

Plant functional traits in studies of vegetation changes in response to grazing and mowing: towards a use of more specific traits

Funkční vlastnosti rostlin ve studiu vegetačních změn v důsledku změny obhospodařování pastvou a kosením

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Plants' abilities to function are difficult to evaluate directly in the field. Therefore, a number of attempts have been made to determine easily measurable surrogates – plant functional traits (PFTs). In particular, the value of PFTs as tools for predicting vegetation responses to management (i.e., grazing and mowing) is the focus of a large number of studies. However, recent studies using PFTs to predict the effect of pasture management in different regions did not give consistent predictions for the same set of PFTs. This lead to the suggestion that more specific traits better suited for a specific region be used in the future. We consider the identification of the most adaptative traits for surviving grazing and mowing in different biomes an important goal. Using temperate grasslands in Europe as an example, we show that (i) plant height, often considered as the best predictor of species response to grassland management, is coupled with other more relevant functional traits, and that (ii) clonal traits have important, often neglected functions in the response of species to grassland management. We conclude that single traits cannot be the only basis for predicting vegetation changes under pasture management and, therefore, a functional analysis of the trade-off between key traits is needed.

Key words: clonality, disturbance, grassland, management, persistence traits, phenology, vegetative regeneration

Introduction

Large domesticated herbivores grazing pastures, or fed fodder harvested from meadows, are a key socio-economic and ecological issue in different ecosystems around the world. The resulting plant communities are traditionally managed for these purposes and survive harvesting, trampling and manuring (e.g., Vera 2000). Changes in intensity or timing of these processes result in changes in taxonomical and functional composition and subsequent changes in ecosystem functioning (Bakker 1989, Milchunas & Lauenroth 1993, Díaz et al. 2007). This explains the great interest in monitoring the impact of grazing and mowing on plant communities for the purpose of preserving their biodiversity and economic or aesthetic values.

Several theories about the effect of herbivory on plant communities in terms of species traits have been developed, which predict specific plant responses to grazing (see review by Díaz et al. 2007). The classical assumptions that resulted in the boom of plant trait studies are summarized by Noy-Meir et al. (1989):

(i) Grazing affects plant species unequally (i.e., some are favoured and others suppressed). (ii) Prolonged grazing results in stable communities. (iii) The main driver of species change under grazing is the intensity independent of weather and/or soil conditions. (iv) Species in different communities respond in a consistent manner (decrease or increase) to changes in the intensity of grazing. (v) Decreasing and increasing species, respectively, share specific morphological, physiological and life-history attributes (plant functional traits; PFTs). (vi) The relative composition of PFTs in different communities and different regions reflects the grazing intensity.

In order to better predict vegetation response to human activities, such as changes in grazing and mowing, based on the above hypotheses, vegetation changes were assessed in terms of a common set of PFTs (McIntyre et al. 1999a). For this a common set of functional traits needs to be agreed and their predictive value assessed under different grazing and mowing regimes, and in different regions (Weiher et al. 1999, McIntyre et al. 1999b). Plant ecologists in general agree on which ecological functions are relevant for dispersal, establishment and persistence of plant species. For example, in the list proposed by Weiher et al. (1999) the following ecological functions relevant to the persistence of plants in a community are listed: seed production, competitive ability, plasticity, space-holding capacity/longevity, space-acquiring potential, vegetative regeneration and disturbance avoidance. These ecological functions should be expressed and quantified by easily measurable traits such as seed number and seed mass, above-ground biomass, plant height, plant longevity, specific leaf area (SLA).

After agreeing a common set of traits, the next step is to test the predictive value of these common PFTs in different vegetation types and climatic conditions (McIntyre et al. 1999a, Díaz et al. 2001, de Bello et al. 2005). This challenge has been addressed by a number of plant ecologists (see the papers published in *Journal of Vegetation Science*, *Applied Vegetation Science*, *Journal of Applied Ecology*, etc.). Despite the first encouraging results (Díaz et al. 2001), the same traits do not consistently indicate species' responses to grazing under different environmental conditions (Vesk et al. 2004a, Osem et al. 2004, Pakeman 2004, de Bello et al. 2005).

This inconsistency in the predictive power of PFTs was confirmed by a recent meta-analysis across continents (Díaz et al. 2007). Nearly 200 individual studies from all continents using 7 common traits (life history, canopy height, growth habit, shoot architecture, growth form, palatability and origin) were inspected for consistency in the response of plants to grazing pressure (Díaz et al. 2007). Overall, the results indicated that increased grazing generally favoured annuals over perennials, small, prostrate and rosette plants over high, erect and tussock plants. These traits were reported as typical of pasture plants already many years ago even before a formal PFT analysis (Harper 1969, see also Milchunas & Lauenroth 1993, Díaz et al. 2007). In addition, the patterns in trait response in the meta-analysis of Díaz et al. (2007) are often strongly influenced by precipitation and/or grazing history, contrary to the original assumptions summarized by Noy-Meir et al. (1989). Thus, the relevance of single traits for predicting vegetation shifts might depend on specific environmental conditions or the historical background of particular grazing and mowing regimes. For further improve-

ment of the PFT approach the use of more specific traits better suited for a particular region was therefore proposed (Díaz et al. 2007).

Here, with particular reference to European temperate grasslands, we assess additional functional traits in different environmental conditions, reveal the complex nature of traditionally assessed traits and investigate the relationships between them and other more relevant traits.

Plant height

The most frequently PFT used to assess species response to pasture management is plant height. This trait is recognized as important for competitive performance and acquiring carbon, and is a fundamental functional trait of plants (Westoby 1998, Westoby et al. 2002). The importance of plant height is obvious when considering the plant kingdom as a whole from small annuals to tall trees (West et al. 1997). However, in studies of vegetation changes in pastures it might not be very informative (Vesk et al. 2004a). Pastures may be composed of a mixture of herbs and shrubs of the same size, so size of a species might not determine its competitive advantage over plants with other regenerative and space occupancy traits. This is due to the fact that vertical growth in different life forms has different costs: in herbaceous plants it is achieved during one season but woody species may take years to attain a similar height (Givnish 1995).

Therefore, instead of using traits as a single predictor of species success under a particular grassland management regime, trade-off between different traits, e.g. those related to competitive ability and avoidance of disturbance by means of low stature or timing of development, needs to be considered. A set of traits that can be used in combination with height to assess these trade-offs are related to shoot architecture (e.g., distribution of leaves along the plant stem, or biomass per unit height) or life cycle. The shoot architecture of herbaceous plants reflects the biomass distribution along the vertical axis of a plant. Although the competitive superiority of high erosulate shoots (i.e., erect leafy shoots) over low rosette shoots is clear, their loss in biomass when e.g., mowed, is not only a function of shoot height. Species with erosulate shoots usually lose all their leaves and the apical meristem with the potential to flower, as these shoots are usually monocyclic (Fig. 1), i.e. annual (for explanation see below). The different strategies of plants differing in shoot architecture was studied in Estonian meadows (Liira & Zobel 2000, Liira et al. 2002, Lepik et al. 2004) and grouping according to shoot architecture (and leaf width) proved to explain more of the variability in the response of plants to management, illumination and application of fertilizers, than height alone.

Other studies also indicate that a plant's life cycle needs to be considered together with plant height in assessing species response to pasture management (Vesk et al. 2004a, de Bello et al. 2005). When life cycle information is combined with height, an important plant attribute is the phenological status of shoots in perennial species. Using a similar analogy as Westoby (1998), the above-ground shoots of perennial herbs in a seasonal temperate climate start their growth in spring in a race for light. During the seasonal race for light, species may change their positions from dominant to subordinate or vice versa. Thus comparing small plants at the beginning of the season with tall plants at the end of the season may be meaningless as both may accumulate enough carbon to be able to take part in

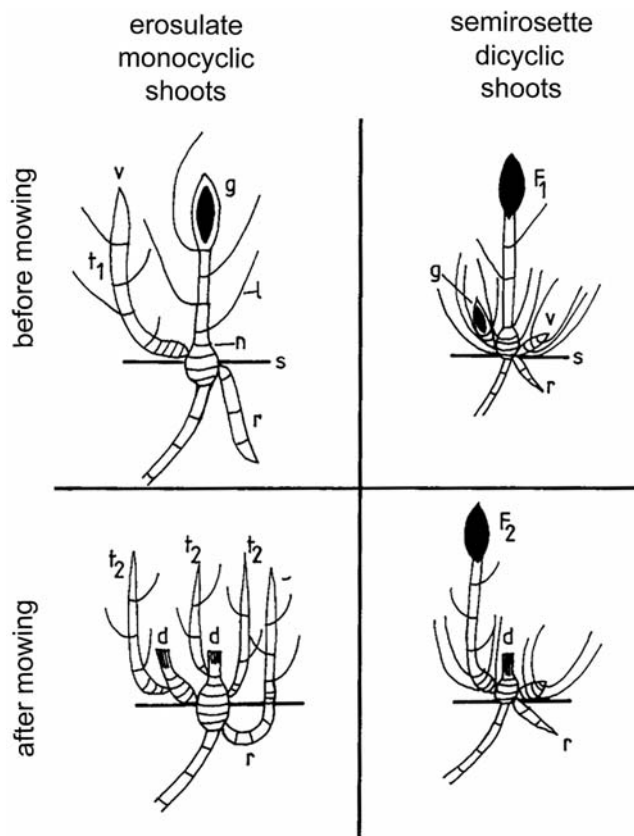


Fig. 1. – Effects of mowing on plants differing in shoot architecture and shoot cyclicality. Mowing plants with erosulate monocyclic shoots results in the loss of both non-flowering and flowering shoots. Plants with semirosette dicyclic shoots, on the other hand, lose only flowering shoots and their vegetative shoots continue to grow and flower next year. v – vegetative apical meristem; g – generative apical meristem; t1 – first generation of erosulate shoots in the season; t2 – second generation of erosulate shoots in the season; d – basal parts of shoots removed by cutting; r – rhizome; n – nodes; s – soil surface; F1 – shoot flowering before mowing; F2 – shoot flowering after mowing. Adapted from Klimešová & Čížková 1996.

the next race (after disturbance or winter). In this case, phenological observations may considerably improve our knowledge of height as a functional trait in herbaceous plants (e.g., Martínková et al. 2002).

In particular, perennial herbs usually consist of several shoots, connected by a rhizome, through which carbon and nutrients may be exchanged. These shoots may or may not be at the same ontogenetic stage. For example, in a species with monocyclic (annual) shoots, all shoots start to grow at the same time, flower and then die at the end of the season. On the other hand, species with dicyclic (biennial) shoots usually have a mixture of shoots: some of them flower (those initiated in the previous season) and some of them remain vegetative (those initiated in the current year). Thus plant height measured as height of flowering shoots reflects different information for monocyclic versus dicyclic shoots. Moreover, the functionality of shoot height differs according to shoot cyclicality: plants with monocyclic

shoots will lose all apical meristems when mown during bolting or flowering, whereas dicyclic shoots lose apical meristems of only half of the shoots (Fig. 1). Vegetative shoots with apical meristems hidden near the soil surface may continue to grow, produce leaves and flower. Thus, herbaceous perennial plants with dicyclic shoots will be favoured in mown meadows (Kahlert et al. 2005).

Summarizing, the importance of plant height in response to grassland management needs to be considered in combination with a set of related traits, namely leaf and shoot architecture, phenology or ramet life span, all of which determine different trade-offs and combinations of traits in response to grazing and mowing regimes.

Overlooked traits such as vegetative reproduction

Several traits associated with plant ecological functions, as proposed by the common core of PFTs (Weiher et al. 1999), are still frequently under-represented. These are the traits related to space acquisition by clonal growth and tolerance of disturbance associated with resprouting ability. This may be because such traits are traditionally considered difficult to measure in the field (Weiher et al. 1999). Currently, however, there are protocols assessing plant traits associated with vegetative regeneration and clonal growth (Cornelissen et al. 2003, Knevel et al. 2003, 2005, Klimešová & Klimeš 2007) and databases containing information, for example, on bud banks and clonal growth of the European flora (database of clonal plants CLO-PLA: <http://clopla.butbn.cas.cz>; LEDA traitbase: www.leda-traitbase.org; Klimešová & Klimeš 2008).

Information on how these traits can be used to predict species responses to grazing and mowing is scarce. Studies conducted so far have shown that these traits are significantly influenced by environmental factors and, for example, their relevance varies along gradients of moisture or nutrient availability (Sammul et al. 2003, Benson et al. 2004, Halassy et al. 2005, Dalgleish & Hartnett 2006, Nicolas et al. 2007). For example, a study across different climatic regions in Spain indicates that clonal growth is more important in response to grazing in humid temperate climates than the semi-arid Mediterranean climate (de Bello et al. 2005). Similarly, the pool of reserve meristems (bud bank) is sensitive to precipitation in Central North America, being more important for vegetative regeneration in wet than arid sites (Dalgleish & Hartnett 2006). Specific information on clonal growth traits in meadows under different management regimes is scarce. For example, frequent branching of short rhizomes in a traditionally managed meadow is considered as important for efficient occupancy of a spot once colonized (Sammul et al. 2004). Similarly, Klimeš (1999) found little vegetative spreading, even in potentially clonally growing plants, in species rich meadows in the White Carpathian Mts (Czech Republic). On the other hand, the most common clonal growth mode was by epigeogenous rhizomes (rhizomes that originate on the soil surface at the shoot base, but are pulled down into the soil by root contraction; Klimešová & Klimeš 2006). This mode of clonal growth is characterized by little lateral spread, large numbers of reserve buds and considerable stores of carbon (Klimeš & Klimešová 2000). Storage of carbon seems to be more important for resprouting of plants in meadows than clonal spread, as it enables fast re-occupancy of the canopy after mowing (Klimeš & Klimešová 2002).

We thus hypothesize that, for some vegetation types and especially in more humid-temperate conditions dominated by perennial herbaceous plants, traits of below-ground or-

gans can be key predictors of species response to grazing and mowing. Studies indicate little lateral spread via clonal growth in managed compared to abandoned meadows and the prevalence of clonal growth organs specialized for bud banks and/or carbon storing. This might indicate that persistence and fast re-occupancy of the canopy after mowing is a key strategy for meadow plants, similarly to that of resprouters in pastures and fire-prone areas (Hendrickson & Briske 1997, Benson et al. 2004, Vesk et al. 2004b, Olano et al. 2006).

Combining height with other traits in determining species strategies in grasslands

A combination of height and other related traits can give better indication of the different responses to mowing and grazing. One way of combining of key functional traits with different height strategies of plants and assessing the response to grassland management, is to use cluster analyses to identify “syndromes of traits” (McIntyre et al. 1999b). This classical approach, as illustrated in Fig. 2 for 95 species in a dry oligotrophic species-rich meadow in the White Carpathians (Czech Republic), can provide an analytical tool for including trait

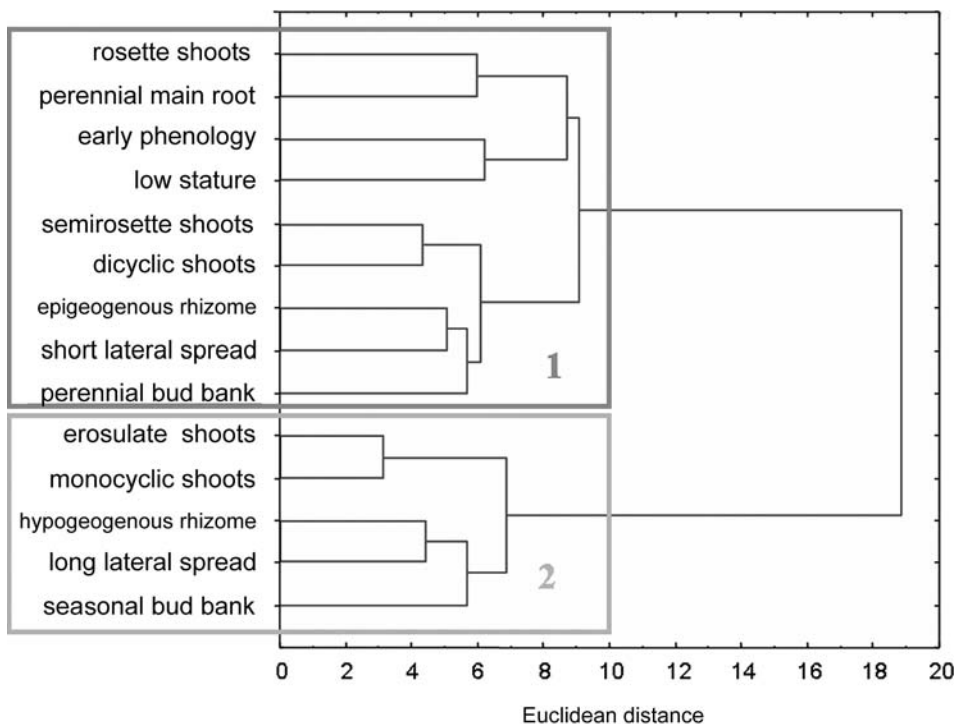


Fig. 2. – Cluster analysis of plant traits based on their co-occurrence in 95 species growing in a dry species-rich meadow in the Čertoryje Nature Reserve (White Carpathians, Czech Republic). Euclidean distance was used as a measure of sample dissimilarity (Orlói 1978). Group 1: traits typical of dominant species, Group 2: traits typical of less common species.

trade-offs within a particular species pool. In this case, the cluster analysis shows that early, low-growing rosette plants usually have dicyclic shoots and an epigeogenous rhizome or tap roots and thus have a limited potential for spreading laterally whereas late tall-growing erosulate plants have monocyclic shoots and a hypogeogenous rhizome. Thus, height alone does not reflect the complete range of strategies for coping with grassland management. The next step would be to test how these different groups respond to mowing or grazing.

The determination of strategies or emergent groups delimited on the basis of clusters of functional traits (see Lavorel et al. 1999), however, may not always be suitable for predicting vegetation changes under grassland management, as rare combinations of traits, which might make a plant particularly successful, may be missed. For example, a potential dominant in the oligotrophic species-rich meadows in the White Carpathians is the grass *Molinia arundinacea* (Klimeš & Klimešová 2002), which is characterized by traits of both groups: rosette shoots, restricted lateral spread, hypogeogenic rhizome, monocyclic shoots and late phenology. For this the approach of McGill et al. (2006) could be used to prioritize the factors (in our case traits) in order to ascertain which traits are the best predictors of long-term success in a given system (see also Lepš et al. 2006).

In conclusion, we strongly recommend that in the use of PFTs to assess species composition changes under grassland management, one should (i) consider more specific traits, in particular shoot architecture, life cycle and vegetative reproduction, the bud bank and carbon storage, in association with height, and (ii) integrate this information and assess how a combination of traits determines competitive advantage/disadvantage of species subjected to mowing or grazing. To achieve this, a single ad hoc chosen trait is unlikely to predict accurately vegetation changes under grassland management for which a functional analysis of trade-offs of key traits among species in plant communities is needed.

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Souhrn

Ekologická funkce rostliny je obtížně měřitelná, proto je snaha o nalezení pomocných parametrů, které nazýváme funkční vlastnosti rostlin. Tyto funkční vlastnosti bývají často využívány jako prediktory vegetačních změn následkem změny obhospodařování kosením nebo pastvou. Současné studie však docházejí k závěru, že v různých geografických regionech jsou při stejných změnách obhospodařování zvýhodněny rostliny charakterizované různou sadou funkčních vlastností, a predikce na širší geografické škále tedy není možná. Tento fakt je považován za důsledek současných selekčních tlaků biotických a abiotických faktorů na funkční vlastnosti v různých regionálních flórách. Jako řešení bylo navrženo používat specifitější funkční vlastnosti rostlin, které lépe odráží regionální podmínky.

Na příkladě evropských temperátních trávníků ukazujeme, které specifické funkční vlastnosti mohou být v tomto případě relevantní, a jak nejčastěji studovaná vlastnost, výška rostliny, souvisí s jinými funkčními vlastnostmi rostliny. Závěrem konstatujeme, že jednoduché vlastnosti rostlin zkoumané samostatně nemohou být podkladem pro predikci změn po skončení obhospodařování a funkční analýza rostlin studovaného společenstva je nezbytná.

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