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Tolerance and resistance of plants to disturbance

PhD Thesis

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Chapter 1

Introduction

As sedentary organisms, plants are often exposed to various types of disturbance, which can be considered as one of the most important sources of uncertainty in their lives (Bergelson et al. 1993, Firbank 1993, Schippers et al. 2001). Disturbance events, originating in activities of pathogens, herbivores, man and from phenomena such as wind-damage, frost, drought, soil erosion or fire, are components virtually of all world's ecosystems and are associated with the partial or total destruction of the plant biomass (Grime 2001). Hence, disturbance events can vary not only in their severity, but also in their predictability and frequency. Naturally, plants developed impressive diversity of ways how to reduce negative consequences of disturbance on their fitness.

Generally, the plant individual has two options how to successfully cope with disturbance: tolerate or resist it. Tolerance to disturbance is enabled by resprouting from axillary or adventitious buds and results in some degree of compensation of lost biomass. Resistance is connected with production of defense mechanisms, which minimize the probability to be negatively affected by disturbance event. Since the production of defense mechanisms has at least physiological limitations, for example it is not possible to resist intensive fires or hurricanes, it stand to reason that resistance to disturbance is applicable mainly for conditions with less severe disturbance events originating for example in radiance, pathogens or herbivores. On the other hand, tolerance to disturbance seems to be more universal strategy (see the Table 1) as the resprouting from buds could be realized in a broader spectrum of disturbance severity, even if plant body is entirely fragmented by severe disturbance (e.g. Latzel et al. 2008, Martínková et al. 2004 a, b, 2006, 2008).

The understanding how plants cope with disturbances, which are among the most important factors shaping plants communities, provides better insight into functioning of majority of biotical systems and gives us a tool to their management and/or protection. This thesis aims to uncover some aspects of *tolerance* and *resistance* of herbs to disturbance on the level of a plant individual as well as a whole plant community.

Table 1. Possible strategies of plant individuals in coping with disturbance events differing in severity, predictability and frequency.

Severity	Predictability	Frequency	Strategy
low	low	low	tolerance/resistance
low	low	high	tolerance/resistance
low	high	low	tolerance/resistance
low	high	high	tolerance/resistance
high	high	high	tolerance
high	high	low	tolerance
high	low	high	tolerance
high	low	low	untenable

Tolerance to disturbance: resprouting of herbs

To predict globally plant community responses to environmental change and to address hypotheses about the mechanisms underlying these responses, usage of plant functional traits reflecting basic plant ecological functions was proposed (e.g. Noy-Meir et al. 1989, Weiher et al. 1999) Majority of published literature engaged in prediction of community dynamics in disturbed environments, consider traits such as canopy height, life history, and shoot architecture (Díaz et al. 2007) but often overlooked traits directly connected with the tolerance to disturbance, for example bud bank formation Therefore, the proposal to use of vegetative regeneration from the bud bank in prediction of vegetation response to a given disturbance regime is naturally one of the main goals of this thesis.

The resprouting of plants from the bud bank after disturbance, has received substantial attention mainly in fire prone habitats of Australia, South Africa or the Mediterranean Basin, where many woody species cope with recurrent fire disturbance by resprouting from lignotubers (Bell & Ojeda 1999, Lloret et al. 1999, Cruz et al. 2003, Verdaguer & Ojeda 2005) and in studies of plant response to herbivory (Del-Val & Crawley 2005, McIntire & Hik 2005, Suwa & Tomomi 2008, Zhao et al. 2008). However, the resprouting of plants from the bud bank should not be considered only in context with the abovementioned factors. Intensive exploitation of European nature leads also to constant disturbance pressures on many plant species and magnitude and severity of disturbance on these plots may exceed traditionally studied systems. Plants of mown grasslands, arable lands, belts around roads, urban or industrial zones and alike are facing to recurrent severe disturbance events and only those capable to survive such harsh regimes are able to inhabit these areas. Nonetheless, in the light of the scanty interest, there is lack of information about the role of biotic and abiotic factors affecting the resprouting of severely injured herbacous plants.

Resistance to disturbance: induced defenses

Herbivory is an important biotical factor negatively affecting many plant species. It is natural that, besides the regrowth after damage (tolerance), plants have developed various defense mechanisms to protect themselves. Such defenses could be classified as constitutive or induced. The first is usually present during a whole plants life in a form of mechanical or biochemical compounds and is accompanied by fitness costs when herbivores are not present (Bergelson & Purrington 1996, Purrington 2000). Induced defense allows triggering of mechanical or biochemical defenses in plants only when they are under attack by herbivores and thus allows minimize significantly fitness costs of protection (Herms & Mattson 1992, Zangerl & Bazzaz 1992, Agrawal et al. 1998).

Some clonal plants are able to spread the signal of herbivore attack to distant, interconnected and not attacked ramets (Gómez et al. 2006). This information's headstart facilitate

them to be prepared on herbivores before they truly come. However, if interconnected ramets are being induced after inadequate reaction to herbivore attack, for example, if the herbivore is less motive or not so abundant, costs of induced defense can outweighed its benefits and such induced plant could be weakened compare to not induced and can significantly lose in competition for limited resources.

As costs of induced defenses have received considerable interest (e.g. Cipollini 2002, Cipollini et al. 2003, Dietrich et al. 2005, Zavala et al. 2004), their benefits have been often neglected in experimental studies even when quantification of benefits is an important aspect that deserves more attention in order to estimate the cost-benefit balance necessary to understand the evolution of induced protection (Agrawal 2000).

Objectives and content of the thesis

The main objectives of this thesis are: (i) interpret the most used plant functional traits considered as relevant to disturbance response of species in man-made habitats and discuss relevance of some so far omitted persistence traits for plants for regularly managed temperate meadows, (ii) assess and compare the role of resprouting of herbs with other common plants traits in selected man-made habitats, (iii) interpret the role of nutrients availability on resprouting and seeding strategy of two related resprouting species (*Plantago lanceolata and P. media*) and finally, (iv) evaluate the costs and benefits of resistance to disturbance in a model clonal species *Trifolium repens*.

Chapter 2 summarizes most frequently used plant functional traits that are considered as appropriately predicting species responses to disturbance in grasslands, and investigate the relationships of these traits with other, so far omitted but possibly more relevant traits.

Chapter 3 concerns in the role of vegetative and generative regeneration together with other selected plant traits after disturbance in urban plant communities. As urban flora of Central Europe host numerous non-native species, particular respect is taken on regenerative abilities of exotic species.

Chapter 4 is focused on evaluating of the role of nutrients availability on vegetative and generative regeneration strategy of two related ribworts (*Plantago lanceolata* and *P. media*). Tested is if there is a general tendency for resprouting in nutrient poor and for seeding in nutrient rich conditions.

Chapter 5 evaluates the costs and benefits of induced defenses in a clonal plant *Trifolium repens.*

Chapter 6 summarizes outputs of this thesis.

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Tolerance to disturbance: resprouting of herbs

Chapter 2

Jitka Klimešová, Vít Latzel, Francesco deBello & Jan M van Groenendael - **Plant functional traits in studies of vegetation changes under grazing and mowing: towards a use of more specific traits.** *Preslia* [in press]

Plants' abilities to perform ecological functions are difficult to evaluate directly in the field. Therefore, a number of attempts were made to determine easily measurable proxies - plant functional traits (PFTs). In particular, the value of PFTs as tools for predicting vegetation responses to management (i.e. grazing and mowing) was the focus of a large number of researches. However, recent studies searching for consistency in PFT predictions concerning pasture management in different regions did not confirm a consistent predictive value of the same set of PFTs. The use of more specific traits better suited for a specific region was suggested for future studies. We consider this an important goal that can help us select the most adaptative traits in response to grazing and mowing for different biomes. Using temperate grasslands in Europe as an example, we showed that (a) plant height, often considered as the best predictor of species response to grassland management, is coupled with other more relevant functional traits, and that (b) clonal traits have important, often neglected functions in the response of species to grassland management. We concluded that simple traits cannot be the only basis for predictions of vegetation changes under pasture management and, therefore, a functional analysis of the trade-off between key traits is needed.

Jitka Klimešová, Vít Latzel, Francesco deBello & Jan M van Groenendael – **Funkční vlastnosti rostlin ve studiích vegetačních změn po pasení a kosení: postup k užití více specifických vlastností.** *Preslia* [in press]

Je velmi obtížné vyhodnotit ekologické funkce rozličných vlastností rostlin přímo v terénu. Z tohoto důvodu bylo navrženo několik postupů k určení jednoduše měřitelných „zjednodušení" - funkčních vlastností rostlin (PFT). Mnoho výzkumníků se zaměřilo zejména na použití PFT jako pomůcky při předpovídání odpovědí rostlin na různý typ managementu (například pastvu či kosení). Ovšem nejnovější studie nepodpořily konzistentní prediktabilitu stejného souboru PFT týkající se managementu spásaných společenstev různých regionů. Proto bylo navrženo používat více specifické vlastnosti rostlin, které budou vhodné pro daný region. V tomto vidíme důležitý cíl, který nám může pomoci vybrat nejvíce přizpůsobivé vlastnosti odpovědí rostlin na pasení nebo kosení v různých biomech. Ukazujeme na příkladu temperátních luk, že (a) výška rostliny, často považovaná jako nejlepší prediktor odpovědi rostlinných druhů na management, je propojena s dalšími, více

důležitými funkčními vlastnostmi a že (b) klonální vlastnosti rostlin mají důležitou, často opomíjenou funkci v odpovědi rostlinných druhů na management luk. Uzavíráme, že jednoduše měřitelné vlastnosti rostlin nemohou být základem pro předpovídání vegetačních změn na pastvách a je tudíž nutná funkční analýza různých trade-offs mezi klíčovými vlastnostmi rostlin.

Chapter 3

Vít Latzel, Stanislav Mihulka & Jitka Klimešová - **Plant traits and regeneration of urban plant community after disturbance: Does the bud bank play any role?** Appl Veg Sci (2008) 11: 387-394.

Main questions of this study were: What is the relative role of the bud bank, seed and various species traits in the regeneration of urban plant communities after severe disturbances? Do invasive and exotic species, highly abundant on disturbed communities, regenerate better than native species after disturbance?
Results revealed that the bud bank played a key role in regeneration in the plots where the resprouting of herbs was not inhibited by herbicide. In the plots with herbicide treatment, the seed bank was important in re-establishing vegetation after disturbance. Exclusion of the bud bank by using herbicide allowed the establishment of small annuals, whereas biennials were successful in plots where the bud bank was not inhibited. Exotic species with a long residence time in the local flora were successful in plots where regeneration from the bud bank was excluded, whereas species with short residence times or that were invasive were suppressed by both types of disturbance.
We conclude that in response to various types of disturbance, species with different regeneration strategies (either seeds or bud bank) were promoted. Exotic species were suppressed primarily by disturbance, which suggests that factors other than just regenerative capability contributed to the high abundance of exotics in urban communities

Vít Latzel, Stanislav Mihulka & Jitka Klimešová – **Rostlinné vlastnosti a regenerace městských ruderálů po narušení: hraje banka pupenů nějakou roli? ?** Appl Veg Sci (2008) 11: 387-394.

Hlavní otázky této studie byly: Jaká je relativní role banky pupenů, semen a různých rostlinných vlastností při regeneraci ruderálního společenstva po silném narušení? Regenerují po narušení invazní a nepůvodní druhy, které jsou v narušovaných společenstvech velmi hojné, lépe oproti původním druhům?

Výsledky odhalily, že banka pupenů hraje klíčovou roli při regeneraci v plochách, kde nebyla vegetativní regenerace potlačena použitím herbicidu. Naopak vyloučením banky pupenů pomocí herbicidu odhalilo důležitost semen při regeneraci po narušení. Potlačení banky pupenů za pomoci herbicidu umožnilo uchycení drobných jednoletých druhů, zatímco dvouletky byly více úspěšné v plochách, kde banka pupenů nebyla potlačena. Nepůvodní druhy obývající lokální flóru dlouhou dobu byly úspěšné v plochách, kde byla zamezena regenerace z banky pupenů, zatímco druhy s krátkou dobou výskytu nebo invazní druhy byly potlačeny oběma typu narušením.
Uzavíráme, že jsou podporovány druhy s různými regeneračními strategiemi (regenerace ze semen či banky pupenů) v závislosti na typu narušení. Nepůvodní druhy byly potlačeny experimentálním narušením, což naznačuje, že i jiné faktory než právě regenerační schopnost přispívá k jejich vysokému výskytu v městských rostlinných společenstvech.

Chapter 4

Vít Latzel & Jitka Klimešová - **Fitness of resprouters versus seeders in relation to nutrient availability in two *Plantago* species differing by nutrient demands**. Manuscript [Basic and Applied Ecology, under review]

Two contrasting strategies of plants from disturbed areas, resprouters investing to storage and capable of vegetative regeneration after disturbance and seeders investing into seed production and regenerating form seeds, are reported to depend on nutrient availability. While resprouting is predicted to be enhanced in nutrient poor conditions, seeding prevails in nutrient rich conditions. To test this idea we assess fitness of individuals regenerated from seeds and from root fragments in two species with contrasting nutrient demands and hypothesized that 1) plants with higher nutrient demands have higher fitness as seeder without respect to nutrient availability or 2) both species will have higher fitness as resprouter in lower nutrient availability and as seeder in higher nutrient availability. We also manipulated nutrient availability prior and after disturbance. We support the first and rejected the second hypothesis in pot experiment with *Plantago lanceolata*, with high and *Plantago media,* with low nutrient demands. Moreover, high nutrient availability prior the disturbance negatively affected resprouting success, but the growth and fitness of successfully regenerated individuals was enhanced at higher nutrient availability. We concluded that resprouting from roots after disturbance is affected by nutrient availability, however, because the effect considerably differs on individual life-history stages, resulting life history variability might buffer against resprouter/seeder dichotomy up to some threshold of disturbance severity and frequency.

Vít Latzel & Jitka Klimešová – **Reprodukční úspěch jedinců regenerovaných vegetativně oproti jedincům regenerovaných generativně v souvislosti s dostupností živin u dvou druhů jitrocelů lišícími se nároky na živiny.** Rukopis

Dvě kontrastní strategie rostlin narušovaných stanovišť: „respouters“ mající schopnost vegetativně regenerovat po narušení a investující tak do zásobních látek a “seeders” investující do produkce semen z nichž po narušení regenerují, jsou považovány za závislé na dostupnosti živin. Zatímco v živinami chudých podmínkách je předpovídaná výhoda vegetativní regenerace, regenerace ze semen by měla převažovat v živinami bohatých podmínkách. Abychom otestovali tuto hypotézu, stanovili jsme fitness jedinců regenerujících ze semen a z kořenových fragmentů u dvou druhů s kontrastními nároky na živiny. Předpokládali jsme, že 1) druh s vyšším nárokem na živiny má vyšší fitness při regeneraci ze semen bez ohledu na dostupnost živin nebo 2) že oba druhy budou mít vyšší fitness při malé dostupnosti živin pokud regenerují vegetativně a naopak budou mít vyšší fitness v živinami bohatých podmínkách, pokud regenerují ze semen. Dále jsme manipulovali dostupnost živin před i po narušení. V květináčovém experimentu s druhy *Plantago lanceolata* (vysoké nároky na živiny) a *P. media* (malé nároky na živiny) jsme nemohli zamítnout první hypotézu avšak druhou ano. Navíc jsme zjistili, že vysoká hladina živin před narušením negativně ovlivnila regenerační úspěch, avšak růst a fitness úspěšně regenerovaných jedinců byl zvýšen vyšší hladinou živin. Vyvozujeme, že regenerace z kořenů po narušení je ovlivněna hladinou živin, ovšem, protože efekt živin se významně liší mezi jednotlivými životními obdobími rostlin, vyplývající life history variabilita může tlumit dichotomii mezi strategiemi regenerace ze semen a vegetativní regenerace až do určité síly disturbance a frekvence.

Resistance to disturbance: induced defenses

Chapter 5

Sara Gómez, Vít Latzel, Yolanda Verhulst & Josef F. Stuefer - **Costs and benefits of induced resistance in a clonal plant network.** Oecologia (2007) 153: 921–930.

Plant defense theory suggests that inducible resistance has evolved to reduce the costs of constitutive defense expression. To assess the functional and potentially adaptive value of induced resistance it is necessary to quantify the costs and benefits associated with this plastic response. The ecological and evolutionary viability of induced defenses ultimately depends on the long-term balance between advantageous and disadvantageous consequences of defense induction. Stoloniferous plants can use their inter-ramet connections to share resources and signals and to systemically activate defense expression after local herbivory. This network-specific early-warning system may confer clonal plants with potentially high benefits. However, systemic defense induction can also be costly if local herbivory is not followed by a subsequent attack on connected ramets. We found significant costs and benefits of systemic induced resistance by comparing growth and performance of induced and control plants of the stoloniferous herb Trifolium repens in the presence and absence of herbivores.

Sara Gómez, Vít Latzel, Yolanda Verhulst & Josef F. Stuefer – Náklady a výhody indukované obrany u klonální sítě rostlin. Oecologia (2007) 153: 921–930.

Teorie rostlinné obrany předpokládá, že indukovaná obrana se vyvinula v důsledku redukce nákladů běžné u konstitutivní obrany. Pro vyhodnocení funkční a potenciální adaptivní hodnoty indukované obrany je třeba vyhodnotit jak náklady tak i výhody spojenými s plastickou odpovědí. Ekologická a evoluční životaschopnost indukované obrany závisí na dlouhodobé vyváženosti mezi výhodnými a nevýhodnými následky indukované obrany. Oddenkaté rostliny mohou využít propojení jejich ramet a sdílet tak zdroje a signály a tím systémově aktivovat obranné mechanismy po lokálním útoku herbivorů. Tento propojený varovný systém může poskytnout klonálním rostlinám potenciální výhody. Avšak systémová obrana může být také nákladná pokud lokální útok herbivorů není následován útokem na ostatní ramety. Našli jsme průkazné náklady a výhody systémové indukované obrany pomocí srovnání růstu indukovaných a kontrolních rostlin jetele plazivého v přítomnosti a absenci herbivorů.

Chapter 6

Summary of results

The main objectives of this thesis were: (i) interpretating the most used plant attributes considered as relevant to disturbance response of species in man-made habitats and proposing a set of more specific traits, (ii) assessing and comparing the role of resprouting of herbs with other common plant traits in selected man-made habitats, (iii) interpretating the role of nutrient availability in the resprouting and seeding strategy of two related species (*Plantago lanceolata and P. media*), and (iv) evaluating the costs and benefits of resistance to disturbance in the model clonal species *Trifolium repens*.
Each objective has been dealt with in one chapter and a summary is presented in this chapter.

Tolerance to disturbance

Plant functional traits in grasslands

The plant functional traits (PFTs) approach in predicting vegetation responses to disturbance (grazing or mowing) worldwide is discussed in the second chapter. As the predictability of most used PFTs is limited by local environmental factors, we attempt to propose more specific plant traits. We found out that the most frequent PFT used in published literature is plant height. Nonetheless, plant height itself only roughly reflects their functionality in disturbed environments because of the trade-offs between various traits related with height. Therefore, we suggest using particularly leaf and shoot architecture, phenology or ramet life span simultaneously with plant height. This approach should also take into account the mentioned trade-offs between traits and plant height. We also propose to use vegetative regeneration from the bud bank to predict vegetation response to a given disturbance regime, as this persistence trait is largely neglected. Resprouting allows plants to tolerate a broad spectrum of disturbance regimes and could therefore be a good predictor of species response to disturbance, as we demonstrate in the third chapter of this thesis.

The role of resprouting of herbs together with other common plants traits in selected man-made habitats

The inconsiderable role of resprouting in herb regeneration after disturbance (was confirmed by our study of three urban plant communities (Chapter 3). Although these communities consisted predominately of annuals and short-lived perennials, i.e. species regenerating mainly from seeds, resprouting played a significant role here and affected the redevelopment of community dynamics after disturbance. Resprouting from the bud bank was mainly related to annual and biennial species, as perennials were predominantly suppressed by disturbance. The advantage of resprouters over seeders in particular conditions could be observed not only in their fast regrowth after disturbance and finishing their reproductive cycle, but also in their higher competitive ability in comparison with some species that only regenerate from seeds.

Besides resprouting from the bud bank, also forming a permanent seed bank was an attribute of species that were able to successfully regenerate after disturbance. Invasive species, highly abundant in European urban communities, were suppressed by disturbance, which indicates that invasibility of the observed introduced species was facilitated by factors other than their superior regenerative abilities as is usually assumed.

Effect of nutrients on resprouting of two related species

The effect of nutrient availability on resprouting and seeding strategies is dealt with in the fourth chapter. Our results suggest that different allocation strategies of plants with different nutrient demands might result in a dichotomy of seeding/resprouting strategies, as we found that species differing in their nutrient demands also differed in their regenerative strategies. Whereas species with higher nutrient demands were better seeders than resprouters, species with lower nutrient demands were more successful as resprouters than seeders. We also proved that resprouting strategy is affected by nutrient availability both prior and after disturbance, however, responses of different life-history stages differ. The resulting life history variability in reaction to disturbance may reduce the effect of disturbance (varying in severity, frequency and predictability) up to a threshold before the dichotomy of resprouter/seeder strategies is established. At the same time this may be a reason for the versatility of the system and the lack of a simple explanation for the evolution pathways of resprouter/seeder dichotomy in different taxa.

Resistance to disturbance

Induced defence

The last chapter demonstrates that the activation of induced defenses in the clonal species *Trifolium repens* is a beneficial strategy in preventing damages caused by invertebrates. As induced plants suffered considerably less by herbivory than uninduced ones, we proved potential advantage of the induced individuals that correctly respond to triggering signal of herbivore attack. However, we also point at the reverse side of the induced resistance system and demonstrate its drawback in terms of insufficient interpretation of the type and/or intensity of herbivory exposure.

General conclusion

This thesis demonstrates that both tolerance and resistance of plants to disturbance are beneficial strategies in coping with various types of disturbance events in different conditions. We demonstrated that resprouting of herbs after severe disturbance has a considerable impact on redevelopment dynamics of herbaceous communities and is affected by the productivity of the habitat. We pointed out that the invasibility of at least some species is facilitated by other factors than their better regenerative capabilities as compared to native species. We also proved and evaluated the advantages and disadvantages of resistance to disturbance in terms of the induced defence system in the clonal plant *Trifolium repens* and outlined the cost-benefit balance which is necessary to understand the mechanisms in the evolution of induced plant defences.

Prospects for future research

Plants traits are not fixed but conditioned by their genetic variation and evolutionary change. According to recent opinions, plants can actively respond to disturbance or stress not only in circumstances as demonstrated for example in this thesis, i.e. in a morphologic-physiological context, but also in their rapid genetic modification. It has been demonstrated that plants have mechanisms to quickly respond to stress by a „re-arrangement“ of their genetic expression and thus successfully overcome a changed environment not depending on their genetic variability in the sense of the neo-Darwinian theory. This aspect is called the epigenetic phenomenon and thanks to DNA methylation or histone modifications, plants can modify the phenotype very quickly. This aspect is described quite in detail at the level of cell biology, however, the epigenetic factor is still unexplored in the real word. This is a challenge for us and provides us with new targets for future research.

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Curriculum Vitae

Born: 24th January 1978 in České Budějovice, Czech Republic.

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1999-2001: bachelor degree, bachelor work: Response of three Ranunculus species on competition and nutrient enhancement. Supervisor: Prof. Jan Š. Lepš
2001-2004: master degree, diploma thesis: Influence of competition and nutrients to growth of three *Ranunculus* species. Supervisor: Prof. Jan Š. Lepš

Scientific research: bud bank functioning, maternal effect

Stay abroad
2005:Department of Experimental Plant Ecology, Radbout University, Nijmegen, The Netherlands.

Presentation on conferences

Sara Gómez, Vít Latzel, Yolanda Verhulst & Josef F. Stuefer: The importance of being connected. Induced systemic resistance to herbivory in ramets of a clonal plant network. The 13th Symposium on Insect-Plant Relationships (SIP13), Uppsala, Sweden, July 29 – August 2, 2007. Poster. Best Poster Award.

Vít Latzel, Stanislav Mihulka & Jitka Klimešová: The role of the bud bank in disturbed biotopes. The 20th Annual Conference of the Plant Population Biology Section of the Ecological Society of Germany, Switzerland and Austria, 17-19 May 2007, Poster.

Vít Latzel, Stanislav Mihulka & Jitka Klimešová: Plant Functional Traits in a man-Made Habitat.19th Annual conference of the Section Plant Population Biology of the Ecological Society of Germany, Switzerland and Austria. 24 - 27 May 2006 Halle/Saale, Germany, Poster.

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Vít Latzel (2007) Je výhodné být on-line, aneb K čemu je dobrý rostlinám intranet?Vesmír 11: 688.