



Research article

Changes in biomass allocation in species rich meadow after abandonment: Ecological strategy or allometry?



Alena Bartušková^{a,*}, Jiří Doležal^{a,b}, Štěpán Janeček^{a,c}, Vojtěch Lanta^{b,d}, Jitka Klimešová^a

^a Institute of Botany, Czech Academy of Sciences, Dukelská 135, 379 01 Třeboň, Czech Republic

^b University of South Bohemia, Faculty of Sciences, Department of Botany, Branišovská 31, 370 05 České Budějovice, Czech Republic

^c Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, 128 44 Praha 2, Czech Republic

^d University of Turku, Department of Biology, Section of Ecology, FIN-20014, Turku, Finland

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ABSTRACT

Plants respond to changes in biotic and abiotic conditions by altering the allocation of biomass to organs with different functions. The degree to which this response is limited by architectural constraints and follows the rules of the allocation theory has rarely been studied at the community level for several reasons: environmental factors affecting plants in a community are of complex nature with contradictory effects, plants in a community tend to be similar in size, which limits the capability to recognize allometry, and only rarely are plant communities so species rich that robust regression analysis is feasible. We tested whether the often reported effect of meadow abandonment increasing investment into supportive structures due to an increasing competitive milieu is caused by changed allocation strategy of resident species or by an allometric effect. For the study we examined biomass allocation to leaf blades, petioles and stems in 41 plant species in two species rich temperate European meadows differing in water availability (dry versus wet) and subjected to abandonment. Biomass allocation between organs with supportive versus photosynthetic function in meadow species followed a general allocation pattern (allometric exponent 0.75), irrespective of the management. The observed changes in relative investment into supportive structures after abandonment were caused only by the increasing size of the resident species. The effect was restricted to wet meadow, while in dry meadow the reaction of the species was diverse – probably due to low competition after abandonment.

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Plant nomenclature

Kubát et al. (2002).

Introduction

One of the basic questions in comparative plant ecology is how plants allocate their resources to different functions (Bazzaz and Grace, 1997). The allocation of biomass to plant organs is presumed to be a reflection of actual plant life function demands, but this has its constraints. For example, when biomass is allocated to one organ or function, it is at the expense of other organs or functions; this implies trade-offs (Weiner, 2004). Furthermore, biomass allocation is limited by architectural constraints and these change with plant size. Between individual organs there are, therefore, frequent

allometrically scaled relationships (Niklas, 1994a,b; Enquist and Niklas, 2002). Residual variation of these relationships is considered to reflect the ecologically induced variations in biomass allocation within and across species (Zens and Webb, 2002; McCarthy and Enquist, 2007).

Understanding the strategy in resource allocation in plants therefore needs to separate the contribution of two components: alteration in allocation might be simply the result of size, which is called 'apparent' or 'passive' plasticity, or active changes in allocation relationships, called 'real' plasticity (McConnaughay and Coleman, 1999; Wright and McConnaughay, 2002). There are many experimental, usually intraspecific studies dealing with the influence of different resource availabilities on changes in biomass investment with mainly light, nutrients, water and CO₂ being considered (Poorter et al., 2011 and reference therein); allometric effects are, however, seldom explicitly tested (Janeček et al., 2014). Studies of resource allocation under field conditions are comparatively rare (Niklas, 1994a; Metcalf et al., 2006; Fraterrigo et al., 2006; Niu et al., 2008, 2009; Minden and Kleyer, 2011), and they

* Corresponding author. Tel.: +420 384 721 156.

E-mail address: alena.bartuskova@ibot.cas.cz (A. Bartušková).

separate the effect of plant size on the observed allocation of plant biomass and evaluate the response of a whole community even more rarely (Minden and Kleyer, 2011; Niu et al., 2009). The reasons for this are manifold: changes in the allocation strategy of plants under complex environmental effects faced usually by communities bring about contradictory effects of altered competition milieu, nutrient availability, disturbance regime, litter accumulation, etc. (Fortunel et al., 2009; Robson et al., 2009); communities might not be enough species rich to allow robust regression analysis; and species in a community tend to be similar in size. The plants in one community are filtered by certain environmental conditions (Díaz et al., 1998; Westoby and Wright, 2006) and therefore represent only a tiny fraction of the variability in the plant kingdom. In case the similarity concerns plant size, as in herbaceous communities, this could hinder the possibility of recognizing the general allometric pattern described by Enquist and Niklas (2002) for plants across different ecosystems (Robinson, 2004; Tilman et al., 2004; Poorter et al., 2011).

Having all those obstacles in mind we aimed to test whether the common observation that with increasing competition plants invest preferably into supporting organs at the expense of assimilation organs is due to active change in allocation strategy or simply due to allometry. As the biomass of leaves scales with the $3/4$ power of the stem biomass (Enquist and Niklas, 2002), the whole effect might be due to an increase of plant size with increasing aboveground competition. We selected a species rich temperate meadow subjected to abandonment as a model community. An advantage of meadow communities is that they represent the most species rich communities on a small scale recorded by researchers (Wilson et al., 2012) and therefore allow for examining biomass allocation of a large number of species growing in one community under the same conditions. Although all species in the meadow community are herbaceous and small, there is still some variability in stature (Klimešová et al., 2010), at least in species rich stands.

With the changing demands of the human society, the meadows have been exposed to alterations of management and in recent decades, abandonment has become one of the particularly highlighted threats to highly diverse meadow communities (Huhta, 1997; Baur et al., 2006). Abandonment above all other effects is associated with increasing competitive milieu and consequent successional changes resulting in decreasing species richness and changes in species composition towards woody species (Falińska, 1999; Kahmen and Poschlod, 2004; Doležal et al., 2011). In the dense vegetation cover of a meadow, competition for light plays an important role and the coexistence of species differing in size is enabled by the equalizing effect of regular mowing which allows the persistence of small plants regarded as weaker competitors (Zobel, 1992; Klimeš and Klimešová, 2001; Klimešová et al., 2010). A first response of resident species to altered competitive milieu, before any species-exclusion happens, is an increase in size and a change in biomass allocation to different organs, resulting in an increased allocation to stems, petioles, i.e. into supportive structures as they are all key components in the competition for light (Kull and Zobel, 1991; Givnish, 1995; Westoby et al., 2002; Poorter et al., 2011; de Bello et al., 2012).

Therefore, this study aims to elucidate the role of variation in biomass allocation of plants for two contrasting meadows after a change in management. We expect that the biomass allocation on the community level will be affected by the time since the cessation of mowing. The biomass allocation in response to the cessation of mowing was tested for 41 common species in wet and dry meadows both one and three years after abandonment at the peak of community development in June, just before traditional mowing, and at the end of the season in October. The following questions were considered:

- (i) Are the absolute and relative aboveground biomass allocations at community level in the meadows affected by location, management, season and/or year?
- (ii) Can a deviation from the general allometric relationship ($\alpha=0.75$) among supportive biomass and biomass of leaf blades for plants in a community be found and is it related to management change?
- (iii) Is the interspecific response to abandonment comparable to the intraspecific response?

Materials and methods

Site description

These experiments were conducted in two species-rich meadows, differing in water availability, that have already been used to study management impact on community functioning (Lepš, 1999, 2004; Klimeš et al., 2000). The dry meadow is located in the Bílé Karpaty Mts., south eastern Czech Republic, in the Čertoryje Nature Reserve (48°54' N, 17°25' E) at 440 m a.s.l. The area receives an average of 650 mm precipitation annually and has a mean annual temperature of 8 °C (Tolasz et al., 2007). The dryness is mainly caused by the high permeability of deep soils on a flysch bedrock. The meadow is on calcium-rich soil with scattered *Quercus* spp. trees, classified as *Bromion* alliance (Chytrý, 2007). There are up to 70 species/m² (Klimeš et al., 2000). The wet meadow is situated in the southern part of the Czech Republic in Ohrazení (48°57' N, 14°36' E), at 500 m a.s.l. The mean annual temperature is 7–8 °C and precipitation is 700 mm (Tolasz et al., 2007). Clay deposits near the soil surface prevent quick rain water infiltration. This meadow is on acidic soil and is classified as *Molinia* alliance (Chytrý, 2007). There are 35–40 species per 0.25 m² (Lepš, 2004). The meadows are mown in June (dry meadow) or July (wet meadow) and have been mown annually for at least 10 years before the experiment started. The wet meadow has a higher productivity of aboveground biomass (dry biomass 320 g m⁻²) than the dry meadow (dry biomass 250 g m⁻²) (de Bello et al., 2012).

Experiment

The dataset included 12,708 individually measured plant parts (leaves, stems, flowers) from 6129 plant individuals belonging to 41 common meadow species. The data were collected in traditionally mown and recently abandoned plots in both meadows, twice during the growing season: in early June before mowing and in mid-October at the end of the growing period in both 2006 and 2008. The experiment was set up in June 2005, in a randomized block design on regularly mown meadows. Six blocks were selected in the dry meadow and five blocks in the wet meadow. Each block contained nine permanent plots (three rows of three) in which either the fallow treatment (i.e. abandonment) was applied from 2005, or mowing was continued (for further details on experimental set up, see Klimešová et al., 2010). Out of all species only those species occurring in all of the selected plots in a given meadow in June 2006 were selected for data collection, resulting in 22 and 19 target species occurring on the dry and wet meadows respectively (Table 1).

A minimum 2–6 randomly selected shoots of each target species were harvested in each block – from two plots differing in management in June 2006 and in two other plots at other collection dates. Sampled shoots were transported in a cooling box to the laboratory where they were partitioned into blades, petioles, stems and reproductive parts. Samples were oven dried at 80 °C for 24 h and then weighed.

For later analysis, the petiole biomass with the stem biomass were combined as they are both supportive organs of leaf blades

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