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Influence of management on cover and seed production of *Brachypodium pinnatum* (L.) Beauv. in a calcareous grassland

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Summary

1 Abundance (cover) and seed production of *Brachypodium pinnatum* (L.) Beauv. were assessed in calcareous grassland plots which had been subject to six experimental management types for 16 years.

2 Management strongly influenced cover of *B. pinnatum*. Cover was highest in burned plots (71%), followed by plots that were abandoned (48%). Although all mowing regimes (yearly, every 2nd year and every 5th year in summer, and yearly in autumn) reduced cover of *B. pinnatum* (4–21%), the extent of reduction was found to depend on the respective mowing time and frequency.

3 Inflorescence formation and seed production depended on type and frequency of biomass removal and were not simply a function of the abundance of the species. Seed production was highest in burned plots (1000 seeds m^{-2}) followed by plots that were abandoned, mown in autumn, or mown every 5th year in summer (about 100 seeds m^{-2} each). In plots that had been mown yearly or every second year in summer, *B. pinnatum* was still present but produced hardly any seeds.

4 Since seed production of *B. pinnatum* depends on the management regime, grassland management may be used to control the spread of *B. pinnatum* by sexual reproduction.

Keywords: cutting regime, Mesobrometum, reproductive output, seed set, sexual recruitment

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Introduction

One of the most important threats to biodiversity in calcareous grassland in continental western Europe is the abandonment of traditional land use followed by successional change of the vegetation (Willems 1983; Bobbink & Willems 1987). An important process reducing floristic diversity in this type of vegetation during early succession is the increase in dominance of the grass species *Brachypodium pinnatum* (L.) Beauv. (Bobbink & Willems 1987). Increasing dominance of *B. pinnatum* has been reported from throughout the distribution area of calcareous grassland in western Europe (Hope-Simpson 1940; Willems 1983; Hakes 1988; Acutis & Cavalleto 1989; Coquillard 1995). Control of

B. pinnatum has often become the immediate objective of management in nature reserves of this habitat type. Re-introduction of grazing (Hakes 1988), mowing regimes (Krüsi 1981; Bobbink & Willems 1991) and change of mowing time from autumn to summer (Bobbink & Willems 1991) have proved to be effective to prevent or break the single-species dominance of *B. pinnatum* and restore species-rich grassland.

Recently, many authors have focused on the species' physiology and clonal growth strategy to understand why this species is so successful in fallow grassland. Important characteristics seem to be the formation of a dense litter canopy combined with the independence from sexual reproduction (Kienzle 1984; Bobbink & Willems 1991; Mitchley & Willems 1995), internal cycling of nutrients or carbohydrates (Werner 1983; Bobbink *et al.* 1989; Stöcklin & Gisi 1989), a clonal 'foraging' strategy (de Kroon & Knoops 1990), and highly efficient nutrient uptake (Bobbink *et al.* 1989; Bobbink 1991). However, the last point has not always been confirmed (Ryser & Lambers 1995; Wilson *et al.* 1995).

While ecophysiological traits and the vegetative reproduction of *B. pinnatum* have been extensively studied, the propagation by seeds has received little attention (see Bornkamm 1961; Zimmermann 1979; Willems & Bobbink 1990). It has been generally assumed that sexual reproduction plays a minor role for the local spread of this species (Grime *et al.* 1988), therefore, it has never been thoroughly examined.

The possibility of grassland colonization by *B. pinnatum* through establishment of seedlings was first suggested by Willems & Bobbink (1990) who observed seed dispersal and first stages of establishment outside a "front line" of existing clones. The occurrence of sexual reproduction and the establishment of seedlings suggest that the level of seed production may ultimately determine the probability of colonization. This draws attention to the question of how management regimes do affect the amount of seeds produced by *B. pinnatum*.

The present study examines how different types of management measures influence seed production of *B. pinnatum*. Cover and seed production of *B. pinnatum* were determined on plots of calcareous grassland on which four different mowing regimes were implemented, as well as burning and abandonment. The following questions were pursued: (1) Do different management types influence cover and seed production of *B. pinnatum?* (2) Which types of grassland management are most effective to prevent the spread of *B. pinnatum* by sexual reproduction?

Methods

STUDY SITE

The study site is located in the Jura mountains of northern Switzerland near Schaffhausen (47°45'50" N, 8°36'36" E). It is situated at 700 m a.s.l. on an ESE-facing slope with an inclination of 12°. The soil type is rendzina on a γ-marl limestone (Ryser *et al.* 1995), the vegetation nutrient-poor, calcareous grassland (Mesobrometum erecti, Zoller 1954). The climatic conditions consist of an average annual precipitation of 910 mm in Merishausen, *c.* 1 km north of the study site (572 m a.s.l.) and an average mean temperature of 8.0 °C in Schaffhausen (437 m a.s.l.). Prior to the experimental treatments, the site had been mown annually between mid June and mid July for at least 20 years (Bronhofer 1956; Krüsi 1981).

EXPERIMENTAL TREATMENTS

In 1978, 18 permanent plots, each 5 m x 10 m, had been established at the study site (Krüsi

1981). In the plots, the following six management regimes (each with three replicates) have been applied regularly since then (Fig. 1): cutting in early July, yearly (J1); every 2nd year (J2; cut in odd years); and every 5th year (J5; last cut in 1992); yearly cutting in October (O1); yearly burning in February/March (BU); and abandonment (AB). The treatments will be referred to by their abbreviations.

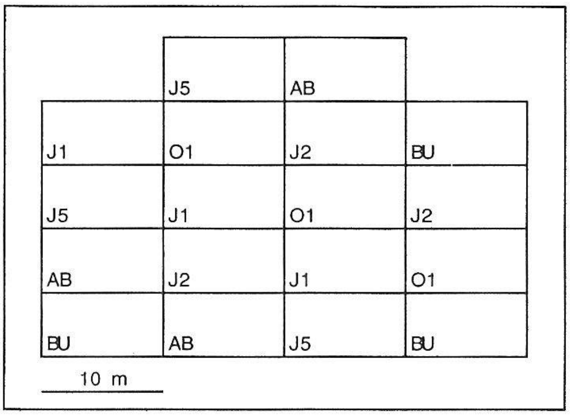

Fig. 1. Arrangement of the 18 plots with six different management types on the ESE-slope of the calcareous grassland studied. Plots measured 5 m x 10 m. AB: abandoned; BU: burned in late winter; J1, J2, J5: mown every year, every 2nd, and every 5th year in early July; O1: mown yearly in autumn.

COVER

In July 1994 shortly before cutting (J1 plots) and in October (all other treatments), the cover of *B. pinnatum* was determined in each plot to characterize the vegetative performance in relation to the respective management applied. In five squares (1 m x 1 m), positioned along one diagonal of each plot, cover values of *B. pinnatum* > 20% were estimated to the nearest 5%, values < 20% to the nearest 1%.

SEED PRODUCTION

Prior to the collection of seed data, cover of *B. pinnatum* was mapped on a 1 : 250 scale. Four density classes (0–5, 5–15, 15–25, 25–75% cover) were distinguished.

In early July, the number of inflorescences of *B. pinnatum* per unit area was recorded in each plot. Within each density class represented on a plot, three sample squares (1 m x 1 m) were chosen systematically. In these 1-m^2 plots inflorescences were counted. Obtained inflorescence numbers were weighted by the extent of their respective density classes to calculate the average number of inflorescences per squaremeter on each plot.

In mid August when spikes were fully ripe but not broken apart yet, the number of flowers per inflorescence and the seed set (percentage of flowers which developed into seeds) were determined. For two cover strata, 5–25% (two of the original strata combined) and 25–75% cover, eight inflorescences were collected in each plot; from two patches of the stratum, one inflorescence was chosen at random. The three closest inflorescences nearby were identified and all four were collected. The low number of inflorescences on some plots set limits to better randomization. For each spike the number of flowers was determined. The number of flowers in the third spikelet was multiplied with the number of spikelets of the inflorescence.

The seed set was determined in each sample of eight inflorescences. All caryopses were collected, and a random sample of 50 selected. Seed set could unambiguously be determined by counting the number of developed caryopses out of the 50 caryopses. The germination rate was determined in the greenhouse with 20 of these developed caryopses per plot.

STATISTICAL ANALYSES

For the statistical analysis, the plot means were calculated for all variables. The effect of management on the variables was investigated by one-way analyses of variance. In addition, a non-paramentric test (Kruskal-

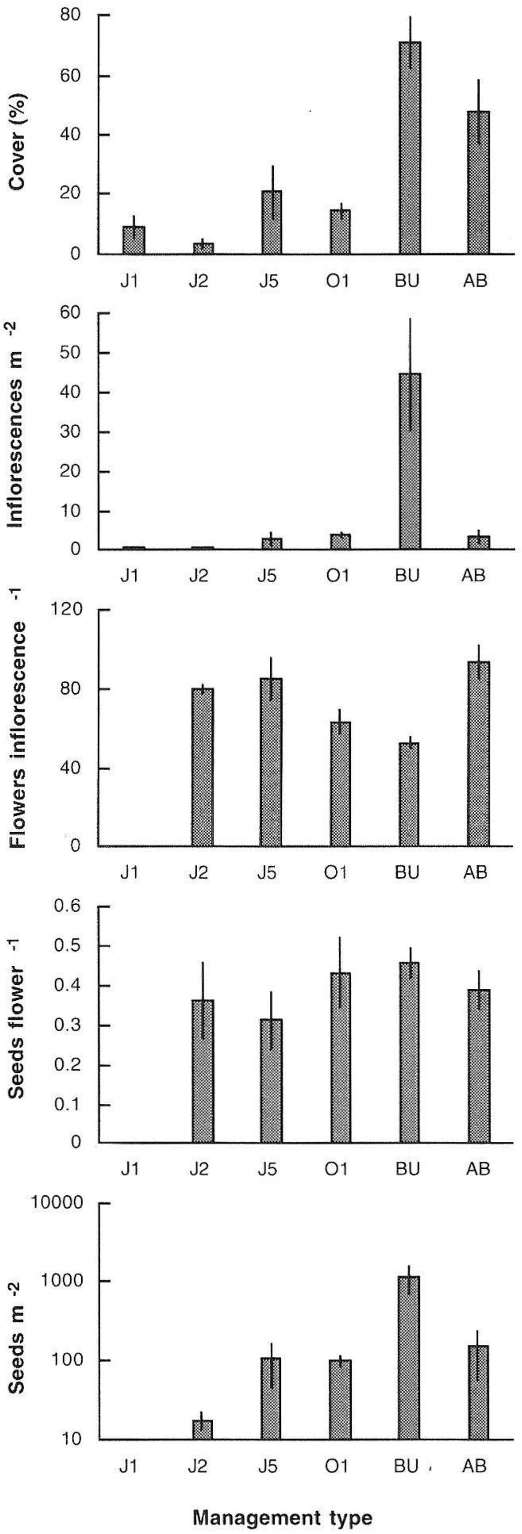

Fig. 2. *Cover, flower and seed production, and estimated seed yield of* Brachypodium pinnatum *per unit area in plots with different management (abbreviations as in Fig. 1; means ± 1SE). For J1, the number of flowers and seeds could not be determined due to mowing.*

Wallis) was applied to check for effects of non-normal data distribution; all values of $P < 0.05$ listed in the following chapter are maintained below this value, also in the non-parametric test. All parametric tests were performed with log- or arcsin-squareroot transformed data.

Results

The different management treatments had strong effects on the performance of *B. pinnatum* in the permanent plots (Fig. 2; Table 1). Cover was significantly different among treatments ($P < 0.001$), and varied by a factor of 20. It was high in burned and in abandoned plots, and low in plots with mowing treatments.

The number of inflorescences per unit area varied by a factor of about 50 ($P < 0.01$). The highest values were, again, obtained in burned plots. The number of flowers per inflorescence varied to a lesser extent (Fig. 2, $P < 0.01$), it was around twice as large on abandoned plots as on burned ones. The size of inflorescences, therefore, seemed to be negatively correlated with the relative density of inflorescences. The seed set per flower was generally around 0.4 and was not significantly influenced by management ($P > 0.05$). The average germination rate in the greenhouse was 11.7%, it did not show any management effects, either ($P > 0.05$).

From the variables above, the number of seeds per squaremeter was calculated (Fig. 2). Management strongly affected seed production. The highest number of seeds was produced on burned plots (*c.* 1000 m^{-2}), followed by the treatments O1, AB, and J5 (around 100 seeds m^{-2} each), and J2 plots (20 seeds m^{-2}). No ripe seeds were produced in J1 due to early annual mowing.

The result, that relative seed production ("seed production" in relation to "vegetative

Table 1. Results of analyses of variance of the effect of different management regimes on cover, seed production, and germination rate of Brachypodium pinnatum *(***$P < 0.001$, **$P < 0.01$, $^{ns}P > 0.05$)*

Variable	$df_{treat., res.}$	$SS_{treatment}$	$SS_{residual}$	F-ratio	r^2
Vegetative cover	5, 12	1.5	0.25	14.0***	0.85
Inflorescences m^{-2}	5, 12	7.4	2.2	7.9**	0.78
Flowers inflorescence^{-1}	4, 9‡	0.12	0.029	9.3**	0.80
Seed set (seeds flower^{-1})	4, 9‡	0.046	0.15	0.71^{ns}	0.24
Germination rate	4, 9‡	0.052	0.28	0.41^{ns}	0.15

‡no measurements were made in plots cut in summer (J1)

cover") was highest in burned plots, followed by plots mown in autumn shows, that seed production is not simply a function of the vegetative abundance of *B. pinnatum.*

Discussion

Cover

The abundance of *B. pinnatum* under different treatments found in the present study agrees largely with results of earlier work on restoration and management of species-rich calcareous grasslands in western Europe on the fact that summer mowing is adequate to reduce the abundance of *B. pinnatum* and to increase species diversity (Krüsi 1981; Hakes 1988; Bobbink & Willems 1991, and references therein). In the most comprehensive study on the impact of cutting regimes on the performance of *B. pinnatum* (Bobbink & Willems 1991), summer cutting was successfully tested as an alternative to traditional mowing in November, which had proved to be insufficient to control *B. pinnatum* during the years before. In contrast to this, cover of *B. pinnatum* in the present experiment was also low under late annual mowing in October.

Seed production

Seeds were produced in five management types with exception of annual summer cutting (J1) where inflorescences were removed before seed dispersal. However, the form of grassland management was crucial to the amount of seeds produced by *B. pinnatum.* Of the three levels of observation (number of inflorescences, size of inflorescences, seed set; cf. Fig. 2) the number of inflorescences was the most important determinant of total seed production per unit area. Seed production depended directly on the type and frequency of biomass removal and not only through the effect of these treatments on the cover of the species (Fig. 2).

Zimmermann (1979) found high fertility of *B. pinnatum* on burned meadows and suggested that diurnal regime of light and temperature near the soil surface may determine the number of inflorescences formed by the rhizomes. Absence of litter on burned plots may thus positively affect the formation of inflorescences. The data of this study support this hypothesis. High numbers of inflorescences (in relation to cover) were found in plots burned in late winter and to a lesser degree in plots mown in October. Treatments with litter layers (AB, J5, J2) led to comparatively low seed production. High numbers of inflorescences on plots that were free from litter have also been reported for *Molinia caerulea* (Grant *et al.* 1963).

Implications for management

The role that sexual reproduction plays in the rapid spread of *B. pinnatum* has hardly been considered in literature (Kienzle 1984; Grime *et al.* 1988; Hakes 1988). Kienzle (1984) assumed that *B. pinnatum* clones in the Swiss Jura expand from forest fringes into the open grassland exclusively by stolons. However, in Dutch chalk grassland colonization of *B. pinnatum* was observed outside the "front line" of existing clones (Willems & Bobbink 1990). First findings of an allozyme study with plant material from the same site as the data presented here revealed a high genetic variability of *B. pinnatum* (unpubl. data) which may indicate frequent sexual reproduction.

Besides the availability of microsites for establishment, the amount of seeds may play an important role for the colonization of adjacent grasslands. Unfortunately, no data are available on dispersal distances. But once introduced, *B. pinnatum* can successfully occupy habitats by clonal growth and build up almost monospecific stands, even where inflorescences are not formed (Grime *et al.* 1988).

The results of this study suggest that seed production resulting from specific managements should be observed. Where potentially spreading populations exist, it is necessary to consider management measures not only with respect to the vegetative performance of *B. pinnatum,* but also regarding the levels of seed production and dispersal. Burning of the vegetation appears to be a particularly inadequate management. However, cutting in autumn (which is sometimes applied to help certain rare species) may also favour sexual recruitment of *B. pinnatum.* In this case mowing biannually in summer should be considered an effective alternative, because it addresses a combination of management objectives, including the control of vegetative cover and seed production of *B. pinnatum.*

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