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Strategies in aboveground space occupancy in herbs from disturbed habitats

Ph.D. Thesis

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ANNOTATION

Disturbance is an important phenomenon affecting plant lives and shaping plant strategies in disturbed habitats. A variety of ecological concepts on individual plant response to injury has been proposed for specific natural ecosystems or growth forms. In central Europe, man-made habitats are often cases of disturbed places, so the aim of the thesis was to apply four chosen concepts on them.

The thesis is composed of four original studies performed in two model ecosystems: recurrently disturbed ruderal place and regularly mown central European meadow. The occupying of the aboveground space after a disturbance event was studied here either as renovation of biomass or architecture. Regenerative strategies in herbs occupying disturbed habitats were described and confronted with concepts proposed originally for ecosystems subjected to natural disturbance regimes.

DECLARATION [IN CZECH]

Prohlašuji, že svoji disertační práci jsem vypracovala samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

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Alena Bartušková

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LIST OF PAPERS AND AUTHOR'S CONTRIBUTION

The thesis is based on the following papers (listed chronologically):

Klimešová J, **Kociánová A** and Martínková J (2008): Weeds that can do both tricks: vegetative versus generative regeneration of short-lived root-sprouting herbs *Rorippa palustris* and *Barbarea vulgaris*. *Weed Research* 48(2): 131-135, (IF= 1.622).

Alena Bartušková participated in experiment preparation and revision of the manuscript; and was responsible for experiment realization, data assembly and statistical analysis.

Bartušková A and Klimešová J (2010): Reiteration in the short lived root-sprouting herb *Rorippa palustris*: does the origin of buds matter? *Botany* 88(7): 630-638, (IF= 1.098).

Alena Bartušková participated in experiment preparation and was responsible for experiment realization, data assembly, statistical analysis and writing the manuscript.

Klimešová J, Janeček Š, **Bartušková A**, Lanta V. and Doležal J (2010): How is regeneration of plants after mowing affected by shoot size in two species-rich meadows with different water supply? *Folia Geobotanica* 45(3): 225-238, (IF=1.229).

Alena Bartušková participated in data collection in the field and following sample processing in the laboratory.

Bartušková A, Doležal J, Janeček Š, Klimešová J and Lanta V: Changes in allocation pattern in grassland plants after land use change: allometry or various strategies in biomass partitioning (manuscript).

Alena Bartušková participated in data collection in the field and following sample processing in the laboratory; and was responsible for data assembly, partially for statistical analysis and for writing the manuscript.

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CHAPTER I

General introduction

INTRODUCTION

General introduction

Disturbance is an important phenomenon affecting plant lives, which leads, according to its severity, to the loss of some biomass in affected plants (Bellingham and Sparrow 2000, Grime 2001). The disturbance takes place in many types of habitats worldwide. Whether caused by abiotic factors, such as fire, flooding, drought, frost or soil erosion, or by pathogens, herbivores and also man, each type of disturbance varies also in frequency and predictability (Iwasa and Kubo 1997, Grime 2001). Combination of all these factors shapes plant strategies in disturbed habitats.

Grime (1977, 2001) supposed that coping with disturbance and adapting to resource dynamic are the major points of ecological variation in plants, so the CSR triangle theory was proposed. The vertices of the triangle are occupied by the C (competitive), S (stress tolerant) and R (ruderal) strategies. Individual species are placed at the location where they fit with respect to the CSR strategies. This system is largely applicable; nevertheless, the level of plant individuals is here neglected. If we undertake an excursion in one vertex of the Grime's triangle, where plants face the disturbance, we cannot find surviving individuals, but just their descendants grown up from seeds.

None universal theory exists. A variety of ecological strategy schemes have been proposed, however, directly on the individual level, only some of them are applicable. The problem of many concepts lay in their high specificity or in constraint possibilities of studying some ecosystems or objects, e.g. trees. The following concepts seem to meet our requirements: (i) resprouter/seedler strategy from fire-prone areas, (ii) compensation concept used mainly in context of herbivory (iii) reiteration of an architectural model described especially in trees and (iv) regenerative strategies of plants in highly competitive environment of a regularly mown meadow.

Resprouter versus seedler

In fire-prone areas of Australia, South Africa and the Mediterranean Basin, fire events destroy aboveground vegetation and expose bare ground repeatedly in a period of several years (Bell and Ojeda 1999, Cruz et al. 2003, Pausas and Verdú 2005). Plant individuals cope with such event either by regenerating from unaffected reserve meristems ("resprouter"), or they do not survive but rely on the seed bank in

the soil ("seeder" or "non-sprouter") to re-establish their populations (e.g. Bell and Ojeda 1999, Vesik and Westoby 2004b). Resprouters are often slow growing species with small seed production but higher investment into belowground storage and reserve meristem formation. On the contrary, seeders are fast growing and flower early in the ontogeny (Bond and Midgley 2003, Pausas and Verdú 2005). However, tested on trees, shrubs and rarely on perennial herbs, short-lived species were excluded from looking for such dichotomy (Bellingham and Sparrow 2000, Vesik et al. 2004).

Compensation of biomass and seed production

Plants may tolerate the disturbance, i.e. they compensate for the lost biomass via dormant meristems and carbohydrate reserves (Agrawal et al. 2004). The concept of compensatory growth (i.e. biomass or seed production of injured in comparison with uninjured plants) was originally used for studying the effects of herbivory on plants. Considering the ability of maximal recovery of lost plant biomass to be the best indicator of the herbivore-plant relationship, the biomass response was most often used to explain it. Besides that, plant fitness was observed, where possible, mainly in monocarpic species (e.g. Rautio et al. 2005, Brody et al. 2007). Studies revealed differences in the compensatory response (overcompensation, compensation and undercompensation) according to the damage level of the plants, nutrient availability, and disturbance timing (McNaughton 1983, Belsky 1986, Maschinski and Whitham 1989, Lehtilä K 2000, Huhta et al. 2003, Wise and Abrahamson 2005). However often not considered, internal plant factors are vertical distribution of meristems (Huhta et al. 2003, Vesik and Westoby 2004a), plant size (Falster and Westoby 2005) or carbon storage (Sosnová and Klimešová 2009).

Reiteration of architecture

The function and fate of meristems result in final architecture of a plant (Sussex and Kerk 2001). Hallé et al. (1978), on the basis of reiteration (i.e. repetition of the architectural unit within the whole architectural model of the plant) observed in the tree architecture, distinguished several architectural models. The reiteration of the architectural unit is a result of a damage, environmental stress or optimal conditions and, according to the basic model resemblance, the reiterated unit may be complete or incomplete - partial (Hallé 1999). The reiteration concept got recently out of its descriptive function and received a more ecological dimension (Woolley et al. 2008),

which was also extended from tropical trees to temperate forest trees (Millet et al. 1999, Ishii and Ford 2001). However, studies examining reiterated structures in herbs are scarce (Dubard 1903, Carlsson and Callaghan 1990; Zhang et al. 2009).

Biomass allocation

It is assumed that allocation should maximize fecundity and overall lifetime fitness (Bazzaz and Grace 1997). Allocation is also important in the integration of a plant's response to stress, including maintaining phloem translocation and channelling carbon to provide chemicals involved in the responses. This carbon comes not only from allocation of recently assimilated carbon but also from mobilization from previously stored reserves (Geiger and Servaites 1991). Plants with relatively high non-structural materials (e.g., herbaceous plants) are more flexible in redeployment than those with relatively high structural materials (e.g., long-lived trees); and plants which occupy habitats with highly variable environments have a higher flexibility of allocation and redeployment because they must track changes of environment (Bazzaz and Grace 1997).

Biomass allocation is the result of the tendency to enhance allocation to the organ that acquires the most limiting resource, which is called "Optimal partitioning theory" (Bloom et al. 1985). This, however, is constrained by many trade-offs during the plant lifetime and also by allometric relationships between plant organs sizes (Tilman 1988, Enquist and Niklas 2002, Weiner 2004).

Recurrently disturbed habitats by humans in Central Europe

Central Europe lack ecosystems which are characterised by natural disturbance regimes except for small sized river banks. On the other hand, large scale artificial and semi-natural ecosystems affected by regular disturbance caused by human activities like (i) arable fields and (ii) grasslands are very common. Aim of the study was to apply existing concepts on plant response to disturbance on those habitats to solve question whether the abovementioned concepts represent universal tools for studying plant response to disturbance.

(i) Arable fields and other man-made habitats

In Central Europe, among most disturbed places, belong man-made habitats. Disturbance events are characterized here as frequent, unpredictable or predictable

and severe, often causing exposure of bare ground. Such places are dominated by species that are characterized by high production of small seeds and rather short life-cycle enabling them to finish the life-cycle between two consecutive disturbances (Harper 1977, Grime 2001). This, however, is not necessary for all plant species inhabiting severely disturbed places. Some of them were moreover found to possess the ability to regenerate from reserve meristems on remained plant parts, most often belowground organs such as roots or rhizomes (Korsmo 1930, Hamdoun 1972, Martínková et al. 2004, Klimešová and Klimeš 2007). As Grime (2001) proposed, multiple regenerative strategies in one species enhance the ability to inhabit a variety of environments. Considering the fact that disturbance events may create very different conditions, the combination of several regenerative strategies seems to be advantageous also in coping with the variable disturbance events, typical for man-made habitats.

Applied concepts:

Resprouter-seeder concept (Case study 1). Weeds of arable land rely either on surviving the disturbance events (e.g. ploughing) as seeds or they have a large regeneration capacity in fragmented roots or stems (Irmisch 1857, Rauh 1937). Nevertheless, the combination of the respective strategies was observed even in short-lived weedy herbs, which should generally behave as seeders (Martínková et al. 2004, Malíková et al. 2010). Such intermediate forms disrupt the easy dichotomy in regenerative strategies.

Compensation of biomass production and reiteration of architecture (Case study 2). The dormant meristems, which give rise to new shoots, are represented by two groups of buds: (i) axillary buds arising in the leaf axils and present at each node of the stem and (ii) adventitious buds, whose *de novo* formation is extended not only to stems, but to leaves or roots too (Esau 1966, Kerstetter and Hake 1997). Axillary buds belong to standard “equipment” of a plant, but adventitious buds on roots, which is the most often placement, are found just in 10% of the central European flora species (Klimešová and Klimeš 2003). The study by Dubard (1903) indicates that the differences in anatomy and placement of buds of different origin may also affect the compensatory response together with the quality of the reiterated architectural model.

(ii) Grasslands

Together with pastures, hay meadows are the most often cases of managed grasslands in Central Europe. Meadows are managed for several goals, including providing hay for domestic animals or conservation of species-rich areas (Gibson 2009). It is a very specific habitat, joining in itself composition of predominantly perennial, often clonal and highly-competitive plant species and a regular disturbance – mowing, leaving only up to five centimetres biomass at least once a year. Mowing favours grasses in particular and prevents the expansion of woody plants (Gibson 2009). High numbers of species are found to coexist especially in oligotrophic, traditionally managed European hay meadows, which are appreciated therefore and mechanisms of species coexistence have been largely studied here (e.g. Kull and Zobel 1991, Zobel 1992, Klimeš and Klimešová 2001). Mowing is one of the main factors affecting the species composition, namely through alteration of the competitive environment of the plants (Gibson 2009).

Applied concepts:

Biomass compensation in relation to plant size (Case study 3). One of the main resources to compete for aboveground is light and the competition increases in crowded communities. The higher competitive ability is in this case connected with the presumption of larger plants (Givnish 1982, Grime 2001). However, larger plants are generally penalized by higher structural costs, continuing maintenance costs and by disadvantages in water transport to height (Westoby et al. 2002). Longer time to achieve reproductive height was moreover observed in these plants (Sun and Frelich 2011). In meadows plant species differing in size coexist. We may consider the regular disturbance - mowing to be an equalizing process preventing competitive exclusion of small species. Although it was proposed that larger plants lose by mowing proportionally more leaf canopy than smaller plants (Zobel 1992, Klimeš and Klimešová 2001), little is known about the consequent regenerative ability.

Biomass allocation (Case study 4). In changing environment, the biomass allocation pattern may be very plastic (McConnaughay and Coleman 1999, Poorter et al. 2011). This was studied mainly in pot experiments, studies performed in natural communities and under competition are scarce (Fraterrigo et al. 2006, Niu et al. 2009). In regularly mown meadow, the cessation of mowing represents strong change in environmental conditions including enhanced competition for light or litter

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accumulation (Grime 2001, Huhta et al. 2001). Under crowded conditions, larger plants are in advantage because of better light availability (Anten and Hirose 1999) and after cessation of mowing also seed production of large late flowering species is not time-limited any more (Kahmen and Poschlod 2004). Thus we may consider enhanced allocation to biomass of stems and other supportive organs such as petioles, to cope with the impact of large dominant species, and consequently changed biomass partitioning pattern in reaction to management ceasing.

OBJECTIVES AND CONTENT OF THE THESIS

The main objective of the thesis was to test some hypotheses on plant strategies in aboveground space occupancy of plants from disturbed habitats using manipulative experiments. We focused on three main plant parameters: fecundity, shoot biomass, shoot architecture and biomass partitioning among shoot organs (stem, leaf, flower) and we studied them in four case studies performed in two model ecosystems: recurrently disturbed ruderal place inhabited by short lived monocarpic plants and regularly mown central European meadow. By comparison of the studied plant parameters of disturbed and undisturbed plants we aimed to answer following questions: (i) Do resprouting individuals have higher fecundity than individuals regenerating from seeds at the time of disturbance? (ii) Does shoot biomass and shoot architecture differ in relation to type of buds from which the shoot emerge? (iii) Does biomass compensation in meadow plants depend on shoot size? and (iv) Do meadow plants invest more to supportive structures after abandonment and if yes, is observed higher proportion of stem to leaf biomass caused by allometry (increasing shoot size)?

Case study 1 (Chapter II) deals with comparison of the vegetative and generative regeneration following a severe disturbance in two short-lived herbs *Rorippa palustris* and *Barbarea vulgaris*. The neglected ability of regeneration from adventitious bud on roots is here highlighted.

Case study 2 (Chapter III) focuses on the compensatory growth after hard damage and describes differences in the architecture of reiterated structures from the basal axillary buds and from the adventitious buds on roots in *Rorippa palustris*.

Case study 3 (Chapter IV) describes the compensatory growth of 41 meadow plants after mowing and gives it in the relationship with the proportion of removed biomass and plant size. Another studied aspect is the effect of water availability on these features.

Case study 4 (Chapter V) follows changes in biomass allocation pattern in 41 meadow plants after cessation of regular mowing management, again on the example of two meadows differing in the water availability.

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CHAPTER II

Weeds that can do both tricks: vegetative *versus* generative regeneration of short-lived root-sprouting herbs *Rorippa palustris* and *Barbarea vulgaris*

Klimešová J, Kociánová A and Martínková J (2008): Weed Research 48(2): 131-135

Weeds that can do both tricks: vegetative *versus* generative regeneration of short-lived root-sprouting herbs *Rorippa palustris* and *Barbarea vulgaris*

Abstract

Weeds of arable land have two strategies for coping with severe disturbance: they have either a very short life cycle and survive disturbance events (ploughing) as seeds or they rely on an underground bud bank and a large regeneration capacity from fragmented roots or stems. Representatives of the respective strategies differ in their investments: annual weeds invest in generative structures and production of easily dispersable or durable seeds, whereas perennial weeds invest preferentially to underground storage organs bearing buds which serve for vegetative propagation. Even when perennial weeds may also produce seeds under favourable conditions, these may serve for further field infestation and spreading. However, the ability of some short-lived annual weeds to regenerate from roots is often overlooked in studies on mechanisms for disturbance survival.

Here, we show that short-lived weeds capable of adventitious sprouting from roots may be very successful in vegetative regeneration from root fragments. Using a pot experiment, short-lived root sprouters were found to have higher (*Rorippa palustris*) or the same (*Barbarea vulgaris*) fitness when regenerating from root fragments as when regenerating from seed. Even though this finding needs to be tested on other species and in different experimental settings, the results indicate the potential importance of adventitious sprouting from roots in short lived plants. Better knowledge of this phenomenon is crucial for understanding both the population dynamics of short-lived root-sprouters in disturbed habitats and the ruderal strategy of plants generally.

Abstrakt

Polní plevely čelí silnému narušení pomocí dvou strategií: Mají buď velice krátký životní cyklus a přežívají jednotlivá narušení (orbu) ve formě semen nebo spoléhají na podzemní banku pupenů a velkou regenerační schopnost fragmentovaných kořenů nebo stonků. Představitelé opačných strategií se liší v investicích: jednoleté plevely investují do generativních struktur a produkce lehce šířitelných nebo vytrvalých semen, naopak vytrvalé plevely přednostně investují do podzemních zásobních orgánů nesoucích pupeny, které slouží k vegetativnímu rozšiřování. I když mohou vytrvalé plevely produkovat semena i za nepříznivých podmínek, mohou semena sloužit k dalšímu zamoření polí a šíření. Schopnost regenerace z kořenů některých krátkověkých jednoletých plevelů je však při studiu mechanismů přežívání narušení často přehlížena.

Zde ukazujeme, že krátkověké plevely schopné adventivního odnožování z kořenů mohou být velice úspěšné ve vegetativní regeneraci z kořenových fragmentů. Květináčový experiment odhalil, že krátkověké druhy odnožující z kořenů měly vyšší (*Rorippa palustris*) nebo stejné (*Barbarea vulgaris*) fitness, když regenerovaly z kořenových fragmentů i ze semen. Přestože tato zjištění musí být testována i na jiných druzích a za jiného experimentálního uspořádání, výsledky naznačují, jaký význam má adventivní odnožování z kořenů u krátkověkých rostlin.

Lepší poznání tohoto jevu je klíčové jak pro lepší porozumění populační dynamiky krátkověkých druhů odnožujících z kořenů na narušovaných místech, tak pro pochopení ruderální strategie rostlin obecně.

Následující pasáž o rozsahu 9 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném originále disertační práce uloženém na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.

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CHAPTER III

Reiteration in the short lived root-sprouting herb *Rorippa palustris*: does the origin of buds matter?

Bartušková A and Klimešová J (2010): Botany 88(7): 630-638

Reiteration in the short lived root-sprouting herb *Rorippa palustris*:

does the origin of buds matter?

Abstract

Regrowth of injured plants occurs from dormant meristems. Its success is known to be dependent on extrinsic factors such as severity of injury and nutrient availability, although little is known about the effect of intrinsic factors. We conducted a growth chamber experiment with the short lived root-sprouting herb *Rorippa palustris*, where we evaluated the role of bud origin on plant regrowth after disturbance. In particular, we investigated whether shoots sprouting from either axillary or adventitious buds differ in compensatory growth and architecture. We triggered resprouting from axillary versus adventitious buds by two levels of disturbance: i) removal of the whole aboveground biomass with axillary buds on the stem base and adventitious buds on roots left intact; and ii) removal of whole aboveground biomass including axillary buds on the stem base and only adventitious buds left intact. Despite the fact that the adventitious buds were larger and contained more leaf primordia than axillary buds at the time of disturbance, the latter preferentially resprouted when both types of buds were present. Both axillary and adventitious shoots compensated for lost aboveground biomass, nevertheless only axillary shoots compensated for fruit production. Shoot reiteration after injury was only partial in both types of shoot; however, adventitious shoots differed in more architectural characteristics from uninjured plants than axillary shoots. We confirmed that output of plant regeneration after disturbance depends also on intrinsic factors such as origin of buds.

Abstrakt

Rostliny po narušení opětovně vyrůstají z dormantních meristémů. Je známo, že úspěch obnovy je závislý na vnějších faktorech, jako je míra narušení a dostupnost živin, málo je však známo o vlivu vnitřních faktorů. V experimentu provedeném v klimaboxu s krátkověkým bylinným druhem *Rorippa palustris* schopným odnožovat z kořenů jsme odhadovaly roli původu pupenů ve schopnosti obnovy rostliny po narušení. Zejména jsme zkoumaly, zda se prýty vyrostlé buď z axilárních, nebo z adventivních pupenů liší v kompenzačním růstu a v architektuře. Spustily jsme odnožování z axilárních versus adventivních pupenů pomocí dvou hladin narušení: i) odstranění veškeré nadzemní biomasy za ponechání axilárních pupenů na bázi stonku a adventivních pupenů neporušených; a ii) odstranění veškeré nadzemní biomasy včetně axilárních pupenů na bázi stonku za ponechání pouze adventivních pupenů neporušených. I přes to, že adventivní pupeny byly v době narušení větší a obsahovaly více listových primordií než axilární pupeny, když byly přítomny oba typy pupenů, axilární přednostně vyrůstaly v prýty. Axilární i adventivní prýty kompenzovaly ztracenou biomasu, avšak adventivní prýty se lišily od nenarušených rostlin ve více charakteristikách architektury než prýty axilární. Potvrdily jsme, že výsledek regenerace rostlin po narušení závisí také na vnitřních faktorech, jako je původ pupenů.

Následující pasáž o rozsahu 17 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném originále disertační práce uloženém na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.

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CHAPTER IV

How is regeneration of plants after mowing affected by shoot size in two species-rich meadows with different water supply?

Klimešová J, Janeček Š, Bartušková A, Lanta V and Doležal J (2010):

Folia Geobotanica 45(3): 225-238

How is regeneration of plants after mowing affected by shoot size in two species-rich meadows with different water supply?

Abstract

Mowing of a meadow is an example of an equalizing process which reduces differences among species by removing aboveground biomass approximately 5 cm above ground. This regular disturbance that affects all plants prevents competitive exclusion of small species and thus allows coexistence of numerous species differing in shoot size. In this paper we search for the mechanism behind this by comparing the shoot biomass of 41 common species in dry and wet species-rich meadows in mown and recently abandoned plots in June (before mowing) and in October. We asked the following questions: i) Do the plants differ in proportion of biomass lost by mowing? ii) Are the mown plants able to compensate for biomass lost by mowing? iii) Is the compensatory ability of mown plants related to their size? iv) Is the compensatory ability of plants related to severity of disturbance (removed biomass)? v) Does water availability in meadows affect these features? Our results revealed that the earlier explanation of equalization of meadow plants after mowing due to the fact that larger plants lose proportionally more biomass than small plants does not represent the entire mechanism. Even when larger plants in the wet meadow lost more biomass, the proportion of lost biomass was not dependent on plant size, and compensation ability (growth of mown in comparison with unmown plants) was not related to the lost biomass in this meadow type. On the contrary, the observed pattern could be explained by different compensation abilities of small versus tall plants. In addition, according to our expectations, the compensation for lost biomass in the wet meadow was higher than in the dry one.

Abstrakt

Kosení luk je příkladem vyrovnávacího procesu, který odstraněním biomasy přibližně 5 cm nad zemí zmenšuje mezidruhové rozdíly. Toto pravidelné narušení, které ovlivňuje všechny rostliny, zamezuje kompetitivnímu vyloučení malých druhů, čímž umožňuje koexistenci mnoha druhů lišících se velikostí prýtu. V tomto článku jsme pomocí srovnání biomasy prýtů u 41 běžných druhů suché a vlhké druhově bohaté louky na kosených a nedávno opuštěných plochách v červnu (před kosením) a v říjnu hledali mechanismus v pozadí tohoto jevu. Položili jsme si následující otázky: i) Liší se rostliny v proporcí biomasy ztracené kosením? ii) Jsou kosené rostliny schopné kompenzovat biomasu ztracenou při pokosení? iii) Je schopnost kompenzace pokosených rostlin úměrná jejich velikosti? iv) Je schopnost kompenzace úměrná míře narušení (odstraněné biomase)? v) Ovlivňuje dosažitelnost vody na louce tyto schopnosti? Naše výsledky odhalily, že dřívější vysvětlování vyrovnávacího procesu u lučních rostlin po pokosení skrze to, že větší rostliny ztratí proporčně více biomasy než rostliny malé, nevystihuje celý mechanismus. I když větší rostliny ztratily na vlhké louce více biomasy, proporce ztracené biomasy nebyla úměrná velikosti rostlin, a schopnost kompenzace (růst pokosených ve srovnání s nekosenými rostlinami) nebyla v tomto typu louky úměrná ztrátě biomasy. Na druhou stranu, sledovaný vzor může být vysvětlen pomocí různé schopnosti kompenzace malých oproti velkým rostlinám. Navíc byla, podle našich předpokladů, schopnost kompenzace ztracené biomasy vyšší na vlhké louce než na louce suché.

Následující pasáž o rozsahu 19 stran obsahuje skutečnosti chráněné autorskými právy a je obsažena pouze v archivovaném originále disertační práce uloženém na Přírodovědecké fakultě Jihočeské univerzity v Českých Budějovicích.

REGENERATION AFTER MOWING

*Publikace vyšla tiskem v časopise Folia Geobotanica.
Podíl studenta na publikaci: 15%*

CHAPTER V

Changes in allocation pattern in grassland plants after land use change: allometry or various strategies in biomass partitioning.

Bartušková A, Doležal J, Janeček Š, Klimešová J and Lanta V (manuscript)

Changes in allocation pattern in grassland plants after land use change: allometry or various strategies in biomass partitioning.

Abstract

Theory expects that allocation of biomass in plants after change of management responds to new demands due to increased competition, availability of nutrients etc. We tested this hypothesis on two recently abandoned species rich grasslands differing in species pool. Although cessation of mowing resulted in larger shoot biomass of meadow herbs, only few of them showed change in relative investment into stems, leaf blades and reproductive organs. On the community level, only plants from the wet meadow increased investments into stems at the expense of other aboveground organs whereas plants from the dry meadow did not change the investments. Because the biomass of stems versus leaves showed allometric pattern only in 10 out of 16 analyses, we were not able to fully separate the effect of size in changed biomass partitioning. These results were caused by different shoot architectures of meadow forbs and their specific seasonal development and responses to management. We therefore concluded that when studying interspecific relationships between biomass investment, shoot architectures and their developmental trajectories should be taken into account.

Abstrakt

Teorie předpokládá, že po změně managementu alokace biomasy u rostlin reaguje na nové nároky zvýšené kompetice, změněné dostupnosti živin apod. Tuto hypotézu jsme testovali na dvou nedávno opuštěných druhově bohatých loukách lišících se druhovým zastoupením. Přestože ukončení kosení vedlo ke zvětšení biomasy lučních druhů, jen u několika druhů se ukázala změna v relativní investici do stonků, listových čepelí a generativních orgánů. Na úrovni společenstva, pouze rostliny na vlhké louce zvýšily investice do stonků na úkor ostatních nadzemních orgánů, přičemž rostliny ze suché louky investice nezměnily. Protože biomasa stonků oproti biomase listů ukázala alometrický vztah pouze v deseti z 16 analýz, nebyli jsme tedy schopni plně odstranit vliv velikosti na změny v rozdělení biomasy. Tyto výsledky byly způsobené různou architekturou prýtu u lučních bylin a jejich specifickým sezónním vývojem a odpovědí na management. Při studiu mezidruhových vztahů v investicích do biomasy tedy musíme brát v úvahu i architekturu a vývoj prýtů.

Podíl studenta na publikaci: 60%

Plant nomenclature Kubát et al. (2002)

One of the basic questions in comparative plant ecology is how plant allocates its resources to different functions (Bazzaz and Grace 1997). The allocation of biomass has been generally predicted via optimal partitioning theory (OPT) suggesting the largest allocation to the organ that acquires the most limiting resource (Bloom et al. 1985). When, however, biomass is allocated to one organ or function, it is at the expense of other organs or functions, which imply tradeoffs (Weiner 2004). In order to support all plant functions biomass partitioning is limited by architectural constraints, which change with plant size, and therefore between individual organs are often found allometrically scaled relationships (Niklas 1994a, b). The fact that the standing biomass of leaves scales as the $\frac{3}{4}$ power of the standing biomass of stems and as the $\frac{3}{4}$ power of the root biomass (Enquist and Niklas 2002) cause methodological difficulties when studying OPT. Some of the plasticity in allocation is simply the result of size, and is called 'apparent' (McConnaughay and Coleman 1999) or 'passive plasticity' (Wright and McConnaughay 2002) and should be distinguished from "real" plasticity.

There are many studies dealing with influence of different resource availabilities on the plasticity of allocation, mainly light, nutrients, water or CO₂ (see review by Poorter et al. 2011). However, much less effort was invested to study an impact of varied managements directly in the field conditions. Among couple of studies which were done so far (Fraterrigo et al. 2006, Niu et al. 2008, 2009) only one separated effect of plant size on observed allocation (Niu et al. 2009). According to this study investments into generative structures in Tibetan alpine grassland generally increased in grazed plots and decreased in fertilized plots while passive plasticity due to allometry was less often. Changes in allocation strategy of plants under complex effect of varied management, which bring about altered competition milieu, nutrient availability, disturbance regime, litter accumulation etc. (Fortunel et al. 2009, Robson et al. 2009), are therefore still poorly known.

To evaluate effect of changed management on biomass partitioning of plants we used semi-natural grasslands of temperate Europe, which are conspicuous by high plant diversity. With changing demands of the human society, the grasslands have ever been exposed to alterations of management including grazing, mowing or abandonment. Especially in last decades, abandonment became one of the very often mentioned threats for highly diverse meadow communities

(Huhta 1997, Baur et al. 2006). Management cessation is followed here by successional changes resulting in decreasing species richness and changes in species composition toward woody species (Falińska 1999, Kahmen and Poschlod 2004). We may consider competition as main mechanism to stay at the beginning of proposed changes. In the dense vegetation cover of the meadow, competition for light play important role and coexistence of species differing in size have been explained via equalizing process of the regular mowing, which allows persistence of smaller 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 exclusion happens, should be recognized as a change in biomass allocation to different organs. We could expect increased allocation to stem and petioles, as other supportive structures, because they are key components in competition for light (Givnish 1995). Also plant height that reflects investment in supportive organs is generally considered to increase under crowded conditions in order to provide prior access to light (Kull and Zobel 1991, Westoby et al. 2002, de Bello et al. 2012). Therefore we expect increased relative investments into stems (on the expense of leaf blades), however, we have no presumption, whether the relationship between the biomass of supportive organs and blades will be allometric, or, on the contrary, we will reveal some shift in biomass partitioning strategy. We can also expect that resident species will differ in their allocation pattern, some of them keeping pace in competition for light and investing more to stems while some of them being suppressed and investing more to leaf blades.

Questions:

- (i) Are there changes in the biomass partitioning in plants subjected to land use change?
- (ii) Is the change just the effect of allometric scaling or is it caused by the shift in biomass partitioning strategy?
- (iii) Is the response to abandonment independent of species pool, i.e. consistent between two sites differing by water availability?

Methods

Site description

Our experiment was conducted in two species-rich meadows differing in moisture that had already been used to study management impact on community functioning (Lepš 1999, 2004; Klimeš et al. 2000). First site (further called dry meadow) is located in Bílé Karpaty Mts., in the southeastern part of the Czech Republic, in 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 (Tolász et al. 2007). The meadow on calcium-rich soil with scattered *Quercus* spp. trees belongs to *Bromion* alliance (Chytrý 2007). Second site (further called wet meadow) is situated in the southern part of the Czech Republic in the locality Ohrazení (48°57' N, 14°36' E), at 500 m a.s.l. The mean annual temperature is 7-8°C and precipitation 700 mm (Tolász et al. 2007). This meadow on acidic soil is classified as *Molinion* alliance (Chytrý 2007). Both meadows are regularly once a year mown in June (dry meadow) or July (wet meadow) and had been mown for at least 10 years before the experiment started.

Experiment

The data set included 12708 individually measured plant parts (leaves, stems, flowers) in 6129 plant individuals belonging to 41 meadow species. The data were collected in traditionally mown and recently abandoned plots in both meadows, two times during the growing season (early June before mowing, mid October at the end of growing period) in 2006 and 2008 (one and three years after the onset of the experiment). The experiment was set up in June 2005, in a randomised block design on regularly mown meadow. Six blocks were designated in the dry meadow and five blocks in the wet meadow. Each block contained 9 permanent plots (3 rows of 3) in which either the fallow treatment (i.e. cessation of mowing) was applied beginning in 2005, or mowing was continued (for further details of experimental set up, see Klimešová et al. 2010, Lanta et al. 2011). Only those species occurring in all the selected plots in a given meadow in June 2006 were selected for data collection, resulting in 22 species from the dry meadow and 19 species from the wet meadow (Table 1).

In June 2006 and June 2008, just before the mowing in the experimental plots took place, at least 2-6 randomly selected shoots of each target species were harvested in each block, respectively, in two plots with contrasting management in 2006 and in two other plots in 2008. Sampled shoots were transported in a cooling box to the laboratory, where they were partitioned into blades, petioles, stems and reproductive biomass. Samples were oven dried at 80°C for 24 hours and then weighed.

For later analysis, we decided to merge biomasses of petioles, where present, with those of stems, because of the similar function to support foliage efficiently (Niinemets et al. 2007). Stems, moreover, have the function of supporting flowers or fruits. The biomass of stems, whether with or without petioles, is further called biomass of supportive organs. The photosynthetic function of stems and petioles, we assumed to be negligible with respect to blades.

Table 1. List of studied species and abbreviations of their names used in figures.

Dry meadow		Wet meadow	
<i>Betonica officinalis</i> L.	BeOf	<i>Angelica sylvestris</i> L.	AnSy
<i>Bromus erectus</i> HUDS.	BrEr	<i>Betonica officinalis</i> L.	BeOf
<i>Carex montana</i> L.	CaMo	<i>Carex hartmanii</i> CAJANDER	CxHa
<i>Cirsium pannonicum</i> (L. fil.) LINK	CiPa	<i>Carex pallescens</i> L.	CxPal
<i>Clematis recta</i> L.	ClRe	<i>Carex panicea</i> L.	CxPan
<i>Filipendula vulgaris</i> MOENCH	FiVu	<i>Deschampsia cespitosa</i> (L.) PB.	DeCe
<i>Fragaria vesca</i> L.	FrVe	<i>Galium boreale</i> L.	GaBo
<i>Geranium sanguineum</i> L.	GeSa	<i>Holcus lanatus</i> L.	HoLa
<i>Helianthemum grandiflorum</i> (SCOP.) DC.	HeGr	<i>Juncus effusus</i> L.	JuEf
<i>Inula salicina</i> L.	InSa	<i>Lathyrus pratensis</i> L.	LaPr
<i>Lathyrus niger</i> (L.) BERNH.	LaNi	<i>Lysimachia vulgaris</i> L.	LyVu
<i>Molinia arundinacea</i> SCHRANK	MoAr	<i>Molinia caerulea</i> (L.) MOENCH	MoCa
<i>Leontodon autumnalis</i> L.	LeAu	<i>Potentilla erecta</i> (L.) RÄUSCHEL	PoEr
<i>Plantago lanceolata</i> L.	PLa	<i>Ranunculus acris</i> L.	RaAc
<i>Potentilla alba</i> L.	PoAl	<i>Ranunculus auricomus</i> agg.	RaAu
<i>Primula veris</i> L.	PrVe	<i>Rumex acetosa</i> L.	RuAc
<i>Prunella grandiflora</i> (L.) SCHOLLER	PrGr	<i>Sanguisorba officinalis</i> L.	SaOf
<i>Ranunculus polyanthemus</i> L.	RaPo	<i>Selinum carvifolia</i> (L.) L.	SeCa
<i>Salvia pratensis</i> L.	SaPr	<i>Viola palustris</i> L.	ViPa
<i>Serratula tinctoria</i> L.	SeTi		
<i>Pyrethrum corymbosum</i> (L.) SCOP.	PyCo		
<i>Trifolium montanum</i> L.	TrMo		

Data analysis

We analyzed all the species from both localities together. In the common test, the effect of locality (dry, wet), management (mowing, fallowing), year (2006, 2008) and season (June, October) and their interactions on the biomass allocation, expressed either by the absolute values or proportion of biomass allocated in assimilative (blades), supportive (stems and petioles) and reproductive (flowers and fruits) organs, was analyzed using a generalized mixed effect model (GLMM) because the data represent a hierarchical split-plot design with both fixed and random effect factors. Each species was considered a “main-plot” and represented a factor with a random effect nested in the locality. Treatment, locality, year and season were the categorical fixed effect factors. In the separate analyses for each species, the categorical fixed effect factors included the treatment, year and season while the block was factor with a random effect. All the tests were based on the restricted maximum likelihood (REML) approach. The statistical significance of the main effects and interactions were assessed by computing Bayesian highest probability (HPD) intervals using Markov chain Monte Carlo simulations, as this is favoured over normal confidence limits for GLMMs. Analyses were done using the lme4 and languageR packages in the R program (R Development Core Team 2008). Graphs illustrating differences in mean absolute and relative investment in individual organs between sites were done in STATISTICA program (Anon 1996). Non overlapping standard error bars were used to describe differences.

Principal Component Analysis (PCA) was finally used to assess overall intercorrelations of biomass values allocated in individual organs and their differences between two localities, within the growing season and between the years in mown and fallow plots. The relation to main tested variables was assessed by their passive projection to the PCA ordination plane using centroids of four factor level combinations (16 centroids in total). The same method was used to assess the intercorrelations of biomass proportions in individual species and the differences between mown and fallow treatment in June, for both localities separately (44 centroids – the dry meadow, 38 centroids – the wet meadow). The ordination analysis and visualization of their results were carried out using the Canoco and CanoDraw programs (ter Braak and Šmilauer 1998).

Regressions were used to reveal allometric relationships between biomass allocated to supportive organs and blades. Consequently, similarity to the APT model (Enquist and Niklas 2002) was assessed by comparisons of slopes. Both were performed with the SMATR program (Falster et al. 2006). In correlation graphs, data were fitted using standardised major axis (SMA) techniques. This technique minimises the sum of squares in both x and y dimensions (for details, see Warton et al. 2006).

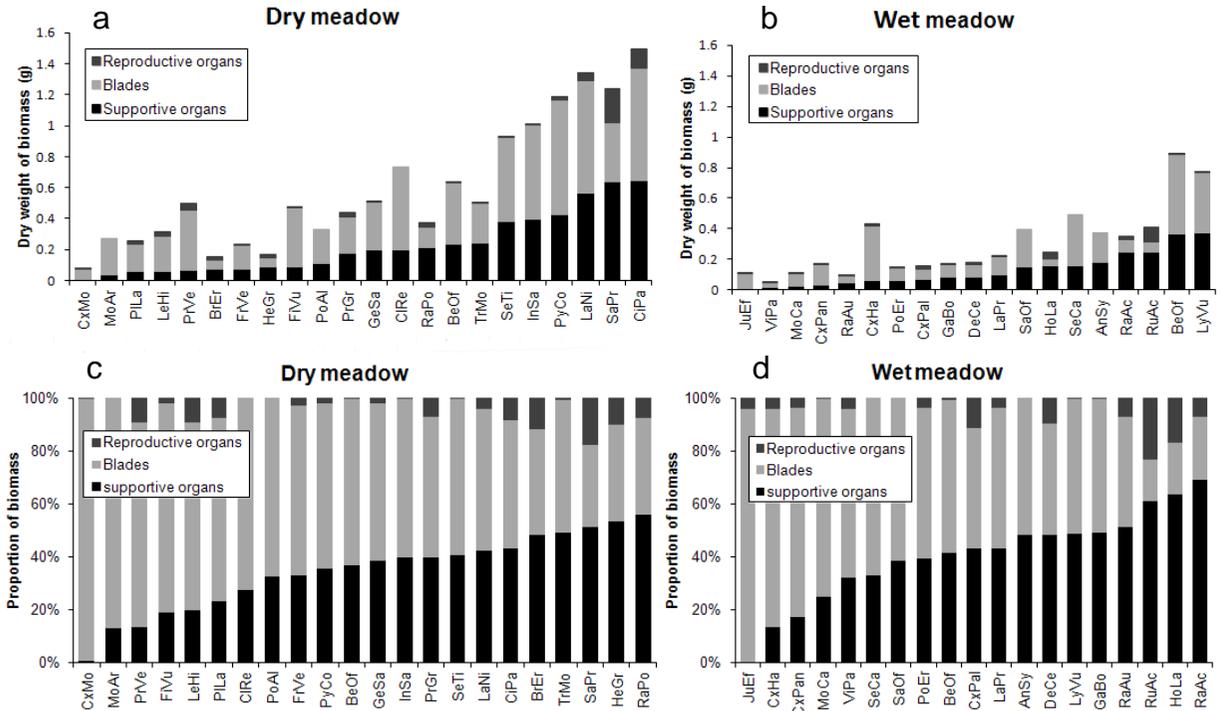


Figure 1. Mean absolute (a, b) and relative values (c, d) of biomass investment into different organs in species of dry (a, c) and the wet meadow (b, d), calculated for each species from shoots sampled in regularly mown plots before mowing in June 2006 and 2008. Species name abbreviations are given in Table 1.

Results

Biomass partitioning response at the species level

Species of both meadows differed under normal management regime in biomass allocation and also in biomass partitioning pattern, as shown on mean values in June (Fig. 1). Among all species, the maximal average biomass of one shoot was 1.5 g in the dry meadow, compared to 0.9 g in the wet meadow (Fig. 1a, b). The

investment in supportive organs ranged till 56% in the dry and 69% in the wet meadow. Maximal investment in reproductive organs was 18% in the dry and 23% in the wet meadow; however, some species did not even flower at the time of mowing (Fig. 1c, d).

In the dry meadow in June just three species (*Filipendula vulgaris*, *Helianthemum grandiflorum*, *Potentilla alba*) out of 22 increased the percentage investment in supportive organs in fallow plots; by contrast, four species (*Bromus erectus*, *Cirsium pannonicum*, *Leontodon autumnalis*, *Plantago lanceolata*) markedly decreased the same investment. Two species (*Salvia pratensis*, *Ranunculus polyanthemos*) invested relatively less into reproductive organs in fallow plots and one species (*Primula veris*) even increased the investment (Fig. 2).

In the wet meadow in June six species (*Deschampsia cespitosa*, *Galium boreale*, *Lathyrus pratensis*, *Lysimachia vulgaris*, *Potentilla erecta*, *Selinum carvifolia*) increased the relative investment into supportive organs in fallow plots, none decreased the investments. Increase of relative investment in reproductive organs was found in one species (*Carex palescens*) in fallow plots. The other species showed unclear or none reaction to the cessation of mowing (Fig. 2).

In October the plants with late phenology, which did not show differences in June, had markedly higher absolute and relative investment in supportive and reproductive organs in fallow plots than in mown plots. Among them erosulate forb *Inula salicina*, semirosette forb *Serratula tintoria* and dominant grass species *Molinia arundinacea* and *Molinia caerulea* (data not shown) were conspicuous.

Biomass allocation at the community level

In the dry meadow in June in comparison to the wet meadow, there were higher absolute investments in supportive organs, blades and also reproductive organs; however, lower percentage investment in supportive organs was observed (Fig. 3). In October plants regenerated after mowing had higher absolute investment in blades in the dry meadow, the other investments were comparable to the wet meadow. Consequently, the autumnal proportional investment in blades was higher here (Fig. 3).

In the common test (Table 2), all factors including *locality* (dry, wet), *management* (mowing, fallowing), and *season* (June, October) had significant effect on both absolute and relative values of the biomass allocation, except the factor *year* (2006, 2008) having no effect on the absolute values. No effect was found in

the interaction of all factors. The most significant effect had the combination of the *treatment* and the *season* (Fig. 4). No effect had the interaction of the *treatment* and the *year*, which together with significant effect of the *locality* indicates the importance of different species composition in both meadows. The effects of all factors are illustrated in Figures 3 and 4.

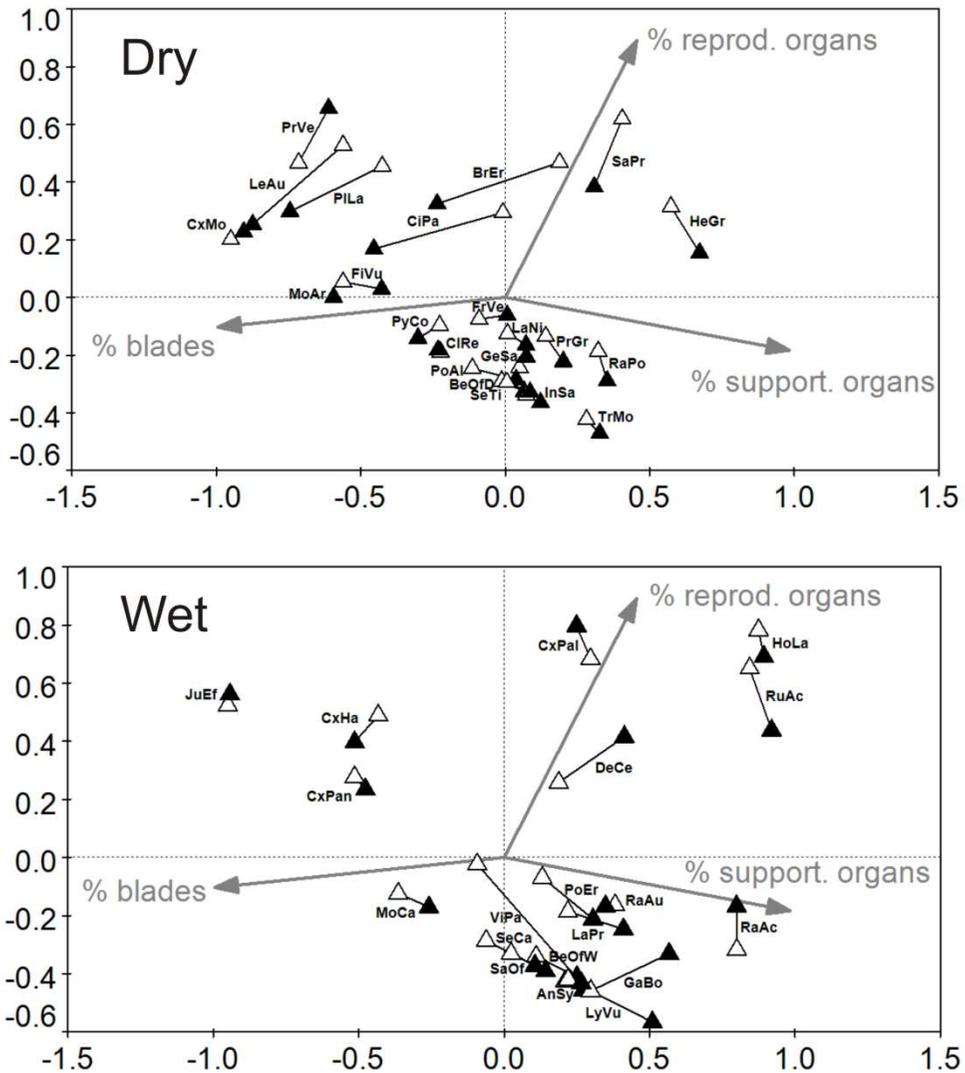


Figure 2. PCA ordination of percentage of biomass allocated to individual organs with passively projected centroids of individual species values in mown (Δ) and fallow treatment (\blacktriangle) in June. Species name abbreviations are given in Table 1.

Table 2. Results of testing for the effects of locality (dry, wet), management (mowing, fallowing), year (2006, 2008) and season (June, October) and their interactions on the biomass allocation, expressed either by the absolute values or proportion of biomass allocated in blades, supportive (stems and petioles) and reproductive (flowers and fruites) organs, using GLMM for all data. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, a $p < 0.1$.

	Blades		Supportive organs		Reproductive organs	
	abs	%	abs	%	abs	%
Locality (L)	11.32**	4.64*	2.92a	4.01a	3.67a	n.s.
Treatment (T)	147.18***	127.01***	138.52***	181.52***	12.98***	n.s.
Year (Y)	n.s.	13.29***	n.s.	8.90**	n.s.	15.39***
Season (S)	222.16***	96.62***	91.16**	21.02***	29.59***	370.76***
loc:treat	32.30***	n.s.	7.57**	n.s.	n.s.	n.s.
loc:year	1.42a	7.26**	n.s.	5.52a	n.s.	n.s.
treat:year	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.
loc:season	38.49***	n.s.	6.03*	2.48a	n.s.	23.56***
treatm:season	n.s.	110.41***	39.51***	114.02***	36.14***	22.19***
year:season	4.8*	3.51a	7.48**	10.98***	n.s.	6.42*
loc:treat:year	n.s.	n.s.	n.s.	n.s.	3.23a	n.s.
loc:treatm:season	n.s.	38.29***	17.81***	40.94***	10.89**	5.81*
loc:year:season	6.82*	11.94***	n.s.	12.10***	n.s.	3.90*
treatm:year:season	9.95**	n.s.	n.s.	n.s.	n.s.	n.s.
loc:treatm:year:season	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.

The response to abandonment was slightly different in both meadows. In the dry meadow in June higher absolute investment in blades together with supportive organs in fallow plots led in their unchanged proportion in comparison to regularly mown plots. It indicates that plants in fallow plots were just larger. The same amount of biomass was invested in reproductive organs therefore the lower proportion of reproductive biomass in fallow plots was just the effect of the rest of the biomass components. In October the absolute investments in blades and supportive organs were higher in fallow plots. Also markedly higher investment in reproductive organs was observed in fallow plots in 2008, which was even higher than in June, and thus indicates realization of sexual reproduction in phenologically late species. It was caused by the fact that in mown plots just blades regenerated, whereas biomass of supportive organs and reproductive organs was nearly at minimum. It was also reflected by changed biomass proportions between fallow and mown plots.

In the wet meadow, differences between mown and fallow plots in absolute investment in blades and supportive organs did not appear till 2008, when the biomasses of both organs in fallow plots exceeded those in mown plots. But not in the same range, so that in comparing mown and fallow plots, it led to the decreased proportion of biomass of blades and increased proportion of supportive organs in fallow plots. The biomass of reproductive organs differed neither in absolute nor in

relative values. In October the absolute investment in blades in fallow plots was slightly higher just in 2006 whereas in 2008 the biomass of the blades was the same. The absolute together with relative investment in supportive organs were higher in fallow plots in both years.

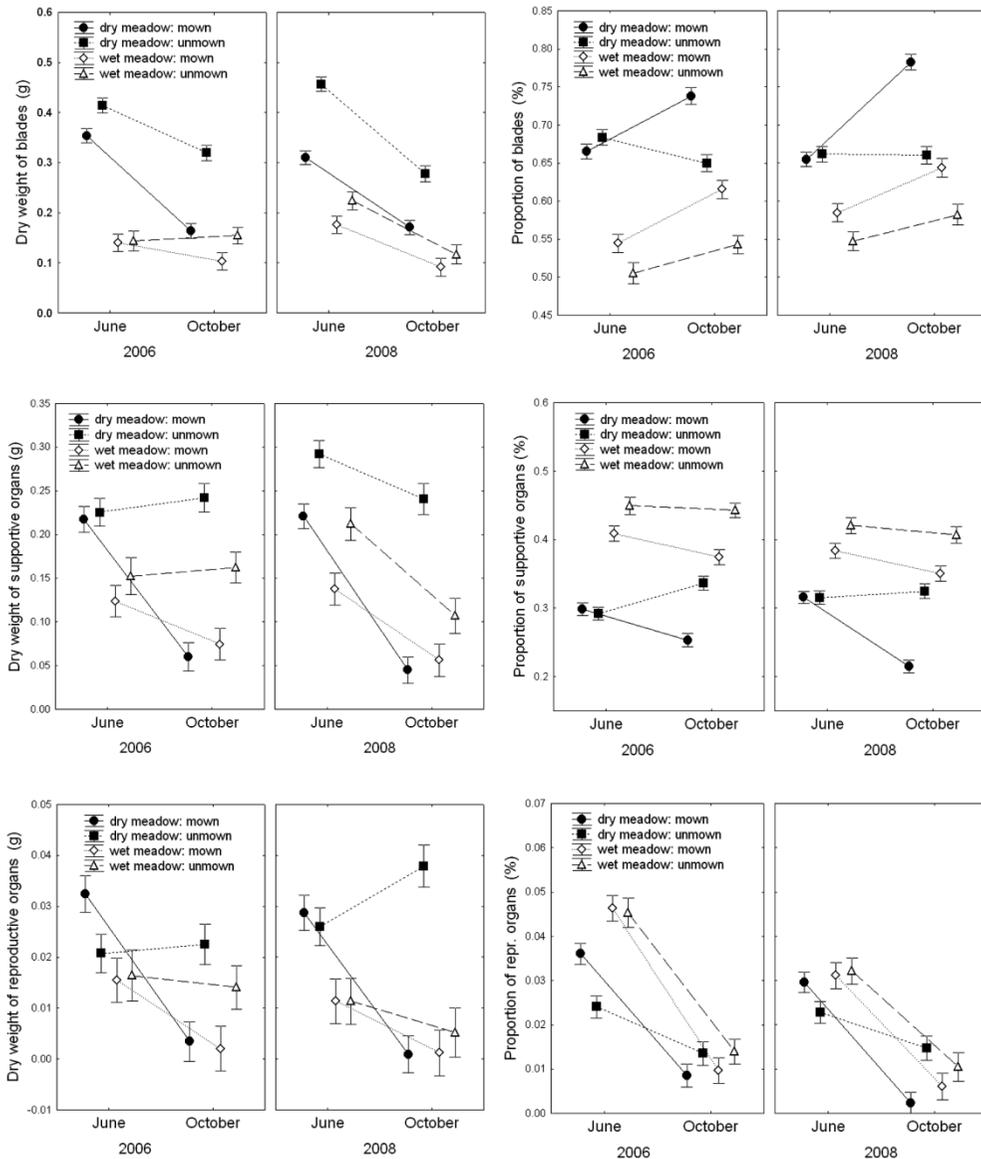


Figure 3. Biomass allocation in individual organs: absolute and relative values. The differences between two localities, within the growing season and between the years in mown and fallow plots are shown (mean, bars denote standard error)

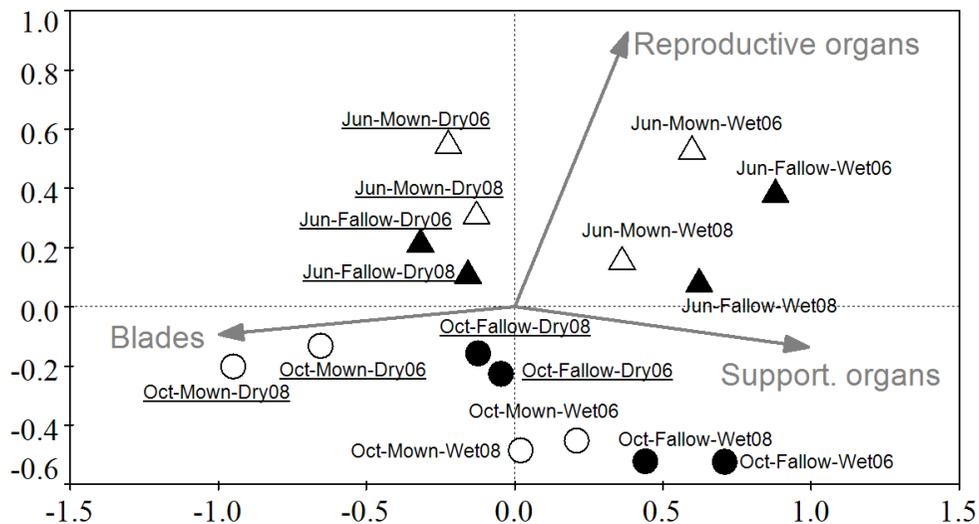


Figure 4. PCA ordination of biomass allocated to individual organs with passively projected centroids of four factor level combinations. The combinations of the season and the management, influencing most the differences in biomass allocation, are marked with different symbols and fill.

Allometry

Allometric relationships between biomass of blades and biomass of supportive organs for studied species were found just at some harvest times and more or less independently on the treatment (Fig. 5). In the dry meadow, significant correlations were found in all harvests in June and in the fallow treatment in October 2006. On the contrary, the allometric relationships were found in the wet meadow in all October harvests; however, in June only in the fallow treatment in 2006.

Slopes of the fitted lines differed significantly between the localities in both comparable cases of fallow treatments in June and October 2006, whereas lower slopes were found in the dry meadow. This indicates that although the biomass of blades was the same in both meadows, investment of the biomass into supportive organs in the dry meadow was higher than in the wet meadow. Some variability between years was observed in the dry meadow, where the slopes significantly differed between 2006 and 2008 in fallow treatments in June. No differences were found in the wet meadow.

When comparing our data with the Enquist and Niklas (2002) APT model, in which slope of the relationship between stem mass and leaf mass was 0.75, we obtained values ranging from 0.37 to 0.99. Significantly lower proved only three regression slopes, all in the dry meadow, namely, both mown and fallow treatments in June 2008 and fallow treatment in October 2006.

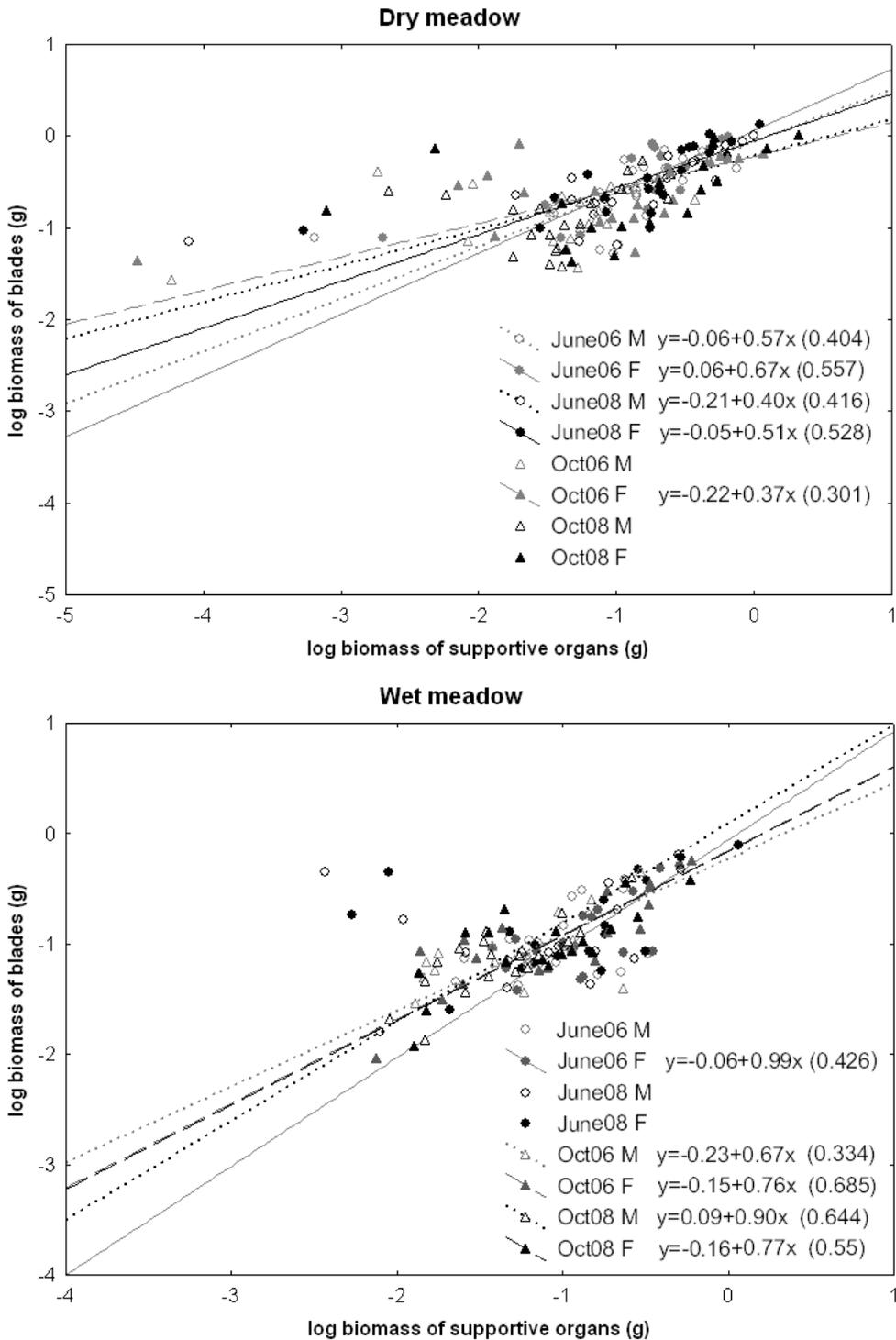


Figure 5. Interspecific log-log relationships between biomass of supportive organs and biomass of blades in the dry and wet meadow in each harvest: June/October, 2006/2008, M-mown treatment/F-fallow treatment. The SMA regression equations are written in every case, where $p < 0.05$; values of R^2 are given in parentheses. The symbols represent the mean value for each species in each harvest.

Discussion

Meadow plants under short term abandonment produced larger shoots but relative investments into supportive structures increased only in wet meadow and on both meadows only in several species. Abandonment also led to shift towards later timing in investment into reproductive organs in several phenologically late species. Allometric relationship between investments into supportive structures and leaf blades was found only in 10 out of 16 of analyzed datasets for community response to treatments reflecting methodological problems when applying this method on meadow herbs.

Site specific effects

Response to abandonment in our studied meadows was driven by the species composition. In the wet meadow, several species responded to the management cessation by increasing the investment into supportive organs, more or less at the expense of the blades, while other species did not show any significant response. On the other hand, in the dry meadow, much diverse reactions were observed among studied species. Whereas only three species increased relative investment in supportive organs, four other species declined this investment, and the rest showed no reaction. Similar mixture of positive and negative effects on growth was observed by Niu et al. (2008) in Tibetan alpine meadow after fertilization. The authors of cited study, however, revealed consistent and opposite responses of different functional groups in a meadow, namely graminoids and forbs (Niu et al. 2008), the effect that we could not support by own data. For example grass species *Bromus erectus*, decreased the investment into supportive structures similarly to several forbs, and in the wet meadow another grass species *Deschampsia cespitosa* increased the supportive investment together with some other forb species.

Effect of abandonment on biomass partitioning

In Central European meadow communities, all aboveground plant parts are produced during the course of a growing season which is interrupted by mowing. After mowing the ability to compensate for the lost biomass is key factor determining the biomass allocation late in the season and is affected by plant size and shoot architecture (Klimešová et al. 2010). On the contrary, in the fallow treatment, competition for light is crucial. Large plants are usually phenologically late and when they are not subjected to mowing, they may flower and accumulate biomass later in

the season (Kahmen and Poschlod 2004, Sun and Frelich 2011). Resulting large biomass and tall canopy cause considerably lower light availability inside the stand (Anten and Hirose 1999). Also in our study, some phenologically late species profited from the mowing cessation and some, but not all, small species were suppressed. It was observed, that tall herbs and herbs increasing their biomass after abandonment slowly increase their dominance after abandonment, whereas smaller herbs quickly decrease the abundance (Huhta et al. 2001, Kahmenn and Poschlod 2004, Niu et al. 2008, Lanta et al. 2011, Klimešová et al. 2011). In our study, small herb *Primula veris*, which showed increased investments into flowering in fallow plots represents exception as it is forest species and shade tolerance enable it to survive also in abandoned meadow.

Allometry and shoot architecture of meadow plants

Crucial for understanding of biomass partitioning strategy is separation of allometric effect in biomass partitioning. This attempt is frequently used in experimental studies examining one species and its phenotypic plasticity as response to nutrients, competition, etc. (Poorter et al. 2011). On the other hand, studies comparing several species usually do not examine effect of environmental conditions on the interspecific allometric relationship but evaluate scaling of organs per se (Metcalfe et al. 2006, Niklas 1994a). While study by Niu et al. (2009) is first to examine effect of management changes on interspecific allocation relationship between aboveground vegetative and generative biomass, our study is first to examine the pattern for relationship between investments into leaf blades versus supportive organs. While in study by Niu et al. (2009) authors were able to test whether plants in treated alpine meadow show the same of different scaling of reproductive to vegetative biomass we fail to do so for nearly half of the analyses.

The reason for the lack of relationship between leaf blades and supporting organs in our dataset were probably (A) small differences in plant sizes and (B) high diversity of shoot architectures of meadow herbs.

A - Reasons why scaling among stems and leaves show a linear relationship in dry the meadow in June and in the wet meadow in October may be due to differences in seasonal development and establishment of size hierarchies in both meadows. In the dry meadow, the peak of development was in June, whereas in the second half of growing season plants growth is limited by dryness. On the other hand, in the wet meadow, suitable conditions for growth start later in a season

due to spring high water table and continue for longer time and therefore peak of development with larger size inequalities among species is attained in the second half of the season.

B - The shoot of meadow plants may have following architectures (i) vegetative shoot is composed from leaves (rosette shoot) and stem is produced only to bear inflorescence; (ii) vegetative shoot lack stems and is formed only by leaves but generative shoot bear both leaves and inflorescence (semirosette shoot); (iii) vegetative as well as generative shoots are composed by leafy stems (erosulate shoots). While architecture of rosette and erosulate shoots is not affected by management, plants with semirosette shoots (the most common type in meadow) are usually flowering and showing semirosette shoots in the first part of the season before management, whereas in the second part of the season they form non-flowering rosette shoots (Klimešová et al. 2008). The effect of changed architecture of majority of resident species after management is observable on Figures 3 and 4 where changes in allocation from June (before mowing) to October (after mowing) are visible.

Plasticity in biomass allocation in meadow herbs have therefore not only allometric but also so far unrecognized architectural constrains. Specifically, decreasing investment into stems in several herbs from dry meadow is attributable to lack of flowering, which is connected with stem formation.

Conclusion

Our study revealed that higher competitive milieu in meadows after abandonment results in site specific biomass investments into blades versus supportive structures due to different species pools and different architectures of meadow herbs. We pointed out that size dependent change in biomass investments are difficult to recognize due to diverse herb architectures and their variation through growing season and as a consequence of management. Future studies would profit from comparisons of experimental results with developmental trajectories of different architectural types of herbs.

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BIOMASS ALLOCATION

CHAPTER VI

Summary of results

SUMMARY OF RESULTS

Summary of results

This thesis extended the knowledge of plant strategies and confirmed that chosen ecological strategy concepts are applicable not only to naturally disturbed ecosystems but also to ecosystems disturbed by human activities and thus are not constrained by the specificity of their original purpose. The case studies answered following questions:

(i) Do resprouting individuals have higher fecundity than individuals regenerating from seeds at the time of disturbance?

Short-lived herbs are capable of adventitious sprouting from roots may be very successful in vegetative regeneration from root fragments. Using a pot experiment, short-lived root sprouters were found to have higher (*Rorippa palustris*) or the same (*Barbarea vulgaris*) fitness when regenerating from root fragments as when regenerating from seed.

(ii) Does shoot biomass and shoot architecture differ in relation to type of buds from which the shoot emerge?

Despite the fact that the adventitious buds were larger and contained more leaf primordia than axillary buds at the time of disturbance, the latter preferentially resprouted when both types of buds were present. Both axillary and adventitious shoots compensated for lost aboveground biomass, nevertheless only axillary shoots compensated for fruit production. Shoot reiteration after injury was only partial in both types of shoot; however, adventitious shoots differed in more architectural characteristics from uninjured plants than axillary shoots. We confirmed that output of plant regeneration after disturbance depends also on intrinsic factors such as origin of buds.

(iii) Does biomass compensation in meadow plants depend on shoot size?

Our results revealed that the earlier explanation of equalization of meadow plants after mowing due to the fact that larger plants lose proportionally more biomass than small plants does not represent the entire mechanism. Even when larger plants in the wet meadow lost more biomass (similarly as in dry meadow), the proportion of lost biomass was not dependent on plant size, and compensation ability (growth of mown in comparison with unmown plants) was not related to the lost biomass in this

meadow type. On the contrary, the observed pattern could be explained by different compensation abilities of small versus tall plants. In addition, according to our expectations, the compensation for lost biomass in the wet meadow was higher than in the dry one.

(iv) Do meadow plants invest more to supportive structures after abandonment and if yes, is observed higher proportion of stem to leaf biomass caused by allometry (increasing shoot size)?

Although cessation of mowing resulted in larger shoot biomass of meadow herbs, only few of them showed change in relative investment into stems, leaf blades and generative organs. On the community level, only plants from the wet meadow increased investments into stems at the expense of other aboveground organs whereas plants from the dry meadow did not change the investments. Because the biomass of stems versus leaves showed allometric pattern only in 10 out of 16 analyses, we were not able to fully separate the effect of size in changed biomass partitioning. These results were caused by different shoot architectures of meadow forbs and their specific seasonal development and responses to management. We therefore concluded that when studying intraspecific relationships between biomass investment, shoot architectures and their developmental trajectories should be taken into account.

Perspectives

The case studies, although variable in the subject matter, bring one similar message. It is not necessary to form new concepts in ecology of disturbed ecosystems but it is possible to apply the existing concepts to other situations. Man-made disturbed habitats have numerous characteristics in common with natural ecosystems and their research might profit from applications of methodologies used elsewhere. For understanding plant response to disturbance generalized approach and large scale comparisons of different systems and disturbance regimes would be necessary.