

Multiple Regenerative Strategies of Short-Lived Species: An Effect on Geographical Distribution, Preference of Human-Made Habitats and Invasive Status

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Abstract It is expected that plant species with multiple regenerative strategies have a wider ecological amplitude and geographical distribution. However there is still an anxious question why species with multiple regenerative strategies are not more frequent. In the presented work we asked whether short-lived plants with a potential bud bank *i)* have a wider geographical distribution, *ii)* occur more frequently in human-made habitats and *iii)* more frequently possess invasive status in comparison with the short-lived species without this additional regenerative strategy. Results show that short-lived plants with a potential bud bank are *i)* more widely geographically distributed, *ii)* under-represented in natural habitats and weakly over-represented in habitats disturbed by human activities and *iii)* contrary to expectation, less numerous among neophytes than species without a potential bud bank. This suggests that short-lived root-sprouters are more habitat-specialized when compared with such plants without adventitious bud-bank formation, but are more widely geographically distributed. A higher frequency of multiple regeneration strategies seems to be restricted by costs of having this ability in habitats or situations without a disturbance regime.

Keywords Disturbance · Multiple regenerative strategies · Phylogenetic independent contrasts · Potential bud bank · Resprouting from roots · Short-lived species

Introduction

A regenerative strategy allows plant species to establish new populations, to maintain its existing ones and to enlarge them. The regenerative strategy allows plant

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individuals to pass on genetic information to the next generation or after injury to its body, regenerate from preserved parts or even multiply from a disintegrated body (Harper 1977; Richards 1986). According to Grime (2001) five types of regenerative strategies are recognizable: vegetative expansion, seasonal regeneration, persistent seeds, numerous wind-dispersed seeds and persistent seedlings. Although trade-offs between regenerative strategies are often observed in a population (Bellingham and Sparrow 2000; Chaloupecká and Lepš 2004; Clarke and Dorji 2008) different regenerative strategies can be mutually compatible (Grime 2001; Mandák and Pyšek 2001a,b; Pausas et al. 2006; Klimešová et al. 2008). Grime (2001) mentions that the multiple regenerative strategies bring about advantages in a variable and unpredictable environment and he asks: “Why then do not more species evolve multiple forms of regeneration?” Consequentially he proposes that it is because some regenerative modes are restricted to certain lineages.

Grime (2001) illustrates his ideas on common perennial species. We found a group of short-lived plants to be equally suitable for testing multiple regenerative strategies hypotheses. Short-lived species represent a clearly defined group of plant species comprising those with and without multiple strategies of regeneration. Multiple regenerative strategies in the short-lived species represent a co-occurrence of *i*) generative regeneration from a seed bank and *ii*) vegetative regeneration by adventitious sprouting from roots and/or hypocotyle (Klimešová 2003; Martínková et al. 2004a,b, 2008; Klimešová and Klimeš 2007; Klimešová et al. 2008; Malíková et al. 2010). In short-lived species, adventitious sprouting from roots plays a key role especially in disturbed habitats (Fig. 1) (Klimešová and Martínková 2004; Martínková et al. 2006) because it may enhance plant colonization capacity in highly disturbed habitats, enable it to persist there or even invade new areas.

In the study we test Grime’s idea that multiple strategies of regeneration enlarge the range of conditions in which regeneration occur and widen the ecological amplitude of the plant. Applying this hypothesis to a model group of short-lived species we test whether root-sprouting enables short-lived plants *i*) to a wider

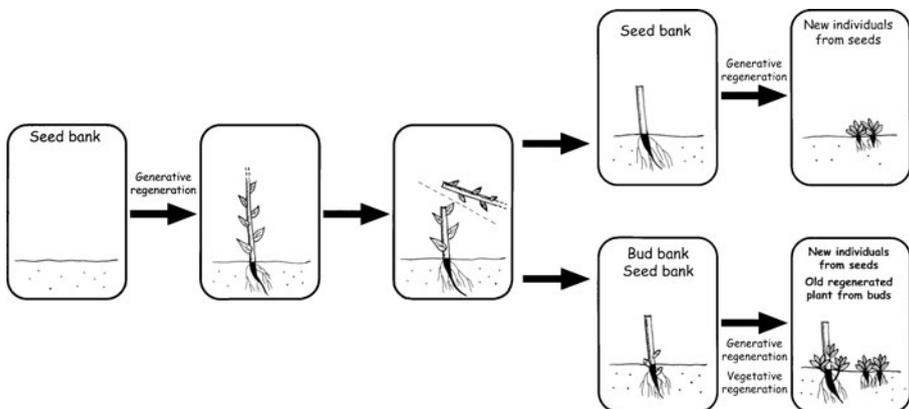


Fig. 1 Diagram comparing regeneration after disturbance of a short-lived species without the ability of resprouting – death of injured individual followed by generative regeneration of population from the seed bank (top pictures) – with a short-lived species with the ability of resprouting – vegetative regeneration of injured individual from the bud bank and generative regeneration of population from seeds (bottom pictures)

geographical distribution, *ii*) to tolerate higher impact of human-made disturbance, and *iii*) to be more common among recently spreading plants (neophytes) in comparison to non-sprouting short-lived plants.

Material and Methods

Short-Lived Species

As a source of plant species for the analyses we selected CLO-PLA3 – a database of plant traits concerning clonal growth and vegetative regeneration of Central European species. (Klimešová and Klimeš 2006). For this study, we selected all species classified in the database as biennials or short-lived perennials. In total, 288 short-lived species were found. In CLO-PLA3 database, 37 of these species were classified as root-sprouters and 240 as not sprouting from roots. The remaining 11 species were classified as unclear cases and were excluded. List of short-lived species acted in the analyses is in the Electronic Supplementary Material 1.

Species Characteristics

To answer questions mentioned in the introduction, we focused on the geographical distribution of short-lived species, their tolerance to a disturbance and invasive behaviour. In the BioFlor database (Klotz et al. 2002), we selected the following three characters, which corresponded to our demands and were available for all 277 short-lived species.

1. **Number of floristic zones** (Kühn and Klotz 2002a). The number of floristic zones in which the species occur is a proxy of the range of geographical distribution and diversity of environmental conditions. In the database nine floristic zones spanning the entire globe are defined: arctic, boreal, northern temperate, southern temperate, submeridional, meridional, subtropical, tropical, austral and/or antarctic.
2. **Hemeroby** (Klotz and Kühn 2002). This system of seven hemerobic levels describes how close to nature or how far away from nature is a vegetation unit where species occur. The advantage of the system is that several levels in which a plant species may occur can be assigned. Thus, one might determine amplitude of hemerobic levels as a surrogate for tolerance to human impacts on vegetation. Values of this characteristic ranges from the lowest grade, used for plants avoiding human-affected habitats, to the highest one, used for plants strongly associated with them. Even if hemeroby seems to carry an element of circular argument, we believe that using such characteristics for studying root-sprouting is fully acceptable. Classification of hemeroby was done without knowing which species is capable of root-sprouting. Hemeroby classification was published in BioFlor (Klotz et al. 2002), and a list of root-sprouting species in CLO-PLA (Klimešová and Klimeš 2006).

Three variables were used for each species: maximum hemeroby – the highest level of hemeroby for the species, minimum hemeroby – the lowest level of hemeroby for the species, and range of hemeroby.

3. **Proportion of neophytes** (Kühn and Klotz 2002b) – after 1500 AD aliens among root-sprouters and not root-sprouting species.

In less than 0.5% of all cases, information on this characteristics was not available. In that case the information was replaced by the mean of all species.

Statistical Analyses

To compare number of floristic zones and hemeroby characteristics between root-sprouting and non-sprouting short-lived species, 1-way ANOVAs were performed. Proportion of neophytes among root-sprouters and non root-sprouting plants was analyzed using a χ^2 test. All statistics were done using STATISTICA version 7.0 (StatSoft, Inc. 2005).

As some traits were inherited from ancestors of extant plants and are not necessarily adaptive in environments inhabited by their descendants today, species are not independent entities. If phylogenetic relationships between species explain the observed variation, then causality of the correlation between the traits is questionable. To remove the effect of phylogeny from the relationship root-sprouting and selected plant traits, we calculated phylogenetically independent contrasts. Instead of directly comparing values of traits among species, contrasts between values obtained for species at individual nodes of the phylogenetic tree are considered (phylogenetically independent contrast – PIC). We used this approach to evaluate the effect of root-sprouting on hemeroby and the number of floristic zones. We used the phylogenetic tree compiled by Durka (2002) as the source of the phylogenetic relationships among species. As root-sprouting was defined as a dichotomous variable, we used the “brunch” procedure (Purvis 1991). This approach assumes that under the null model half of the contrast in indicator values calculated at nodes is positive and half negative, and the mean value of the contrasts is zero (P value in Table 1). Therefore, we used the two-tailed sign test and the one-tailed t-test for testing. The calculations were performed using STATISTICA for Windows, version 7.0, and the CAIC program (Purvis and Rambaut 1995).

To analyze proportion of neophytes among root-sprouters and non root-sprouting plants, only a traditional analysis (TIP) considering individual species as independent entities were used as both variables are dichotomous (see above).

Results

The Number of Floristic Zones

We tested the assumption that root-sprouting plants have a broader tolerance to environmental factors, and consequentially they should be distributed over more floristic zones. In the PIC analysis on a number of floristic zones in which root-sprouting or not root-sprouting species occur, we found that root-sprouting plants are distributed in more floristic zones than plants that do not sprout from roots (number of zones: $P=0.03$, $t=2.8$, $d.f.=27$, $P=0.008$). A traditional analysis without application of PIC did not show this relationship (Table 1).

Table 1 Results of the statistical analyses comparing characteristics of root-sprouting vs non-sprouting short-lived species. Results of analyses (F , P or χ^2), degrees of freedom and P -values are shown. Relation of resprouting vs non-sprouting species is displayed. A. Traditional tests without an application of phylogenetically independent contrast – PIC. B. Tests after application of PIC. Number of neophytes cannot be tested using PIC since variable is dichotomous

Characteristics	F , χ^2 , P	d.f.	P	RS vs non-RS species
A				
Number of floristic zones	$F=2.29$	d.f.=1	$P=0.13$	RS=non-RS
Minimum hemeroby	$F=1.01$	d.f.=1	$P=0.32$	RS=non-RS
Maximum hemeroby	$F=1.14$	d.f.=1	$P=0.29$	RS=non-RS
Range of hemeroby	$F=0.11$	d.f.=1	$P=0.11$	RS=non-RS
Number of neophytes				
With <i>Oenothera</i> spp.	$\chi^2=72.5$	d.f.=1	$P<0.0001$	RS<non-RS
Without <i>Oenothera</i> spp.	$\chi^2=16.5$	d.f.=1	$P<0.0001$	RS<non-RS
B				
Number of floristic zones	$P=0.03$	d.f.=27	$P=0.008$	RS>non-RS
Minimum hemeroby	$P=0.47$	d.f.=27	$P=0.01$	RS<non-RS
Maximum hemeroby	$P=0.5$	d.f.=27	$P=0.07$	RS=non-RS
Range of hemeroby	$P=1$	d.f.=27	$P=0.85$	RS=non-RS

Hemeroby

We tested whether root-sprouting short-lived plants tolerate a wider range of intensity of disturbance caused by human activities than short-lived plants that do not sprout from roots. However on the basis of the PIC as well as TIP analysis we reject this hypothesis (Table 1).

PIC analysis showed that the minimum hemeroby tolerated by short-lived root-sprouting plants was higher than that of plants that do not sprout from roots (minimum hemeroby: $P=0.47$, $t=2.6$, d.f.=27, $P=0.01$) (Table 1). In TIP analysis this relationship was not found (Table 1). This indicates that root-sprouters fail to persist in more natural habitats where disturbance is usually less frequent or less severe, thus their strategy is narrower in this respect.

Maximum hemeroby was not found to be different between root-sprouters and not root-sprouting species in both types of analyses (Table 1).

Proportion of Neophytes

The proportion of neophytes among root-sprouters was 16.7%, the rest of root-sprouters was classified as archeophytes, among herbs not sprouting from roots 37.5% are neophytes. Neophytes were more frequent among short-lived plants not sprouting from roots than in short-lived root-sprouters ($\chi^2=72.5$, d.f.=1, $P<0.0001$) (Table 1). This trend persisted even after the species-rich genus of *Oenothera*, in which root-sprouting is generally poorly known, was removed from the analysis ($\chi^2=16.5$, d.f.=1, $P<0.0001$) (Table 1).

Discussion

Our analyses reveal that short-lived species with an additive mode of regeneration, i.e., root-sprouting, are more widely geographically distributed and therefore tolerate more diverse climatic conditions than other short-lived plants. Short-lived root-sprouters are also under-represented in habitats not affected by humans and under-represented among the neophytes.

Grime (2001) proposed that presence of multiple regenerative strategies enlarge conditions in which regeneration of perennial plant species occur and therefore widen ecological amplitude of such species. He also suggested the advantage of multiple regenerative strategies in a variable and unpredictable environment. On the basis of presented work on the short-lived species, we have to supplement Grime's findings because short-lived species need some specifications especially on ecological niche. The number of floristic zones occupied by short-lived root-sprouters is higher than the number of zones occupied by short-lived plants without root-sprouting ability, however their ecological niche is narrower. The ecological niche of short-lived root-sprouting species is restricted to places with certain affection by human activity, supposedly a specific disturbance regime causing plant injury during the vegetative season (Malíková et al. 2010).

Grime's anxious question "Why then do not more species evolve multiple forms of regeneration?" needs more complex analysis as well. A simple explanation that it is due to restriction of plant lineages evolution seems to be too single-sided. It is true that presence of root-sprouting is concentrated to certain families (Rauh 1937) for example Brassicaceae, Onagraceae, Scrophulariaceae etc., however the presented results indicate that multiple regenerative strategies could not be only beneficial but could bring about costs and thus hinder spread of populations outside certain habitats and also the more common occurrence of the trait among species.

Although multiple regenerative strategies of short-lived monocarps have attracted little attention to date, an analogous system with co-occurring regenerative strategies exists: fire prone areas. At fire-prone areas, except plants regenerating exclusively from seed (seeders), plant species with multiple regenerative strategies occur as well (Midgley 1996). These species survive fire by resprouting from a bud bank and they can also regenerate from seeds. Similarly to our studied short-lived resprouting species, at fire prone areas, resprouters attain a lower stature and are outcompeted by seeders in conditions where disturbance is excluded (Midgley 1996; Bellingham and Sparrow 2000). This points at the existence of certain costs resprouting ability brings about under conditions without disturbance: Species with the ability of resprouting have a lower height, a slower growth and a lower seed production than species without resprouting due to formation of buds and storage of carbon in organs out of reach of a disturbance (Midgley 1996). Although the cost of bud formation is probably negligible (Vesk and Westoby 2004) carbon is stored in below-ground organs at the expense of growth of above-ground biomass (Sosnová and Klimešová 2009). Partitioning of carbon between growth and storage affects the competitive ability of plants and could result in a lower performance and thus also the occurrence of short-lived root-sprouters in undisturbed vegetation.

Our findings also support the theoretical study by Archer and Webb (2006). They found that coexistence of persistence and dispersal strategy, i.e., mixed strategy, is

evolutionary favored only when the acting disturbance is large scale and all individuals in a population are injured. Experimental data with short-lived *Oenothera* spp. support this theory as well (Martínková et al. 2006).

Although our study represents a first insight into the effect of resprouting on niche breadth in the short-lived species, there are other studies evaluating traits of common *versus* rare species, what is an analogy to Grime's question. Overall, literature results suggest that of the traits, regenerative properties of plants, e.g., size and production of seeds, seed bank formation and vegetative regeneration have different context specific effects on plant distribution (Kelly and Woodward 1996; Eriksson and Jakobsson 1998; Murray et al. 2002; Lososová et al. 2008). A positive correlation between ecological niche and geographical distribution is usually found, even though such a comparison is problematic when niche breadth is surrogated by species abundance in a community (e.g., Lososová et al. 2008). In the work by Rey Benayas et al. (1999) where both niche breadth and species abundance were separated, ecological specialists with broad geographical distribution were found. It seems that accurate separation of species distribution and breadth of ecological niche can reveal interesting ecological relationships, not only in the case of short-lived resprouters and multiple regenerative strategies, but also in other ecological questions.

Conclusions

The results indicate that root-sprouting in short-lived herbs occupy more variable climatic conditions, but they are specialists restricted to the communities with a certain disturbance regime probably because bud-bank formation brings about costs and growth reduction when a disturbance event does not come. Higher frequency of multiple regeneration strategies, namely adventitious resprouting and production of seeds, among short-lived plant species seems to be restricted by costs of having this ability in habitats or situations without a disturbance regime.

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