

Annuals sprouting adventitiously from the hypocotyl: their compensatory growth and implications for weed management

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Abstract: Habitats, disturbed severely at least once a year, are often dominated by annual plants, which avoid disturbance by means of a short life span and massive production of seeds. Contrary to perennials, they lack pools of reserve meristems and storage carbon in below-ground organs necessary for vegetative regeneration after disturbance. However, some annuals are able to initiate a bud bank on the hypocotyl after loss of their shoot.

In three experiments, we investigated how the timing of disturbance or population origin affects adventitious bud formation on the hypocotyl for regeneration and compensatory growth in some annual weeds.

The best regenerative abilities were observed in *Kickxia spuria* and *K. elatine*, with 87% and 80% of individuals regenerating, respectively, followed by *Microrrhinum minus* with almost 70%. Less than 30% of individuals regenerated in *Euphorbia peplus* and *Anagallis arvensis*. The time of injury did not affect the regeneration capacity of species for which the timing was examined, nor their consequent compensatory growth.

The best compensation for biomass and fruit production was observed in *M. minus*, albeit two populations differed in this respect. The injured plants were shorter and produced more shoots than intact plants. Mechanical control of weeds capable of forming adventitious buds on hypocotyl by harrowing, brushing, or cutting may not be sufficient in organically farmed lands.

Key words: bud bank; disturbance; hypocotyl; vegetative regeneration; weed control

Introduction

Disturbance events are common in most habitats, and occur over a range of intensities and frequencies (Noble & Slatyer 1980; White & Pickett 1985; Spooner 2005). On highly productive, severely and regularly disturbed biotopes, for example arable fields, annual species are more common than perennials or biennials (Bellingham & Sparrow 2000). Since annuals neither possess storage assimilates or buds near the ground or below ground neither traits necessary for vegetative regeneration after loss of aboveground biomass, population survival after damage relies mainly on regeneration from seeds produced between the disturbance events (Grime 2001).

However, many annuals are able to tolerate moderate disturbance and, in some species, injured plants may have a higher fitness than intact plants. Increased fitness following injury is referred to as overcompensation. Vigorous branching after loss of apical dominance may be one mechanism responsible for overcompensation (Paige & Whithman 1987; Maschinski & Whithman 1989; Bergelson & Crawley 1992; Aarssen 1995;

Lehtilä & Syrjänen 1995; Bergelson & Purrington 1996; Lennartsson et al. 1997; 1998; Huhta et al. 2000, 2003; Hellström et al. 2004). Compensatory growth could also be facilitated by an increase of net photosynthetic activity (Whitfield et al. 1980; Trumble et al. 1993; Thomson et al. 2003) as well as a change in resource allocation from roots to shoots (McNaughton 1983; Stafford 1989; Trumble et al. 1993).

When disturbance is severe and results in loss of all above ground organs, only those annuals that are capable of adventitious sprouting from otherwise meristemless roots and/or hypocotyl may potentially survive. However, the ability of annuals to form buds de novo and regenerate vegetatively from them was not sufficiently studied to evaluate its potential role in the weediness of such species. The few experiments done so far were focused predominantly on regeneration of *Rorippa palustris* from root fragments (Martínková et al. 2004a,b, 2006, 2008; Klimešová et al. 2007) or *Linum usitatissimum* and *Euphorbia geniculata* from the hypocotyl (Adams 1924; Crooks 1933; Rauh 1937; Eggers 1946; Link & Eggers 1946; Kigel et al. 1992;

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Ishikawa et al. 1997). Experiments with *Rorippa palustris* found that plants that regenerated from root fragments can finish their life cycle and even produce more seeds than plants regenerating from seeds (Klimešová et al. 2008). Moreover, most of the above-mentioned studies evaluating adventitious bud formation on the hypocotyl dealt mainly with anatomy and histology and did not evaluate the consequences for the life history of plants.

To fill this lack of information about the role of hypocotyl resprouting in annuals, three experiments were established on weedy species common in Central Europe known to form adventitious buds on the hypocotyl (*Kickxia elatine*, *K. spuria*, *Anagallis arvensis*, *Euphorbia peplus* and *Microrrhinum minus*; Klimešová 2003, Klimešová & Klimeš 2006, 2008) with the aim to answer the following questions: 1) Does adventitious sprouting from the hypocotyl enable completion of the life cycle? 2) How are biomass and seed production of regenerated plants affected in comparison with intact plants (compensation/overcompensation)? 3) Does disturbance timing affect resprouting and compensation? 4) Is there variation among populations in resprouting and compensatory growth? 5) What are the implications for weed management?

Methods

The study consisted of three parts, all carried out in a cultivation chamber. In the first part, regeneration and compensation of *Kickxia elatine* and *K. spuria* were examined, while in the second and third parts, differences in regeneration and compensatory growth between populations were examined for *Euphorbia peplus*, *Anagallis arvensis* and *Microrrhinum minus*. All plants were planted in pots with 9 cm in diameter and 7 cm depth, filled with a mixture of soil and bare sand at a ratio of 2:3. Plants were fertilized every 40 days by standard fertilizer (ASB Grünland; nutrients per plant: nitrogen – 0.025 g, phosphorus – 0.015 g, kalium – 0.0175 g). Temperature and light conditions were controlled: both *Kickxia* species were cultivated at a mean temperature of 22°C/12°C (day/night), with the other species at a mean temperature of 22°C/20°C (day/night). Light conditions were maintained at a 14h/10h (light/dark) photoperiod. The mean air humidity was regulated at 70%.

Experiment 1: *Kickxia elatine* and *K. spuria*

Seeds of both species were collected from a natural population around Řitovice, central Bohemia. Seeds were stratified for three weeks at 4°C before sowing.

Three cohorts were established for both species. Seeds were sown in 10-day intervals, and each cohort consisted of 10 individuals. Plants from each cohort were divided into two groups: five individuals were treated, five served as a control.

All treated plants were injured (aerial tissue excised below the cotyledons) at the same time: the youngest cohort consisted of 10 day old plants, while the oldest cohort was 30 days old at the time of injury. All plants were in vegetative phase at the time of injury. The experiment was terminated 160 days after excision.

Experiment 2: *Euphorbia peplus* and *Anagallis arvensis*

Seeds of three populations of *E. peplus* and *A. arvensis* were collected from the urban habitats of Mladá Boleslav,

Kněžnice u Jíčina and Kopidno (*E. peplus*) and České Budějovice, Kopidno and Zliv (*A. arvensis*), the Czech Republic. For every population, seeds were collected at least from 20 plant individuals. Seeds were stratified for three weeks at 4°C temperature prior to planting. Twenty individuals of each population were divided into two groups: ten were excised below the cotyledons 30 days after germination, and ten untreated plants served as controls. All plants were in the vegetative stage at the time of injury. The experiment was terminated 143 days after excision.

Experiment 3: *Microrrhinum minus*

Seeds of two populations of *M. minus* were collected, one from České Budějovice and the other from Tábor, the Czech Republic. Plants of the first population were collected from an urban habitat with infrequent disturbance, while plants of the second population were from an industrial locality that was regularly disturbed. For every population, seeds were collected at least from 20 plant individuals. Sixty individuals from each population were divided into two groups: half of them were treated, and half were kept as a control. Treated plants were divided into groups of ten individuals and excised below the cotyledons at 20, 35, and 50 days after germination respectively. Plants belonging to the oldest cohort were flowering; the youngest plants were in the vegetative stage at the time of injury. The experiment was terminated 152 days after excision, and all measurements described below were taken.

Measured characteristics

The following plant characteristics were assessed in the experiments: the amount of initial (excised) biomass for all treated plants, the number of regenerating individuals, stem length (the main stem for untreated plants, the longest adventitious shoot for treated plants), number of branches (all axillary branches of untreated plants, all adventitious shoots emerged from the hypocotyl of treated plants), length of the longest branch (*K. spuria* and *K. elatine*), the number of flowers and fruits, shoot biomass, and root biomass (for *Kickxia* and *Microrrhinum*). Biomass was expressed as oven-dry weight (dried at 80°C for 24 hrs). The quantity of seeds of every plant of both *Kickxia* species was estimated from the number of fruits for an individual plant multiplied by the mean number of seeds per fruit. This number was obtained by averaging the number of seeds of three fruits for every harvested plant. Examination of seed weight and germinability was done only for *K. elatine*, since only this species produced sufficient numbers of seeds for testing. Three replications of 20 stratified seeds per plant were placed on moist filter paper in petri dishes for three weeks; the number of germinated seeds was recorded daily.

Statistical analyses

The impact on regeneration capacity of treated plants from the various populations or cohorts, and of the initial biomass, was evaluated by ANOVA in Generalized Linear Models with a binomial distribution (regenerated: yes/no). The effect of plant size at the moment of injury on subsequent regrowth and reproduction was evaluated by regressions. The effect of cohort or population for control plants or the effect of injury for lumped cohorts and populations in *Kickxia elatine*, *K. spuria*, *E. peplus* and *A. arvensis* (first and second experiment) were analyzed by one-way ANOVA. The effect of population and treatment in *M. minus* (third experiment) was analyzed by two-way ANOVA. All statistical analyses were performed using STATISTICA 7.

Table 1. Comparisons of growth and reproductive characteristics of intact and excised plants of *K. elatine* and *K. spuria*. Mean values and standard errors are shown. P-values: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns $p > 0.1$; N/A not available.

Attribute	<i>Kickxia elatine</i>			<i>Kickxia spuria</i>		
	Injury	Control	P	Injury	Control	P
Length of the stem [cm]	75.5 ± 7.6	72.7 ± 6.8	ns	27.0 ± 5.7	53.8 ± 5.4	***
Length of the longest branch	38.2 ± 7.8	61.2 ± 7	*	14.4 ± 2.2	26.1 ± 2.2	***
Number of branches	2.4 ± 0.62	6.4 ± 0.56	***	0.6 ± 0.24	1.9 ± 0.2	***
Root biomass [g]	0.34 ± 0.04	0.49 ± 0.04	*	0.21 ± 0.039	0.39 ± 0.037	***
Shoot biomass [g]	0.83 ± 0.13	1.8 ± 0.12	***	0.53 ± 0.11	1.55 ± 0.10	***
Total biomass [g]	1.18 ± 0.17	2.35 ± 0.15	***	0.74 ± 0.14	1.94 ± 0.13	***
R/S biomass	0.42 ± 0.019	0.27 ± 0.017	***	0.3 ± 0.038	0.26 ± 0.036	ns
Flowers	8.58 ± 5.67	35.69 ± 5.07	***	9.62 ± 3.48	30.93 ± 3.35	***
Fruits	17.7 ± 3.13	23.4 ± 2.8	***	0.62 ± 0.95	7.86 ± 0.92	***
Fruits + Flowers	26.25 ± 4.45	59.09 ± 4	***	10.24 ± 3.65	38.82 ± 3.5	***
Seeds per fruit	12.59 ± 1.03	12.8 ± 0.92	ns	9.7 ± 1.23	16.5 ± 1.18	***
Seeds per plant	233 ± 55.7	317 ± 49.8	ns	6.38 ± 1.5	145 ± 22.7	***
Seed weight [g]	0.0252 ± 0.014	0.0337 ± 0.012	ns	N/A	N/A	N/A
Seed germinability [%]	71.3 ± 5.6	74.3 ± 5.3	ns	N/A	N/A	N/A

Results

Experiment 1: *Kickxia elatine* and *K. spuria*

Kickxia elatine

80% of individuals regenerated after excision. Plant age ($p = 1$, Wald stat. = 0) and amount of initial above ground biomass ($p = 0.99$, Wald stat. = 0.001) did not affect regeneration.

Comparisons of cohorts of undisturbed (control) plants revealed that individuals of different ages varied only in the length of the stem and the longest branch, with older individuals having longer stems and branches ($p = 0.0033$, $F = 9.53$). No significant differences were observed in the other measured criteria. Consequently, plants had similar trends in growth and reproduction between cohorts in individual treatments. Since some cohorts consisted of less than 5 regenerated individuals and no differences between cohorts were found, further analysis was done on the cumulative dataset and treated plants from all cohorts were summarized in one group. Regenerated plants had shorter and fewer branches, produced fewer flowers, fruits, and biomass, and had a higher root-to-shoot ratio than intact plants (Table 1). Seed weight, number of seeds per fruit or plant and seed germinability did not differ between regenerated and control plants. Thus, plants from the studied population were not able to compensate for biomass loss but compensated in terms of seed production.

Kickxia spuria

87% of the individuals regenerated after injury. Neither plant age ($p = 0.999$, Wald stat. = 0.00004), nor amount of initial above-ground biomass ($p = 0.999$, Wald stat. = 0.00013) affected the regeneration capacity of the treated individuals.

Intact plants from different cohorts did not differ in any of the measured criteria and therefore, as for *K. elatine*, we grouped treated individuals from all cohorts together prior to analysis (Table 1).

Regenerated individuals of *K. spuria* were smaller, produced less biomass, fewer and shorter branches, fewer flowers, fruits and seeds per fruit and per plant than control plants. Regenerated plants had the same RS ratio as intact individuals. Thus, plants from the studied population were not able to compensate either for biomass loss or seed production.

Experiment 2: *Euphorbia peplus* and *Anagallis arvensis*

Euphorbia peplus

Comparisons of intact plants from different populations revealed no differences in any of the measured criteria (data not shown). Differences in regeneration capacity of treated plants between populations were also not found ($p = 0.14$, Wald stat. = 3.89). As there were no differences, we grouped all treated individuals prior to analysis of compensation.

27% of the treated individuals regenerated from the hypocotyl. The amount of initial biomass did not significantly affect regeneration capacity ($p = 0.75$, Wald stat. = 0.56), however, it altered the subsequent fruit production: the greater the initial biomass, the lower the fruit production ($p = 0.033$, $R^2_{adj} = 0.56$). Regenerated plants created fewer branches, fruits and above ground biomass in comparison with intact plants, but they had longer stems and produced more flowers (Table 2). Injured plants were not able to compensate for biomass or seed production.

Anagallis arvensis

Comparisons of intact plants from different populations revealed no differences in any of the measured criteria (data not shown). Differences in regeneration capacity between populations were not found ($p = 0.84$, Wald stat. = 0.34). As for *Euphorbia peplus*, treated individuals from all populations were grouped prior to analysis of compensation.

30% of the treated individuals regenerated from the hypocotyl. The amount of initial biomass did not significantly affect regeneration, neither the capacity of

Table 2. Comparisons of growth and reproductive characteristics of intact and excised plants of *E. peplus* and *A. arvensis*. Mean values and standard errors are shown. P-values: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns $p > 0.1$.

Attribute	<i>Euphorbia peplus</i>			<i>Anagallis arvensis</i>		
	Injury	Control	P	Injury	Control	P
Length of the stem [cm]	11.63 ± 0.48	9.97 ± 0.25	**	15.8 ± 2.77	43.1 ± 1.43	***
Number of branches	4.5 ± 1.17	11.85 ± 0.6	***	4.11 ± 0.82	7.0 ± 0.68	*
Shoot biomass [g]	0.36 ± 0.17	1.19 ± 0.087	***	0.27 ± 0.23	1.76 ± 0.11	***
Flowers	43.4 ± 8.78	3.07 ± 4.53	***	4.88 ± 2.16	8.43 ± 1.17	Ns
Fruits	31.25 ± 15.7	131.37 ± 8.1	***	6 ± 9.35	71.8 ± 4.8	***
Fruits + Flowers	74.63 ± 18.69	134.43 ± 9.65	***	10.88 ± 9.36	80.23 ± 4.8	***

Table 3. Comparisons of growth and reproductive characteristics of intact and excised plants between populations of *M. minus*. Two-way ANOVA, mean values and standard errors are shown. P-values: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; real value is shown: 0.05 < $p < 0.1$; ns $p > 0.1$.

Attribute	Population 1		Population 2		Population effect	Treatment effect	Pop x Treatment effect
	Injury	Control	Injury	Control	P-level	P-level	P-level
Length of the stem [cm]	34.36 ± 1.03	41.25 ± 1.49	35.3 ± 0.99	36.8 ± 1.48	Ns	**	*
Number of branches	4.2 ± 0.56	7.4 ± 0.8	4.6 ± 0.38	5.0 ± 0.56	0.097	**	*
Root biomass [g]	0.062 ± 0.007	0.048 ± 0.009	0.055 ± 0.015	0.023 ± 0.022	Ns	ns	ns
Shoot biomass [g]	0.819 ± 0.056	0.99 ± 0.082	0.757 ± 0.046	0.603 ± 0.069	**	ns	*
Total biomass [g]	1.02 ± 0.07	1.19 ± 0.1	0.812 ± 0.07	0.653 ± 0.11	*	ns	ns
R/S biomass	0.075 ± 0.006	0.047 ± 0.009	0.072 ± 0.018	0.038 ± 0.027	Ns	0.064	ns
Flowers	77.14 ± 7.06	60.6 ± 10.23	43.65 ± 4.13	26.0 ± 6.16	***	*	ns
Fruits	61.9 ± 6.28	76.5 ± 9.09	52.6 ± 6.04	46.7 ± 9.0	*	ns	ns
Fruits + Flowers	139.1 ± 11.9	137.1 ± 17.2	96.25 ± 7.81	72.7 ± 11.64	***	ns	ns
Fruit biomass [g]	0.140 ± 0.013	0.158 ± 0.019	0.142 ± 0.046	0.233 ± 0.068	Ns	ns	ns

treated individuals ($p = 0.91$, Wald stat. = 0.17) nor their consequent growth and reproduction (analyses not shown). Regenerated individuals had shorter stems, less above ground biomass, and fewer flowers and fruits (Table 2) than control plants. Thus, injured plants were not able to compensate for biomass or seed production.

Experiment 3: *Microrrhinum minus*

Microrrhinum minus

No differences were observed for regeneration capacity between populations: 67% from the first population and 70% of the individuals of the second population regenerated, respectively ($p = 0.7814$, Wald stat. = 0.08). The timing of treatment affected only the number of branches in the first population: branching was the highest in plants injured 50 days after germination and the lowest in plants treated 10 days after germination ($p = 0.0062$, $F = 5.16$). However, final biomass production was similar between these groups ($p = 0.31$, $F = 1.23$).

Intact plants differed between populations: plants from the first population produced greater biomass than plants from the second population (Table 3). The initial biomass was greater for plants treated 50 days after germination, while lowest for the youngest (10 days after germination) in both populations (pop.1: $p = 0.00011$, $F = 13.012$, pop. 2: $p = 0.00002$, $F = 17.226$). Although the amount of initial biomass

did not affect the regenerative capacity of treated plants (pop.1: $p = 0.4874$, Wald stat. = 2.4331 pop.2: $p = 0.9603$, Wald stat. = 0.2981), larger plants at the moment of injury (without consideration of disturbance timing) from the first population produced more above ground biomass ($p = 0.03$, R^2 adj = 0.2244), below ground biomass ($p = 0.011$, R^2 adj = 0.2928), and total biomass ($p = 0.021$, R^2 adj = 0.25102542) following regeneration. Also, greater initial biomass was associated with increased branch number in the second population ($p = 0.048$, R^2 adj = 0.2).

Since the timing of injury did not affect the regenerative ability of plants from both populations and had only a significant effect on subsequent branching of the first population and no direct effect on biomass production, we grouped regenerated individuals from all excision times together for individual populations (first group: 20 individuals from the first population, second group: 21 individuals from the second population). Analyses of interaction between both population and treatment effect revealed that individuals differed in responses to excision (Table 3). Regenerated individuals from the first population compensated for biomass loss after injury, whereas treated individuals from the second population overcompensated for biomass loss (see Fig. 1a). Populations differed in response to treatment in the length of the stem (Fig. 1b) and the number of branches (Fig. 1c). Analysis of branch number (Table 3) revealed that

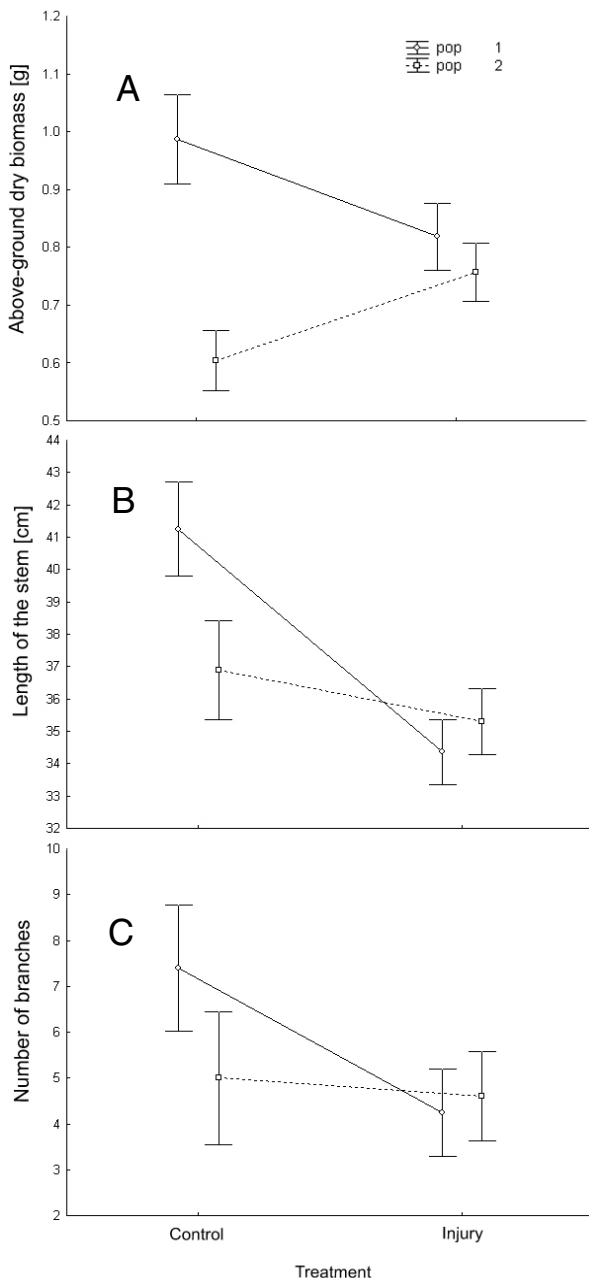


Fig. 1. Average values and standard deviations for growth characteristics of control and injured plants from two populations of *Microrrhinum minus*. A – shoot biomass; B – length of the stem; C – number of branches.

treated plants created fewer branches than control plants.

Individuals from the first population had lower growth than individuals of the second population after injury. Nevertheless, a similar compensatory growth was found for the production of flowers and fruits for both populations.

Discussion

It seems likely that (over)compensatory growth after damage of some annuals can occur even when disturbance removes all axillary buds, if the disturbance oc-

curs in the beginning of the growing season, which might allow plants to finish their life cycle. Differing compensatory growth of *M. minus* plants from various population indicated that (over)compensation could vary between populations depending on their disturbance history.

Injury timing

Kickxia elatine and *K. spuria* species had the greatest regenerative abilities with 80% and 87% of individuals regenerating, respectively, followed by *Microrrhinum minus* with almost 70% regeneration. The worst regeneration from the hypocotyl was recorded for *Euphorbia peplus* and *Anagallis arvensis* species, with only 30% regeneration.

Surprisingly, no age effect on regeneration was observed in the experiments, even when the age of seedlings varied between 10 and 30 days (or 50 days for *M. minus*). Data in the literature are contradictory: histological observations showed a decreased ability of the hypocotyl to produce epidermal buds from the beginning of its growth up to 60 day old plants of *Linum usitatissimum* (Link & Eggers 1946). Ecological observations of resprouting ability, on the other hand, showed increasing production of hypocotyl buds after excision of the primary shoot in *Euphorbia geniculata* (Kigel et al. 1992).

It seems that decreasing ability to form exogenous adventitious buds on the hypocotyl does not hinder regeneration. Moreover, older plants have the advantage of larger size, a bigger root system and larger amount of storage compounds.

Even the switch between vegetative and generative growth seems not to decrease the resprouting abilities of the studied annuals as the oldest injured plants of *M. minus* were already flowering. This is due to the fact that all of the studied plants may be considered as iteroparous annuals sensu Harper (1977). They start to produce flowers very early in ontogeny and in favourable conditions their shoots continue to grow and produce additional shoot modules consisting of an internode, node and leaf subtending either a side branch or flower. Such endless (unterminated) growth in the chamber room was also responsible for the fact that injured plants were delayed in phenology in comparison with control plants. A harvest in an arable field, similarly as in the experiments, would terminate the growth of plants prior to senescence caused by the end of the season.

Compensatory growth and differences among populations

A higher number of branches was observed in intact plants than regenerated individuals; branching was responsible for (over)compensation in *M. minus*. This was caused by the fact that branches of intact plants (axillary branches of the primary stem) were shorter than branches of treated individuals (adventitious shoots resprouting from the hypocotyl). Most studies demonstrating compensation also refer to vigorous branch-

ing (from axillary meristems) after tissue removal as a mechanism (Benner 1988; Maschinski & Whitham 1989; Lennartsson et al. 1997, 1998; Huhta et al. 2000) and overcompensation as a mere byproduct of reduced apical dominance (Aarssen 1995; Bergelson & Crawley 1992; Paige 1994; Huhta et al. 2003).

Due to the small regeneration abilities of *E. pepplus* and *A. arvensis*, we were only able to evaluate the effect of population origin on regeneration for *M. minus*. Overcompensating individuals of *M. minus* from the habitat with high and predictable disturbance events were of smaller stature and more branched. Smaller plants could reduce the risk of high biomass loss after disturbance without affecting their competitive ability and overcompensatory re-growth relative to that of the population from a habitat with less regular disturbances.

Lennartsson et al. (1997) found that plants of *Gentianella campestris* from localities varying by disturbance history also differed in their compensatory growth. They deduced that overcompensation is an adaptive trait that has an evolutionary history related to habitats with a high and predictable risk of damage (Lennartsson et al. 1997).

Implications for weed management

In Europe, the studied species predominantly occupy root crop communities and ruderal habitats. Regeneration from seeds after disturbance is the main strategy in such communities (Grime 2001). However, as we demonstrated, some plants can regenerate vegetatively as well. This previously overlooked life-history trait surely has an effect on plant population structure and dynamics (Klimešová & Klimeš 2003, 2007). For example, on organically farmed lands, weed control is usually carried out mechanically, by harrowing, rotary cultivation, or brushing (Rasmussen & Ascard 1996). Nevertheless, such control may not be effective, particularly early in the growing season, if there are weeds capable of vegetative regeneration. Relative growth rates of seedlings may differ from that of plants resprouting from the bud bank, as sprouters could have a competitive advantage over seedlings due to stored starch reserves and an existing root system (Loehle 2000; Latzel et al. 2008). Even sparse weed cover can negatively alter crop growth by impacting the red-far-red ratio perceived by the crop (Rejcan & Swanton 2004). Consistent suppression of generatively regenerating plants by those regenerated vegetatively has been reported in annually disturbed arable fields in northern Colombia (Denslow 1985) and in urban plant communities (Latzel et al. 2008). Thus, weeds regenerating from the hypocotyl could negatively affect the growth of crops on fields even where the suggested control cut height of 5 cm (Andreasen et al. 2002) is used.

On the other hand, our results came from a chamber experiment where conditions for plant growth were ideal. Growth of a weed is influenced by the crop as well and shading was found to reduce adventitious bud formation on the hypocotyl of *Linum usitatissimum*

(Eggers 1946). Thus, the necessary next step in understanding the weedy status of adventitiously sprouting annuals is to examine their growth in the field.

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