Applied Vegetation Science 11: 387-394, 2008
doi: 10.3170/2008-7-18487, published online 14 May 2008

Plant traits and regeneration of urban plant communities after disturbance: Does the bud bank play any role?

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Abstract
Questions: 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 in disturbed communities, regenerate better than native species after disturbance?
Methods: Hand tilling was applied to three urban plant communities with and without additional herbicide treatment to exclude regeneration from the bud bank. Plant traits were determined from the literature and databases. Species responses to the treatments were evaluated with RDA analyses in CANOCO. Linear models were applied to identify traits that could predict the responses of species to disturbance.
Results: The bud bank played a key role in regeneration in the plots without 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 and perennials were successful in plots where the bud bank was not inhibited by herbicide. 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.
Conclusion: 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.

Keywords: Community response; Exotic plant species; Functional trait; Man-made habitat; Roundup; Seed bank; Urban flora.

Nomenclature: Dostál (1989).

Abbreviation: RDA = Redundancy Analysis.

Introduction

Frequent disturbances play a major role in shaping plant communities in urban environments. Trampling, vehicular movement and building activities recurrently affect vegetation and, hence, only those species capable of regenerating after repeated disturbance become residents of urban habitats (Benvenuti 2004). While a specific set of regenerative traits is typical for particular crops on arable land due to the characteristic timing of management, soil or climatic factors (Lososová et al. 2006a), the species composition of urban environments may be related to the diverse regeneration strategies of those species (Prach et al. 2001; Lososová et al. 2006b). Here, we advocate that vegetative regeneration may play a role in re-establishing vegetation in urban settings, in addition to contributions from the seed bank and seed dispersal. There are several reasons to expect the participation of the bud bank in regeneration in urban environments including: (1) perennial herbs have below-ground organs bearing stored carbon and buds for spring regeneration and resprouting after disturbance (Klimešová & Klimeš 2003; 2007); (2) short lived species are capable of vegetative regeneration as demonstrated in experiments and in field observations (Martínková et al. 2004a,b; 2006; 2008; Klimešová et al. 2007) and (3) species resprouting from the bud bank (resprouters) are reported in severely disturbed communities (Cruz et al. 2002; Vesk & Westoby 2004; Vesk 2006). Despite the fact that existence of this dichotomy of regenerative strategies has, so far, only been tested for fire prone communities and woody species (Vesk et al. 2004), we can expect similar regeneration responses after disturbance in herbaceous communities.

A combination of several regenerative strategies in one species may act as insurance for surviving an unpredictable disturbance; species with multiple regenerative strategies are more likely to inhabit a variety of environments (Grime 2001). Multiple regeneration strategies might be very useful for invasive exotic species (Tassin et al. 2007; Theoharides & Dukes 2007), which are common in the urban flora. Thus, we make two predictions:

1. The urban plant community contains species which are capable of resprouting from the bud bank after a severe disturbance.

2. Invasive exotic species will increase after disturbance but non-invasive exotics and native species will not increase.

To test these predictions, severe disturbances (hand tilling) were applied during the growing season to mimic disturbances caused, for example, by vehicular movement or construction activities. We compared our treated plots with those which remained undisturbed and those where regeneration from the bud bank after disturbance was inhibited by herbicide application. Two different approaches were used to evaluate the data. In the first case, we directly compared regeneration of species after disturbance with and without the contribution of the bud bank. In the second approach, we tested whether the bud bank can predict a species' percentage cover after experimental disturbance, and if any differences were related to the status of the species as exotic, invasive or native.

Methods

Study area

The study was conducted at three sites in the city of České Budějovice in south Bohemia (Czech Republic). Two study sites were located near the hypermarket Globus (Globus 1: 49°0'10.153" N, 14°26'53.258" E; Globus 2: 48°59'59.008" N, 14°27'5.834" E), while a third study site was situated near the Úsilné neighbourhood (49°0'45.055" N, 14°30'48.938" E). Mean annual temperature of the experimental sites was ca. 8 °C and mean annual precipitation ranged from 800 mm to 1000 mm (Tolasz 2007). The area of each study site was ca. 10 000 m^2. All sites originated as a consequence of construction activities, which have been continuing on these sites for several years. Study sites were chosen carefully according to their similarities in species composition (ca. 80% of species occurred at all sites) and soil type (shallow slate soil with up to 10% stones of ca. 5 cm long). Annuals and short-lived perennials with mainly ruderal or competitive-ruderal life strategies (*sensu* Grime 2001) dominated the vegetation.

Experimental design

Six experimental blocks (3 m × 7 m) were established at each of the three study sites beginning in June 2006. In all blocks, three 1 m × 1 m plots were subjected to different treatments (54 plots). The three treatments included (1) a control without disturbance, (2) tilled, which allowed regeneration from both seeds and bud bank and (3) a tilled/herbicide combination, with regeneration possible only from seeds. For the disturbance treatments, plants were mown and the soil of selected plots was manually dug to a depth of ca. 10 cm. The disturbance resulted in fragmentation of entire plants and their partial burial. Exclusion of regeneration from the bud bank in the tilled/herbicide plots was attained by herbicide application, using a glyphosate solution (Roundup®) one week prior to the disturbance treatment. Roundup is commonly used for the control of a broad spectrum of annual and perennial weeds in various agricultural, industrial and domestic situations (Yu et al. 2007). Glyphosate (N-[phosphonomethyl] glycine) inhibits specific plant enzymes, resulting in reduced production of secondary metabolites and the death of the treated plants (Steinrücken & Amrhein 1980; Schönbrunn et al. 2001).

Vegetation sampling and analysis

Species cover was estimated using a net with a 10 cm × 10 cm mesh to visualize each of the 54 plots before the applied treatments in June 2006 and at the end of the experiment in September 2006.

Species were included in the analysis if they occurred in at least two sites and in three plots at a study site (35 of 47 species). The effect of individual disturbance regimes on overall species abundance was tested with ANOVA (Anon. 2006). Species responses to experimental treatments were evaluated with multivariate methods in CANOCO version 4.5 (ter Braak & Šmilauer 2002). According to the length of the gradient from a preliminary Detrended Correspondence Analysis (DCA), a linear model was used (Redundancy Analysis, RDA). The percentage covers for individual species from all experimental sites were analysed together with the type of experimental site as a co-variable. Percent species covers were log transformed prior to analysis (Lepš & Šmilauer 2003). The statistical significance of the environmental variable (disturbance regime) was evaluated with a Monte Carlo permutation test (499 permutations). The whole variability of species covers at all sites and under all treatments during the experiment (species covers before manipulation and at the end of experiment) was evaluated using PCA.

For evaluating the respective roles of the bud bank and seeds after disturbance, differences in species cover between disturbed plots (tilled and tilled/herbicide treatments) were analysed using pairwise t-tests for dependent samples (Anon. 2006). The compared pairs were plots subjected to the respective disturbance treatments within a block. Effect of study site was not taken into account so there were no more than 18 pairs in each *t*-test.

Table 1. Univariate general linear models for the most relevant traits as single predictors for both treatments. The following traits did not significantly predict species response to disturbance treatments and are not shown including *tap root persistence*, *storage organ presence*, *age of first flowering*, *genet life span*, *Raunkiaer's life forms*, *seed weight, seed size and plant height*. R^2_{adj} is the adjusted R^2; n is the number of species members of a given trait, p-values: * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$; real p-value is shown: $0.05 < p < 0.1$, NS = $p > 0.1$. Response + or – = positive or negative response to soil disturbance

Trait	Category	Tilled/herbicide R^2_{adj}	Tilled/herbicide Response	Tilled/herbicide F	Tilled/herbicide p-value	Tilled R^2_{adj}	Tilled Response	Tilled F	Tilled p-value
Guild	Legumes ($n = 4$)	0.103	-	4.91	*	0	-	0	NS
Canopy structure	Semirosette ($n = 16$)	0.056	+	3.02	0.091	0	+	0	NS
	Height: Small ($n = 18$)	0.080	+	3.95	0.055	0	+	0	NS
C-S-R strategies *sensu* Grime	C ($n = 8$)	0.081	-	4.04	0.053	0	+	0	NS
	CR ($n = 13$)	0.056	+	3.05	0.09	0	+	0	NS
Life cycle	Annuals ($n = 17$)	0.296	+	15.27	***	0.159	+	7.43	**
	Perennials ($n = 15$)	0.297	-	15.36	***	0.189	-	8.93	**
Seed bank longevity	Seed bank: long term ($n = 30$)	0.130	+	6.07	*	0.096	+	4.6	*
	Seed bank: transient ($n = 28$)	0.075	-	3.74	0.062	0	-	0	NS
Fruit/seed type	Silique ($n = 3$)	0.144	+	6.74	*	0.093	+	4.73	*
	Legume ($n = 4$)	0.103	-	4.91	*	0	-	0	NS
	Capsule ($n = 6$)	0	-	0	NS	0.149	-	6.96	0.01
Invasibility	Invasive ($n = 10$)	0.104	-	4.94	*	0.246	-	12.11	**
Residence time	Archeophyte ($n = 16$)	0.095	+	4.58	*	0	+	0	NS
	Neophyte ($n = 4$)	0.088	-	4.28	*	0.068	-	3.99	0.07

Predicting species response by traits

We selected 17 plant traits relevant to regeneration after disturbance (Table 1). Traits were collected from available databases including CloPla (Klimešová & Klimeš 2006), BiolFlor (Klotz et al. 2002) and the "Catalogue of alien plants of the Czech Republic" (Pyšek et al. 2002).

Traits, including quantitative values, were categorized by fuzzy coding to account for species variability for a given trait and to handle similar variables (Pakeman 2004). We also included residence time in the flora and invasive status of species in the analysis. These characteristics, however, cannot be seen as plant functional traits and were analysed separately.

As proxies to the species response to disturbance regime (dependent variables), individual species scores, obtained from the first canonical axis of the previous RDA for the respective disturbance treatment vs control were used. Two regression models were constructed to assess whether some of the traits (independent variables) could predict the response of species to disturbance regime (dependent variables). In the first step, stepwise linear regression was used, in which the trait was included if $P < 0.05$ (Table 2). In the second step, the relevance of each selected trait to the disturbance regime was tested using univariate general linear model analysis (Table 1). See de Bello et al. (2005) for a more detailed explanation of this statistical approach.

Results

Vegetation response

Disturbance regime significantly affected plant species abundance (ANOVA, $F = 58.3$, $p < 0.0001$). The highest mean plant cover was observed in the control plots (mean cover: 21.2%, SE = 0.97), while the lowest mean cover was in plots where plants regenerated only from seeds (mean cover: 8.93%, SE = 0.64). Mean plant cover was intermediate (mean cover: 17.46%, SE = 0.83) in plots with both regeneration strategies. While species composition in control plots and tilled plots (regeneration of plants from the bud bank and seeds) underwent similar changes during the season (the same direction of arrows in the PCA, Fig. 1), plots where

Table 2. Traits that significantly predicted species responses in respect to soil disturbance treatments using stepwise linear regression. For each trait, standardized B-values indicate sign and magnitude of the predicted response to disturbance regime in each treatment separately. In both disturbance treatments, the order in which stepwise regression included the traits into the model is respected. Invasive status and residence time in the flora were evaluated separately and added to the table.

Tilled/herbicide treatment Traits	B	Tilled treatment Traits	B
Legumes	– 0.35	Bud bank; below-ground	0.42
Seed bank: long-term	0.40	Perennial	– 0.71
Perennial	– 0.54	Capsule	– 0.30
Invasive	– 0.42	Invasive	– 0.52
Archeophyte	0.41		

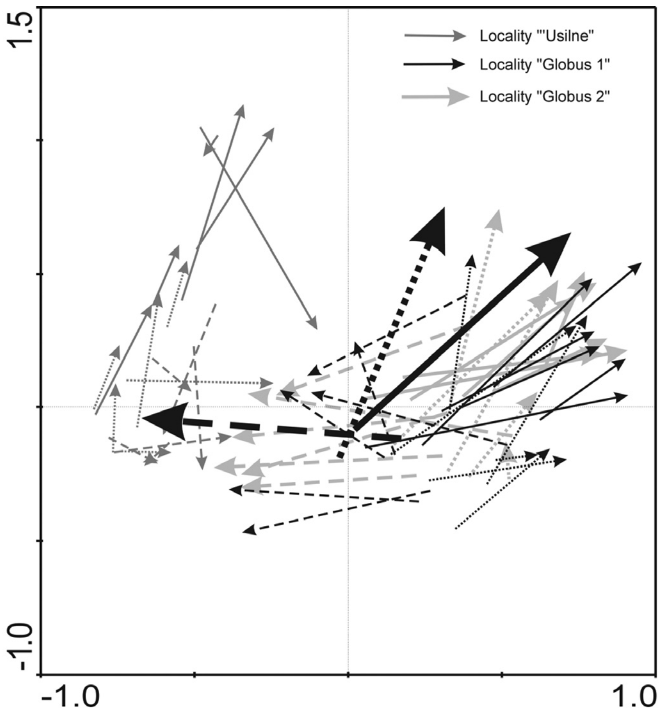

Fig. 1. PCA ordination diagram representing the projection of all plots at all study sites during the experiment in České Budějovice, Czech Republic. Arrows show direction of vegetation change from June 2006 to September 2006 and connect centroids of species composition on the individual plot. Solid arrows = control plots, dashed arrows = tilled/herbicide treatment, stippled arrows = tilled treatment. Highlighted arrows show generalized projection for all treatments and all study sites. Cumulative percentage variance of data set: first and second axis 49.2%.

regeneration from the bud bank was excluded (tilled/herbicide treatment) had arrows in a different direction from other treatments (Fig. 1).

Regeneration of short-lived perennials, such as *Barbarea vulgaris* and *Daucus carota*, increased in the treatment with both seed and bud banks (tilled treatment), while annuals, such as *Tripleurospermum inodorum*, *Erysimum durum* and *Capsella bursa-pastoris*, were successful in the plots where only regeneration from seeds could occur (tilled/herbicide treatment). On the other hand, species such as *Cirsium vulgare*, *Epilobium ciliatum* and *Plantago major* were the most frequent in the control plots (RDA analysis, Fig. 2).

Comparisons between tilled and tilled/herbicide disturbance treatments showed apparent differences in cover of regenerated species as well. *Trifolium hybridum* (t = 5.93, p < 0.0001), *Trifolium repens* (t = 3.31, p = 0.0041), *Polygonum aviculare* (t = 3.36, p = 0.0037), *Daucus carota* (t = 3.04, p = 0.0074) and *Artemisia vulgaris* (t = 3.73, p = 0.0025) were more abundant in tilled plots. On the other hand, *Tripleurospermum inodorum* (t = –2.19, p = 0.0302), *Erysimum durum* (t = –3.91, p = 0.0062) and *Capsella bursa-pastoris* (t = –2.47, p = 0.0251) were more abundant in plots where only regeneration from seeds (tilled/herbicide treatment) was possible (see Fig. 3, t-test for dependent samples).

Plant trait predictive value

A persistent seed bank and a long time residence of exotics in the flora were selected as the best predictive traits of species response for plots where regeneration from the bud bank was excluded (tilled/herbicide treatment; Table 2). On the other hand, perennials, legumes and invasive species were significantly reduced in disturbance treatments.

The presence of a below-ground bud bank was the best predictive trait of species response in the plots where the herbicide was not applied before disturbance (till treatment). Perennials, invasive species and species with capsule fruits had reduced regeneration in those plots (Table 2).

We also analysed the relevance of selected traits to regeneration in relation to disturbance regime for each trait independently (Table 1). Annuals and species with small stature and a persistent seed bank, exotic species with long residence time in the flora and species with a siliqua fruit type responded positively to disturbance when regeneration was only possible from seed (i.e. tilled/herbicide treatment). Invasive species, perennials, legumes and species with a short residence time in the seedbank had lower percentage covers after the tilled/herbicide treatment. In the tilled treatment, annuals, species forming a persistent seed bank and species with a siliqua fruit type had higher percentage covers, while perennials and invasive species had lower percentage covers.

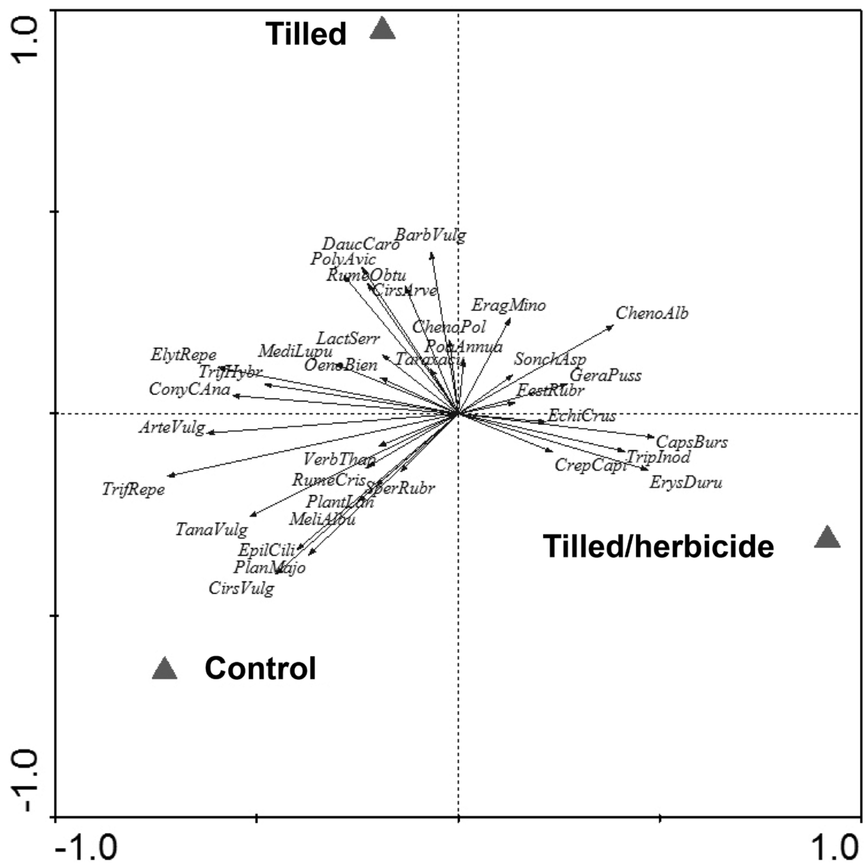

Fig. 2. Ordination diagram showing the result of the RDA based on Canoco for all study sites in České Budějovice, Czech Republic. Trace: 0.213, $F = 6.911$, $p = 0.002$.
Abbreviations of species names: ArteVulg = *Artemisia vulgaris*; BarbVulg = *Barbarea vulgaris*; CapsBurs = *Capsella bursa-pastoris*; CirsArve = *Cirsium arvensis*; CirsVulg = *Cirsium vulgare*; ConyCana = *Conyza canadensis*; CrepCapi = *Crepis capillaris*; DaucCaro = *Daucus carota*; EchiCrus = *Echinochloa crus-galli*; ElytRepe = *Elytrigia repens*; EpiCili = *Epilobium ciliatum*; EragMino = *Eragrostis minor*; ErysDuru = *Erysimum durum*; FestRubr = *Festuca rubra*; GeraPuss = *Geranium pusillum*; ChenoAlb = *Chenopodium album*; ChenoPoly = *Chenopodium polyspermum*; LactSerr = *Lactuca serriola*; MediLupu = *Medicago lupulina*; MeliAlbu = *Melilotus albus*; OenoBien = *Oenothera biennis*; PlanMajo = *Plantago major*; PlanLanc = *Plantago lanceolata*; PoaAnnua = *Poa annua*; PolyAvic = *Polygonum aviculare*; RumeCris = *Rumex crispus*; RumeObtu = *Rumex obtusifolius*; SonchAsp = *Sonchus asper*; SperRubr = *Spergularia rubra*; TanaVulg = *Tanacetum vulgare*; Taraxu: =*Taraxacum* spec.; TrifHybr = *Trifolium hybridum*; TrifRepe = *Trifolium repens*; TripInod = *Tripleurospermum inodorum*; VerbThaps = *Verbascum thapsus*.

Discussion

The nature of the redevelopment of vegetation after disturbance by tillage depends on whether or not herbicide has been applied, because herbicide reduces the relative contribution of vegetative sprouting in comparison to regeneration from seeds. This result from our study supports our prediction that the bud bank plays a role in regeneration of the urban plant community. The bud bank played a role, not only in the vegetative regeneration of perennial species after disturbance, but also in annuals and biennials, e.g. the annual *Polygonum aviculare* and the biennials *Barbarea vulgaris* and *Oenothera biennis*.

Regeneration of small annual species without storage roots was hindered, probably by the fast regeneration of resprouters from the bud bank, e.g. *Tripleurospermum inodorum*, *Erysimum durum* and *Capsella bursa-pastoris* (Fig. 3). Even though annuals are the most common life form in disturbed habitats, because of their faster growth rates compared to perennials (Grime 2001), the relative growth rates of seedlings may differ from those of species resprouting from the bud bank (Klimešová et al. 2008). Therefore, sprouters could have an advantage over seedlings because of stored starch reserves and pre-existing root systems (Loehle 2000). Consistent suppression of

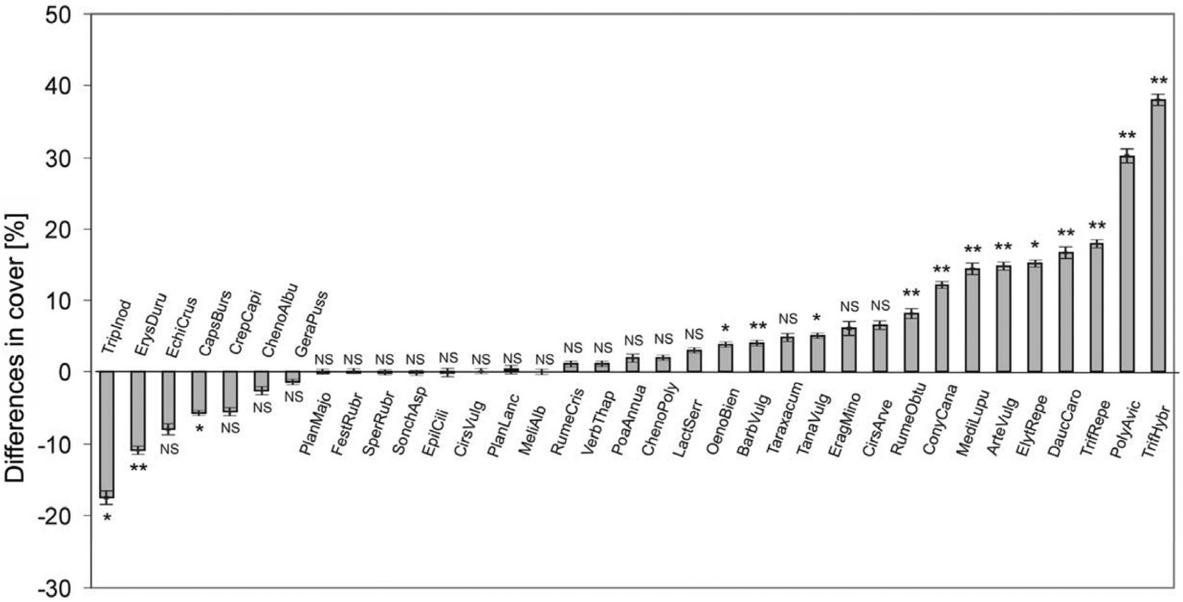

Fig. 3. Differences in mean species cover between till and till/herbicide treatments for all sites in České Budějovice, Czech Republic. Positive values of cover: species formed a higher mean cover on plots with the tilled treatment, values ca. 0: species had the same mean cover in both disturbed treatments, negative values: species had a higher cover in the tilled/herbicide treatment. Differences were analysed by pairwise *T*-test for dependent samples for individual species. Compared pairs were plots subjected to respective disturbance treatments within a block (see Methods). Statistically significant differences based on pairwise comparisons: * = $p < 0.05$; ** = $p < 0.01$; NS = $p > 0.05$.

species regenerating both by seed and vegetative means was also reported in annually disturbed arable fields in northern Colombia (Denslow 1985). Such suppression of seeders might be a consequence of reduced germination caused, for example, by differences in red-far-red light ratio (Rejcan & Swanton 2004) or microclimate because of the alteration of the level of shade in the environment (Aarssen & Epp 1990; McPhee & Aarssen 2001).

Disturbance by either tilling or herbicide suppressed invasive species, contrary to our expectation. Invasive species recorded on our sites were represented mainly by tall competitive species, e.g. *Tanacetum vulgare, Cirsium arvense, Cirsium vulgare* and *Conyza canadensis*, which differ in regenerative strategies from shorter invasive annuals (Hodkinson & Thomson 1997).

Archeophytes, the species resident in the Czech flora before the discovery of America in the 15th century, were the only exotics that were successful in regenerating in disturbed plots where regeneration from the bud bank was excluded. This was probably because archeophytes are often small arable species with a persistent seed bank, which profit from suppressed competition. On the other hand, neophytes are mostly perennial species, which are reduced by both disturbance treatments.

This study demonstrates that sprouting from the bud bank is crucial in severely disturbed, man-made habitats where regeneration from seeds is usually considered the main regeneration strategy. Despite the fact that urban plant communities of central Europe are susceptible to invasions by exotic species, these invasions have probably been facilitated by factors other than superior regenerative abilities as is commonly assumed.

Conclusions

This study shows that vegetative regeneration from the bud bank can play an important role in the re-establishment of vegetation after disturbances in urban environments. The advantage of vegetative regeneration could be seen, not only in the fast re-establishment of these species, but also in the higher competitive ability of these species in comparison to species that regenerate only by seeds. Species that regenerated rapidly after disturbance also tended to be annual species, which were present in the seed bank. A perennial life strategy was characteristic of plant species that responded negatively to disturbance. Invasive species, contrary to our expectations, were suppressed by disturbance, whereas archeophytes regenerated successfully in plots where vegetative resprouting from the bud bank was inhibited. Coexistence of various regenerative strategies in the urban environment is probably indicative of habitats with a variety of disturbances differing in their timing and severity.

Acknowledgements. We are indebted to Francesco de Bello and Beth A. Middleton for comments and to Keith Edwards for language correction. Financial support from the Grant Agency of the Czech Republic (GA206/03/H034, GD206/08/H044, 206/03/P155), Institute of Botany AS CR (AV0Z60050516) and Ministry of the Environment of the Czech Republic (SPII2d1/37/07) is acknowledged.

References

Anon. 2006. *STATISTICA (data analysis software system), version 7.1*. www.statsoft.com. Tulsa, OK, US.

Aarssen, L.W & Epp, G.A. 1990. Neighbour manipulations in natural vegetation: a review. *Journal of Vegetation Science* 1: 13-30.

Benvenuti, S. 2004. Weed dynamics in the Mediterranean urban ecosystem: ecology, biodiversity and management. *Weed Research* 44: 341-354.

Cruz, A., Pérez, B., Quintana, J.R. & Moreno, J.M. 2002. Resprouting in the Mediterranean-type shrub *Erica australis* affected by soil resource availability. *Jounal of Vegetation Science* 13: 641-650.

de Bello, F., Lepš, J. & Sebastia, M.T. 2005. Predictive value of plant traits to grazing along a climatic gradient in the Mediterranean. *Journal of Applied Ecology* 42: 824-833.

Denslow, J.S. 1985. Disturbance-mediated coexistence of species. In: Pickett S.T.A. & White P.S. (eds.) *The ecology of natural disturbance and patch dynamics,* pp. 307-323. Academic Press, San Diego, CA, US.

Dostál, J. 1989. *Nová květena ČSSR*. Academia Press, Praha, CZ.

Grime, J.P. 2001. *Plant strategies, vegetation process, and ecosystem properties*, 2nd. ed. Wiley, Chichester, UK.

Hodkinson, D.J. & Thomson, K. 1997. Plant dispersal: the role of man. *Journal of Applied Ecology* 34: 1484-1496.

Klimešová, J. & Klimeš, L. 2003. Resprouting of herbs in disturbed habitats: is it adequately described by Billingham-Sparrow's model? *Oikos* 103: 225-229.

Klimešová, J. & Klimeš, L. 2006. *CLO-PLA3 – A database of clonal plants in central Europe*. http://www.clopla.butbn.cas.cz [Institute of Botany, AS CR]

Klimešová, J. & Klimeš, L. 2007. Bud banks and their role in vegetative regeneration - A literature review and proposal for simple classification and assessment. *Perspectives in Plant Ecology, Evolution and Systematics* 8: 115-129

Klimešová, J., Sosnová, M. & Martínková, J. 2007. Life-history variation in the short-lived herb *Rorippa palustris*: effect of germination date and injury timing. *Plant Ecology* 189: 237-246.

Klimešová, J., Kociánová, A. & 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: 131-135.

Klotz et al. 2002. BIOLFLOR - Eine Datenbank mit biologisch-ökologischen Merkmalen zur Flora von Deutschland. *Schriftenreihe für Vegetationskunde* 38: 1-334.

Lepš, J. & Šmilauer, P. 2003. *Multivariate analysis of ecological data using CANOCO*. Cambridge University Press, Cambridge, UK.

Loehle, C. 2000. Strategy space and the disturbance spectrum: a life-history model for tree species coexistence. *The American Naturalist* 156: 14-33.

Lososová, Z., Chytrý, M., Cimalová, Š., Otýpková, Z., Pyšek, P. & Tichý, L. 2006a. Classification of weed vegetation of arable land in the Czech Republic and Slovakia. *Folia Geobotanica* 41: 259-273.

Lososová, Z., Chytrý, M., Kühn, I., Hájek, O., Horáková, V., Pyšek, P. & Tichý, L. 2006b. Patterns of plant traits in annual vegetation of man-made habitats in central Europe. *Perspectives in Plant Ecology, Evolution and Systematics* 8: 69-81.

McPhee, Ch.S. & Aarssen, L.W. 2001. The separation of above- and belowground competition in plants. A review and critique of methology. *Plant Ecology* 152: 119-136.

Martínková, J., Klimešová, J. & Mihulka, S. 2004a. Resprouting after disturbance: an experimental study with short-lived monocarpic herbs. *Folia Geobotanica* 39: 1-12.

Martínková, J., Kočvarová, M. & Klimešová, J. 2004b. Resprouting after disturbance in the short-lived herb *Rorippa palustris* (Brassicaceae): an experiment with juveniles. *Acta Oecologia* 25: 143-150.

Martínková, J., Klimešová, J. & Mihulka, S. 2006. Vegetative regeneration of biennial *Oenothera* species after disturbance: Field observations and experiment. *Flora* 201: 287-297.

Martínková, J., Klimešová, J. & Mihulka, S. 2008. Compensation of seed production after severe injury in the short-lived herb *Barbarea vulgaris*. *Basic and Applied Ecology* 9: 44-54.

Pakeman, R.J. 2004. Consistency of plant species and trait responses to grazing along a productivity gradient. A multi-site analysis. *Journal of Ecology* 92: 893-905.

Prach, K., Pyšek, P. & Bastl, M. 2001. Spontaneous vegetation succession in human-disturbed habitats: A pattern across sere. *Applied Vegetation Science* 4: 83-88.

Pyšek, P., Sádlo, J. & Mandák, B. 2002. Catalogue of alien plants of the Czech Republic. *Preslia* 174: 97-186.

Rejcan, I. & Swanton, C. J. 2004. Red-far-red ratio of reflected light: a hypothesis of why early-season weed control is important in corn. *Weed Science* 52: 774-778.

Schönbrunn, E., Eschenburg, S., Shuttleworth, W.A., Schloss, J.V., Amrhein, N., Evans, J.N.S. & Kabsch, W. 2001. Interaction of the herbicide glyphosate with its target enzyme 5-enolpyruvylshikimate 3-phosphate synthase in atomic detail. *Proceedings of theNational Academy of Science of the United States of America* 98: 1376-1380.

Steinrücken, H.C. & Amrhein, N. 1980. The herbicide glyphosate is a potent inhibitor of 5-enolpyruvyl-shikimic acid-3-phosphate synthase. *Biochemical and Biophysical Research Communications* 94: 1207–1212.

ter Braak, C.J.F. & Šmilauer, P. 2002. *CANOCO reference manual and user's guide to Canoco for Windows: software for canonical community ordination (Version 4.5)*. Microcomputer Power, Ithaca, NY, US.

Tassin, J., Riviere, J.N. & Clergeau, P. 2007. Reproductive versus vegetative recruitment of the invasive tree *Schinus terebinthifolius*: Implications for restoration on Reunion

Island. *Restoration Ecology* 15: 412-419.
Theoharides, K.A. & Dukes, J.S. 2007. Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytologist* 176: 256-273.
Tolasz, R. 2007. *Climate atlas of Czechia*. Český hydrometeorologický ústav Olomouc: Univerzita Palackého v Olomouci, Oloumouc, CZ.
Vesk, P.A., Warton, I. & Westoby, M. 2004. Sprouting by semi-arid plants: testing a dichotomy and predictive traits. *Oikos* 107: 72-89.
Vesk, P.A. & Westoby M. 2004. Sprouting ability across diverse disturbances and vegetation types worldwide. *Journal of Ecology* 92: 310-320.
Vesk, P.A. 2006. Plant size and resprouting ability: trading tolerance and avoidance of damage? *Journal of Ecology* 94: 1027-1034.
Yu, Q., Cairns, A. & Powles, S. 2007. Glyphosate, paraquat and ACCase multiple herbicide resistance evolved in a *Lolium rigidum* biotype. *Planta* 225: 499-513.

Received 31 May 2007;
Accepted 11 February 2008;
Co-ordinating Editor: B.A. Middleton.