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

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Summary

Weeds of arable land have two strategies for coping with severe disturbance: they have either a very short life cycle and survive disturbance events (ploughing) as seeds or they rely on an underground bud bank and a large regeneration capacity from fragmented roots or stems. Representatives of the respective strategies differ in their investments: annual weeds invest in generative structures and production of easily dispersible or durable seeds, whereas perennial weeds invest preferentially to underground storage organs bearing buds which serve for vegetative propagation. Even when perennial weeds may also produce seeds under favourable conditions, these may serve for further field infestation and spreading. However, the ability of some short-lived annual weeds to regenerate from roots is often overlooked in studies on mechanisms for disturbance survival. Here, we show that short-lived weeds capable of adventitious sprouting from roots may be very successful in vegetative regeneration from root fragments. Using a pot experiment, short-lived root sprouters were found to have higher (*Rorippa palustris*) or the same (*Barbarea vulgaris*) fitness when regenerating from root fragments as when regenerating from seed. Even though this finding needs to be tested on other species and in different experimental settings, the results indicate the potential importance of adventitious sprouting from roots in short-lived plants. Better knowledge of this phenomenon is crucial for understanding both the population dynamics of short-lived root-sprouters in disturbed habitats and the ruderal strategy of plants generally.

Keywords: adventitious buds, annual, biennial, Brassicaceae, disturbance, fitness, resprouting, vegetative regeneration.

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Introduction

Disturbance is an important environmental factor in numerous plant communities and, as such, shapes plant strategies. It is defined as a mechanism, which limits plant biomass by causing its partial or total destruction (Grime, 2001). Disturbance avoidance, characterised by a short life cycle and large seed production, is a typical strategy of plants inhabiting highly disturbed habitats (Bellingham & Sparrow, 2000; Grime, 2001), although there are ecosystems where tolerance to disturbance is an alternative strategy (Noble & Slatyer, 1980; van der Meijden *et al.*, 1988; Barrat-Segretain *et al.*, 1998; Bond & Midgley, 2001; Klimešová & Klimeš, 2003). It is expected that plants tolerating disturbance should have only moderate reduction of fitness after injury (Agrawal, 2000). Cases were reported where grazed plants have higher fitness than ungrazed in several short-lived species (overcompensation) (Paige & Whitham, 1987; Lennartsson *et al.*, 1998; Huhta *et al.*, 2000, 2003; Paige

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et al., 2001) and were interpreted as a mutualism between herbivore and plant. However, the ability of plants to compensate for lost biomass or seed production is constrained by trade-offs with resistance traits, pre-destruction fecundity or competitive ability (Aarssen & Irwin, 1991; Aarssen, 1995; Simons & Johnston, 1999; Strauss & Agrawal, 1999; Rautio *et al.*, 2005) and may be explained solely as a plant response to lost apical dominance.

Experiments studying the response of short-lived plants to herbivory are based on an idea that herbivores leave some plants untouched (Stowe *et al.*, 2000). If grazed plants left more descendants than ungrazed plants, then there is a good chance to spread the ability to resprout into the next generation. However, severe and large-scale disturbances, for example on arable land or in fire prone areas, leave few plants intact. Thus, any seeds produced by surviving plants contribute substantially to the next generation and the ability to resprout may spread in the population. The two opposite strategies, resprouters and seeders, are reported in communities subjected to severe, recurrent disturbance (Vesk & Westoby, 2004). This is in accordance with the model by Achter and Webb (2006), which predicts a mixed regenerative strategy in conditions when a disturbance affects not only the target plant but its neighbours as well. A large-scale disturbance would favour large production of dispersible and/or durable seeds and vegetative regeneration. In fire-prone areas, these strategies are represented by different species, while on arable land, they may be found in one species in perennial weeds. For example, *Cirsium arvense* produces numerous light seeds and can resprout from roots fragments. Here, we wanted to test if the two regenerative strategies may co-exist in a population of short-lived plant species with ability to resprout from roots and produce many light seeds. It was expected that such plants have a higher fitness when regenerating from root fragments than when regenerating from seeds after a disturbance.

To test this idea, an arable field was chosen as a model and two short-lived weedy species, which are capable of producing a high number of seeds as well as regenerating from root fragments, were studied. We asked the question whether the plants would attain a higher fitness (seed production) as resprouters (individuals which survive severe injury) or seeders (individuals which establish from seeds after disturbance).

Methods

Rorippa palustris (L.) Besser and *Barbarea vulgaris* W.T. Aiton were used in the experiment. Both species are from the Brassicaceae family, occurring originally in river banks subjected to disturbance by flooding, which may cause fragmentation of the root system. Secondarily, they are even more common in wet arable fields where disturbance of the root system is also of great importance. They are able to resprout from root fragments, form adventitious buds and roots and survive severe disturbance (Klimešová, 2003). On the other hand, they are supposed to be typical representatives of the ruderal strategy; they produce numerous seeds, have a short life cycle and form a permanent seedbank. *Rorippa palustris* is usually an annual species, even if it may behave as a biennial or short-lived perennial (Klimešová *et al.*, 2004). *Barbarea vulgaris* is usually biennial, but it may be a short-lived perennial as well (MacDonald & Cavers, 1991).

We sampled 10 over-wintering plants of *R. palustris*, 15 one-year-old vegetative rosettes and 15 two-year-old flowering plants of *B. vulgaris* on ruderal localities (South Bohemia, Czech Republic) in April 2003. Seeds were sampled from the same populations in the preceding summer. Plants were kept over night in wet and dark conditions. Root fragments were cut from each plant the following day. Because of the different sizes of the root systems, the number of fragments from individual species differed. In *R. palustris*, roots were cut into four categories: thick/long ($F1$, $>0.5/6$ cm), thick/short ($F2$, $>0.5/3$ cm), thin/long ($F3$, $<0.5/6$ cm) and thin/short ($F4$, $<0.5/3$ cm). Roots of flowering plants of *B. vulgaris* were cut into two size categories: thick ($F1$, $>0.5/3$ cm) and thin ($F2$, $<0.5/3$ cm); only the thin fragments ($F2$, $<0.5/3$ cm) were cut from vegetative rosettes, as a result of the insufficient size of the root system. Fragments were planted separately into containers ($15 \times 15 \times 15$ cm) filled with a mixture of common garden soil and sand (1:5). Fragments were laid horizontally and covered by a 1 cm thick layer of soil mixture. Seeds collected in the same locality were planted (10 replicates) in the same size containers with the same soil mixture.

Plants of *R. palustris* were kept in a glasshouse without temperature regulation and additional light; they were watered regularly. Flowering was induced naturally by prolonging the day. All but five plants fruited during the next 2 months and the experiment was terminated. *Barbarea vulgaris* plants were kept outdoors in a container and watered when needed. Plants were fertilised by tablet fertiliser each 6 weeks and overwintered without additional water supply, nor frost protection. Flowering was induced naturally by cold in the winter. The experiment was terminated the following year, after seeds were matured and plants were still alive. After termination of the experiment, plants were harvested, roots washed and both above-ground and below-ground biomass dried at 80°C for 24 h and then weighed. The number of fruits was then counted.

We used a similar model as that employed by Kelly (1989) to evaluate if an annual strategy is more beneficial than a biennial strategy in short-lived plants with life-history variation. It was expected that the seeder and resprouter strategies will render the same benefit (B-resprouter = B-seeder) when the mean number of seeds produced by the seeder is equal to the mean number of seeds produced by the resprouter × probability of resprouter survival.

Results

Fruit production of plants growing from root fragments and seeds was compared in the pot experiment. In the annual *R. palustris*, fitness was higher in plants regenerating from root fragments than from seeds (Table 1), whereas production of fruits in both types of plants was the same in *B. vulgaris* (Table 2). Because of the low mortality of plants from root fragments in *R. palustris*, and their high seed production, the benefit to resprout was higher in this species than the benefit to establish from seed (B-resprouter = 391; B-seeder = 117; Table 1). On the other hand, there was higher mortality in resprouter, and the seed production of the resprouter was the same as that of the seeder, in *B. vulgaris* and thus the benefit to be a seeder was higher than to be a resprouter (B-resprouter = 104; B-seeder = 150; Table 2).

Discussion

Growth comparisons of plants differing by mode of regeneration (root fragment versus seed) at the time of disturbance revealed that vegetatively regenerating plants can contribute substantially to seed production of the population and its ability to regenerate into the next generation. The adventitious sprouting in these short-lived plants growing on arable land may explain the high infestation of field margins and other ruderal habitats by these species.

Even though our experiment could not elucidate details about the dependence of resprouting on timing of disturbance in relation to life cycle, we have some knowledge from preceding studies. Both species are able to resprout from an age of 6 weeks (Martínková *et al.*, 2004; J. Martínková unpubl. obs.), thus, up to a certain age/size, their population survival is dependent on the seedbank. Later on in ontogeny, the root-sprouting ability of *R. palustris* is higher in the second part of the season than the first part, with a minimum around the summer solstice (Klimešová *et al.*, 2007). The best compensation of seed production in plants of *B. vulgaris* resprouting from roots in comparison with untouched plants was found in over-wintering yet not flowering

Table 1 Growth and fitness parameters of *Rorippa palustris* plants established from root fragments (*F*1–4, *F*) and seeds (*S*) in a pot experiment (mean ± SD)

Rorippa palustris	*F*1 (*n*1 = 10)	*F*2 (*n*1 = 10)	*F*3 (*n*1 = 10)	*F*4 (*n*1 = 10)	*S* (*n*1 = 20)	*F* (*n*1 = 40)	ANOVA
Survival	100% (*n*2 = 10)	90% (*n*2 = 9)	100% (*n*2 = 10)	80% (*n*2 = 8)	100% (*n*2 = 20)	92.5% (*n*2 = 37)	–
Below-ground biomass	0.575 ± 0.163	0.438 ± 0.148	0.260 ± 0.123	0.351 ± 0.112	0.192 ± 0.075	0.408 ± 0.180	***
Above-ground biomass.	2.981 ± 0.918	2.151 ± 0.480	1.273 ± 0.385	1.138 ± 0.513	0.770 ± 0.305	1.919 ± 0.964	***
Root/shoot ratio	0.198 ± 0.055	0.207 ± 0.064	0.222 ± 0.125	0.399 ± 0.362	0.258 ± 0.064	0.250 ± 0.181	NS
Number of fruits	708.403 ± 225.572	464.778 ± 150.093	292.300 ± 116.504	226.000 ± 132.634	117.950 ± 105.876	432.379 ± 246.744	***
Number of fruits/biomass	225.235 ± 38.332	220.754 ± 71.407	225.467 ± 53.435	202.982 ± 64.031	139.553 ± 98.464	219.396 ± 55.602	**
Survival × number of fruits	672.6	376.47	292.3	144.64	117.95	391	–

Comparison of all plants from root fragments irrespective of size (*F*) and number of seeds (*S*) were tested by ANOVA and results are shown in last column of the table (data for numbers of fruits/biomass were log (x + 1) transformed). ANOVA: $^{**}P < 0.01$; $^{***}P < 0.001$; NS, $P > 0.05$; –, not tested. Number of plants in treatment: *n*1, number of replications; *n*2, number of surviving plants.

Table 2 Growth and fitness parameters of *Barbarea vulgaris* plants established from root fragments (*F*1, *F*2, *F*) and seeds (*S*) in a pot experiment (mean ± SD)

Barbarea vulgaris	*F*1 (*n*1 = 15)	*F*2 (*n*1 = 15)	*S* (*n*1 = 15)	*F* (*n*1 = 30)	ANOVA
Survival	26.7% (*n*2 = 4)	73.3% (*n*2 = 11)	86.7% (*n*2 = 13)	50% (*n*2 = 15)	
Below-ground biomass	2.061 ± 0.605	2.513 ± 0.662	1.660 ± 0.630	2.392 ± 0.659	*
Above-ground biomass	3.138 ± 0.273	4.203 ± 1.246	3.322 ± 1.493	3.919 ± 1.167	NS
Root/shoot ratio	0.668 ± 0.239	0.617 ± 0.152	0.521 ± 0.078	0.631 ± 0.171	*
Number of fruits	174.500 ± 31.932	221.455 ± 62.305	173.308 ± 70.028	208.933 ± 58.764	NS
Number of fruits/biomass	55.49 ± 7.48	53.67 ± 10.48	54.06 ± 8.22	54.152 ± 9.550	NS
Survival × mean number of fruits	46.59	162.32	150.25	104.46	–

Comparison of all plants from root fragments irrespective of age of injured plants (*F*) and seeds (*S*) were tested by ANOVA and results are shown in last column of the table (data for numbers of fruits/biomass were log (x + 1) transformed). ANOVA: *$P < 0.05$; NS, $P > 0.05$; –, not tested. Number of plants in treatment: *n*1, number of replications; *n*2, number of surviving plants.

plants, in comparison with earlier or latter phenological stages (Martínková *et al.*, 2007).

Germination is possible throughout the season in both species (Grime *et al.*, 1988; MacDonald & Cavers, 1991); however, it is probably more sensitive to moisture, light and temperature fluctuations than vegetative regeneration. On the other hand, the seedbank is much richer than the bud bank in both species (Klimešová *et al.*, 2004). Also, the question of repeated disturbance remains unsolved: is a seeder with a storage tap-root more successful in regenerating than a resprouter with a bunch of slender adventitious roots?

Despite many unsolved questions, it is clear that some short-lived root sprouters possess a unique strategy of coping with disturbance. Adventitious buds do not fit into the bet hedging strategy, which is expected for axillary buds. According to this, axillary buds have three possible fates: flowering, branching or dormancy (Bonser & Aarssen, 1996). On the other hand, adventitious buds may be considered as rescue buds activated or even formed *de novo* only after severe injury (potential bud bank; Klimešová & Klimeš, 2007). In the studied species, they are not used for flowering or branching until the plants are severely disturbed. They enable not only survival after severe injury, but guarantee high seed production, which is necessary for the long-term survival of populations of monocarpic species.

The ability to regenerate vegetatively in short-lived species should be taken into account when considering the ruderal strategy of plants inhabiting disturbed habitats, such as arable fields, as it is more widespread in short-lived monocarpic plants than previously thought. The list of short-lived plants resprouting adventitiously from roots in the central European flora is given in Table 3 (source CLO-PLA3, Klimešová & Klimeš, 2006) and includes 23 species which deserve our attention to test if their weedy status is not affected by the ability to sprout adventitiously.

Table 3 Monocarpic plants resprouting adventitiously from roots in the Central European flora (Klimešová & Klimeš, 2006)

Species	Family	Weedy status	Life history
Alliaria petiolata	*Brassicaceae*	Envir	*b*, *p*
Anchusa officinalis	*Boraginaceae*	Envir	*a*, *b*, *p*
Arabis hirsuta	*Brassicaceae*		*b*, *p*
Arabis turrita	*Brassicaceae*		*b*, *p*
Barbarea vulgaris	*Brassicaceae*	Envir	*b*, *p*
Barbarea stricta	*Brassicaceae*	Envir	*b*
Brassica oleracea	*Brassicaceae*	Arable, envir	*a*, *b*, *p*
Cnidium dubium	*Apiaceae*		*b*
Diplotaxis muralis	*Brassicaceae*	Arable, envir	*b*
Isatis tinctoria	*Brassicaceae*	Envir	*b*, *p*
Jasione montana	*Campanulaceae*		*b*, *p*
Knautia arvensis	*Dipsacaceae*	Arable, envir	*b*, *p*
Medicago lupulina	*Fabaceae*	Arable	*a*, *b*
Oenothera biennis	*Onagraceae*	Envir	*b*
Oenothera issleri	*Onagraceae*	Envir	*b*
Orobanche caryophyllacea	*Orobanchaceae*		*b*, *p*
Orobanche flava	*Orobanchaceae*		*b*, *p*
Orobanche minor	*Orobanchaceae*	Arable	*b*, *p*
Picris hieracioides	*Asteraceae*	Envir	*b*, *p*
Reseda lutea	*Resedaceaea*	Envir	*b*, *p*
Rorippa palustris	*Brassicaceae*	Arable, envir	*a*, *b*
Scabiosa columbaria	*Dipsacaceae*		*b*, *p*
Senecio jacobaea	*Asteraceae*	Envir	*b*, *p*

Weedy status: envir, environmental weed; arable, weed on arable land; life history: *a*, annual; *b*, biennial; *p*, perennial, according to different sources.

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