32	0.0	0.0	80	14.6	12.5	96
11.8	4.2	144	20.5	3.4	176	6.3	6.3	16	18.8	6.3	16	20.8	2.1	48	18.8	2.1	48
11.3	2.5	80	28.1	6.3	160	18.8	0.0	16	-	-	0	12.5	0.0	64	12.5	0.0	64
26.6	0.0	64	18.8	6.3	80	-	-	0	38.8	1.3	80	18.8	2.5	80	31.3	0.0	48
24.0	2.1	96	17.0	0.0	112	6.3	0.0	16	18.8	0.0	32	15.6	3.1	32	37.5	0.0	16
4.2	0.0	96	3.6	1.8	112	-	-	0	18.8	6.3	16	9.4	0.0	64	3.1	0.0	64
3.1	0.0	64	0.0	0.0	64	0.0	0.0	16	6.3	0.0	16	0.0	0.0	64	2.1	0.0	48
21.9	7.3	96	17.0	8.9	112	43.8	0.0	16	10.9	1.6	64	22.5	5.0	80	31.3	10.4	48
13.4	0.9	112	1.6	0.0	64	6.3	1.6	64	4.2	0.0	48	10.4	0.0	96	10.4	0.0	96
14.1	1.6	64	17.2	12.5	64	12.5	0.0	32	15.6	3.1	32	21.9	3.1	32	12.5	9.4	32