Litter and living plants have contrasting effects on seedling recruitment in subalpine grasslands

Vegetace a opad mají opačný vliv na vzcházení semenáčů v subalpinských travinných společenstevech

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In the internal French Alps, subalpine grasslands become dominated by the tussock grass, *Festuca paniculata,* when mowing ceases. Does litter or living plants affect seedling recruitment in these subalpine communities, and does this vary between mown and unmown grasslands? Can the vegetation patterns observed in the field be related to the effects of *F. paniculata* ? These hypotheses were tested using both a field and pot experiment. Seedlings of *Bromus erectus,* a subordinate species in these grasslands, were used as phytometers in both experiments. At both mown and unmown subalpine grassland sites in the French Alps, a removal experiment was established. This field experiment included removal of litter and living vegetation in order to differentiate their respective effect on seedling establishment. Vegetation and litter had contrasting effects. Vegetation affected the recruitment success of *B. erectus* by limiting seedling growth at the mown site and survival at the unmown site. Litter modified recruitment only at the unmown site, where it increased survival but limited growth. Survival and growth of seedlings responded to different environmental factors. Survival was determined more by soil moisture, while growth probably depended more on light availability. Where there is a thick litter layer, as is the case in unmown subalpine grasslands, the competitive effect of vegetation can be counterbalanced by an increase in soil moisture due to the litter reducing rate of evaporation of water. The effect on seedlings of the presence of *Festuca paniculata*, the dominant species at these sites, was also quantified using a pot experiment, including a cutting treatment. This experiment showed that the competitive effect of the vegetation could be largely explained by the inhibitory effect on growth of the dominant species, *F. paniculata*. This study provides a better understanding of the processes that result in conservative plants, such as *F. paniculata,* becoming dominant in these subalpine environments upon cessation of traditional management practices.

Keywords: *Bromus erectus*, competition, facilitation, *Festuca paniculata*, growth, litter, recruitment, survival

Introduction

The biodiversity of subalpine grasslands in the Alps is under threat due to the abandonment of agricultural practices such as mowing (MacDonald et al. 2000, Tasser & Tappeiner 2002). The cessation of mowing often leads to plant communities becoming strongly dominated by large and tough caespitose grasses, such as *Festuca paniculata,* in the southern parts of the French, Italian and Swiss Alps (Jouglet & Dorée 1991, Vittoz et al. 2005, Quétier et al. 2007). *Festuca paniculata* (L.) Schinz & Thell can be very abundant in such subalpine grasslands (Quétier et al. 2007). It is a tall plant with a conservative strategy (i.e. thick leaves, high carbon content, low decomposability, vegetative height: 30–50 cm) and produces a thick layer of litter (Gross et al. 2007). This layer is likely to affect other species, in particular via seedling recruitment, which could explain the lower diversity in such grasslands compared to mown grasslands. However, recruitment processes in mountain grasslands are largely unknown (Stampfli & Zeiter 2004). In this study, one of the objectives was to determine whether the deep litter layer produced by *F. paniculata* can affect seedling recruitment in subalpine plant communities.

Seedlings recruitment is widely recognized to be of primary importance in the maintenance of diversity and coexistence of species (Grubb 1977, Fenner & Kitajima 1999, Burt-Smith et al. 2003, Zeiter et al. 2006). In established communities, the microenvironment is altered by the presence of adult plants and this can affect the establishment of seedlings (Suding & Goldberg 1999). Such biotic interactions between seedling and adult plants can result from competition for resources, facilitation (protection from grazing and from physical damage) and/or via the amount of litter. The effect of plant litter on neighbouring plants can differ from that of living vegetation (Foster & Gross 1997, Suding & Goldberg 1999, Violle et al. 2006). For example, while living plants limit the growth of neighbouring plants by competing for resources, litter can enhance their growth by reducing evaporation of water from the soil. However the effect of litter remains unclear, especially in subalpine grasslands. Depending on the situation, litter decreases (Jensen & Meyer 2001, Wilby & Brown 2001, see Facelli & Pickett 1991b, Xiong & Nilsson 1999 for a review) or increases seedling recruitment (Xiong et al. 2003, Eckstein & Donath 2005, Violle et al. 2006). Indeed, litter can exert different kinds of effects: chemical, physical or mechanical, which can limit the growth of plants (Carson & Peterson 1990, Facelli & Pickett 1991b, Rotundo & Aguiar 2005). These negative effects, however, can be counterbalanced by its ability to retain water, enhance nutrient availability or protect plants from lethal frosts or herbivory (Eckstein & Donath 2005, Violle et al. 2006, see for a review Facelli & Pickett 1991a, b). Young plants are often more affected by the presence of litter than adult plants (Xiong et al. 2003) because the leaves of seedlings are often under the litter layer and as they are shallow rooted they are more vulnerable to variations in soil surface moisture. More generally, the absence of reserves makes seedlings highly sensitive to any environmental factor. Where litter quantities are greater than 200 $g \cdot m^{-2}$, which is the case in subalpine grasslands in the Southern Alps that are not mown, the effects of the litter are generally negative (Xiong & Nilsson 1999, Violle et al. 2006). Given the observation that biodiversity decreases with increase in litter that occurs with an increase in the abundance *F. paniculata* (Quétier et al. 2007), it is predicted that the main effect of litter in such subalpine grasslands will be negative.

The following hypotheses were investigated: (i) Litter and living vegetation have a negative effect on seedlings recruitment in subalpine grasslands; (ii) The effect of vegetation (the whole community) is largely due to the negative effect of the dominant species, *F. paniculata*. The first hypothesis was tested using a field experiment. This experiment focussed on two typical types of subalpine grasslands (Jouglet & Dorée 1991): one that has been continuously mown for several centuries, and the other unmown for several decades. To test the second hypothesis, a pot experiment was conducted to determine the effect of monospecific stands of *Festuca paniculata* on seedling recruitment.

Material and methods

Study site

The field experiment was done in subalpine grasslands in the French Alps (Villar d'Arène, Hautes-Alpes, 44°59'N, 6°23'E), at an altitude of 1900 m a.s.l. Average temperatures varied between –1.6° C in January and 14° C in July/August (interpolated from the nearby Besse-en Oisans meteorological station, alt. 1470 m, reference period 1953–1990, Météo France). Two sites, representative of the two main subalpine grassland types in the study area (Jouglet & Dorée 1991), separated by ca 100 m and both facing south-west, were chosen. The first site had been mown for over a century to produce hay for winter feed. At the second site mowing ceased 35 years ago (Quétier et al. 2007). Both of these sites are dominated by *Festuca paniculata* (L.) Schinz & Thell, a large tussock grass producing abundant litter (Table 1). Where mowing occurs, the abundance of *F. paniculata* is limited to only 38% of the biomass, whereas cessation of mowing results in it increasing to over 70% of the biomass, with consequent reductions in total species diversity (Quétier et al. 2007). Mown and unmown sites were located on the same soil type, which had the same available water content (Gross et al. 2008).

Field experiment

A removal field experiment was conducted to investigate the biotic interactions at the two sites. There were three replicates at each site. Within each replicate, three 1.2 × 1.2 m plots were selected for the different treatments. Thus, there were 18 plots at both sites. The first treatment (–V–L) was the removal of vegetation and litter, first by means of an application of a systemic herbicide (glyphosate, Roundup®) on 10 May 2004, and then the green biomass and litter were removed by hand two weeks later. The second treatment (–V+L), determined the effect of litter, with the litter present before the glyphosate treatment left on the soil and the poisoned green biomass (which differed from the original litter and thus could be easily identified) removed. The third treatment was the control (+V+L), in which the vegetation and litter was left intact. Roots that extended into the plots from the surrounding vegetation were severed down to a depth of 20 cm around the –V–L and –V+L plots using a knife. During the experiment, treatments were inspected and weeded by hand every two weeks. *Bromus erectus* Huds. was used as a phytometer to assess the biotic interactions in each treatment. *Bromus erectus* is a subordinate perennial species of caespitose grass making up only 0.2% of the biomass in these grasslands. Seeds of *B. erectus* were collected at the end of July 2003 from populations at the same site as used for the experiment and stored at ambient temperature (15–20° C) in paper bags in the dark. In May 2004, seeds were germinated on potting compost in the laboratory. Three weeks later, all the seedlings had two leaves and they were transplanted one week prior to canopy closure (24–28 May 2004). This period corresponds to the time when seeds germinate during the snowmelt and reach the two leaf stage, equivalent to the state they reached in the laboratory. Eight seedlings were planted in each plot. Seedlings were planted 20 cm from the plot edges in a square 80 × 80 cm pattern, with one seedling at each corner and one seedling in the middle of each side with seedlings separated by at least 40 cm. Seedling naked roots were planted directly into small holes. A total of 144 seedlings (eight seedlings × three treatments × three replicates × two sites) were transplanted. No mortality occurred

Table 1. – Features of the two experimental sites. The percentage interception of light was measured above the litter layer. Relative cover data were obtained from the experimental plots (2005), while abundances (frequencies from a transect-point method), living and litter biomass data are from Quétier et al. (2007) for the same fields (sampled in July 2004). Differences between the two sites in relative cover of bare soil and litter were significant ($F_{1,22} = 9.64$, $P = 0.005$ for bare soil, and $F_{1,22} = 7.73$, $P = 0.011$ for litter). Dominant species are those that make up 80% of abundance.

Site	Management	Altitude (m a.s.l.)	Dominant species	Slope	Above-ground living biomass (g·m^{-2})	Litter biomass (g·m^{-2})	Light inter-ception (%)	Bare soil cover (%)	Litter cover (%)
Mown	Mowing Mown in August every year (one harvest)	1990	*Festuca paniculata* (38%) *Meum athamanticum* (13%) *Festuca nigrescens* (10%) *Festuca laevigata* (8%) *Trifolium alpinum* (5%) *Carex sempervirens* (4%)	20°	268.8 ±4.9	76.6 ±1	37.0	4.6	22.4
Unmown	No mowing Formerly mown 50 years ago	1960	*Festuca paniculata* (70%) *Festuca nigrescens* (9%) *Festuca laevigata* (8%)	26°	417.8 ±82.1	392.3 ±41.6	51.2	0.7	56.7

during the two weeks following transplantation. Seedling survival and growth, two components of fitness via which competition can be measured, were quantified (Aarssen & Keogh 2002, Violle et al. 2006). Survival and growth were monitored on 14 September 2004. Growth was measured as the change in number of leaves, as all seedlings had the same number of leaves (two leaves) when they were transplanted. The number of leaves is significantly correlated with the root square transformation of seedling biomass ($F_{1,332} = 5172$, $P < 0.0001$, $R^2 = 0.94$), which was measured in the pot experiment carried out under many different conditions, including competition and nutrient addition. Soil moisture was measured in each treatment at both sites during 2005 using 10 TDR probes/plot (mini TRASE system1, Soil Moisture Equipment Corporation, Santa Barbara, CA, USA) on 14 dates during the period June to 15 September, which corresponds to a range of dry periods after rainfall of 1 to 26 days. The data presented is the average for the 14 dates. Probes were buried at a depth of 15 cm and measurements recorded at midday. It is acknowledged that these measurements were made one year after the seedling recruitment experiment. However, at the field site, the moisture measurements were consistent throughout the season and differences between treatments remained constant (Gross et al. 2008). In the –V treatments, new plants were individually killed using Roundup®. Light transmittance above and below the canopy but above the litter was measured on the 14 July 2004 at three randomly selected locations at each site, using a 1 m long measuring rod fitted with a PhotoActive Radiation sensor (LI-191 Line Quantum Sensor, LI-COR). Bare soil and litter cover were estimated visually at each site in twelve 40 × 40 cm quadrats, within which the numbers of 2.5 × 2.5 cm cells with bare soil, litter and vegetation were counted on three occasions between 24–25 May 2005 and complete canopy closure in mid-June. This period coincides with the first critical growth phase of seedlings after snow melt (personal observation).

Pot experiment

To determine the effect of the dominant species in the grassland, a pot experiment was conducted. Individuals of *F. paniculata* were collected from the field in August 2003 and planted in 28 cm diameter pots (corresponding to 615.7 cm^2 of soil surface) in November 2003. Sixteen tillers of *F. paniculata* were randomly chosen and planted in a regular pattern in each pot (hereafter referred to as a matrix). Control pots did not contain *F. paniculata* plants. Pots remained in a glasshouse during winter and were then placed in March 2004 in the experimental garden of the Joseph Fourier Alpine Station at Grenoble (altitude 200 m a.s.l.). The potting soil (16 l in each pot) consisted of a mixture of sand (2/3), clay (vermiculite 1/4) and a potting mixture (1/12, Fertiligène®). Fertilizer was applied in May 2004 to all the pots in the form of 7.2 g of Fertiltop® (16-8-10+4MgO+oligoelements), which corresponds to 1.152 g nitrogen per pot. The vegetation in half of the pots was cut to a height of 5 cm in June 2004 to simulate mowing. There were thus three different treatments (control, matrix, matrix cut). There were seven replicates per treatment, resulting in a total of 21 pots. Seedlings of *B. erectus* from the same group as those used for the field experiment were transplanted into the pots during 17–21 May 2004. Seven seedlings of *Bromus erectus* were planted in each pot, arranged in a circle with each seedling between two adult tillers of *F. paniculata.* Control pots were planted in the same way with the same distance between seedlings. Pots were watered daily to avoid water limitation. Light availability at ground level was measured on 11 July 2004 between 11:00 and 15:00 with a PhotoActive Radiation (PAR) sensor (LI-191 Line Quantum Sensor, LI-COR). PAR was measured at four points in each pot and averaged. The experiment was harvested on 15 July 2004, when seedlings had reached a size (based on leaf number) equivalent to that in the field at the end of the growing season (the number varied between 5 and 15 across the treatments in both experiments). Seedling above ground biomass was dried for three days at 65°C, and weighed. An allometric relationship was established between the number of leaves and seedling biomass ($R^2 = 0.94$, $F_{1,331} = 5172$, $P < 0.0001$). This allowed field growth results to be compared with those of the pot experiment.

Data analyses

Field experiment: Environmental variables.

Environmental data were analysed using an analysis of variance with treatment and site (for cover data) as explanatory variables. For moisture data, the average for the 14 dates was used. Sampling was carried out one year after the experiment, but this was acceptable because plot order remained consistent between sampling dates.

Field experiment: Performance variables.

To test the role of biotic and abiotic factors on seedling performance, analyses were conducted as follows. Seedling survival in the field was analysed using a logistic regression model (Wrigley 2002). Sites were analysed separately to avoid pseudo-replication. A first analysis tested the treatments (–V–L, –V+L, +V+L) as a fixed factor to determine whether vegetation and/or litter removal affected seedling survival, followed by pair-wise comparisons corrected by Bonferroni adjustments (Abdi 2007). Growth in the field was analysed in a similar manner using analysis of variance. A first analysis tested the effects of litter and vegetation followed by post-hoc Student tests corrected by Bonferroni adjustments (Abdi 2007) to compare the treatments.

Field experiment: Performance × Environment interaction.

For each performance measure (survival and growth), a second analysis was conducted to determine whether one or several environmental factors influenced survival and growth. Light availability and moisture were treated as fixed continuous factors, when conducting an independent analysis for each of these variables and each site. Logistic regression models were used for the analysis of each performance variable and survival, and an analysis of variance for growth.

Pot experiment.

The effect *F. paniculata* had on the performance of *B. erectus* seedlings was determined. Treatment (control, matrix, and cut) was a fixed factor. Survival was analysed using a logistic fit log-likelihood. Growth was analysed using an analysis of variance. The effect of light was then tested as a fixed factor, as in the analysis of the results of the field experiment.

All analyses were conducted using JMP 5.0.1 software (SAS Institute 2002, Cary, North Carolina, USA).

Results

Environmental variables

Soil moisture during the growing season was similar at the two sites in the absence of litter or vegetation (28.1% vs. 28.5% for the mown and unmown sites, respectively; Fig. 1, Table 2). Litter alone significantly increased soil moisture at the unmown site (+3%, comparing –V–L to –V+L, $F_{2,15} = 104.7$, $P < 0.0001$). Vegetation and litter combined reduced soil moisture, especially at the unmown site (–8%, comparing –V–L to +V+L, $F_{2,15} = 104.7$, $P < 0.0001$) but also at the mown site (– 3.5%, $F_{2,15} = 102.9$, $P < 0.0001$, Table 3). Vegetation decreased light availability at both sites ($F_{1,8} = 113.62$, $P = 0.0001$, Table 2 & 3, Fig. 2).

Vegetation, litter and ground cover differed significantly between the two sites. In spring, the mown site was characterized by high vegetation and low litter cover (Table 1), whereas at the unmown site, more than half of the area was covered by litter and consequently there was a lower vegetation cover. There was little bare soil at the unmown site, while at the mown site more bare ground was visible.

Field experiment: Plant-plant interactions

The effect of vegetation on seedlings measured in addition to that of the litter was always zero or negative. At mown sites, vegetation did not modify survival (Fig. 1), but did limit the growth of seedlings (Fig. 2). Even though light decreased in the presence of vegetation, no significant effects of light on growth were detected ($F_{1,7} = 5.08$, $P = 0.0588$). There was also no apparent relationship with moisture ($F_{1,7} = 4.04$, $P = 0.084$, Table 4).

At the unmown site, vegetation reduced survival of the seedlings to only 8.3% (Fig.1). This was linked to soil moisture ($W = 5.63$, $P = 0.018$, Fig. 1, Table 4). There was no

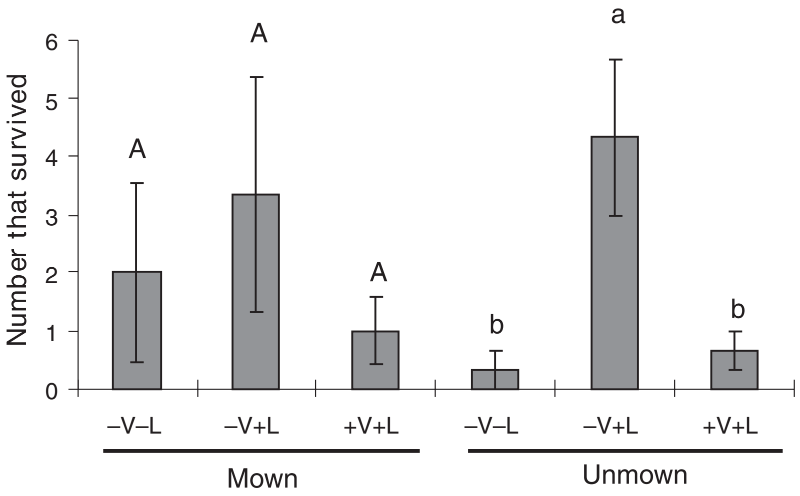

Fig. 1. – Mean survival of seedlings of *Bromus* e*rectus* at the end of the season at mown and unmown sites under different treatments: without vegetation and without litter (-V-L), without vegetation and with litter (-V+L) and with vegetation and litter (+V+L). Histograms refer to the average number of seedlings that survived of the eight that were planted. Bars indicate standard errors. Different letters indicate significant differences between treatments

Table 2. – Levels of light and moisture recorded in each treatment and site in the field experiment and in each matrix treatment of the pot experiment. Light availability was measured in terms of Photosynthetic Active Radiation, in µmol·m^{-2}·s^{-1}. Moisture was not measured in the pot experiment as the pots were kept moist by watering (n.a. – not available).

Experiment	Site	Treatment	Light availability (µmol·m^{-2}·s^{-1})	Moisture (%)
Field experiment	Mown	–V–L	1469±39	28.1±0.5
		–V+L	n.a.	28.2±0.4
		+V+L	930±98	24.7±0.2
	Unmown	–V–L	1512±7	28.5±1.2
		–V+L	n.a.	31.5±0.1
		+V+L	739±63	17.7±1.5
Pot experiment	Control	1928.6±31	n.a.	
	Matrix	1284.2±95	n.a.	
	Matrix cut	1521.2±65	n.a.	

Table 3. – Analyses of the response of environmental variables to the treatments in the field and pot experiments. For the field experiment, each site (mown and unmown) was tested separately. Litter and vegetation treatments correspond to the –V-L, –V+L, +V+L treatments. For the pot experiment, Matrix factor included the following modalities: Controls, Matrix and Matrix cut. Moisture was not tested as pots were kept moist.

Experiment	Environmental variable	Site	Source	DF	Sum of Sq.	F	P
Field experiment	Light availability	Mown	Litter & Vegetation treatment	1	871922.4	65.1	< 0.0001
		Unmown	Litter & Vegetation treatment	1	1793617.8	374.5	< 0.0001
	Moisture	Mown	Litter & Vegetation treatment	2	48.5	48.9	< 0.0001
		Unmown	Litter & Vegetation treatment	2	629.8	104.8	< 0.0001
Pot experiment	Light availability		Matrix	2	1699580.1	22.5	< 0.0001

relationship between survival and light available at ground level (W = 0.37, P = 0.54). Additional effects on growth were not detectable (Fig. 2). There was no correlation between growth and light ($F_{1,2} = 10.40$, P = 0.19) or moisture ($F_{1,14} = 2.98$, P = 0,11, Table 4).

Field experiment: effect of litter

At the mown sites there was no significant difference in seedling survival between plots with and without litter (Figs 1 & 2). At the unmown sites, litter significantly enhanced *Bromus erectus* seedling survival (increase from 4% to 54%). This was linked to soil moisture (W = 5.63, P = 0.018, Fig. 1, Table 4). There was no relationship between survival and light availability at ground level (W = 0.24, P = 0.62 at the mown site, W = 0.37, P = 0.54 at the unmown site). This positive facilitation effect on seedling survival was compensated for by the negative effect of litter on growth (Fig. 2).

Pot experiment

The treatments did not significantly affect seedling survival (W = 0.33, P = 0.85). Survival was high (96 to 100%) in all pots. A negative effect of *F. paniculata* on seedling growth was observed (Fig. 3) and simulated mowing did not modify this effect ($F_{2,42} = 46.3$, $P < 0.0001$). These responses were not significantly related to light availability if the results of the whole experiment are taken into consideration ($F_{1,46} = 1.01$, P = 0.32), as cutting increased light availability without any consequent increases in the growth of the seedlings.

Discussion

In French subalpine grasslands, litter and vegetation had contrasting effects on seedlings, depending on the site and the fitness parameter considered. Litter had both facilitative and negative effects, while living vegetation was always competitive. This competition is likely to be linked to the negative effect that *F. paniculata* had on seedlings in the pot experiment.

Plant-plant interactions

Living plants inhibited seedling growth at the mown site and limited seedling survival at the unmown site. Vegetation always significantly reduced light availability in the field, which affected growth. In mown grassland, limitation of seedling growth can also be explained by mechanisms other than competition for light. In the pot experiment, *F. paniculata* had a negative effect on seedling growth whether cut or not. This effect could not be due solely to competition for light, especially when mown. Moreover, light intensity was reduced less in this experiment than in the field. Competition for water is also not likely to have occurred in the pots. It is hypothesized that *F. paniculata* competes with seedlings for light and soil resources. Root competition is probably a key factor limiting seedling growth, at least in mown meadows. Nitrogen limitation due to competition with *F. paniculata* for this resource could also limit growth, taking into account the ability of this species to store nitrogen (unpublished data). Phosphorus limitation could also be important in subalpine grasslands, because of nitrogen deposition at high altitudes (see Litaor et al. 2005 and references therein). *Festuca paniculata* is a very resilient and conservative species (Quétier et al. 2007), but mowing could increase its rate of acquisition of

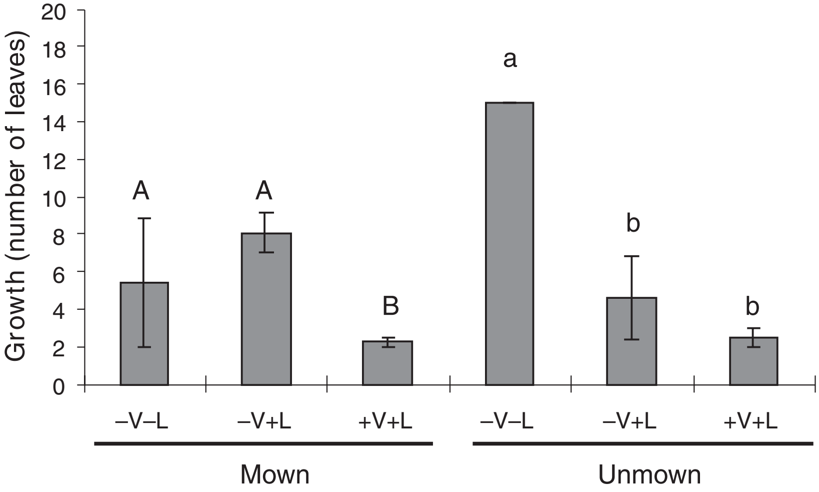

Fig. 2. – Mean growth, measured in terms of the number of leaves, of *Bromus* e*rectus* seedlings at the end of the season at mown and unmown sites under different treatments: without vegetation and without litter (–V–L), without vegetation and with litter (–V+L) and with vegetation and litter (+V+L). Histograms refer to number of leaves on the seedlings at the end of the experiment. Bars indicate standard errors. Different letters indicate significant differences between treatments.

Table 4. – Analyses of the performance of *Bromus erectus* seedlings in the field and pot experiments and its correlation with environmental variables. For the field experiment, each site (mown and unmown) was tested separately. Litter and vegetation treatments corresponded to the –V–L, –V+L, +V+L treatments. Growth was analysed using analyses of variance. Survival analyses were performed using a logistic regression model (W = Wald chi-square). For the pot experiment, Matrix factor included the following modalities: Control, Matrix and Matrix cut. Moisture was not tested as pots were kept moist. Nparm: number of parameters.

Experiment	Performance measure	Site	Factor	Nparm	DF	W	P
Field experiment	Survival	Mown	Litter & Vegetation treatment	2	2	4.9	0.09
			Light availability	1	1	0.2	0.62
			Moisture	1	1	0.0	0.83
		Un-mown	Litter & Vegetation treatment	2	2	15.4	**0.0004**
			Light availability	1	1	0.4	0.54
			Moisture	1	1	5.6	**0.018**
			Source	DF	Sum of Sq.	F	P
	Growth	Mown	Litter & Vegetation treatment	2	89.2	14.8	**0.0002**
			Light availability	1	40.2	5.1	0.0588
			Moisture	1	35.0	4.0	0.084
		Un-mown	Litter & Vegetation treatment	2	104.2	7.5	**0.0068**
			Light availability	1	95.5	10.4	0.19
			Moisture	1	34.2	3.0	0.11
	Performance measure		Source	Nparm	DF	W	P
Pot experiment	Survival		Matrix	2	2	0.3	0.85
			Source	DF	Sum of Sq.	F	P
	Growth		Matrix	2	156.3	18.5	< 0.0001
			Light availability	1	0.8	0.2	0.66

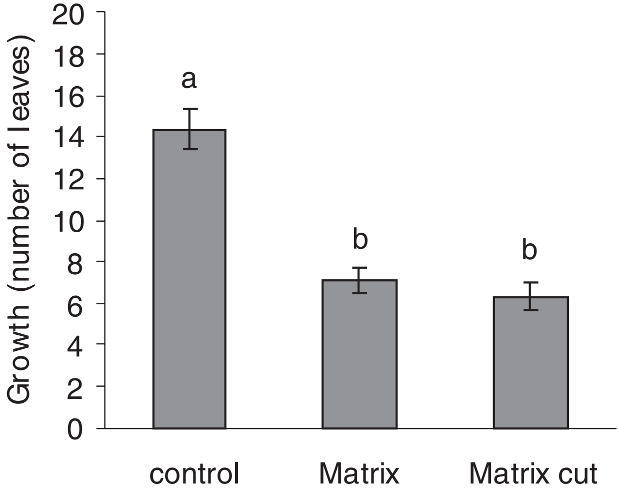

Fig. 3. Growth of seedlings of *Bromus erectus* grown under different conditions and recorded at the end of the season in the pot experiment: Control, Matrix, Matrix cut. Bars indicate standard errors. Different letters indicate significant differences between treatments.

resources as it removes a high proportion of its aboveground biomass. Robson et al. (2007) found a faster relative rate of mineral-N turnover in subalpine mown fields. Another mechanism could be inhibition of growth by chemical compounds produced by *F. paniculata* (Inderjit & Callaway 2003, Viard-Crétat et al. 2009). In mown grasslands, other vegetation and *F. paniculata* could compete for soil nutrients and hence limit seedling growth. In the unmown community, survival was limited by competition for light and soil water. Survival and growth are two components of a plant's response to different factors of the environment (Howard & Goldberg 2001). Survival is often linked to mortality factors such as a sudden shortage of water (Goldberg et al. 1999, Hastwell & Facelli 2003). Higher mortalities under vegetation could be the result of temporary depletions in water supply. In the absence of a treatment including vegetation but excluding litter, which would have allowed a formal test of the interactions between litter and vegetation, these conclusions have to be considered with caution. However, this situation does not exist in natural plant communities and such a treatment would not have been informative in terms of understanding the ability of seedling to establish in these communities.

Effect of litter

Litter had no effect at the mown site, where the amounts of litter are largely limited by repeated removal of living biomass before the death of the leaves in autumn. Our results show a strong facilitation effect of litter on the survival of *Bromus erectus* seedlings at the unmown site. Seedlings survived significantly better under litter than on bare soil. Soils were moister under a litter layer, and litter may have protected the soil and/or seedlings from desiccation (Eckstein & Donath 2005). Other mechanisms, such as protection from herbivores or lethal frosts, cannot be excluded. However, seedling growth was limited by litter. The reduction in growth due to litter at the unmown site could have resulted from shading, phytotoxic effects of leachates, or the energy needed to penetrate the mat of litter (Facelli & Pickett 1991a, Tilman 1993). The possibility that litter could trap seeds by preventing their roots from reaching the soil was not tested. The differences between mown and unmown sites may be due to the thick litter layer present at the unmown site in spring (Table 1) when seedlings need to find appropriate conditions when they switch from their reserves to photosynthesis in order to grow. This result suggests that the effect of litter is commensurate with its abundance, which differs from the hypothesis that small amounts of litter have facilitative effects, whereas amounts greater than 200 $g \cdot m^{-2}$ decrease seedling recruitment (Xiong & Nilsson 1999, Violle et al. 2006). The presence of litter simultaneously induces facilitation and competition (Tilman 1993, Foster & Gross 1997). As in previous studies, negative effects on growth and positive effects on survival were observed (Facelli & Pickett 1991a, b, Goldberg & Novoplansky 1997, Goldberg et al. 1999, Suding & Goldberg 2001).

Limitations on survival, growth and establishment success in mown and unmown grasslands

The first important outcome of this study is the importance of the demographic parameters considered (Howard & Goldberg 2001). Both survival and growth are important in the harsh abiotic conditions found in subalpine grasslands. Growth was probably limited by competition for soil nutrients in the mown grasslands and more limited by carbon acquisition under the thick litter layer present in unmown grasslands. Survival was dependent on the availability of soil water in unmown grasslands, indicating that desiccation can result in the mortality of seedlings in subalpine grasslands. This has consequences for the strategies and traits of species that adapt to environmental constraints (Cingolani et al. 2007). These processes, measured at the seedling stage for one phytometer species explain how species specialized in soil resource acquisition may succeed in mown grasslands, while species investing in carbon acquisition and storage via taller statures and conservation strategies dominate in unmown grasslands. This second strategy favours in turn the accumulation of poorly decomposable litter. Heterogeneity in the litter mat may allow other species to establish in gaps in the litter in unmown grasslands providing their seedlings can survive desiccation. These conclusions correlate well with what is observed in the field (Quétier et al. 2007), but need to be verified by incorporating the relative degrees of stress experienced by species in a community depending on their own niche optima (Liancourt et al. 2005).

Competitive/facilitative effects of Festuca paniculata and its litter

Another conclusion concerns the diverse roles of litter and living vegetation in the recruitment of subalpine species such as *Bromus erectus*. It is shown that the thick litter layer present on soil after tissue death can modify seedling recruitment in subalpine grasslands. This is particularly important at, for example, high altitudes where the conservative strategies adopted by plants result in the litter layer being poorly decomposable. While there is intense competition between plants with high resource acquisition abilities (Berendse & Elberse 1990), any potential litter effect is likely to be more pronounced when the plant community is dominated by conservative species with slowly decomposing tissues (Quested & Eriksson

2006). Plant competition and litter effects are not independent (Suding & Goldberg 1999). It is likely that the plant-plant and litter-plant interactions will differ in intensity for plants with acquisitive or conservative strategies, respectively. In subalpine grasslands in the French Alps, *F. paniculata* simultaneously competes with seedlings of subordinate species for resources and via a very significant litter effect. A topic for further research would be to investigate how trade-offs between plants adopting acquisition/conservation strategies affect not only resource acquisition, but also tissue decomposition, which may be important in harsh environments such as subalpine grasslands.

Conclusions

Festuca paniculata exerts a competitive effect that could explain the observed negative effects of vegetation on seedlings in natural communities. Its litter, however, also reduces the rate of evaporation and thus the drying out of soil. In mown grasslands, competition reduced growth while in unmown grasslands, seedlings benefited from facilitation and survived better, but competition again limited their growth. In unmown grasslands, which are of lower diversity, *F. paniculata* may strongly influence the establishment of seedlings of *B. erectus*. In agriculturally abandoned fields in the Southern French Alps, conservative species such as *Festuca paniculata* may, however, be able to grow better under thick litter layers. Recruitment mechanisms, such as those investigated in this study, may partly account for the abundance patterns and strategies observed in subalpine grasslands, which are a result of species filtering based on different competitive responses.

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Souhrn

Ve vnitří části francouzských Alp se na subalpinských trávnících, které přestaly být koseny, stala dominantním druhem trsnatá tráva *Festuca paniculata*. Článek si klade otázku, zda je vzcházení semenáčů v těchto společenstev ovlivňováno opadem nebo živou vegetací a zda se vliv těchto dvou faktorů liší na sečených a nesečených loukách, a nakolik se projevuje dominance *F. paniculata*. Hypotézy byly testovány pomocí terénních a nádobových pokusů, jako fytometr byl použit druh *Bromus erectus*. V terénním pokusu byla na sečených i nesečených loukách odebrána biomasa jak vegetace, tak opadu a vyjádřen tak vliv obou faktorů na vzcházení semenáčů. Vliv vegetace a opadu byl opačný. Vegetace omezovala růst semenáčů *Bromus erectus* na sečených plochách a snižovala jejich přežívání na nesečených plochách, zatímco opad měl vliv pouze na nesečené louce, kde zlepšoval přežívání semenáčů, ale omezoval jejich růst. Přežívání semenáčů záviselo více na půdní vlhkosti, jejich růst spíše na dostupnosti světla. Na místech se silnou vrstvou opadu, která se vytváří na nesečených loukách, je kompetitivní působení vegetace kompenzováno zvýšenou vlhkostí v důsledku nižší evaporace.

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