

## Original article

Insect herbivory and grass competition in a calcareous grassland:  
results from a plant removal experimentEmmanuel Corcket <sup>a,\*</sup>, Ragan M. Callaway <sup>b</sup>, Richard Michalet <sup>c</sup><sup>a</sup> Laboratoire d'Ecologie Alpine, Université Joseph Fourier, B.P. 53, 38041 Grenoble cedex 9, France<sup>b</sup> Division of Biological Sciences, University of Montana, Missoula, MT 59812, USA<sup>c</sup> Laboratoire d'Ecologie des Communautés, Université Bordeaux I, 33405 Talence, France

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## Abstract

We compared the effects of herbivory by grasshoppers and neighbourhood competition on two dominant grasses, *Bromus erectus* and *Brachypodium pinnatum*, in a calcareous grassland in the French Alps. In a fully factorial design, herbivory was reduced by insecticide spraying and competition was reduced by removal of neighbouring plants. The effects of herbivory and competition were species-dependent. *Bromus*, a stress-tolerant species, was strongly affected by competition, but not by herbivory. In contrast, the more competitive species, *Brachypodium*, was negatively affected by herbivory, but only when neighbouring vegetation was removed. The greatest herbivory pressure on isolated targets of *Brachypodium* is likely to be due to the indirect effects of experimental gaps, i.e. more favourable microclimatic and foraging conditions for grasshoppers. This suggests that herbivory by insects may be a confounding factor in many plant removal experiments. Field experiments designed to study the combined effects of competition and herbivory should take into account the indirect effects induced by experimental gaps.

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Keywords: *Brachypodium pinnatum*; *Bromus erectus*; Competition; Grasshopper; Removal experiment

## 1. Introduction

The effects of insect herbivory on ecosystem processes and plant community structure have been widely documented and include increased nutrient turnover (Blumer and Diemer, 1996; Mulder et al., 1999; Belovsky and Slade, 2000), shifts in community composition and altered plant performances (Brown, 1985; Olff and Ritchie, 1998; Escarré et al., 1999). The course of plant succession may also be altered by insect herbivory (McBrien et al., 1983; Brown, 1984; Brown and Gange, 1992) due to the preference of particular insect types for habitats of different successional stages (Brown, 1984) or to the successional status of target plants (Leps et al., 2001).

Competition is also a major force in plant communities, determining vegetation composition (Grime, 1973; Reader et al., 1994), plant performance (Goldberg, 1987), and patterns of succession in many habitats (Tilman, 1990). The most

common manner to measure the intensity of competition in the field is to perform neighbour removal experiments (Goldberg and Scheiner, 1993; Markham and Chanway, 1996), i.e. to compare responses of target individuals with or without neighbouring vegetation. Some experimental studies have combined the effects of herbivory and plant competition (Rodriguez and Brown, 1998; Van et al., 1998), and typically use a factorial design of competitor removal and herbivory exclusion with cages or insecticide (Rees and Brown, 1992; Thébaud et al., 1996; Dormann et al., 2000; Fowler, 2002; Olofsson et al., 2002). The comparative importance of herbivory and competition has been shown to vary among study systems, particular target plant species, and the species of herbivore investigated (Dormann et al., 2000; Corcket et al., 2002). Very few studies have focused specifically on insect herbivory and competition among grass species (Clay et al., 1993).

In an abandoned pasture in Canada, Reader (1992) demonstrated that herbivory by slugs may confound measurements of competition intensity determined by removal experiments. In that study, plant survival was reduced by

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herbivory when the plant was surrounded by its neighbours, suggesting that removing a plant's neighbours may reduce food and shelter for slugs. In this case, herbivory mimicked the effects of competition since it decreased the performance of targets with neighbours, which may be described as “apparent competition” (Holt, 1977). This may create serious bias in studies assessing plant interactions using removal experiments. Even so, few competition studies have explicitly considered this confounding effect (Van der Wal et al., 2000).

The purpose of our study was to compare the effects of foliar herbivory by insects and the effects of plant competition on two target grasses which are dominant in calcareous grasslands of the French Alps. We tested the responses of the dominant grasses to herbivory and competition with plants neighbouring, and whether herbivory might be a confounding factor in our experiment. Finally, we attempted to assess the long-term effects of insect herbivory and plant competition on plant dominance in calcareous grasslands.

## 2. Materials and methods

The field site, “Liche Petet” (45°10'N, 5°50'E, 700 m a.s.l.), is a calcareous grassland located near Grenoble, in the foothills of the French Alps. The vegetation structure is typical of prairies classed as *Mesobromion* communities in phytosociological classifications (Braun-Blanquet and Moor, 1938); this vegetation type is widespread in Western Europe (Willems, 1982; Royer, 1985). At Liche Petet, vegetation is dominated by *Bromus erectus* and *Brachypodium pinnatum* (respectively, 54% and 14% of vegetation density; see data in Corcket et al., 2002). Although these two perennial grasses may co-exist in the same habitat, *B. erectus* is an early-successional species in comparison to *B. pinnatum* (Royer, 1972; Barbaro and Cozic, 1998; Fekete et al., 2000). The impact of grazing mammals in the grasslands at Liche Petet is minimal, with only several days of sheep grazing permitted per year. Grasshoppers are often abundant in *Mesobromion* grasslands (Voisin, 1986), and when they are they cause significant damage to plants (Voisin, 1995; Corcket et al., 2002). This is the case in Liche Petet, where the dominant grasshopper species are *Euchorthippus declivus* Brisout and *Chortippus biguttulus* Linné (Corcket et al., 2002). Grasshoppers are “edge-eaters” and leave rounded, scalloped-marks on the edge of the grass blades they eat. Herbivory marks from grasshoppers are unlikely to be confused with marks from other herbivores such as small mammals or gastropods, which were not detected at the experimental site. Herbivory by large mammals, particularly sheep, was prevented by erecting fences around the experimental area. No evidence of herbivory by other invertebrates (snails or slugs) or vertebrates (rodents) was detected in the experimental site.

The loss of leaf tissue to herbivores may lead to a loss of photosynthetic production. If the incision is deep enough (more than half of the width of the blade), the leaf is greatly weakened and the top end of the blade may be cut. Herbivory

damage may also increase water loss at the edge of the herbivory marks. Overall, we assumed that an increase in the number of marks of herbivory on an individual plant may lead to reduced fitness and decreased growth, especially in stressful environments. For each dominant grass, *B. erectus* and *B. pinnatum*, 60 target individuals were randomly sampled. When a randomly chosen target was close to another conspecific clump, we checked to be sure that the individual was not connected to the clump, especially for *B. pinnatum*, which is a clonal species. Each target individual was randomly assigned to an experimental treatment, which included two levels of competition and two levels of herbivory. Each treatment combination was replicated 15 times. Target individuals were at least 30 cm from other targets.

Competition intensity was assessed through neighbour removals. For half of the targets, we clipped all aboveground vegetation at the ground level within a radius of 15 cm. We clipped all regrowth as often as necessary. In such field experiments, we were able to measure diffuse competition experienced by target species, i.e. summed intra- and inter-specific effects of neighbourhood. When the growth of target species without neighbours is significantly greater than the growth of target species with neighbours, competitive effects are assumed.

To decrease herbivory, we sprayed insecticide on individual target grasses (15 with neighbours and 15 without neighbours for each species). We did not spray both targets and neighbours in order to avoid confounding indirect effects of herbivory which could have masked the direct effect of herbivory on our targets (Crawley, 1989; Escarré et al., 1999). Shoots were included inside a plastic bottle with the bottom removed, 9-cm in width, and insecticide was sprayed through the bottleneck. Every 10–15 days from June to October 1999, treated target individuals received five sprays of a 0.5 ml/l water solution of insecticide (Decis™; active ingredient: Deltamethrin dosed 25 g/l). This treatment provided a negligible amount of water to target plants (0.2 ml per spray), in comparison to natural rainfall (ca. 605 mm during the course of the experiment; Météo-France, 1999).

Measurements of the intensity of leaf damage experienced by the grasses were conducted using a relative scale graduated from 0 to 5 (described in Corcket et al., 2002). This subjective non-linear scale was especially developed to assess herbivory non-destructively in the field. The level “0” indicated no damage, “1” indicated very few marks on the blades, and “5” indicated that more than half of the estimated foliar area was eaten. Levels “2–4” were assigned as intermediate levels of herbivory, according to the number and the width of herbivory marks on the blades. We recorded the damage experienced by *Bromus* and *Brachypodium* in June, August, and October 1999. These data did not meet the assumptions of normality and were square root transformed prior to analysis.

We quantified the growth of target individuals by counting the number of leaves with at least half of their blade area remaining green. This non-destructive measurement allowed

us to collect data on the growth of our target individuals at the different dates throughout the season. Previous studies have shown that, for *B. erectus* and *B. pinnatum*, leaf number is significantly related to total biomass (Corcket et al., 2003). These data were not normally distributed (Shapiro-Wilk tests), and therefore, were also square root-transformed.

We tested the effects of insecticide and neighbourhood removal on damage and leaf numbers using two-way ANOVAs (neighbour  $\times$  insecticide). Six models of analysis were designed, combining each species (*B. erectus*, *B. pinnatum*) and each date (June, i.e. before the experimental treatments; August; October). Tukey tests were also performed within each model.

Microclimate at the ground level was measured within clumps of *Bromus* and *Brachypodium* and on bare soil, where vegetation was removed within a 30 cm diameter to simulate removal conditions. Hobo® H8 Pro Series climatic sensors (Onset Computer Corporation, Bourne, MA, USA) were placed 2 cm above the ground, with two replications for each microsite. Air temperature and vapour pressure deficit (VPD) were recorded each hour for 22 days from late June to late July 1999. We used data at 16:00 h, which corresponded to mean maximal temperature and VPD during the period of record. Data of the two replicates per microsite (*Bromus*, *Brachypodium*, bare soil) were plotted. Results were expressed as mean  $\pm$  1 standard error (S.E.) for these 22 days.

Phytotoxic or stimulatory effects of insecticide (Crawley, 1989) on *Bromus* and *Brachypodium* were tested in a common garden experiment. Thirty individuals of each species were grown from local seeds and transplanted into pots. For each species, half of the target individuals were sprayed with insecticide, as described above. Shoot length and leaf number were measured in July (before spraying) and September 1999, and differences in plant performances between September and July were calculated. Shoot length and leaf number variations were normal without any transformation (Shapiro-Wilk test), allowing us to perform a two-way MANOVA (species  $\times$  insecticide, with shoot length and leaf number as dependent variables).

### 3. Results

In the common garden experiment, neither shoot length nor leaf number of the target grasses were affected by insecticide treatments ( $P > 0.4$ ), indicating that the insecticide did not have phytotoxic or stimulatory effects on *Bromus* and *Brachypodium*.

In the field, insecticide decreased herbivory levels on treated plants, but was not sufficient to completely exclude herbivory on targets. Damage measured on targets sprayed with insecticide decreased during the course of the experiment (from  $1.15 \pm 0.14$  in June to  $0.47 \pm 0.11$  in October,  $Z = -3.80$ ,  $P < 0.001$ , Wilcoxon signed ranks test), whereas no significant changes were observed for targets not sprayed (from  $0.85 \pm 0.11$  in June to  $0.83 \pm 0.15$  in October,  $Z = -0.60$ ,  $P = 0.952$ , Wilcoxon signed ranks test).

Leaf numbers of target species were very similar in June 1999, before the experimental treatments were applied (Table 1 and Fig. 1A). For *Bromus*, leaf number was not affected by experimental treatments in August, but increased significantly in October in the neighbour removal treatment. There was no effect of insecticide on *Bromus* leaf number, neither as main effect nor first order interaction (Table 1 and Fig. 1B,C). In contrast, leaf number of *Brachypodium* increased significantly in August for targets sprayed by insecticide (Table 1 and Fig. 1B) and in October for *Brachypodium* individuals without neighbours and sprayed with insecticide (Table 1 and Fig. 1C).

Prior to initiation of the experiment, *Bromus* targets showed differences in herbivory damage among the treatment groups. Specifically, the targets, which were randomly assigned to the neighbourhood removal treatment, had significantly more herbivory marks than the others (Table 2 and Fig. 2A). Nevertheless, this difference disappeared when experimental treatments were performed, suggesting that leaf damage was not affected by experimental treatments over the course of the experiment (Table 2 and Fig. 2B,C). Prior to initiation of the experiment, targets of *Brachypodium* were very similar among treatments (Table 2 and Fig. 2A). The insecticide treatment significantly decreased damage to *Brachypodium* at the end of the experiment. In October, damage experienced by *Brachypodium* increased with the neighbour removal treatment but the interaction neighbour  $\times$  insecticide was not significant (Table 2 and Fig. 2C). Damage increased to a maximum intensity in August for both species (Fig. 2).

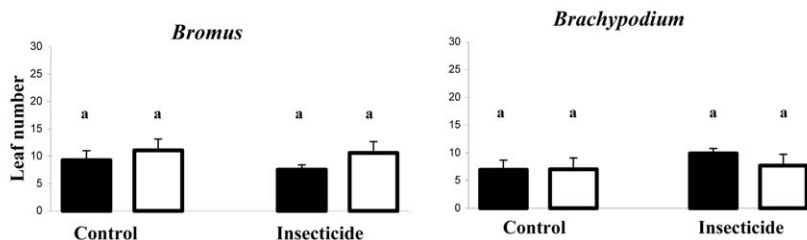
Mean maximal aboveground temperatures were  $35.0 \pm 0.9$  °C on bare soil,  $33.4 \pm 0.7$  °C in *Bromus* swards, and  $33.3 \pm 0.8$  °C in *Brachypodium* swards. Mean maximal VPDs were  $2.67 \pm 0.20$  kPa on bare soil,  $1.78 \pm 0.14$  kPa in

Table 1

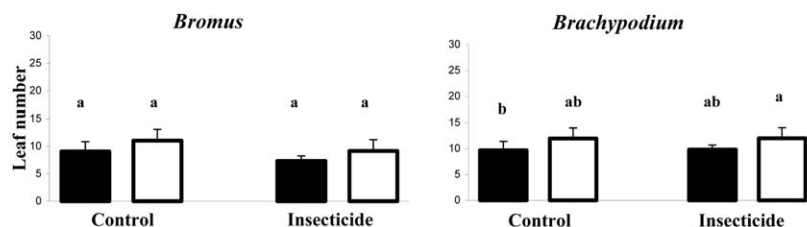
Results of two-way ANOVAs (neighbour  $\times$  insecticide) on the growth (square root of the number of leaves) of *Bromus* and *Brachypodium*, in June, August and October 1999. \*, \*\*, \*\*\* denote significance at  $P$  level  $<0.05$ ,  $<0.01$  and  $0.001$ , respectively

Species	Source	d.f.	F-value		
			June	August	October
<i>Bromus</i>	Neighbour	1	1.6	3.1	16.7 ***
	Insecticide	1	0.2	0.5	0.2
	Neighbour $\times$ insecticide	1	0.0	0.0	0.0
<i>Brachypodium</i>	Neighbour	1	0.7	2.2	2.7
	Insecticide	1	2.2	4.2 *	8.7 **
	Neighbour $\times$ insecticide	1	0.7	0.7	4.6 *

## A. June



## B. August



## C. October

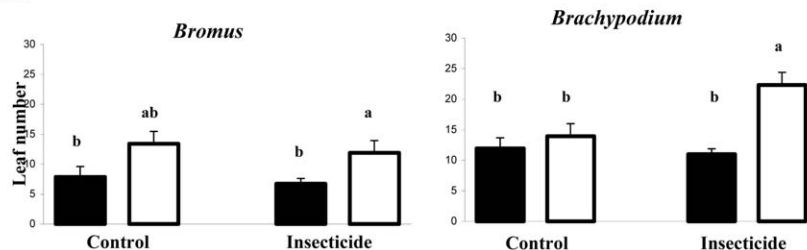


Fig. 1. Means ( $\pm 1$  S.E.) of leaf number for *B. erectus* and *B. pinnatum* in June (A), August (B), and October (C) 1999 for control and sprayed individuals, with (black bars ■) and without (white bars □) neighbours.

Table 2

Results of two-way ANOVAs (neighbour  $\times$  insecticide) on the intensity of herbivory (square root of damage) of *Bromus* and *Brachypodium*, in June, August and October 1999. \*, \*\*, \*\*\* denote significance at  $P$  level  $<0.05$ ,  $<0.01$  and  $0.001$ , respectively

Species	Source	d.f.	F-value		
			June	August	October
<i>Bromus</i>	Neighbour	1	8.7 **	3.1	0.1
	Insecticide	1	1.5	2.9	0.1
	Neighbour $\times$ insecticide	1	2.2	2.1	0.2
<i>Brachypodium</i>	Neighbour	1	0.0	1.1	4.4 *
	Insecticide	1	0.7	1.7	4.7 *
	Neighbour $\times$ insecticide	1	0.3	1.9	1.8

*Bromus* swards, and  $2.24 \pm 0.19$  kPa in *Brachypodium* swards. Summarised, temperature was  $1.5^\circ\text{C}$  warmer and VPD was at least  $0.43$  kPa higher at the bare site than within the grasses. VPD was  $0.46$  kPa higher within *Brachypodium* than within *Bromus* swards.

#### 4. Discussion

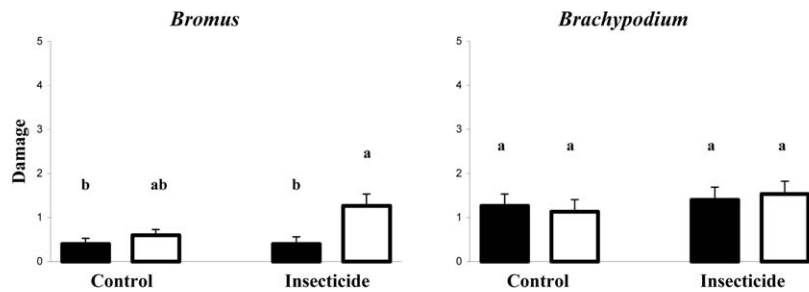
##### 4.1. Species-dependent responses

Each species responded differently to the experimental treatments. *B. erectus* was strongly affected by plant neigh-

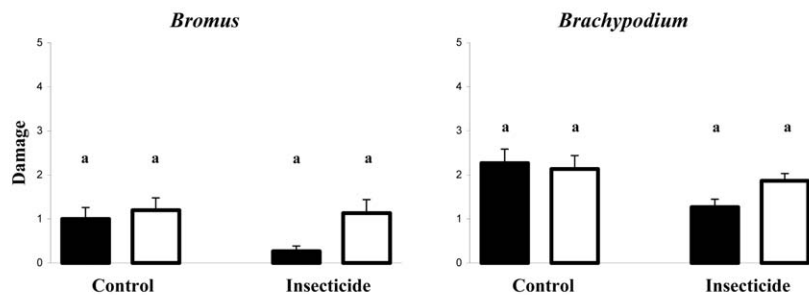
bourhood removal but not by insecticide treatment, whereas *B. pinnatum* was above all affected by insecticide spraying in combination with neighbour removal. These results contrast with those of other field experiments, which found that neighbour removal affected all species while the effects of reducing herbivory treatments were specific to only a few species (Dormann et al., 2000; Greiling and Kichanan, 2002).

The greater sensitivity of *Brachypodium* to herbivory suggests that these grasshoppers may be somewhat specific in their host choice, as documented in several studies (Joern and Lawlor, 1980; Cottam, 1985; Le Gall, 1989; Corcket et al.,

## A. June



## B. August



## C. October

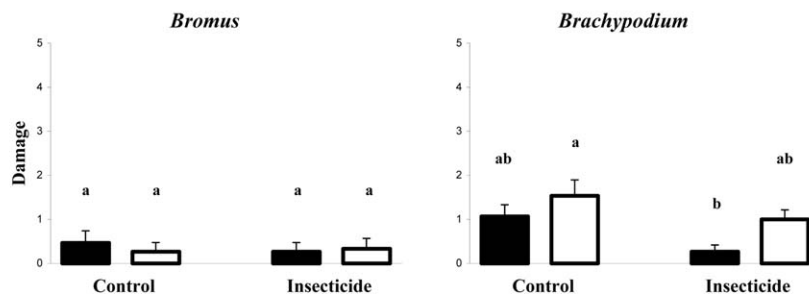


Fig. 2. Means ( $\pm 1$  S.E.) of damage for *B. erectus* and *B. pinnatum* in June (A), August (B), and October (C) 1999 for control and sprayed individuals, with (black bars ■) and without (white bars □) neighbours.

2002). The presence of defence chemicals in target plants (Szentesi, 2002), and particularly trade-offs between secondary metabolites and nutrient contents of leaves (Behmer et al., 2002) may determine the foraging decisions of herbivores. Therefore, stress-tolerant species are often grazed less than fast growing species because they generally allocate more to defence (Grime, 1977; Taylor et al., 1990; Fraser and Grime, 1999; Le Gall, 1989; Jones and Coleman, 1991). This perspective is consistent with our results: *B. erectus* has been shown to be more stress-tolerant than *B. pinnatum* (Barbaro and Cozic, 1998; Corcket et al., 2003). In arctic tundra, McGraw and Chapin (1989) found that a more competitive *Eriophorum* species was more frequently eaten than a less competitive congener. Convergence between stress tolerance and resistance to herbivory was also emphasised by Oksanen and Ranta (1992), who found a consistent relationship between traits for stress tolerance and those involved in grazing

tolerance. The overall positive effect of neighbour removal on leaf number was only significant for *B. erectus*. This is consistent with previous results, which emphasised the important effects of plant competition on the growth of *B. erectus* in *Mesobromion* grasslands (Corcket et al., 2003). In contrast, the response of *B. pinnatum* to neighbourhood competition was not strong and depended on whether or not herbivory was manipulated.

#### 4.2. Herbivory and plant removal: two related factors

The increase in leaf number for *B. pinnatum* when the effects of neighbours and grasshoppers were reduced appeared to be caused by the indirect effects of vegetation removal.

Typically, plant interactions are evaluated in the field by removing neighbouring species or all surrounding vegeta-



tion. We found that grasshopper herbivory was higher on isolated plants than on plants surrounded by neighbours. The reduced growth of *Brachypodium* without neighbours in the high herbivory treatment is consistent with general density-dependent hypotheses of herbivory intensity in which plants with neighbours experience less herbivory than isolated individuals. Several studies have shown that the effects of invertebrate herbivores are stronger in low-density vegetation (Solomon, 1981; Parmesan, 2000). For grasshoppers, this may be explained in part by their use of visual and olfactory signals to locate their primary resource (Le Gall, 1989; Szentesi, 2002). Grasshoppers may preferentially eat isolated plants (our results) or more common plant species (Cottam, 1985) simply because preferred species are easier to locate.

Total removal of vegetation may also induce important changes in microclimate (Reader, 1992; our results), which may directly affect herbivore populations. Several studies have shown that grasshoppers are favoured by an increase in VPD and air temperature (Chopard, 1951; Ritchie, 2000; Corcket et al., 2002).

Our results are consistent with Reader's (Reader, 1992) statement that herbivory may be a confounding factor in plant removal experiments, but Reader found that predation was higher on plants surrounded by neighbours than in the openings and concluded that herbivory established conditions of "apparent competition". In his system, the herbivores were slugs, which are animals requiring mesic habitats and shelter from predators. In our study, we found that *Brachypodium* individuals without neighbours experienced significantly higher herbivory rates. Such a confounding effect in competition studies will overestimate the intensity of competition, and should be avoided or alleviated by minimising the strong indirect effects due to large areas without vegetation. Ideally, targets should be protected against herbivory by caging and/or insecticide spraying, depending on the herbivore involved, or experimental designs should apply intermediate levels of plant removal, such as performed by Goldberg (1987) and Parmesan (2000).

#### 4.3. Herbivory damage and plant growth

The only differences in herbivory damage among our experimental treatments were recorded for *Brachypodium* in October. The significant decrease in damage in the insecticide treatment led to an increase in leaf number for *Brachypodium* targets, but only those without neighbours. This suggests that the negative effects of plant neighbourhood on *Brachypodium* growth were stronger than the positive effects of neighbourhood in reducing herbivory. In contrast, the significant increase in damage without neighbours is consistent with a significant decrease of plant leaf number in these conditions, as compared with insecticide conditions. This indicates that our insecticide treatment was not sufficient to reduce the increase in damage experienced by isolated *Brachypodium* targets, which as mentioned were preferentially

eaten by grasshoppers. However, these data also suggest that measurable, but low levels of herbivory will not significantly reduce *Brachypodium* growth. When we examined the level of damage in relation to differences in plant growth responses, we found that an increase in plant damage from "level 1" (for example, *Brachypodium* sprayed with insecticide and without neighbours in October) to 1.5 (*Brachypodium* without neighbours in October, but not sprayed with insecticide) led to a significant decrease in leaf number. This suggests that the "crucial level" of herbivory, i.e. the level of herbivory, which is necessary to induce significant damage on plants, is between a level of 1 and a level of 1.5 in our relative scale of damage.

#### 4.4. Relationships with other grassland processes

In our study the species, which was negatively affected by herbivory, *B. pinnatum*, is a late successional species in *Mesobromion* communities (Bobbink and Willems, 1993; Barbaro and Cozic, 1998). Therefore, our results are consistent with field approaches showing that herbivory by foliar feeding insects may slow the rate of plant succession (McBrien et al., 1983; Brown, 1985). In contrast, other studies involving belowground invertebrate herbivores (Brown and Gange, 1992; Verschoor et al., 2002) or artificial groups of phytometers (Fraser and Grime, 1999), have shown a converse effect of herbivory on plant secondary succession. In a literature survey, Davidson (1993) found a general effect of herbivores slowing secondary succession in old-fields dominated by grass species.

In our experiment, we excluded sheep from the experimental area and focused on the effects of grasshoppers. However, sheep grazing may strongly interact with grasshoppers. In particular, sheep grazing may dramatically reduce grasshopper populations by increasing larval mortality (Guéguen-Genest and Guéguen, 1987). Sheep and grasshopper herbivory may also have opposite effects, depending on the identity of perennial grasses (Gibson et al., 1987). This may be the case in our study, because grasshoppers eat preferentially *B. pinnatum*, which is usually less preferred by cattle in comparison to *B. erectus* (Delescaille, 1999; Barbaro et al., 2000). Although rarely compared directly, when both types of herbivores co-exist the overall effect will likely be determined by large vertebrate grazers (Gibson et al., 1987).

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