

The effects of mowing and fertilization on carbohydrate reserves and regrowth of grasses: do they promote plant coexistence in species-rich meadows?

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Abstract. After the cessation of regular management and after fertilization a single clonal species tends to dominate in many types of grasslands, whereas in regularly managed meadows these potential dominants usually attain a low cover. It has been hypothesized that plants reaching a high dominance in abandoned and fertilized meadows are selectively suppressed by mowing so that a balanced competition is maintained and competitive exclusion is postponed. We compared regeneration capacity and carbohydrate reserves accumulated by three species of clonal grasses, which markedly increase their dominance in irregularly mown, un-mown or fertilized meadows. Above-ground biomass and the amount of storage carbohydrates of the two largest species, (Molinia arundinacea, Calamagrostis epigejos) were reduced in a mown meadow. This effect was weaker in Bromus erectus, which produces smaller shoots. Shoots of Molinia were most impacted by mowing but their regeneration was efficient due to the large carbohydrate reserves in the shoot bases. Fertilization did not affect Bromus and Calamagrostis. In contrast, fertilized plants of Molinia produced larger storage organs and accumulated more carbohydrates. We conclude that plant size and growth form are important features promoting the ability of potential dominants to tolerate mowing and regenerate after it. Our results confirm that taller plants are selectively suppressed by this type of disturbance, thereby potentially promoting plant coexistence.

Key words: biomass removal, *Bromus, Calamagrostis*, carbohydrate storage, disturbance, management, *Molinia*, plant regrowth, starch, TNC

Introduction

In spite of the relatively short history of meadows in Central Europe (Breymeyer, 1990; Jacobs *et al.*, 1999), these plant communities are among to the most species-rich plant assemblages hosting numerous rare and endangered species. The origin of this diversity has been thoroughly discussed (Breymeyer, 1990; Kull and Zobel, 1991; Zobel, 1992) and several factors, both historical and ecological ones, have been identified as being fundamental to the ecology and maintenance of species-rich meadows (Zobel, 1992, 1997). However, these factors cannot explain the long-term maintenance of high species diversity. An enormous number of hypotheses explaining the coexistence of plants have been suggested, not always mutually exclusive applicable to any situation (Palmer, 1994; Gaston, 1996). For more productive meadows, both theoretical (Palmer, 1994) and empirical studies (Bakker, 1989; Kull and Zobel, 1991; Gusewell et al., 1998; Huhta and Rautio, 1998; Schläpfer et al., 1998; Barthram et al., 1999) suggest that the most important factor responsible for the long-term maintenance of species richness is regular removal of above-ground biomass, either by mowing or grazing. Changes in species composition and shifts in the dominance hierarchy of meadows, which were originally species-rich and have been abandoned or fertilized, indicate the crucial role of biomass removal for the maintenance of species diversity. Abandoned meadows usually become covered with monotonous species-poor vegetation, in which a single grass species tends to dominate. In later stages they are usually invaded by shrubs and overgrown completely (Dzwonko and Loster, 1998; Stampfli and Zeiter, 1999; Klimeš et al., 2000). Out of about 150 to 200 species of vascular plants which usually occur together in individual localities of species-rich meadows, there are very few plants, usually grasses, which become dominants after regular management ceases. Fertilization may result in effects similar to those observed in abandoned meadows: more nutrients are available, species richness declines and a single grass species becomes dominant (Rease and Decker, 1966).

The potentially dominant plants are usually larger than their neighbors and therefore, by mowing, they lose a higher proportion of their biomass than their neighbors. This could be an effective mechanism promoting plant coexistence. Available field data suggest large differences in regrowth of individual plants after mowing. Species which cover and dominance in un-mown meadows have also a high capacity to recover after an increase in disturbance, by means of vegetative growth (Richards and Caldwell, 1985; Donaghy and Fulkerson, 1998). This regeneration process may be faster if carbohydrate reserves are available for regrowth. The relationship between regrowth and carbohydrate storage has recently been questioned because the amount of reserves is usually not limiting for plant regrowth (Richards and Caldwell, 1985; Hogg and Lieffers, 1991a, b). It seems beyond doubt, however that at least the earlier phases of regrowth are largely dependent on carbohydrate reserves and repeated cutting depletes reserves considerably. Large carbohydrate reserves are also beneficial for fertilized plants because during a period of nutrient flush, which is usually short, utilization of the easily available nitrogen can be limited by carbon availability (White, 1973; Baas, 1989). These carbon expenses could be supplied from carbohydrate reserves. Therefore, we expect that the most successful plants in abandoned and fertilized meadows are relatively large and should be capable to regrow fast after mowing or increase their biomass after fertilization, using their reserves of stored carbohydrates.

In general plants are using reserves to buffer temporal changes in their growing conditions (Iwasa and Kubo, 1997; Suzuki and Stuefer. 1999). Carbohydrates are usually considered the main compounds of storage, while nitro-genous compounds are sometimes also included (White, 1973; Heilmeier and Monson, 1994). Carbohydrate reserves play a particularly important role in plant regrowth after a period of inactivity and in recovery after disturbance. In addition, they are used to meet carbon demands for respiration and reproduction (Bradbury and Hofstra, 1977; Chapin et al., 1990; Heilmeier and Monson, 1994). At a smaller time scale the storage is needed to cover expenses during bad weather and nights when photosynthesis is reduced or interrupted (Chapin et al., 1990). Water-soluble carbohydrates play a significant role in freezing tolerance, too (Gunn and Walton, 1985; Chatterton et al., 1989). Carbohydrates accumulate virtually in all plant organs. However, numerous plants develop organs with specialized tissues (Klimeš et al., 1997) where concentrations of storage carbohydrates may reach remarkably high values. The total amount of carbohydrates per plant is higher in species developing storage organs. The importance of carbohydrate storage has repeatedly been demonstrated in various species, especially for regeneration after cutting (Hogg and Lieffers, 1991a, b; Klimešová, 1996; Donaghy and Fulkerson, 1998) and for spring regrowth (Rease and Decker, 1966; Clevering et al., 1995). However, little is known about differences between species in the amount of carbohydrates available for regeneration after a disturbance, within a stand or a plant assemblage.

It can be expected that the ability to attain a high dominance in un-mown meadows is closely associated with efficient clonal growth and effective carbon economy in relation to disturbance by mowing. Plant damage by mowing (biomass removal) should increase with plant size because the level of cutting above the soil surface is the same for all plants. Therefore, by mowing, larger plants lose a higher proportion of their above-ground biomass than small plants. This even holds for the total biomass if there is a positive correlation between above- and below-ground biomass across species. Suppression of the potential dominants reduces the strength of competition, thereby promoting the survival of small and competitively inferior plants. In this way mowing may facilitate plant coexistence. We also expect that plants possessing special organs for storage reach higher concentrations of carbohydrates in comparison with plants without such organs. If expressed in absolute amounts per plant shoot this difference should further increase. Plants with special storage organs should be able to restore their original biomass after a disturbance within a shorter time than plants without them. Finally, we expect that fertilization is more beneficial for plants with large carbohydrate storage than for plants with a small storage because plants with specialized storage organs are able to utilize nutrients more efficiently (Iwasa and Kubo, 1997).

For this study we selected species-rich meadows in the Bílé Karpaty Mts., SE Czech Republic, hosting up to 75 species of vascular plants per m^2 and 99 species per 4 m² (Klimeš et al., 2001). Out of the 100 most frequent species of vascular plants occurring there, 21 species are graminoids. Only three of them (Bromus erectus, Molinia arundinacea and Calamagrostis epigejos) have a tendency to dominate in abandoned or moderately fertilized meadows. These three species are clonal, differ in their growth strategy and also in their preference for habitats along a fertilization and humidity gradient. The first two grasses belong to the dominant plants in the meadows, reaching a cover of up to 10-25% each. Calamagrostis epigejos penetrates sometimes into the meadows from neighboring scrub vegetation but is kept at a very low density by regular management. In abandoned meadows any of the three grasses may reach a cover of 40-70%, which is always accompanied by a significantly lower species diversity (Klimeš et al., 2000). The tendency to dominate in abandoned meadows has been observed in the three grasses repeatedly in several localities, but it is not clear under which circumstances the abundance of a particular grass increases and what are the mechanisms responsible for that.

In particular we tested the following three hypotheses:

(a) Plant sensitivity to mowing (biomass removal) increases with plant size. The larger the plant is, the higher proportion of its biomass is removed (*Bromus* vs. *Molinia* and *Calamagrostis*). (b) Plants with special organs for storage reach the highest concentrations of storage carbohydrates. Their regrowth is more efficient and faster than that of plants without special storage organs (*Molinia* vs. *Calamagrostis*). (c) Vegetative regeneration of mown plants is improved by fertilization, especially in plants with large carbohydrate reserves.

Methods

The experiment was carried out in the core of the National Nature Reserve of Čertoryje, Bílé Karpaty Mts., SE Czech Republic (48°54′ N, 17°25′ E). Mean monthly temperatures were 9.4 °C and the mean annual precipitation was 464.1 mm during the last 10 years. The experimental area was situated in meadows with scattered *Quercus* spp. trees, at an altitude of 430–440 m a.s.l., on a SW-faced slope with an inclination of about 5°. These are closed-canopy meadows on relatively deep calcium-rich soils, drying out in summer and mown once a year, with an above-ground biomass of about 250 g m⁻² in June before the harvest (Klimeš, 1995, 1999). There are no distinct seasons supporting different groups of plants during a year so that all species, including a few annuals, can be found just before mowing. Species-rich meadows are widespread in the Bílé Karpaty Mts., covering more than 4000 ha, i.e. 5.6% of the total area. Soil conditions estimated close to one of the experimental plots

were as follows: pH [H₂O]: 5.99; total nitrogen: 0.47%; total carbon: 5.45%. Ca: 8.42 mg g⁻¹; K: 0.05 mg g⁻¹; Mg: 0.72 mg g⁻¹; Na: 0.052 mg g⁻¹; P: 0.234 mg g⁻¹ (estimated in a 1 M BaCl₂ extract, with the ICP OES method). The meadow has not been fertilised in the past decades. The maximum above-ground biomass was about 250 g m⁻² in 1998 and the total cover of vascular plants was about 70%.

In April 1997 nine plots, 10×10 m each, were placed and fixed in an apparently homogeneous area. In the plots one of the three potential dominant grasses, i.e., B. erectus, M. arundinacea and C. epigejos, attained a relatively high cover (10-25%; further on called Bromus, Molinia and Calamagrostis meadows, respectively), whereas the other two grasses were either less abundant or missing. Each of the Bromus, Molinia and Calamagrostis meadows was represented by three plots so that the variation of microhabitats of particular grassland types in the studied locality was included in the experiment. The distance between individual plots was 50-300 m. The plots were divided into 25 subplots each. In these subplots, 2×2 m in size, different management regimes were randomly applied, replicated three times. The following regimes will be evaluated in this paper: mowing at the end of June and fertilizing in May (80 g of standard NPK granules per m², containing 11% of nitrogen, 14% of K₂O and 12.4% of P₂O₅), mowing at the end of June and no fertilizing (traditional management, control), moving twice a year – at the end of June and in September and no fertilizing, no mowing and no fertilizing (abandoned subplots). In the individual subplots the management regimes did not change during the 3 years of the experiment.

The central squares, 0.5 m² in size, situated in each subplot were preserved for repeated recordings of species composition (not shown here). Morphological responses and carbon storage were studied in the buffer zones surrounding the central squares. Plant samples of *B. erectus*, *M. arundinacea* and C. epigejos used for carbohydrate analyses were collected on 3rd October 1999. Five to eight individual plant shoots (stems growing above- and below-ground, and leaves) were randomly selected and collected in each subplot. In some subplots additional below-ground parts of plants were sampled to get 2 g of dry tissue for the chemical analyses. In the laboratory plant shoots were separated into above-ground parts and parts growing at the soil surface and below it (further on called below-ground part). The below-ground part was dried, weighed and analyzed for carbohydrate content. The dry samples were ground and weighed, 2 g of the tissue were used for the estimation of sucrose, glucose, fructose, fructans and starch, carbohydrate fractions were estimated using HPCL chromatography. For methodological details see Čížková et al. (1996). Starch was determined in the supernatant by the anthrone method using glucose as standard (McCready et al., 1950). Total non-structural carbohydrates (TNC) were calculated as starch + sucrose + glucose + fructose + fructans.

On above-ground parts of the shoots the following characteristics were measured: length of the longest leaf sheath (the distance between stem base and the insertion of the highest leaf blade – a measure of plant height), length of the longest leaf blade, number of green leaves and above-ground biomass. To evaluate the ability of plants to regenerate in the following season the same characteristics were measured on above-ground parts of plants on 25th May 2000.

Plant size hierarchies were estimated for the 98 most frequent species occurring in the studied area in June 2000. For individual species about 10 shoots were randomly selected in the field. Shoot height was measured *in situ* and the shoots were cut into fractions below and above 10 cm height above the soil surface. Biomass of these two fractions was dried at 90° to constant weight in a drying chamber and weighed.

Species description

Bromus erectus is a perennial grass with epigeogenous (initiated above-ground) sympodial rhizomes (Fig. 1). Its shoots are polycyclic, tillering is intravaginal. In sparse vegetation it forms large distinct tussocks, in closed-canopy meadows its tussocks are small, being formed by a few shoots. It does



Bromus erectus Molinia arundinacea Calamagrostis epigejos

Figure 1. Graphical representation of the three studied grasses, with emphasis on their storage organs.

not develop any special storage organs, its roots are thin and rhizomes are relatively short-lived.

Molinia arundinacea is a perennial grass with hypogeogenous (initiated below-ground) sympodial rhizome consisting of short increments, growing closely to the soil surface (Fig. 1). Its shoots are monocyclic, tillering is intravaginal. The base of the shoots is formed by one or two thickened nodes serving as a storage organ. Roots of M. arundinacea are thick and long. Axillary buds are situated at the base of the stem tuber. Several of them are utilized for spring regrowth in un-mown stands. In regularly mown meadows one bud usually breaks dormancy and multiplying rate is consequently much lower.

Calamagrostis epigejos is a perennial grass with horizontally growing hypogeogenous sympodial rhizomes (Fig. 1). Its shoots are dicyclic. Tillering is intra-vaginal, partial tussocks consist of 1–2 green shoots. Long below-ground rhizomes are formed extra-vaginally.

Results

The concentrations of carbohydrate fractions and TNC strongly differed between the three studied grasses (Table 1, Panel A). The imposed management regimes affected the levels of starch, sucrose and TNC, but not of glucose, fructose and fructans. The significant interaction between species and

	Species (1)	Plot (2)	Management (3)	Interactions					
				(1-3)	(2–3)				
Panel A: Expressed as concentrations									
Starch	***	**	***	***	ns				
Sucrose	***	**	**	ns	ns				
Glucose	***	ns	ns	ns	ns				
Fructose	***	***	ns	ns	ns				
Fructans	***	ns	ns	ns	ns				
TNC	***	**	***	***	ns				
Panel B: Expressed as total amounts per shoot base									
Starch	***	**	***	***	**				
Sucrose	***	**	*** ***		**				
Glucose	***	**	***	***	ns				
Fructose	***	*	***	***	ns				
Fructans	***	ns	***	***	**				
TNC	***	ns	***	***	*				

Table 1. The effects of species, plot and management on carbohydrate fractions

Based on hierarchical ANOVA with plots nested within species.

***p < 0.001; **p < 0.01; *p < 0.05; ns $-p \ge 0.05$.

management found for starch and TNC indicates that the effects of these management regimes were species-specific. The effect of plots was significant for several carbohydrate fractions, too, possibly due to the differences in nutrient availability and/or soil moisture content. In contrast, the effect of management was the same in all plots where the same grass was evaluated (Table 1, Panel A).

Starch was the main storage carbohydrate in all three grasses. The highest concentrations (about 50%) were found in *Molinia*, lower in *Calamagrostis* (about 40%). In *Bromus* it attained the lowest concentration, about 20% of starch (Table 1, Panel A; Fig. 2). Water-soluble carbohydrates (sucrose, fructose and glucose) were stored at markedly lower concentration in all three species. More sucrose was accumulated by *Molinia* than by the other two species, while the highest concentrations of fructose were found in *Calamagrostis*. The highest concentrations of fructans were found in *Bromus*. Patterns



Figure 2. Concentrations of carbohydrate fractions (mean + S.E.) in below-ground parts of shoots in three grasses in October 1999. F – fertilized; 1 – mown once a year; 2- mown twice a year; 0 – abandoned.

of TNC closely followed that of starch. Management significantly affected concentrations of carbohydrates in *Molinia* and *Calamagrostis* only (Fig. 2). Fertilization slightly decreased the concentrations of nearly all fractions of carbohydrates in the three species, although this decrease was usually non-significant. Repeated mowing resulted in a significant depletion of starch and TNC in *Molinia* and *Calamagrostis*, sucrose decreased in repeatedly mown plots with *Molinia* only. Surprisingly, glucose concentration increased in repeatedly mown *Molinia* stands. In abandoned meadows concentrations of most carbohydrate fractions were slightly reduced (Fig. 2), but this effect was usually not significant (Table 1, Panel A).

The total amount of carbohydrates in below-ground parts of shoots differed strongly between the species (Table 1, Panel B) and between management regimes. The strongly significant interaction between species and management regime indicates that the effects of the management regimes were species-specific. For most carbohydrate fractions the response of the grasses to the management was also specific in individual plots (Table 1, Panel B). Molinia accumulated the highest amounts of all carbohydrate fractions (Fig. 3). It was followed by Calamagrostis, whereas Bromus stored negligible amounts of carbohydrates in its shoot bases. The distribution of carbohydrate fractions across treatments within the species (Fig. 3) accurately followed the distribution of below-ground biomass per shoot (Fig. 4). Dry weight of below-ground parts of the shoots and concentrations of starch was strongly correlated for the combined data ($y = 9.1 \ln(x) + 60.0$; $R^2 = 0.66$; n = 108). However, when analyzed separately for individual species, the relationship persisted for Ca*lamagrostis* only $(v = 11.8 \ln(x) + 67.3; R^2 = 0.34; p < 0.0002)$. This indicates that only in Calamagrostis starch concentrations are constrained by the amount of the structural tissue. For sucrose, glucose and fructose the relationship calculated for individual species was always non-significant (results not shown).

Plant morphology and shoot biomass showed strongly significant speciesspecific differences between measurements made in October and May of the subsequent year (Table 2). Management regimes affected all estimated parameters significantly. The response of individual species to management regimes differed strongly within and between years.

Above- and below-ground parts of shoots were smaller in *Bromus* than in the other two grasses. This was true for all parameters, except for the number of leaves per shoot (Fig. 4). The differences between shoot sizes of plants collected in control plots in October and June of the next year were generally small, presumably due to the extremely dry spring in 2000 which resulted in a relatively low biomass of all plants. In contrast, the response to the second cut in September was strong. No species was able to regenerate completely until October when measurements were made. The differences between treatments



Figure 3. Total amount of carbohydrate fractions (mean + SE) in below-ground parts of shoots in three grasses in October 1999. F – fertilized; 1 – mown once a year; 2- mown twice a year; 0 – abandoned.

were smaller by next May, but they still persisted in all three species (Fig. 4). In contrast, the abandoned plots reached much larger values of all parameters in October than in May of the next year. *Molinia* showed the largest differences between the control and abandoned plots. This species was capable of utilizing the 'prolonged season' in abandoned plots more efficiently than *Calamagrostis* and much more than *Bromus*. In May the differences between abandoned and control plots were the largest in *Molinia* for most parameters. These differences were smaller by next May, but they were still larger than in *Calamagrostis*. In *Bromus* most differences disappeared between October and May. The number of leaves was much reduced by the second cut in *Molinia* and *Calamagrostis*, as recorded in October. However, these differences between *Molinia* and *Calamagrostis* disappeared by next May (Fig. 4).



Figure 4. Selected characteristics of tree grasses (mean + SE) in meadows subjected to four management regimes. Estimates were obtained at the end of the season (after the second harvest of plots mown twice a year, in October 1999) and before the first harvest in the subsequent year (May 2000).

The effect of fertilization was generally small. However, *Molinia* showed a significant increase in below-ground biomass. The biomass of the other two grasses did not change.

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	Interactions											
	Year (1)	Species (2)	Plot (3)	Mana (4)	(1–2)	(1–3)	(1-4)	(2–3)	(2–4)	(3-4)	(1–2–4)	(1–3–4)
Below-ground biomass per shoot [g]	-	***	ns	***	_	_	_	_	***	***	-	-
Above-ground biomass per shoot [g]	***	***	***	***	***	ns	***	_	***	***	***	ns
Longest leaf sheath [cm]	***	***	ns	***	***	ns	***	_	***	***	***	ns
Longest leaf blade [cm]	***	***	***	***	***	ns	***	_	***	**	***	*
Number of green leaves per shoot	***	***	***	***	***	*	***	-	***	*	***	ns

Based on hierarchical ANOVAs with plots nested within species.

Mana – management. ***p < 0.001; **p < 0.01; *p < 0.05; ns – $p \ge 0.05$.

Discussion

The concentration of carbohydrates in bases of stems of the three grasses was relatively high. For example, TNC concentrations ranged between 35 and 60%for different species and treatments. The highest concentrations were found in Molinia, the only species with a specialized storage organ. In comparison with other plants studied so far this level of TNC is relatively high. In other rhizomatous graminoids, such as *Phragmites australis*, 30-53% of TNC has been reported (Čížková et al., 1996; Klimeš et al., 1999), 41% of TNC was estimated in rhizomes of un-mown stands of *Phalaris arundinacea* (Klimešová, 1996), up to 19% in Calamagrostis canadensis rhizomes (Hogg and Liefers, 1991a, b), 33-51% in C. villosa (Holub, 1996), and 16-45% of TNC was found in Carex lacustris rhizomes (Roseff and Bernard, 1979). In plants with rhizomes specialized for storage, TNC levels similar to those found in Molinia mown once a year have been reported (e.g. 50-64% in Rumex alpinus - Klimeš et al., 1993; Klimešová and Klimeš, 1996; 60% in rhizomes of Polygonum bistortoides -Mooney and Billings, 1960, 50–55% in tubers of Scirpus maritimus – Clevering et al., 1995). The highest levels of carbohydrates, up to 73%, have been reported from shoot bases of a rhizomatous grass Parodiochloa (Poa) flabellata (Gunn and Walton, 1985). The total amount of carbohydrates in individual shoot bases are likely to be ecologically more relevant than the actual concentrations because they indicate how much carbohydrates are at disposal for regrowth. The three species differed even more strongly when considering absolute amounts of stored carbohydrates instead of concentrations. There are two potential problems associated with this approach. Firstly, the amount of estimated storage does not include all carbohydrates within a plant. In general, storage carbohydrates are available in all parts of the plant, including leaves and roots. Nevertheless, it has been repeatedly shown that the concentrations of storage carbohydrates in roots and leaves are either low or stable and only a small part of this storage can be imported to growth sinks (reviewed by May (1960) and White (1973)). Much of the carbohydrates utilized for regrowth is accumulated in stem bases. Therefore, the presented values are possibly underestimated in *Calamagrostis* only, because its rhizomes certainly contain carbohydrates available for regrowth. These, however, were not included in the analysis. Secondly, not all carbohydrates accumulated by plants are used for regrowth. Under normal conditions a small part of carbohydrates is usually utilized (Klimeš et al., 1999). However, in the case of extreme events, such as burial or repeated cutting, plants are capable of utilizing even more than 75% of their storage (Hogg and Liefers, 1991a, b; Klimeš et al., 1993). Thirdly, not all fractions of storage carbohydrates were analyzed by us. For example, structural carbohydrates (hemicellulose - see Masuzawa and Hogetsu, 1977), cellulose, proteins, organic acids, soluble phenolics, hydrolyzable tannins and

lipids also increase in response to a carbon surplus. However, it is not clear to which extent they can support plant growth (Richards and Caldwell, 1985; Chapin *et al.*, 1990). These fractions are certainly not as important and efficiently used as those compounds included into our analyses (White, 1973). In spite of these problems we believe that the storage of carbohydrates reported here well reflect the amounts available for the plants.

We found the highest concentrations of sucrose in *Molinia*, whereas in *Bromus* fructans was accumulated at the highest concentrations. *Calamagrostis* accumulated more fructose than the other two grasses. Whether these differences have any ecological consequences or not remains unclear because the role of individual fractions of carbohydrates in plants is still poorly known even if their metabolism has been studied in detail (e.g., Ho, 1988; Avigad and Dey, 1997; Geigenberger *et al.*, 1997).

The effect of mowing on carbohydrate reserves was strong. It has been reported that carbohydrates are utilized to promote regrowth during the first 1-2 weeks only. Later, plant growth depends on other factors, such as leaf area and nutrient availability (White, 1973; Richards and Caldwell, 1985; van der Heyden and Stock, 1996). Similarly, spring growth relies on carbohydrate reserves at the initial stage of development only (Mooney and Billings, 1960; Meyer and Hellwig, 1997). Reproduction, which is another stage in the life cycle of a plant with a high demand of carbon, also utilizes stored carbon for a relatively short period (Mooney and Billings, 1960). Nevertheless, in accordance with other studies (Canadell and López-Soria, 1998; but see Körner, 1999) we found that refilling of diminished carbohydrate pools is a relatively slow process. Molinia and Calamagrostis in plots mown twice a year reached one month after the last cut significantly lower starch and TNC levels than plants mown once a year. This difference likely persists over winter. Surprisingly, reserves of *Molinia* plants, which were not cut at all, were also more depleted than those of plants cut once a year (Fig. 2). This can be explained by the enormous accumulation of litter in un-mown Molinia stands. After 3 years of the experiment it formed a considerable thicket substantially reducing light levels on the ground. Even for the relatively strong Molinia shoots it became difficult to penetrate through this thicket. Growth of Molinia was therefore possibly pursued on the expense of reserve carbohydrates.

The effect of fertilization was surprisingly small. The level of nutrients used in the experiment was not very low, as it simulated levels of fertilization used by farmers in the past. However, it seems that the plants may not have been able to efficiently utilize the available nutrients due to unusually dry spring weather conditions during the last few years. The only plant capable of utilizing the added nutrients was *Molinia*, rooting deeper than the other two grasses. However, *Molinia* did not use the nutrients for the growth of leaves and stems, but for its tubers containing carbon storage. Larger carbohydrate reserves under moderate water stress have been reported from other plants, too (Brown and Blaser, 1965; White, 1973; Thomas and James, 1999).

It has been suggested that plants living in seasonal environments and adapted to a low resource supply form large nutrient storages. This suggests that the opportunity cost of the storage is lower in these environments than in conditions, which promote rapid growth and small storage (Chapin, 1980; Chapin et al., 1990). The same principle seems to be valid for carbohydrate storage. In seasonal environments plants with structures specialized for carbon storage are better represented than in more stable conditions (Klimeš et al., 1997). Out of the three studied grasses only Calamagrostis has relatively high nutrient demands (Ellenberg, 1974; Rebele, 2000). Accordingly, it does not form specialized organs for carbon storage and both storage concentration and total carbohydrate storage per shoot is lower in *Calamagrostis* than in *Molinia*, which is a plant of nutrient-poor habitats. However, Bromus accumulated even less carbohydrates, even if it is also a plant of nutrient-poor habitats. These results indicate that the above-mentioned rule is not general and some other factors may interfere. Accordingly, the diversity of clonal growth forms and types of storage organs in any environment is relatively high and a single type usually does not prevail (Klimeš et al., 1997).

The studied grasses differ in their morphology and seasonality. In Bromus the shoot base persists over several seasons. Therefore, no translocation is required to daughter ramets because they originate intravaginally within the mother shoot. Carbohydrate economy is therefore relatively efficient in this species. New tillers of *Calamagrostis* are polycyclic as well, but they are either intra- or extra-vaginal. The extravaginal tillers form relatively long hypogeogenous rhizomes, which are completely dependent on carbohydrates imported from the mother tiller. In Molinia the shoots are monocyclic. Their base is formed by a tuber which overwinters. In spring it regenerates from buds situated at the base of the tuber. After the new tillers are established the tuber dies. Virtually all storage of assimilates is accumulated in tubers and translocated to new tillers in spring only. These differences between the grasses are clearly reflected by the growth pattern after mowing. It would be of interest to know what the effect of mowing would be if it was applied at a lower level above the soil surface. In that case a larger part of the above-ground biomass of Bromus would be removed and consequently Bromus would be much more sensitive to moving. The data collected in the studied locality by Sillinger (1929) fit to this scenario quite well. Bromus attained a surprisingly low abundance in the 1920s, being effectively suppressed by mowing, which was done by hand and its level above the soil surface was certainly considerably lower than today. From the 1950s when machines replaced hand-mowing Bromus could spread and increase in abundance so that in the 1970s it was already as abundant as today (Tlusták, 1972).

Our results show that the effect of mowing on the studied grasses corresponds to the expected order of the three species, based on plant size and presence of storage organs. Could this species-specific response contribute to the coexistence of plants in the studied meadows? The three grasses are not randomly selected representatives of plants occurring in the locality. All of them are relatively successful, in particular situations reaching the highest cover of all plants present, and belong to the tallest plants in the meadows (Fig. 5A), having approximately the same mean stem height – about 70 cm. There are very few plants in the studied meadows, which develop even longer stems. Only two of them are grasses (*Arrhenatherum elatius, Festuca pratensis*). These are mesophilous grasses which are poorly represented in the studied meadows and cannot reach a higher abundance due to a shortage of soil moisture in summer. Plant biomass is not distributed evenly disturbed along a vertical canopy profile. There-



Figure 5. Mean plant height (A) and proportion of their above-ground biomass potentially lost due to mowing at 10 cm above soil surface (B) of the 98 most frequent plant species occurring in the studied area.

fore, the position of the three grasses according to the proportion of biomass potentially lost by mowing shows a pattern markedly different from that based on plant height (Fig. 5A). The studied grasses move towards the center of distribution (compare Fig. 5A and B), differences between them increase considerably and the order of the two larger species reverses. The smallest proportion of biomass lost by mowing was found in *B. erectus* – 68%. *Calamagrostis* lost 79% and *Molinia* 81% of its above-ground biomass, on average.

In the studied meadows, there are very few plants, which are not directly affected by mowing, such as *Ajuga reptans*, which does not reach the level of mowing. On the other hand, *Knautia kitaibelii*, *Lathyrus latifolius* and *Clematis recta* may lose up to 90% of their biomass, if mown at 10 cm above the ground. Among grasses there is no single species losing more biomass by mowing than *Molinia*. *Calamagrostis* is the second grass in this order and is followed by *Trisetum flavescens*, *Festuca pratensis*, *Brachypodium pinnatum*, *Dactylis glomerata*, *Arrhenatherum elatius*, *Bromus erectus*, etc. Among graminoids the lowest proportion of biomass removed by mowing was found in *Carex caryophyllea* (12%), *Sieglingia decumbens*, *Festuca rubra*, *F. rupicola*, *Holcus lanatus*, *Carex montana*, etc. Most of these graminoids belong either to dominants recorded by Sillinger (1929) (*Carex montana* and *Carex caryophyllea*) or are representatives of plants for which the studied meadows are marginal in respect to their nutrient and soil moisture demands (*Festuca rubra*, *Holcus lanatus*).

These data show that *Molinia* and *Calamagrostis* are the largest grasses in the studied meadows, which lose a high proportion of their biomass by mowing. Therefore, they are suppressed by mowing more than any other graminoids. This negative effect was probably partly reduced (but not removed) by their access to large carbohydrate reserves stored below-ground. In contrast, *Bromus* is a medium-sized plant which is affected by mowing to an extent comparable to several other graminoids. This pattern is in agreement with our predictions. Therefore, we conclude that mowing, which is selective in its effect on individual plants, acts as a factor promoting plant coexistence in meadows by suppressing potential dominants.

Conclusions

(a) The proportion of above-ground biomass lost by mowing increases from *Bromus* to *Calamagrostis* and *Molinia*. A reversed order was found for the magnitude of the effect of mowing on shoot regrowth and on depletion of carbohydrate reserves. (b) *Molinia*, a species developing tubers specialized in carbohydrate storage, accumulates the highest concentrations and amounts of carbohydrates per shoot. In spite of the large negative short-term effect of

repeated mowing on regrowth of *Molinia* this species is able to recover in the next season as efficiently as *Calamagrostis* which is less disturbed by mowing. (c) Fertilization did not affect plant growth. However, shoots of fertilized *Molinia* developed larger storage organs containing a higher amount of storage carbohydrates. The effect of fertilization on *Bromus* and *Calamagrostis*, grasses lacking special storage organs, was negligible.

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