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Plant dispersal and establishment

Important factors affecting species composition of meadow communities

Ph.D. Thesis

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Annotation

Mechanisms maintaining species diversity in managed meadows are not still well understood. To assess the effect of several important factors on species composition of meadow communities, species regeneration abilities were studied in the course of several years. The research was based on manipulative experiments, where species establishment and survival in seed addition experiments as well as during natural regeneration was observed. By comparison of species establishment in intact and disturbed vegetation, effect of dispersal limitation, abiotic conditions and competition was assessed as well as regeneration ability of different functional groups.

Declaration [in Czech]

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

Prohlašuji, že v souladu s § 47b zákona č. 111/1998 Sb. v platném znění souhlasím se zveřejněním své disertační práce, a to v úpravě vzniklé vypuštěním vyznačených částí archivovaných Přírodovědeckou fakultou elektronickou cestou ve veřejně přístupné části databáze STAG provozované Jihočeskou univerzitou v Českých Budějovicích na jejích internetových stránkách, a to se zachováním mého autorského práva k odevzdanému textu této kvalifikační práce. Souhlasím dále s tím, aby toutéž elektronickou cestou byly v souladu s uvedeným ustanovením zákona č. 111/1998 Sb. zveřejněny posudky školitele a oponentů práce i záznam o průběhu a výsledku obhajoby kvalifikační práce. Rovněž souhlasím s porovnáním textu mé kvalifikační práce s databází kvalifikačních prací Theses.cz provozovanou Národním registrem vysokoškolských kvalifikačních prací a systémem na odhalování plagiátů.

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List of papers and manuscripts with author's contribution

The thesis is based on the following papers:

I. **Vítová A.** & Lepš J. (2011) Experimental assessment of dispersal and habitat limitation in an oligotrophic wet meadow. Plant Ecology, 212, 1231−1242 (IF = 1.829).
AV designed and established the experiment together with JL. AV was responsible for data collection in the field, partially for statistical analysis and for writing the manuscript.

II. Švamberková E., **Vítová A.** & Lepš J. The role of biotic interactions in plant community assembly: What is the community species pool? *Manuscript.*
AV designed and established the experiment together with JL and EŠ. AV was responsible for data collection in the field in Experiment 1, partially for statistical analysis and for writing the manuscript.

III. **Vítová A.**, Macek P. & Lepš J. (2016) Disentangling the interplay of generative and vegetative propagation among different functional groups during gap colonization in meadows. Functional Ecology, Online Early (IF = 5.210).
AV, PM and JL designed the experiment, AV and PM established it together. AV was responsible for data collection in the field, partially for statistical analysis and for writing the manuscript.

IV. Fibich P., **Vítová A.**, Macek P. & Lepš J. (2013) Establishment and spatial associations of recruits in meadow gaps. Journal of Vegetation Science, 24, 496–505 (IF = 3.372).
AV, PM and JL designed the experiment, AV and PM established it together. PF and AV digitalized positions of recruits. AV participated in writing the manuscript.

Contents

Chapter 1

General introduction

Species composition of meadows

Majority of grasslands in Central Europe is dependent on regular human management. Those that are shaped by extensive traditional management are called seminatural grasslands (or seminatural meadows) and they are subject of this thesis. Their species composition and abundance have been shaped by centuries of regular mowing or pasturing (Cousins et al. 2009). Effect of management differs among species, and its type and timing differing among meadows can increase diversity of species occurring there. In grasslands, diversity is shaped strongly by competition. Management is one of the factors which can influence the intensity of competition, when it removes the biomass and litter and enhances so the performance of species with low competitive ability (Mudrák et al. 2013). Moreover, management can create small-scale disturbances (gaps) (e.g. by mowing tools or by grazing animals), which provide regeneration niches for seedling establishment (Kotorová & Lepš 1999). The traditional management (including occasional gap creation) has usually a positive effect on species richness (Lepš 1999); it is usually not completely homogeneous. Together with other disturbances, it contributes to spatial heterogeneity of vegetation, supporting through environmental variability and opportunities for species regeneration the species coexistence. Thus, grasslands are considered to be dynamic systems where gaps are created and colonized continuously by a mixture of species forming a mosaic in space and time (Bullock et al. 1995), and belong to habitats with extraordinary species diversity, especially on small-spatial scales (Klimeš 1999, Wilson et al. 2012, Chytrý et al. 2015).

Recently, many studies in plant ecology are focused on species distribution and composition (Zechmeister et al. 2003, Klimek et al. 2007). They try to reveal the role of individual processes allowing coexistence of so many species at different spatial scales and in various habitats. Classical niche theory suggests that species composition of plant communities is determined by environmental conditions, which limit the ability of species to survive in the site, and which also determine the biotic interactions in the community (Grubb 1977). Consequently, only limited variation in community composition in sites with similar ecological conditions is expected. Nevertheless, several studies have shown that some species are absent from sites apparently suitable for them (Tilman 1997, Turnbull et al. 2000, Foster & Tilman 2003). This fact cannot be explained only by unsuitable local conditions but also by species availability in surrounding as well as species ability to disperse to the target locality. Thus nowadays, it is generally accepted that species composition is shaped by all, the regional species pool, dispersal limitation and local conditions including both, the abiotic conditions and biotic interactions (Zobel 1997, Fig. 1).

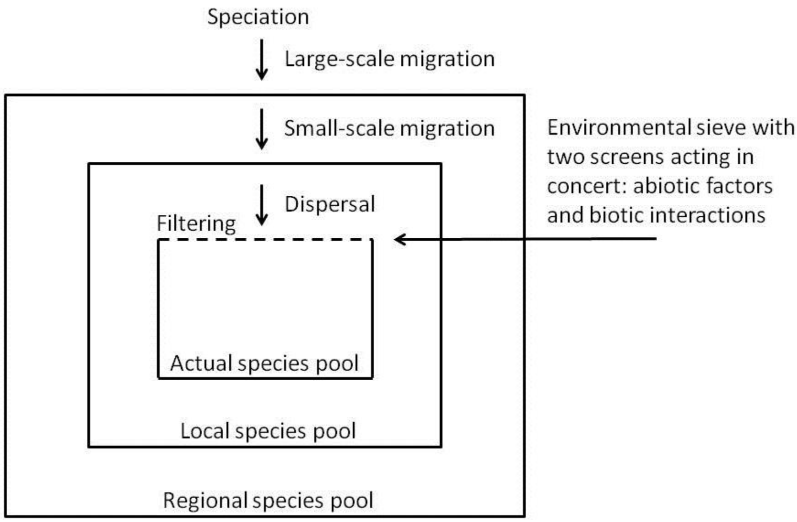

Fig. 1 Species pool according to Zobel (1997).

Species availability

A species has to occur in surrounding or close to the target locality to have a chance to disperse to the site and establish there, i.e. to be a part of regional species pool. (Although I do not exclude the possibility of long-distance dispersal, its probability is generally very low, and so I do not consider it as a factor influencing frequently the community composition.) Regional species pool involves all species in a region (Belyea & Lancaster 1999) and is determined by species evolution and migration ability (Pärtel et al. 1996). However, species from regional species pool has to pass through several filters till it establishes successfully in the community (Zobel 1997, Fig. 1). Firstly, species has to overcome some distance and landscape fragmentation and disperse to the community ("dispersal limitation") and be able to establish and survive there ("habitat or niche limitation"). Both these limitations are strongly influenced by amount of dispersal propagules, when higher propagule pressure can balance low dispersal ability of species or unsuitability of habitat (Stampfli & Zeiter 2008). Further, species composition of community is determined by abiotic conditions of the locality as well as biotic interactions, i.e. community filter (Lambers et al. 2012). Nevertheless, the definition of actual species pool is not consistent depending on if biotic interactions/effect of competition is included or not (compare Zobel 1997 and Butaye et al. 2001).

Species dispersal

Plant dispersal is defined as a movement of seeds and vegetative propagules from maternal plants, differing in type of propagules, dispersal ways, and if it is proceeding in space or time (Poschlod & Biewer 2005). The main purpose of dispersal is to get away from maternal plant to avoid intra-species competition among seedlings and between seedling and maternal plant, to avoid to predation or harsh conditions, and to colonize new sites (Webb 1998). Species potential for dispersal is strongly influenced by the type of propagation. There are many types of clonal propagation but almost none of them is suitable for long-distance dispersal, which is dominated by seeds (Coulson et al. 2001, Jenkins et al. 2007). Nevertheless, there are still many species which can establish in not yet occupied site, but its propagules are not able to disperse to the site (Tilman 1994, Dalling et al. 2002, Zobel et al. 2006) or reach the site in a sufficient amount (Clark et al. 2007). Such species are considered as dispersal limited. And although dispersal is mostly mentioned within the meaning dispersal at large spatial scale, its role at the small scale is no less important, because it provides seeds and propagules for regeneration in available suitable microsites within the community.

Species dispersial can be limited also by seed characteristics, e. g. dispersal potential. If we leave out habitat properties and its history, recent studies show that most species are limited by seed availability (Münzbergová 2004, Poschlod & Biewer 2005, Ehrlén et al. 2006). It seems that seed rain or seed storage in seed bank or both are not sufficient to fully exploit the space available in new open sites suitable for regeneration. In addition to dispersal limitation, insufficient seed availability can be caused by low seed production or their predation (Dalling et al. 2002, Poschlod & Biewer 2005), and generally it is greater at species with large-sized seeds, at ruderal species, and species with relatively short-time seed bank (Clark et al. 2007).

Whereas the distinction between generative and vegetative dispersal is of crucial importance for community functioning, the number of studies concerned with determination of the proportion of dispersal by seeds and/or vegetative propagules in meadow communities is very limited, and the observational studies prevail. In meadows, vegetative propagation usually prevails over generative one (which is rather limited rare event dependent on certain types of disturbance) (Klimeš 1995, Pywell et al. 2003, Sammul et al. 2004). On the other hand, Hodgson et al. (1994) studied over 400 herbaceous plants and concluded that only about 20 % of perennials regenerate solely by vegetative organs, one third of species regenerate only by seeds and remaining species by both. Therefore, a question what is the real role of vegetative and generative propagation in regeneration remains without answer, and unless we want to relay on indirect evidence, it must be solved by manipulative experiments.

Habitat limitation

Habitat limitation means that species distribution is limited by availability of suitable habitats. However, the concept is not consistent in spatial scale – in some studies, effect of habitat limitation is considered at regional scale, but more often it is mixed with evidence for microsite limitation at local scale (Münzbergová & Herben 2005). In our study, we tend to the local scale concept when the species cannot establish in the target community because of unsuitable abiotic conditions or negative biotic interaction (Moore & Elmendorf 2006). Thus, this concept of habitat limitation includes many factors affecting species germination and establishment.

Successful establishment of many species from seeds is a quite improbable event (Zobel et al. 2000). It is dependent very often on certain type of disturbance when open gaps with no vegetation cover or litter are created, resulting in no or decreased competition for light and nutrients. In such disturbed sites, the number of established seedlings is usually higher (Jakobsson & Eriksson 2000, Janeček & Lepš 2005), because seedlings are very sensitive especially to competition, much more than just established plants are. This sensitivity is species specific (Kotorová & Lepš 1999) and species requirements differ between seed germination and seedling establishment (Isselstein et al. 2002). Germination and initial establishment is positively affected by gaps providing more light, usually also more nutrients and lower competition with surrounding vegetation (Křenová & Lepš 1996, Foster & Gross 1997, Morgan 1997). On the other hand, species are more exposed to harsh conditions in gaps (desiccation, herbivores etc.) (Foster et al. 2004, Kolb et al. 2007), which might prevent species establishment. Thus, success of establishment can be more dependent on species already established; the importance of such facilitative effect increases with increasing abiotic stress (e.g. dry or mountain habitats) (Cichini et al. 2011). Therefore, for germination and initial establishment is more important positive effect of gap but for survival it can have in some circumstances also the negative effect (Jakobsson & Eriksson 2000, Foster et al. 2004, Špačková & Lepš 2004, Janeček & Lepš 2005). In real communities (unlike in pot experiments), the ontogenesis of an individual from seed to mature plant is usually rather long process. Seeds of many species can germinate and survive in the community for several years in the seedling stage before they mature or die (Moles & Westoby 2002).

Gaps are relatively common in meadows where they are created by animals (big grazers like deer, but also moles etc.) or as a side-effect of management (missed strokes of scythe in traditional management, or in connection of mowing machinery in modern times). They differ in size, intensity of disturbance and frequency, with which they appear. Thus, we can find in vegetation a mosaic of various gaps varying in their "successional stage" (i.e. in degree by which they are overgrown). Further, gaps are not homogenous, there are different gradients from margins to its center (effect of surrounding vegetation – shading, equalizing mositure and temperature). Although disturbance primarily removes the competition, its effect is very short-term; the colonization of disturbed site starts immediately after disturbance and can last only several years (Hölzel 2005). Nevertheless, it can provide sufficient time for some species to establish. Thus, gaps act as safe sites for emergence of many species (Grubb 1977, Kotorová & Lepš 1999), even though species dependence on gap presence for its recruitment is species specific (Morgan 1997, Hölzel 2005).

Experimental approaches

Whereas the studies of grassland species richness are quite common, including repeated observations of permanent plots to investigate the spatio-temporal dynamics of the communities (e.g. the classical studies starting with Herben et al. 1993), we need experimental manipulations to disentangle the effects of individual factors and to assess the importance of individual processes and mechanisms. Generally, it encompasses two types of manipulation (and their combination). First are sowing experiments, where the propagule and microsite availability is experimentally manipulated, and the second is manipulation of environment, in the study of regeneration, usually artificial creation of microsites, typically artificially created gaps.

Seed sowing experiments

To determine which of these factors is crucial for a species composition of meadow community, seed sowing experiments are usually used. Seeds of resident or non-resident species of target community are added and their emergence and survival is observed. It is expected that resident species have in the community their regeneration niche and abiotic conditions do not restrict their establishment, consequently they should be able to establish themselves. If they establish, it refers to seed limitation, if not to microsite limitation. Thus, the behavior of resident species should serve as a “benchmark“ against which the success of non-resident species should be compared. With non-resident species we cannot assume existence of regeneration niche a priori; their successful establishment in sowing experiment suggests that their regeneration niche exists in the community, and so the establishment is considered to be an evidence of dispersal limitation, whereas failure to establish is evidence of negative biotic interactions or abiotic factors (Turnbull et al. 2000, Foster & Tilman 2003). Turnbull et al. (2000) showed in their summarizing study that approximately 50 % of augmentation experiments concluded in limitation of community by seed availability. In field studies, when non-resident species were introduced to community, seedlings of introduced species were recorded in more than half cases but only in 23 % their establishment can be considered as successful (recorded individuals in reproductive stage). Nevertheless, many studies consider for successful establishment existence of one mature individual.

Nevertheless, seed addition experiments cannot always provide unequivocal results. First, seedling establishment is often highly variable among individual seasons (Špačková & Lepš 2004, Zobel & Kalamees 2005), so that the failure to establish can be quite common, even for the resident species. Further, the observation should be long-term to avoid misleading results (Münzbergová & Herben 2004, Ehrlén et al. 2006). Seeds of many species can germinate but they often cannot establish self-perpetuating viable population. Such population can survive in community for several years in immature stage until they die out (Primack & Miao 1992, Moles & Westoby 2002, Foster & Tilman 2003, Klimeš 2005, Kiviniemi 2008).

Disturbance experiments

Lack of suitable microhabitats for regeneration used to be tested by experiments with some type of disturbance in plots. Although observation of another questions would be also very useful (e.g. changes in colonization along successional gradient, differences in species richness and composition between gaps and surrounding, differences in colonization between gap centre and edges or plant-plant interactions), because such studies are very rare. Moreover, the fate of emerging seedlings is usually followed only for one season so we have very limited information about gap colonization in long-term view (Turnbull et al. 2000). Most of these studies are usually combined with seed addition; natural colonization is observed very rarely.

Further, results depend on many factors such as disturbance intensity, gap size and shape, productivity, land use type, time of gap creation etc. In grasslands, we can observe several types of disturbance with different effect on species diversity – from low-intensity disturbance such as grazing with low efficiency to more intensive and very effective harrowing and turf removal (Pywell et al. 2007). The shape and size of gaps created by such disturbances influence especially the type of prevailing reproductive strategy in gaps when vegetative propagation is more affected by distance from intact surrounding vegetation, i.e. the edge of gap and gap area (Kotanen 1997). Species composition in close surrounding of a gap has also a crucial effect on the course of gap colonization; e.g. especially if species with dominant vegetative propagation are abundant (as usual in many grasslands) (Lanta & Lepš 2009). Species might colonize disturbed sites in different way along productivity gradient, and increased productivity might result in faster closure of gaps (Foster et al. 2004). Similarly, different responses in species establishment are observed among different land-use types (Müller et al. 2014) or between gaps created in different time (Pakeman & Small 2005).

The characteristics of disturbance (especially shape and size of the gaps) and patch dynamics are very often discussed in conservation biology where disturbance is required to restore species-rich communities (Hofmann & Isselstein 2004). Nevertheless, most studies are conducted in forests or extreme grassland habitats with stronger effect of facilitation or competition, representing only small variety of habitats. Considering disturbance as one of the main factor ensuring diversity, we need to observe natural colonization and the processes during gap colonization in more detailed way for longer time and in different habitats to understand diversity.

Aims of the thesis

In this thesis, I focused on disentangling the role of individual factors affecting species composition in meadows. Although studies about species diversity and abundances are common in grassland ecology, detailed manipulative experiments which are monitored for sufficient time period are still missing. I studied establishment and survival of species in differently disturbed sites at meadows for several years to get a more detailed insight into crucial phases of early plant life cycle.

First, I aimed to assess the potential of dispersal limitation and habitat limitation to influence species composition of meadow communities through seed sowing experiment of resident and non-resident species into disturbed plots and intact vegetation. To reflect the fact that the transition from seedling to immature plant is the most sensitive phase of their life cycle, I compared seedling survival in sowing experiment with survival of transplanted immature plants (**Paper I**). The success of establishment for broader variety of species and the time needed for their competitive exclusion was investigated in another seed sowing experiments (**Paper II**).

At smaller spatial scale, natural regeneration of resident species and processes affecting success of their establishment were observed in intact vegetation and during colonization of artificially created gaps in a meadow. Focused on different regeneration strategies of four main functional groups, the role of generative and vegetative propagation during gap colonization was investigated and the regeneration from seed bank, seed rain and vegetative ingrowth was compared (**Paper III**). Further, dynamics and spatial patterns of recruits' establishment during gap colonization were observed as well as the effect of gradient of environmental conditions on the recruitment (**Paper IV**).

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Chapter 2

Experimental assessment of dispersal and habitat limitation in an oligotrophic wet meadow

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Experimental assessment of dispersal and habitat limitation in an oligotrophic wet meadow*

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Abstract

The ability of a non-resident species to establish a viable population when sown or transplanted into a target community is often considered as indirect evidence that its absence in the community is caused by dispersal limitation. We evaluated the importance of dispersal and habitat limitation in an oligotrophic wet meadow community by a sowing experiment where seeds of three resident and three non-resident dicotyledonous species were added to the target community, into disturbed (litter and moss removal by raking) and undisturbed plots. The sowing experiment was supplemented with a transplant experiment, to overcome possible seedling failure in early life stages. Recruitment and survival of seedlings and transplants were monitored for five years. Disturbance increased recruitment, but decreased survival, in both resident and non-resident species. Recruitment was slightly better in the non-resident species, while survival was slightly better in the resident species. Three species reached the reproductive stage at the end of the experiment, one resident and two non-resident. The two non-resident species would probably be able to establish viable populations and consequently their absence can be caused by dispersal limitation. On the contrary, one of the non-resident species was not able to overcome the seedling state, and this inability can cause its absence. Two of resident species failed to establish themselves; this failure to establish is probably related to the prevailing vegetative propagation of these species. This shows that the failure to establish is not sufficient evidence that a species is habitat limited.

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Keywords

habitat limitation, seedling recruitment, species pool, sowing experiment, transplant experiment

Chapter 3

The role of biotic interactions in plant community assembly: What is the community species pool?

Manuscript

The role of biotic interactions in plant community assembly: What is the community species pool?*

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Abstract

Differences in plant species composition between a community and its species pool are considered to reflect the effect of community filters. If we define the species pool as a set of species able to reach a site and form a viable population in a given abiotic environment (i.e. to pass the dispersal and abiotic filter), the difference in species composition should correspond to the effect of biotic interactions. However, most of the operational definitions of the species pool are based on co-occurrence patterns and thus also reflect the effect of biotic relationships, including definitions based on the functional plant traits, Ellenberg indicator values or Beals index. We conducted two seed introduction experiments in an oligotrophic wet meadow with aim of demonstrating that many species excluded by the above definitions from a species pool are in fact able to establish there successfully, if competition is removed. In sowing experiments, we studied the establishment and survival of species after the removal of competition (i.e. in artificial gaps) and in intact vegetation. We also investigated inter-annual variability of seed germination and seedling establishment and competitive exclusion of sown species. The investigated species also included those from very different habitats (i.e. species with very low corresponding Beals index or Ellenberg indicator values that were different from the target community weighted mean). Many of these species were able to grow in the focal wet meadow if competition was removed, but they did not establish and survive in the intact community. These species are thus not limited by abiotic conditions, but by biotic filter. We also recorded a great inter-annual variability in seed germination and seedling establishment. Competitive exclusion of species with

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different ecological requirements could be quite fast (one and half season) in some species, but some non-resident species were able to survive several seasons; the resident species were able to persist in competition. Comparison of realized vegetation composition with the corresponding species pool greatly underestimates the potential impact of the biotic filter if the delimitation of the species pool is based on the realized niches of species and co-occurrence patterns.

Keywords

abiotic filter, biotic filter, competitive exclusion, disturbance, sowing experiment, species pool

Manuscript is prepared for submission.

Chapter 4

Disentangling the interplay of generative and vegetative propagation among different functional groups during gap colonization in meadows

Functional Ecology (2016)

Disentangling the interplay of generative and vegetative propagation among different functional groups during gap colonization in meadows*

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Abstract

1. Meadow plant communities are commonly driven by strong competition, and the colonization of gaps plays an important role in the maintenance of their species diversity. Despite this, species-specific information about the dynamics of vegetative and generative propagation, and on the role of seed bank and seed rain, are rather scarce.
2. In a three year manipulative experiment, we aimed to disentangle the effects of seed bank, seed rain and vegetative propagation in vegetation and during colonization of artificial gaps in a mesotrophic meadow. Vegetative propagation was manipulated by felting, and the presence of the seed bank by soil sterilization using gamma radiation. We focused on the dynamics of four main species groups with different regeneration strategies: dicots, *Cyperaceae*, *Juncaceae* and *Poaceae*. The shift from seedling dominance in early stages towards vegetative resprouts dominating at a later stage in the gap colonization process differed considerably among the four species groups.
3. Dicots and *Juncaceae*, regenerating frequently from the seed bank, acted as pioneer species, and determined species composition of newly disturbed sites. Seed rain became crucial later in the season and resulted in shifting dominance to the more competitive *Poaceae*. Stress-tolerating *Cyperaceae* were colonizing the gaps

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vegetatively mainly towards the end of the experiment. While graminoids showed preference for growing into gaps clonally, dicots propagated vegetatively mostly within intact vegetation.

4. Although seed rain soon equalized seedling numbers in plots with and without a seed bank, the presence of a seed bank proved to be crucial for certain species, and its effect on species diversity remained positive in all functional groups for the duration of the experiment, demonstrating the importance of a seed bank for the maintenance of species diversity. Nevertheless, seedling assembly converged to a similar functional composition in all gap types after three years. We have not detected any competitive effect of vegetative resprouts on seedlings or seedlings on vegetative resprouts throughout the experiment.

5. Each of the three means of regeneration has its unique role in the maintenance of species diversity during gap colonization, and the importance of these roles differs in different functional groups.

Keywords

competition, diversity, seed bank, seed rain, small-scale disturbance, vegetative propagation

Chapter 5

Establishment and spatial associations of recruits in meadow gaps

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Establishment and spatial associations of recruits in meadow gaps*

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Abstract

Questions: What is the spatio-temporal dynamics of recruit (seedlings and vegetative sprouts) establishment in meadow gaps? What processes prevail during recruit establishment? At what spatio-temporal scales do they operate?

Location: A wet meadow in South Bohemia, a region of the Czech Republic.

Methods: We studied spatio-temporal dynamics in pattern of recruits (seedlings and vegetative sprouts) to characterize development and underlying ecological processes during gap colonization. We established four types of artificial gaps laid out in ten replicated blocks. To distinguish the effects of generative vs. vegetative reproduction we used gaps with sterilized and non-sterilized soil (manipulating the seed bank), and manipulated the possibility of clonal spread by inserting mesh or felting along the borders of the gaps.

Results: The majority of recruits appeared during July and August. Recruits were surrounded by empty spaces of 5–9 mm, and formed clumps of 20 mm or more. Clumping of even-aged seedlings and a lower number of vegetative recruits were

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observed in the gaps with non-sterilized soil. Overall, clonal spread was limited to the gap borders, being far less common than recruit establishment from seeds. The recruits emerged preferentially close to the gap centre where the temperature was highest as was the red to far–red ratio (R:FR). However, during the season, the majority of late recruits were observed in the southern, coolest parts of the gaps, reflecting the increasing importance of the facilitative effect of the surrounding vegetation.

Conclusions: Gaps were colonized predominantly from seeds; vegetative propagation was very slow and appeared at the end of the season. The presence of a seed bank enabled earlier gap colonization; the effect of seed rain became increasingly important during the season. The recruits were clumped, which further supports environmentally driven establishment, although other factors (e.g. facilitation) cannot be excluded. For the shortest distances, recruits were absent close neighbours due to the strongest competition. We therefore suggest that there was a spatial continuum between competition and facilitative effects among individual recruits.

Keywords

meadow gap, recruitment, spatial pattern, seed bank, seedlings, vegetative propagation

Chapter 6

General conclusions

General conclusions

Understanding species (in)ability to regenerate in a community is crucial for understanding of the mechanisms maintaining the species diversity. Traditionally, species absence in a community is considered to be caused by dispersal limitation or habitat limitation. In this thesis, we investigated selected factors affecting species dispersal, establishment and survival in a community in detailed way. We demonstrated that successful establishment (i.e. forming a viable population) is affected by a range of factors, importance of each can vary in time and is specific for various community types as well as for individual species. We concentrated on wet mesic and oligotrophic meadows which are regularly mown. We investigated plant species regeneration, both vegetative and from seeds, in disturbed sites as well as in intact vegetation for several consecutive years. Through manipulative experiments we attempted to reveal which factors are crucial for species successful establishment in a community. It seems that a chance to establish from seeds considerably varies in time (not only seasonal variability, but also large variability among individual years) and is influenced by many circumstances; increased chance to establish is often linked with some extreme events appearing once in several years (e.g. extremely wet years). We assessed the role of species dispersal, presence of microsites, removal of competition and other important factors for regeneration of selected species in our localities in those years. The results helped us to understand processes in regeneration at regularly managed meadows. Some of our findings can be also applied in practical conservation biology - they clearly demonstrate which factors are important in management of meadows in Central Europe, which circumstances lead to maintenance of species diversity, suggest which factors suppress the regeneration, and are thus detrimental for the species diversity.

Firstly, we assessed the role of dispersal and habitat limitation (Paper I). In seed sowing and transplant experiments, seeds and transplants of non-resident species were introduced to the community and their survival was observed. By comparison with establishment and survival of resident species, we revealed the effect of habitat suitability and microsite limitation. For both, resident and non-resident species, microsite limitation was observed, their recruitment was higher in disturbed plots where litter and mosses were partially removed by harrowing. Moreover, seed addition of resident species into plots increased their seedling numbers, showing on their seed limitation. Two of three non-residents established in the target community and survived there for several years, so their absence in a community is probably caused by low dispersal potential of the species (heavy seeds, no obvious dispersal mechanism). For another non-resident species we documented inability of transition from seedling to immature plant. Nevertheless, this phase seemed to be crucial for resident species as well. Because both resident and non-resident species germinated well, we concluded that crucial for their successful establishment is the phase of overcoming seedling stage. The chance for this transition to immature plant could be probably increased by species dispersal in a large amount of propagule to the target site (i.e. by increasing propagule pressure). It suggested the importance of propagule pressure when success of species establishment in less suitable habitats could be balanced by higher propagule input and vice versa. This all showed on that establishment from seeds might be, particularly for some species (also the resident ones), a rare event, dependent often on some disturbance. Also, increased propagule pressure might considerably increase the species chance to overcome the seedling stage. Our results could be also used in conservation ecology in re-introduction programs, where transplanting of species would be more successful than seed sowing in species reintroduction.

Regeneration from seeds in intact meadow vegetation is generally low, its success usually depends on some type of disturbance. Such disturbance provides a suitable microsite for species regeneration where the competition is lower. The competition effect of surrounding vegetation on seedlings is probably the most important biotic factor constraining the seedling regeneration, nevertheless, other biotic as well as abiotic factors (desiccation, herbivory, more fluctuating temperature and humidity) are also important causes of seedling mortality. Therefore, we focused on the effect of competition on establishment of species with different varying habitat preferences and varying niche width (Paper II). Species from regional species pool established successfully from seeds if the competition was removed, even in situation, where the target habitat was rather different from their natural habitats. Even species with habitat preferences very different from the target community would be probably able to establish there viable populations if the competition was removed. This suggests that the ecological preferences of most meadow species are not determined so much by their physiological response to environmental conditions, but that the competition (specifically to establish and survive under competitive environment of the target community) is the decisive factor determining the species ecological preferences, i.e. determines where a species will be able to establish and survive. We have also demonstrated, how are these abilities important for various definitions of species pool, and when the comparison of species pool with realized vegetation composition might be used to infer the effect of limitation of species by the effect of competition.

Similarly, strong effect of competition was recorded also during monitoring of natural species regeneration in intact vegetation in comparison with disturbed sites – artificially created gaps (Paper III). Especially in undisturbed vegetation, it resulted in low regeneration from seeds. We tried to contribute to still missing detailed information about the role of vegetative and generative regeneration as well as importance of seed rain and seed bank in species regeneration, even though it is very difficult to find out common rules in seedling establishment. In our case, gaps were colonized rather fast, their cover and composition became similar to intact vegetation in three years. At the beginning, gaps were colonized mostly from seeds, vegetative propagation became dominating in later stages. There were also differences among species groups. Dicots and *Juncaceae* regenerated mostly from the seed bank and were the first colonizing species. Hence, they influenced strongly species composition of newly disturbed sites. Later in the season, seed rain became important and resulted in a shift in species composition from dicots to grasses. Last species group, *Cyperaceae*, seems to be seed limited, regenerating mostly vegetatively. Contrary to gap colonization, we recorded only low numbers of *Poaceae* and *Juncaceae* seedlings in intact vegetation. Seedlings of dicots were frequent there, similarly to gaps. This implies that disturbance is important especially for regeneration of *Poaceae* and *Juncaceae*, which are probably more microsite limited. To conclude, we recorded changes not only in recruit numbers, but also in number of species during gap colonization. The presence of a seed bank was essential for some species, and its presence in gaps had a consistent positive effect on species richness throughout the experiment. Thus, gaps in meadow communities are very important for species regeneration from seeds and maintenance of species diversity, although species group differed in their ability to colonize open spaces through time. The course of colonization can be influenced by type and timing of management, affecting intensity of seed rain as well as disturbance. Due to timing of management, we can inhibit a dominant species (e.g. by cutting in sensitive phase of its phenology) and on the contrary increase abundance of other species, often species that are desirable from the conservation point of view. In our case, meadows are mown at the beginning of June when many species just shed their seeds, so the intensity of their seed rain is very low, which might suppress species relying on regeneration from seed rain.

At the smallest special scale, the seedling establishment is strongly dependent on environmental conditions of target site (Paper IV). Because disturbed sites are usually with sparse or no vegetation, new recruits are exposed to more severe conditions of environment, where the temperature and humidity fluctuate more than in intact vegetation. Furthermore, disturbed sites themselves are not homogenous, we found some gradients of temperature and light in gaps. Most new recruits emerged from seeds without any support from their maternal plant. Seedling survival might be positively affected also by the biotic interactions (facilitation) when species can take advantage of close neighbours. We documented a continuum between competitive and facilitative effects on recruit emergence and establishment. Further, we recorded that species requirements on germination and establishment differed: the seed emergence was higher in gap centre with highest temperature and light. But in time, seedlings survived better in edges of a gap where higher humidity was recorded.

Whereas the traditional theory of community ecology stresses the importance of reaching the competition equilibria for the composition of ecological communities, it seems that two factor studied in the thesis are of extreme importance for the community composition: the ability of propagules to disperse to the target site and the ability to establish a viable population from the propagules in the site. The second factor, is however, strictly constrained by the competition of extant vegetation. Consequently, the competition is important not only for reaching the competition equilibria, but also (and perhaps mainly) for the establishment phase of individual populations. This suggests also the importance of repeated disturbances for the maintenance of the community diversity.

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