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#### Original article

# Effect of mowing and fertilization on biomass and carbohydrate reserves of *Molinia caerulea* at two organizational levels

### Michael Bartoš<sup>a, b, \*</sup>, Štěpán Janeček<sup>a</sup>, Jitka Klimešová<sup>a</sup>

<sup>a</sup> Section of Plant Ecology, Institute of Botany, Academy of Science of the Czech Republic, Dukelská 135, 379 82 Třeboň, Czech Republic
<sup>b</sup> Department of Botany, Faculty of Sciences, University of South Bohemia, Branišovská 31, 370 05 České Budějovice, Czech Republic

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#### ABSTRACT

Individual plant responses to traditional management on European meadows are reported to be contextspecific due to various biotic and abiotic factors. However, the effect of organizational level on which the response is measured is rarely considered. We asked whether plant investment into current and future growth in the clonal grass Molinia caerulea, dominant in a species-rich meadow, expressed per shoot or per growth unit (physically independent part of a clone containing all shoots produced by one overwintering tuber) differs between a mown (biomass harvested at June-July) and an abandoned (left without any management) or fertilized meadow (mown and fertilized). As a measure of investments into current growth we used aboveground biomass and as a measure of investments into future growth we used storage of carbohydrates. Biomass production was higher in managed plots (both mown-fertilized and mown plots) when expressed per growth unit and lower when expressed per shoot. Storage of carbohydrates was not different at the end of the season in plants from differently treated plots when expressed per growth unit, but was significantly reduced for individual shoots from managed plots. This implies that the interpretation of the results from our study depends on organization level and method of plant response assessment (storage vs. growth) and this paradox indicates that considering these factors in a particular study could bring deeper insight into individual responses of plants to changing disturbance regime.

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#### 1. Introduction

Herbivory, namely grazing of herbaceous vegetation by large domestic animals, affects plant growth in many communities. In regions where winter or summer grazing is not possible due to snow cover or drought, grazing is replaced by traditional mowing (Bredenkamp et al., 2002). This management, contrary to direct grazing, non-selectively affects all plants in a community by removing their aboveground biomass, traditionally only once or twice a year. Due to the stronger effect of this type of management on larger and more competitive species than on smaller ones, mowing allows coexistence of a large number of species differing in size and competitive ability (Zobel, 1992; Klimešová et al., 2010) and causes a shift of species composition when the management

E-mail address: bartos@butbn.cas.cz (M. Bartoš).

changes (Huhta, 1996; Wahlman and Milberg, 2002; Stránská, 2004; Janeček and Lepš, 2005).

According to our current knowledge, plants respond to biomass removal by regrowth from dormant meristems and compensate in different degrees for lost biomass, intensify photosynthesis and longevity of rescued biomass (i.e. biomass which was not lost), reduce root growth and increase branching or tillering (Mashinski and Whitham, 1989; Strauss and Agrawal, 1999; but see Murphy and Briske, 1992). Nutrient addition, competition, timing of disturbance (early in the season or later on), severity of defoliation (how much of the aboveground biomass is removed) and frequency (how often biomass is removed) hinder or enhance regrowth and thus tolerance to herbivory (Agrawal, 2000). Usually, compensatory growth is assessed only by measuring aboveground regrowth, but in perennial plants, investments into aboveground biomass might be viewed as an allocation to momentary resource acquisition which is constrained by allocation into storage and thus to survival and future growth (Suzuki and Hutchings, 1997). Therefore carbon investment into perennial belowground organs seems to be important for understanding to processes related with compensatory growth (Stearns, 1992; Iwasa and Kubo, 1997; Hochwender et al., 2000).

<sup>\*</sup> Corresponding author. Section of Plant Ecology, Institute of Botany, Academy of Science of the Czech Republic, Dukelská 135, 379 82 Třeboň, Czech Republic. Tel.: +420 607941107; fax: +420 384721136.

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Carbon stored in plant parts out of reach of disturbance is used for regrowth of aboveground biomass (Adegbola and McKell, 1966; Raese and Decker, 1966; Odgen and Loomis, 1972; Booysen and Nelson, 1975; Iwasa and Kubo, 1997). Dependency of regrowth on carbohydrate reserves is only temporary and lasts until new photosynthetic tissue is formed (Richards and Caldwell, 1985; Hogg and Lieffers, 1991). Nevertheless, carbohydrate storage replenishment can take a much longer time and is species-specific (Menke and Trlica, 1981; Volenec, 1986). Compensation of biomass may be negatively affected when disturbance occurs at the time of a seasonal minimum of carbon storage (i.e. during the period when carbohydrate reserves are depleted for fast growth: Menke and Trlica, 1981; Klimešová, 1996; Nofal et al., 2004; Janeček et al., 2011), thus reducing carbon replenishment before winter (Menke and Trlica, 1983; Klimeš and Klimešová, 2002; but see Sosnová and Klimešová, 2009). Even when storage of carbohydrates at the time of biomass removal is sufficient, their use for regrowth may be hindered by a shortage of nitrogen (Leakey et al., 1977; Mashinski and Whitham, 1989; Wise and Abrahamson, 2005). So far, our knowledge of carbon storage patterns is mainly based on carbohydrate concentrations because the carbohydrate budget per plant is difficult or impossible to assess for clonal plants growing intermingled in a community.

Although changes in species composition after cessation of management or fertilization are well described, individual responses are less known. This is a consequence of the fact that individual responses of perennial herbs, which are mainly clonal, are difficult to follow in the field. Consequently, the majority of studies on which our understanding of plant responses to grazing or mowing are based are carried out either in pot experiments (Cullen et al., 2006; del-Val and Crawley, 2004, 2005; Ferraro and Oesterheld, 2002; Rotundo and Aguiar, 2008) or on monocarpic plants (Huhta et al., 2000a,b,c, 2003; Rautio et al., 2005). When they are performed on perennial species in the field, clonal growth is overlooked (Klimeš and Klimešová, 2002). Exceptions include studies from American rangelands, which examine the response of grass species to grazing at the individual shoot level as well as all shoots of rhizomatous species occurring in a defined area (e.g. Mullahey et al., 1991; Zhang and Romo, 1995), or at shoot and individual plant levels in the case of tussock grasses (e.g. Caldwell et al., 1981; Butler and Briske, 1988; Hendon and Briske, 2002).

Some of the above methodological problems could be overcome by pot experiments, but their ability to mimic natural processes is limited. Although these experiments allow for the study of belowground biomass of plants, they have several drawbacks e.g.: 1) they usually are run without competition which may substantially affect the results of such a study (del-Val and Crawley, 2004); 2) they are conducted with very young plants possessing small storage organs and consequently lower regrowth ability (Wegener and Odasz, 1997). Because pot studies ignore competition, they often report cost of apical dominance, i.e. undisturbed plants show lesser branching than disturbed plants. Overcompensation of lost biomass is repeatedly observed in such studies (Aarssen, 1995; Wise and Abrahamson, 2005), especially when disturbance does not remove more than 25% of the aboveground biomass. When more than 70% of the biomass is removed, plants are not able to compensate for lost biomass (undercompensation) and a cost of resprouting is observed (Huhta et al., 2003; but see Martínková et al., 2008).

The aim of our study was to assess the individual response of a dominant meadow species to abandonment and fertilization, two of the most obvious threats to species-rich meadows (Tasser and Tappeiner, 2002; Isselstein et al., 2005). We did this in terms of biomass and carbon storage. Due to the abovementioned methodological obstacles, we decided to set our experiment in the field and chose a species in which vegetative multiplication and the carbohydrate budget in a storage organ could be assessed. We studied *Molinia caerulea*, which is an important species of wet meadows, being common in cut stands, dominating and spreading after abandonment and finally forming species-poor stands (Hájková et al., 2009). On the other hand, its performance in fertilized meadows is weakened and consequently the species disappears from the community (Lepš, 1999).

Specifically, we asked two questions concerning the performance of *M. caerulea* in traditionally managed, mown, unfertilized plots with recently abandoned (unmown and unfertilized) and fertilized (mown and fertilized) plots: how much affected are (1) aboveground biomass, and (2) carbohydrate storage both at shoot and tussock levels during a season. The shoot level is characterized by one photoactive shoot where biomass of its green aboveground part was considered as a measure of an investments to current growth and carbohydrate storage in its single basal tuber was considered as a measure of an investment to future growth. A tussock level is characterized as a physically independent part of a clone containing all shoots produced by one overwintering tuber, hereafter called growth unit.

#### 2. Material and methods

#### 2.1. Study species

M. caerulea (L.) Moench is a perennial grass species growing in compact tussocks which are composed of densely aggregated shoots (phalanx growth strategy, Lovett Doust, 1981) with their tuberous bases forming a short rhizome. Because the rhizome perennates usually only two years, plant individuals originating from one seed soon form a clone of physically independent units (hereafter called growth units). The flowering shoot is formed by several short basal internodes, the last internode forming a storage organ (tuber) about 3 cm long and 1 cm in diameter, and finally one long internode bearing an inflorescence, which can be up to 150 cm long (Jefferies, 1915); the shoot has up to seven functional leaves of max. 60 cm long. The shoot's longevity is one year; the green aboveground shoot dies off before winter and the only overwintering parts are tubers forming the short rhizome. New shoots arise from buds at the base of a tuber (below storage internode) in the spring (Arber, 1934) or after cutting if the plant is growing on a mown meadow (Fig. 1). M. caerulea usually flowers in July and



**Fig. 1.** A schema of basal parts of growth units (physically independent tussocks) of *Molinia caerulea* growing on abandoned and managed (mown and mown-fertilized) meadow as they look at the end of vegetation season. Arrows point on insertions of photoactive shoots; asterisks point on shoots lost by mowing; A, A<sub>1</sub> – overwintering basal tuber bearing photoactive shoot last year; B – first cohort of this year tubers bearing photoactive shoot for the whole season; B<sub>1</sub> – first cohort of this year tubers bearing photoactive shoot before mowing take place; C – bud for next year shoot, C<sub>1</sub> – second cohort of this year tubers bearing photoactive shoot before mowing take place.

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