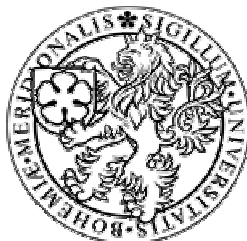


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Adventitious sprouting of short-lived plants in natural populations

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PhD. Thesis

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Annotation

Disturbance is one of most important selective factor causing removal of plant biomass. Man-made habitats are characterized by strong and unpredictable disturbances, providing bare soil surface colonized by plants with short life cycle. Populations of the short-lived plants are, however, vulnerable to the strong disturbance removing all stem parts with reserve axillary meristems in the case it occurs before plant flowering and fruiting. Nevertheless, 2 % of annual and 14 % of biennial plants are able to overcome meristem limitation by adventitious sprouting from hypocotyle or/and roots.

This thesis is composed of four original studies describing the occurrence of adventitious sprouting in natural populations of 22 monocarpic weeds of Central Europe and one species in Indonesia. The studied phenomenon was analyzed in relation to various environmental factors and plant traits in the field and in experimental conditions.

Prohlašuji, že svoji disertační práci jsem vypracoval/a samostatně pouze s použitím pramenů a literatury uvedených v seznamu citované literatury.

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5.8.2011


Lenka Malíková

Author contribution statement

Lenka Malíková, author of this PhD thesis, participated on developing methodology used for data collection, collected almost all basic data and contributed by substantial part in writing.

All co-authors hereby consent to the including of the papers in the PhD thesis of Lenka Malíková.

Prohlašuji, že Lenka Malíková se podílela na spoluautorství následujících článků:

Occurrence of adventitious sprouting in short-lived monocarpic herbs: field study of 22 weedy species

Malíková L., Šmilauer P., Klimešová J. (2010) *Annals of Botany* 105 (6): 905-912.

- Sběr dat a jejich příprava pro statistické zpracování, podíl na psaní textu.

Does potential bank increase tolerance of short lived plant to apical meristem damage?

Klimešová J., Malíková L., Šmilauer P. [manuscript]

- Sběr dat a jejich příprava pro statistické zpracování, podíl na psaní textu.

Compensatory growth of *Euphorbia peplus* regenerating from a bud bank

Latzel V., Malíková L., Klimešová J. (2011) *Botany* 89(5): 313-321.

- Sběr dat v terénu, sběr semen pro experiment.

The invasive annual herb *Euphorbia geniculata* is able to regenerate after severe disturbance by adventitious sprouting

Malíková L., Mudrák O., Klimešová J. (submitted)

- Sběr dat v terénu a provedení nádobového experimentu, příprava dat pro statistické zpracování, hlavní podíl na psaní textu.

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Co-author statement

I would like to confirm that as a co-author of two research papers of Lenka Malíková – *Occurrence of adventitious sprouting in short-lived monocarpic herbs* (that appeared in *Annals of Botany*) and *Does potential bud bank increase the tolerance of short-lived plants to apical meristem damage* (in manuscript), I have contributed with the analysis of collected data. But the definition of sampling design, data collection and transcription, as well as the preparation of manuscripts were done by the other authors.

10 August 2011



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Co-author statement

I would like to confirm that as a co-author of research paper of Lenka Malíková – *The invasive annual herb Euphorbia geniculata is able to regenerate after severe disturbance by adventitious sprouting* (in manuscript), I have contributed with the analysis of collected data. But the definition of sampling design, data collection and transcription, as well as the preparation of manuscripts were done by the other authors.

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I hereby declare that Lenka Malíková substantially contributed to our manuscript “Compensatory growth of *Euphorbia peplus* regenerating from a bud bank” published in the Botany – Botanique. The manuscript is based on the field data of several populations of *E. peplus* collected by Lenka Malíková. Lenka Malíková also significantly contributed to evaluating the data and preparing the manuscript for publication.

I consider her contribution as crucial.



Vít Latzel

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České Budějovice, 30th June 2010


Lenka Malíková

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CHAPTER I

GENERAL INTRODUCTION

DISTURBANCE IN MAN-MADE HABITATS AND PLANT STRATEGIES

Agricultural weeds can be considered as products of human driven evolution as a consequence of anthropogenic disturbance and weed management (Harper 1977). Crop management is very variable mainly due to different crop's demands. Because established fields usually exist for limited period, hence, any adaptation of plants observed in this system can be considered as very fast in relation to truly natural ecosystems.

Man-made habitats are generally characterized by high frequency of severe disturbances. Bare surface of ground is colonized by less competitively successful species (annuals, biennials and short-lived perennials) (Harper 1977; Klemow and Raynal 1983; Löfgren et al. 2000; Grime 2001). Their survival is enabled by large production of seeds and finishing of life cycle between two consecutive disturbances (Harper 1977; Crawley 1986; van der Meijden et al. 1992; Grime 2001). Typical characteristics are small size, high fecundity, short life-span, early onset of maturity and semelopary (Stearns 1992).

Contrary to total damage of plant cover, in the case plant parts remain preserved, plants regenerate vegetatively from bud bank (Korsmo 1930; Wehsarg 1954; Kutschera 1960; Hamdoun 1972; Sosnová 2003). Vegetative regeneration affects biomass production, fecundity, growth form, time of flowering and lifespan of a plant (Kästner et Karrer 1995; Krumbiegel 1998, 1999). Success of tissue renewal is defined by position and utilization of axillary buds (Bellingham and Sparrow 2000; Huhta 2003; Klimešová and Klimeš 2003). Therefore, most disturbance tolerant species are perennial herbs with below-ground organs of stem origin (rhizomes, stolons). On the contrary, most sensitive plants to disturbance are species without underground or basal axillary buds as erosulate annuals and single stemmed trees (Huhta et al. 2003).

Therefore we can conclude that disturbance causes changes in species composition in a community in favor of short-lived species. The short-lived species, however, are more prone to next disturbance event coming sooner than they finish life cycle as they do not form bud bank and regenerate only from seeds (Grime 2001).

ADVENTITIOUSLY SPROUTING SPECIES IN MAN-MADE HABITATS

Inability of short-lived plants to tolerate severe disturbance, however, can be overcome by about 2 % of annual and 14 % biennial species, which are able to regenerate adventitiously by resprouting from the hypocotyl or roots (Table 1, Klimešová et al. 2008). Since roots are growing deeper in the soil than stolons or tubers, adventitious sprouting species have one of most effective mechanism of regeneration after strong disturbance interfering not only aboveground parts of plant, but also upper layer of soil (Klimešová 2003).

Moreover, numerous species are even able to compensate or overcompensate biomass loss and increase fitness in comparison with untouched individuals (Huhta et al. 2003). Meristems kept in dormant state by apical dominance were considered to have bet hedging strategy: in order to provide plant with insurance for one herbivore attack the buds are dormant to be activated by injury (Tuomi et al. 1994; Nilsson et al. 1996). However, overcompensation can be also explained as a side product of apical dominance which enables height growth at the expense of branching under competition (Aarssen 1995).

Compensation ability in biomass production and fitness was usually studied in experimental conditions as comparison of untouched and disturbed plants. Although experiments with short-lived plants lacking ability to form adventitious sprouts from roots or hypocotyle find out that the plants are able to tolerate only low damage (Aarssen 1995; Lennartsson et al. 1997, 1998; Huhta et al. 2000a, 2000b, 2003; Hellström et al. 2004). Manipulations with adventitious sprouters (Martínková et al. 2004, 2008) revealed in experiments that the plants having ability to form adventitious buds on roots are able to overcome meristem limitation, survive severe disturbance and even overcompensate biomass or seed production.

Similarly as success of vegetative regeneration due to axillary branching after damage (Ferraro and Osterheld 2002; Wise and Abrahamson 2007) also adventitious sprouting is affected by environmental factors. Important factors influencing resprouting are: 1. ontogenetical stage of plant and injured part of plant - younger sterile plants are able to regenerate more successfully than flowering and fruiting individuals (Dubart 1903; Klimešová 2003; Martínková et al 2004). 2. soil compaction – apical dominancy prevail in dry and compacted soil, growth of lateral axillar buds and adventitious buds is more tricky (Kutschera and Lichtenegger 1992). 3. nutrient level – resprouting is supported in nutrient poor conditions (Latzel et al. 2009). 4. Timing of injury in the season in relation to day length and carbon storage (Klimešová et al. 2007; Sosnová and Klimešová 2009).

Adventitious sprouting is neglected phenomenon even when it is known by morphologists already for long time (Wydler 1850; Wittrock 1884; Rauh 1938) and studied in manipulative pot experiments by our working group (Klimešová 2003; Martínková et al. 2004; Klimešová et al. 2008; Martínková et al. 2008; Latzel et al. 2009). The occurrence of adventitious sprouting in natural populations of short-lived monocarps and its dependence on extrinsic and intrinsic factors is not known similarly as a relative role of axillary and adventitious bud banks in short-lived species. My theses were designed to contribute to those two areas.

Table 1. List of monocarpic species able to resprout adventitiously from roots and/hypocotyle according to Klimešová 2003.

Life form (a-annual, b-biennial, p-perennial); localization of buds on plant (1-hypocotyle, 2-main root, 3-lateral and adventitious roots); origin (nat-original, ar-archeophyt, species appeared in Europe until 1500 of this epoch, neo-species appeared after 1500 of this epoch, ornam-ornamental species; source (1-Rauh 1937; 2-Beijerick 1887; 3-Korsmo 1930; 4-Kutschera and Lichtenegger 1992; 5-Rothmaler 1988; 6-Reichardt 1857; 7-Wittrock 1884; 8-Dubard 1903; 9-Wehsarg 1954; 10-Irmish 1857; 11-Jäger, pers.com.; 12-Martínková; pers.com.; 13-pers.obs. +-yes, --no, ?-missing data, !-apophyt (original species of Czech flora retailing secondary habitats).

Species	Family	Life-form	Adventitious roots	Spontaneous sprouting	Localization of buds	Origin	Spreading	Resource
<i>Alliaria petiolata</i>	Brassicaceae	a,b,p	-	+	1,2	Nat	+!	1,2,13
<i>Anagallis arvensis</i>	Primulaceae	A	-	+	1,2	Ar	+	1
<i>Anchusa officinalis</i>	Boraginaceae	a,b,p	-	-	2	Ar	+	3
<i>Antirrhinum majus</i>	Scrophulariaceae	A,p	-	+	1	Neo	-	1
<i>Arabis hirsuta</i>	Brassicaceae	B,p	-	+	3	Nat	+!	4
<i>Arabis turrata</i>	Brassicaceae	B,p	+	+	3	Nat	-	5
<i>Barbarea vulgaris</i>	Brassicaceae	B,p	+	-	2,3	Nat	+!	1,3,13
<i>Brassica oleracea</i>	Brassicaceae	a,b,p	-	+	3	Ar	-	2
<i>Centaurium littorale</i>	Gentianaceae	B	+	?	?	Neo	-	7
<i>Cnidium dubium</i>	Apiaceae	B	-	+	3	Nat	-	4
<i>Cymbalaria muralis</i>	Scrophulariaceae	B	-	-	1	Ar	-	1
<i>Diploxys muralis</i>	Brassicaceae	B	-	-	2	Ar	+	1
<i>Isatis tinctoria</i>	Brassicaceae	B,p	-	-	2	Ar	+	8
<i>Jasione montana</i>	Campanulaceae	B	-	-	2	Nat	-	11
<i>Kickxia spuria</i>	Scrophulariaceae	A	-	+	1	Ar	-	1
<i>Kickxia elatine</i>	Scrophulariaceae	A	-	+	1	Ar	-	1
<i>Knautia arvensis</i>	Dipsacaceae	B,p	+	+	2	Nat	+!	3,9
<i>Linaria alpina</i>	Scrophulariaceae	P	-	+	+	orn	-	1
<i>Linaria arvensis</i>	Scrophulariaceae	A	-	+	1	Ar	-	10
<i>Linaria maroccana</i>	Scrophulariaceae	B	-	+	1	Neo	-	1
<i>Linaria purpurea</i>	Scrophulariaceae	P	-	+	1	orn	-	1
<i>Linum usitatissimum</i>	Linaceae	A	-	-	1	Ar	-	1
<i>Medicago lupulina</i>	Fabaceae	A,b	-	+	1,2	Ar	+	6
<i>Mirroredrhinum minus</i>	Scrophulariaceae	A	-	+	1	Ar	+	1
<i>Misopates orontium</i>	Scrophulariaceae	A	-	+	1	Ar	-	1
<i>Oenothera biennis</i>	Onagraceae	B	-	-	2	Neo	+	1,12
<i>Oenothera issleri</i>	Onagraceae	B	-	-	2	Neo	-	12
<i>Orobanche</i>	Orobanchaceae	B,p	-	+	1,3	Nat	-	2
<i>Orobanche caryophyllacea</i>	Orobanchaceae	B,p	-	+	1,3	Nat	-	1
<i>Orobanche flava</i>	Orobanchaceae	B,p	-	+	1	Nat	-	1
<i>Orobanche hederæ</i>	Orobanchaceae	B,p	+	+	1,3	Neo	-	1
<i>Orobanche minor</i>	Orobanchaceae	B,p	+	+	1,3	Neo	-	1
<i>Picris hieracioides</i>	Asteraceae	B,p	-	+	2,3	Nat	-	2,4
<i>Reseda lutea</i>	Resedaceae	B,p	-	+	1,2,3	Ar	+	1,2
<i>Rorippa palustris</i>	Brassicaceae	A,b	+	+	2,3	Nat	+!	13
<i>Scabiosa columbaria</i>	Dipsacaceae	B,p	+	+	2	Nat	-	7
<i>Scabiosa ochroleuca</i>	Dipsacaceae	B,p	+	+	1	Nat	-	7
<i>Senecio jacobaea</i>	Asteraceae	B,p	+	-	2,3	Nat	-	10
<i>Tithymalus exiguus</i>	Euphorbiaceae	B	-	+	1	Ar	+	1
<i>Tithymalus lathyris</i>	Euphorbiaceae	a,b,p	-	+	1	Neo	-	1
<i>Tithymalus peplus</i>	Euphorbiaceae	B	-	+	1	Ar	+	1

AIMS AND OUTLINES OF THESIS

Consequently, the main aims of this thesis are to answer following questions:

1. How often does adventitious sprouting occur in natural populations on species known to have this ability? **(STUDY I)**

2. Which growth characteristics (plant height, number of branches, phenology) and environmental factors (disturbance, nutrient level, moisture, illumination) support regeneration by adventitious sprouting in studied species? **(STUDY I)**

3. Is adventitious sprouting more often in biennial than in annuals? **(STUDY I)**

4. How is the occurrence of adventitious sprouting in plants with reduced apical dominance plants in environment of low competition comparison to prostrate growth forms? **(STUDY I)**

5. What are respective roles of axillary branching and adventitious sprouting after damage of different intensity? **(STUDY II)**

6. Does the resprouting differ among species and populations in field or in experiment? **(STUDY III and IV)**

METHODS

FIELD SURVEY

Monocarpic short-lived herbs that were reported as being capable of adventitious sprouting from the hypocotyle and/or roots were studied in the field (Table 2 in different habitats and environmental conditions mainly in the Czech Republic (Central Europe) from 2005 to 2007 **(STUDY I, II, III)**). Additional to this data collection, invasive tropical weed *Euphorbia geniculata* reported as capable to produce adventitious buds on hypocotyle was studied from 2007 to 2009 in Indonesia (Bali, Java, Sumatra, and the Nias islands) **(STUDY IV)**.

The aim to assess the morphology in at least 30 natural populations per species and at least 20 plants individuals per population was not fulfilled in some rare species (see Table 2). Measured plant traits were as follows: plant height, base width, number of axillary branches, cumulative length of adventitious shoots, length of the longest adventitious shoot, number of adventitious buds, number of adventitious shoots. A disturbance was assessed as an injured or removed main shoot, while phenology was assessed as the main phenological stages (i.e. vegetative, flowering, fruiting).

Communities where sufficient numbers of individuals of a target species occurred were described using phytosociological relevés (van der Maarel 1979). Thus, we also have the following community characteristics: total vegetation cover, cover of individual species and species richness. Species composition was not studied in Indonesia due to difficulties with plant determination. Soil compaction was determined in the field, other environmental characteristics were assessed using Ellenberg indicator values for light, temperature, humidity and nitrogen (Ellenberg 1988).

POT EXPERIMENTS

A pot experiments (**STUDY III and IV**) were performed in a growth chamber at the Institute of Botany ASCR in Třeboň, Czech Republic with controlled climatic conditions. Seeds collected from natural populations examined in field survey were germinated on pure sand in Petri dishes and than planted in pots. Plants were watered regularly, and each pot was fertilized by a fertilizer tablet. Half of plants from each population were injured by clipping when they were in the vegetative stage, having only cotyledonary leaves (**STUDY III and IV**) and after period of vegetative growth (**STUDY III**) the growth of plants was followed until final harvest.

Table 2. List of the 22 studied species with their status in the flora of the Czech Republic, number of sampled populations and total number of sampled and injured individuals during field seasons 2005 and 2006.

Species	Family	Growth form in annual	number of sampled populations	number of sampled individuals	number of injured individuals
Annuals					
<i>Anagallis arvensis</i> L.	Primulaceae	Prostrate	30	1114	78
<i>Arabidopsis thaliana</i> (L.) Heynh.	Brassicaceae	Upright	30	1121	66
<i>Euphorbia exigua</i> L.	Euphorbiaceae	Upright	6	208	33
<i>Euphorbia helioscopia</i> L.	Euphorbiaceae	Upright	30	1085	86
<i>Euphorbia peplus</i> L.	Euphorbiaceae	Upright	31	1407	191
<i>Kickxia spuria</i> (L.) Dumort.	Scrophulariaceae	Prostrate	3	61	0
<i>Kickxia elatine</i> (L.) Dumort.	Scrophulariaceae	Prostrate	2	71	0
<i>Microrrhinum minus</i> (L.) Fourr.	Scrophulariaceae	Upright	31	1257	53
Biennials					
<i>Arabis glabra</i> (L.) Bernh.	Brassicaceae		6	176	13
<i>Arabis hirsute</i> (L.) Scop. <i>sensu stricto</i>	Brassicaceae		2	68	31
<i>Alliaria petiolata</i> (M. Bieb.) Avara et Grande	Brassicaceae		27	993	73
<i>Barbarea vulgaris</i> W.T. Aiton	Brassicaceae		31	1112	12
<i>Barbarea stricta</i> Andrz.	Brassicaceae		10	339	4
<i>Daucus carota</i> L.	Apiaceae		35	1074	162
<i>Diplotaxis muralis</i> (L.) DC.	Brassicaceae		1	30	0
<i>Isatis tinctoria</i> L.	Brassicaceae		2	40	13
<i>Jasione montana</i> L.	Campanulaceae		5	176	1
<i>Medicago lupulina</i> L.	Fabaceae		29	1090	87
<i>Potentilla supina</i> L.	Rosaceae		30	1029	26
<i>Reseda lutea</i> L.	Resedaceae		15	448	28
<i>Reseda luteola</i> L.	Resedaceae		1	20	0
<i>Rorippa palustris</i> (L.) Besser	Brassicaceae		32	1118	45

REFERENCES

- Aarssen LW (1995) Hypotheses for the evolution of apical dominance in plants: implications for the interpretation of overcompensation. *Oikos* 74:149–156
- Beijerinck MW (1887) Wurzelknospen und Nebenwurzeln. *Verhandelingen der Koninklijke Akademie van Wetenschappen* 25(3):1–150.
- Bellingham PJ, Sparrow AD (2000) Resprouting as a life history strategy in plant communities. *Oikos* 98:409–416.
- Dubard M (1903) Recherches sur les plantes a bourgeons radicaux. *Annales des Science Naturalles – Botanique et Biologie Vegetale* 17:109-125.

- Crawley MJ (1986) Plant ecology. Blackwell. Oxford.
- Ellenberg H (1986) Vegetation ecology of central Europe, 4th edn. Cambridge: Cambridge University Press.
- Ferraro DO, Oesterheld M (2002) Effect of defoliation on grass growth. A quantitative review. *Oikos* 98:125–133.
- Grime JP (2001) Plant strategies, vegetation processes and ecosystem properties. John Wiley et Sons, Chichester.
- Hamdoun AM (1972) Regenerative capacity of root fragments of *Cirsium arvense*. *Weed Research* 12:128-136.
- Harper JL (1977) Population biology of plants. Academic Press, London.
- Hellström K, Rautio P, Huhta AP, Tuomi J (2004) Tolerance of an annual hemiparasite, *Euphrasia stricta* agg., to simulated grazing in relation to the host environment. *Flora* 199:247–255.
- Huhta AP, Hellström K, Rautio P, Tuomi J (2000a) A test of the compensatory continuum: fertilization increases and below-ground competition decreases the grazing tolerance of tall wormseed mustard (*Erysimum strictum*). *Evolutionary Ecology* 14:353–372.
- Huhta AP, Lennartsson T, Tuomi J, Rautio P, Laine K (2000b) Tolerance of *Gentianella campestris* in relation to damage intensity: an interplay between apical dominance and herbivory. *Evolutionary Ecology* 14:373–392.
- Huhta AP, Hellström K, Rautio P et Tuomi J (2003) Grazing tolerance of *Gentianella amarella* and other monocarpic herbs: why is tolerance highest at low damage levels? *Plant Ecology* 166:49-61.
- Irmish T (1857) Ueber die Keimung und die Erneuerung Weise von *Convolvulus sepium* and *C. arvensis*, so wie uber hypokotylische Adventivknospen bei kräutigen phanerogamen Phlanzen. *Botanische Zeitung* 15/28:465-474, 489-497.
- Kästner A, Karrer G (1995) Übersicht der Wuchsformtypen als Grundlage für deren Erfassung in der "Flora von Osterreich". *Flora Austriacis Novitatis* 3:1-51.
- Klemow KM, Raynal DJ (1983) Population biology of an annual plant in temporally variable habitat. *Journal of Ecology* 71:691-703.
- Klimešová et al. 2007
- Klimešová J, Kociánová A, Martínková J (2008) Weeds that can do both tricks: vegetative versus generative regeneration of short-lived rootsprouting herbs *Rorippa palustris* and *Barbarea vulgaris*. *Weed Research* 48:131–135.
- Klimešová J (2003) Monokarpické rostliny schopné přežít silnou disturbanci. *Zprávy Čes. Bot. Společ., Praha*, 38, Materiály 19:37-48.
- Klimešová J, Klimeš L (2003) Resprouting of herbs in disturbed habitats: it is adequately described by Bellingham-Sparow's model? *Oikos* 103:225–229.
- Korsmo E (1930) Unkräuter im Ackerbaum der Neuzeit. Verlag von Julius Springer, Berlin, 580 p.

- Krumbiegel A (1998) Growth forms of annual vascular plants in central Europe. *Nordic Journal of Botany* 18:563-575.
- Krumbiegel A (1999) Growth forms of biennial and pluriennial vascular plants in central Europe. *Nordic Journal of Botany* 19:217-226.
- Kutschera L (1960) *Wurzelatlas mitteleuropäischer Ackerkräuter und Kultur-pflanzen*. DLG – Verlang's gmbh, Frankfurt am Main.
- Kutschera L, Lichtenegger E (1992) *Wurzelatlas mitteleuropäischer Grünlandpflanzen*. Band 2. Pteridophyta und Dicotyledoneae (Magnoliopsida). Gustav Fischer, Stuttgart.
- Löfgren P, Eriksson O, Lehtilä K (2000) Population dynamics and the effect of disturbance in the monocarpic herb *Carlina vulgaris* (Asteraceae). *Annales Botanici Fennici* 37:183-192.
- Latzel V, Dospělová L, Klimešová J (2009) Annuals sprouting adventitiously from the hypocotyl: their compensatory growth and implications for weed management. *Biología* 64:923–929.
- Lennartsson T, Tuomi J, Nilsson P (1997) Evidence for an evolutionary history of overcompensation in the grassland biennial *Gentianella campestris* (Gentianaceae). *American Naturalist* 149:1147–1155.
- Lennartsson T, Nilsson P, Tuomi J (1998) Induction of overcompensation in the field gentian, *Gentianella campestris*. *Ecology* 79:1061–1072.
- van der Maarel E (2007) Transformation of cover-abundance values for appropriate numerical treatment – alternatives to the proposals by Podani. *J. Veget. Sci.* 18:767–770.
- Martínková J, Klimešová J, Mihulka S (2004) Resprouting after disturbance: An experimental study with short-lived monocarpic herbs. *Folia Geobotanica* 39:1-12.
- Martínková J, Klimešová J, Mihulka S (2008) Compensation of seed production after severe injury in the short-lived herb *Barbarea vulgaris*. *Basic Applied Ecology* 9:44–54.
- van der Meijden E, Klinkhamer PGL, De Jong TJ, Van Wijk CAM (1992) Meta-population dynamics of biennial plants: how to exploit temporary habitats. *Acta Botanica Neerlandica* 41:249-270.
- Nilsson P, Tuomi J, Astrom M (1996) Bud dormancy as a bet-hedging strategy. *American Naturalist* 147:269-281.
- Rauh W (1937) Die Bildung von Hypocotyl- und Wurzelsprossen und ihre Bedeutung für die Wuchsformen der Pflanzen. *Nova Acta Leopoldiana* 4/24: 395-553.
- Reichardt HW (1857) Beiträge zur Kenntniss hypokotylicher Adventiv-knospen und Wurzelsprosse bei kräutigen Dikotylen. *Verhandlungen der Zoologisch-botanischen Vereins in Wien* 7:235–244.
- Rothmaler W (1988) *Exkursionsflora für die Gebiete der DDR und der BRD*. Band 3. Atlas der Gefäßpflanzen. Volk und Wissen Volkseigener Verlag Berlin.
- Sosnová M, Klimešová J (2009) Life-history variation in the short-lived herb *Rorippa palustris*: The role of carbon storage. *Acta Oecologica* 35:691-697.

- Stearns SC (1992) The evolution of life histories. Oxford: Oxford University Press.
- Tuomi J, Nilsson P, Åström M (1994) Plant compensatory responses bud dormancy as an adaptation to herbivory. *Ecology* 75:1429-1436.
- Wehrsag O (1954) Biologie der Ackerunkräuter. Academia-VerlagGmbH, Berlin.
- Wise MJ, Abrahamson WG (2007) Effects of resource availability on tolerance of herbivory: a review and assessment of three opposing models. *American Naturalist* 169:443–454.
- Wittrock VB (1884) Ueber Wurzelsprossen bei kräutigen Gewächsen, mit besonderer Rücksicht auf ihre verschiedene biologische Bedeutung. *Botanisches Centralblatt* 17(8):227–232, 17(9):257–264.
- Wydler H. (1850) Über subcotyledonare Sprossbildung. *Flora* 8(22):337–338.

CHAPTER II

CASE STUDIES

STUDY I

Occurrence of adventitious sprouting in short-lived monocarpic herbs: field study of 22 weedy species

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ABSTRACT

In this study, we tested 14037 monocarpic herbs of 389 natural populations belonging to 22 species, where growth characteristics and adventitious buds and sprouts were measured in individual plants, species composition and plant cover in communities were evaluated and environmental characteristics were estimated by using Ellenberg indicator values. It was confirmed that adventitious sprouting occurs in natural populations of all but five species examined. Adventitious sprouting was positively affected by plant size and plant injury. Environmental factors including availability of soil nitrogen were not shown to affect adventitious sprouting. Annual and biennial plants did not differ in sprouting, but upright annuals had a lower number of and longer adventitious shoots than prostrate annuals. Field assessment suggests that the potential bud bank on the hypocotyle and roots of annual and biennial herbs supports vegetative regeneration of injured plants in natural populations. This result indicates that adventitious bud formation is a functional trait in the studied plant species and should not be considered only as a teratological feature. This finding raises many questions about the ecology and evolution of this trait. That some annuals and biennials possess a potential bud bank implies that this feature should be considered not only in ecological studies, but also in the

management of weedy and invasive plants, because mechanical disturbance instead of eradication can lead to vegetative regeneration.

INTRODUCTION

Theory predicts that semelparous life history evolves when juvenile survivorship is relatively high compared with the probability of adult survivorship to the next reproductive event (Stearns 1992). The majority of semelparous (monocarpic) plant species have an annual or biennial life cycle and dominate in ecosystems where severe but predictable disturbances detrimentally affect their populations yearly, typically in connection with a seasonal climate, for example summer drought, spring floods and ploughing of arable land. Monocarpic herbs adopt an avoidance strategy characterized by a short life cycle and numerous easily dispersible diaspores (Bellingham and Sparrow 2000; Grime 2001).

The ability of annual herbs to survive an injury is constrained by the scarcity of basal reserve meristems and poor carbon storage (Dina and Klikoff 1974; Otzen 1977; Krumbiegel 1998). Monocarpic herbs with a biennial or shortlived perennial life cycle, by contrast, accumulate reserves and basal meristems (Krumbiegel 1999; Vilela et al. 2008; Sosnová and Klimešová 2009). However, their recovery from damage depends on life-history stage and diminishes with disturbance severity (Huhta et al. 2003; Boege and Marquis 2005) as the costs of recovery may match the costs of intrinsically programmed life-history events (Klimešová et al. 2007).

Despite knowledge about the above-mentioned factors, monocarpic herbs can in reality be subjected to injury and regenerate vegetatively due to different disturbance events with varying intensity, timing and probability, such as herbivory, erosion or anthropogenic activity (Klimešová and Klimeš 2003). Although overlooked in some theoretical studies (Bellingham and Sparrow 2000; Grime 2001), this is accepted, and monocarpic herbs represent a suitable model for studying the fitness consequences of damage (Lennartsson et al. 1997, 1998; Paige 1999; Huhta et al. 2000a, b, c; Hellström et al. 2004; Piippo et al. 2005, 2009; Rautio et al. 2005).

Moreover, about 2% of annuals and 13% of biennial herbs of Central Europe possess the ability to form adventitious buds on the hypocotyle and/or roots (Klimešová and Klimeš 2006). Such buds are formed de novo on organs originally lacking buds and thus provide a plant with additional meristems to those occurring in leaf axils on stem parts (Rauh 1937). This trait contrasts with the expected avoidance strategy of monocarpic herbs, as it brings about a potential for overcoming meristem limitation (Klimešová and Klimeš 2003; Klimešová and Martínková 2004).

Experimental studies have tested whether adventitious bud formation, a morphological trait, might be considered as a pool of meristems for vegetative regeneration in the case of plant injury (potential bud bank sensu Klimešová and Klimeš 2007). The results showed that the formation of adventitious buds in monocarpic short-lived herbs might be an important means to rescue an individual plant and ensure seed production after an injury that was far more severe than expected (Klimešová et al. 2008; Martínková et al. 2008; Latzel et al. 2009). Moreover, plant phenology, life-history stage, carbon storage and plant size are important characteristics constraining resprouting from adventitious buds; photoperiod, nutrient availability, disturbance severity and flooding stress are environmental variables that were found to affect the regeneration process or degree of compensation (Martínková et al. 2004a, b, 2006, 2008; Klimešová et al. 2007, 2008; Sosnová and Klimešová 2009).

Although the capacity to deal with severe injury in monocarpic short-lived herbs was shown under experimental conditions, its role in nature remains unresolved. Apart from a few studies (Martínková et al. 2006; King et al. 2008), the occurrence of resprouting monocarps in the field remains only anecdotally documented in descriptive morphological studies (e.g. Wydler 1850; Reichardt 1857; Wittrock 1884; Beijerinck 1887; Holm 1925; Rauh 1937). Thus, we do not know whether the potential for resprouting is employed by plants in unmanipulated field conditions or if the occurrence of adventitious sprouting is restricted to certain rare situations and thus might be considered as a teratological feature (Penzig 1921–1922).

Due to the scarcity of data on resprouting of monocarpic herbs in field conditions, an analogical system was employed, namely woody resprouters in

fire-prone areas, to make predictions. There is a tendency towards resprouting (i.e. survival and regeneration after fire from the bud bank) in nutrient-poor conditions and towards seeding (i.e. death after fire and regeneration from seeds) in nutrient-rich conditions (Iwasa and Kubo 1997; Bellingham and Sparrow 2000; Buhk et al. 2007; but see Clarke et al. 2005; Knox and Clarke 2005). Resprouters are characterized by low stature and when disturbance is lacking they are overgrown by tall seeders (Midgley 1996). This, however, may not be true in herbs where vertical growth starts each year from zero. When a large-scale severe disturbance affects a community of herbaceous monocarps during the growing season, those possessing adventitious buds will survive and resprout at the expense of storage carbon in roots and those lacking bud banks will die and regenerate from seed. However, as annual and biennial species prevail in habitats subjected to some predictable disturbance, for example ploughing, those plants regenerating from seed might fail to finish the life cycle by the end of the season and thus are not able to outcompete resprouters later on. Therefore, the success of herbaceous monocarpic resprouters will depend more on the ability to compensate for seed production, than just on the ability to survive because they are – contrary to woody resprouters – short living and their populations are dependent on regeneration from seeds.

Compensation ability (fitness and biomass production of injured versus untouched plants) is usually studied as a response of herbs to herbivory. Studies of the dependence on nutrient availability give contrasting, context-specific results (e.g. Ferraro and Osterheld 2002; Wise and Abrahamson 2007). On the other hand, vigour and compensation ability of regenerated root sprouting plants are in contrast to resprouting success supported by nutrient-rich conditions (Martínková et al. 2004a, b, 2008; Latzel and Klimešová 2009). Thus, we may hypothesize that good growing conditions (high nitrogen, sufficient moisture and illumination) will support regeneration by adventitious sprouting in monocarpic short-lived herbs in contrast to resprouters in fire-prone areas (see also Eggers 1946).

Additionally, as biennials usually have the ability to postpone reproduction to later seasons (Klimešová et al. 2007; Martínková et al. 2008), they possess larger carbon storage (Sosnová and Klimešová 2009) and

during a longer life cycle can experience more disturbance events than annuals. Thus, a second hypothesis is that adventitious sprouting will be more common in biennials than in annual herbs and in later phenological phases.

Due to a trade-off between apical dominance (competitive ability) and branching (Aarssen 1995; Bonser and Aarssen 1996; McPhee et al. 1997; Duffy et al. 1999), we expected that plants with reduced apical dominance, those which are not growing in a competitive environment or have a prostrate growth form will have a higher number of adventitious shoots.

The aim here is to test the following hypotheses: (1) good growing conditions (high nitrogen, sufficient moisture and illumination) will support regeneration by adventitious sprouting in short-lived monocarps; (2) adventitious sprouting will be more common in biennials compared with annual herbs and in later phenological phases; and (3) plants with reduced apical dominance, those which are not growing in a competitive environment or having a prostrate growth form will have a higher number of adventitious shoots. To test these hypotheses, the occurrence of adventitious buds and sprouts was assessed in numerous natural populations of 22 species of short-lived monocarpic herbs. As plant characteristics affecting adventitious sprouting, the effects of plant size, growth form, phenology, life history and plant injury were studied, and environmental characteristics studied were vegetation cover as a measure of the competitive milieu, soil compactness and, indirectly (using Ellenberg indicator values), nitrogen status, moisture, light availability and temperature.

METHODS

FIELD DATA

Monocarpic short-lived herbs that were reported as being capable of adventitious sprouting from the hypocotyle and/or roots (Klimešová and Klimeš 2006; Klimešová and de Bello 2009; Table 1) were studied in the field. Populations of annuals and biennials were sampled in different habitats and environmental conditions mainly in the Czech Republic (Central Europe) from 2005 to 2007.

The list of studied species, number of sampled populations and individuals is given in Table 1. The aim to assess the morphology in at least 30 natural populations per species and at least 20 individuals per population was not fulfilled in some rare species. Measured plant traits were as follows: plant height, base width, number of axillary branches, cumulative length of adventitious shoots, length of the longest adventitious shoot, number of adventitious buds and number of adventitious shoots. A disturbance was assessed as an injured or removed main shoot, while phenology was assessed as the main phenological stages (i.e. vegetative, flowering, fruiting).

Communities where sufficient numbers of individuals of a target species occurred were described using phytosociological relevés (van der Maarel 2007): all species in a relevé were determined and their cover estimated (Braun–Blanquet scale $r = 0.05\text{--}0.5\%$, $+ = 0.5\text{--}2.5\%$, $1 = 2.5\text{--}7.5\%$, $2a = 7.5\text{--}15\%$, $2m = 15\text{--}22.5\%$, $2b = 22.5\text{--}37.5\%$, $3 = 37.5\text{--}62.5\%$, $4 = 62.5\text{--}87.5\%$, $5 = 87.5\text{--}100\%$). Thus, the following community characteristics were also assessed: total vegetation cover, cover of individual species and species richness.

Soil cementation was determined using a semiquantitative scale, low, medium and high, according to permeability assessed using a pencil. Other environmental characteristics for the studied populations were assessed using Ellenberg indicator values for light, temperature, humidity and nitrogen (Ellenberg 1986). Values of the environmental characteristics for individual populations were calculated as a weighted average of indicator values for individual species, weighted by the estimated species abundance.

DATA ANALYSIS

The collected dataset (all species were included) was strictly hierarchical in nature, with individual species represented by multiple populations, each with many individuals. Consequently, our hypotheses were tested using linear mixed-effect models or generalized linear mixed-effect models, depending on the nature of a particular response variable (assuming Gaussian, quasi-Poisson or quasi-binomial distributions), with species identity as a random effect and population as a nested effect. The tests were based

on the likelihood-ratio approach, approximating the difference in model deviances with a χ^2 distribution. The two models were fitted using the *lme4* package in R, version 2.8 (R Development Core Team 2008).

Table 1. List of the 22 studied species with their status in the flora of the Czech Republic, number of sampled populations and total number of sampled and injured individuals during field seasons 2005 and 2006

Species	Family	Growth form in annual	Number of sampled populations	Number of sampled individuals	Number of injured individuals
Annuals					
<i>Anagallis arvensis</i> L.	Primulaceae	Prostrate	30	1114	78
<i>Arabidopsis thaliana</i> (L.) Heynh.	Brassicaceae	Upright	30	1121	66
<i>Euphorbia exigua</i> L.	Euphorbiaceae	Upright	6	208	33
<i>Euphorbia helioscopia</i> L.	Euphorbiaceae	Upright	30	1085	86
<i>Euphorbia peplus</i> L.	Euphorbiaceae	Upright	31	1407	191
<i>Kickxia spuria</i> (L.) Dumort.	Scrophulariaceae	Prostrate	3	61	0
<i>Kickxia elatine</i> (L.) Dumort.	Scrophulariaceae	Prostrate	2	71	0
<i>Microrrhinum minus</i> (L.) Fourr.	Scrophulariaceae	Upright	31	1257	53
Biennials					
<i>Arabis glabra</i> (L.) Bernh.	Brassicaceae		6	176	13
<i>Arabis hirsute</i> (L.) Scop. <i>sensu stricto</i>	Brassicaceae		2	68	31
<i>Alliaria petiolata</i> (M. Bieb.) Avara et Grande	Brassicaceae		27	993	73
<i>Barbarea vulgaris</i> W.T. Aiton	Brassicaceae		31	1112	12
<i>Barbarea stricta</i> Andrz.	Brassicaceae		10	339	4
<i>Daucus carota</i> L.	Apiaceae		35	1074	162
<i>Diplotaxis muralis</i> (L.) DC.	Brassicaceae		1	30	0
<i>Isatis tinctoria</i> L.	Brassicaceae		2	40	13
<i>Jasione montana</i> L.	Campanulaceae		5	176	1
<i>Medicago lupulina</i> L.	Fabaceae		29	1090	87
<i>Potentilla supina</i> L.	Rosaceae		30	1029	26
<i>Reseda lutea</i> L.	Resedaceae		15	448	28
<i>Reseda luteola</i> L.	Resedaceae		1	20	0
<i>Rorippa palustris</i> (L.) Besser	Brassicaceae		32	1118	45

Due to the possibility that phylogenetic inertia could affect both the parameters of adventitious resprouting behaviour and the explanatory

variables implied in the hypotheses tested, the tests were also done with phylogenetic correction, using the method of [Desdevises et al. \(2003\)](#).

As the attributes of adventitious sprouting, representing individual response variables in the models, are at least partly related, the results for a particular predictor represent a family of statistical tests, for which Type I errors should be corrected to control for family-level errors. Holm's procedure ([Holm 1979](#)) was employed, which is a more powerful alternative to the traditionally used Bonferroni correction.

RESULTS

Adventitious sprouting was not observed (neither adventitious buds nor shoots were recorded) in five of the 22 studied species: *Euphorbia helioscopia*, *Arabidopsis thaliana*, *Arabis glabra*, *Medicago lupulina* and *Potentilla supina*. The species with the highest number of buds was *Reseda lutea* whereas the species with highest number of shoots was *Isatis tinctoria* (Fig. 1).

EFFECT OF PLANT CHARACTERISTICS ON ADVENTITIOUS SPROUTING

Plant size, measured as shoot base diameter and branch number, was positively correlated with the resprouting intensity of plants, whereas plant height affected resprouting only marginally. Phenological stage and plant injury (defined as the loss of the primary shoot) affected all studied resprouting characteristics, with resprouting being more intensive in late phenological stages and injured plants (Table 2). Differences between biennials and annuals were found only in the length of adventitious shoots, being larger in biennials, whereas the numbers of buds and shoots were not different between the two life-history modes. The species investigated differed in all studied characteristics (Table 3).

Fig 1. Characteristics of adventitious sprouting in the studied species. (A) Populations with adventitious sprouting (%); (B) mean cumulative length of sholte per plant (cm); (C) mean number of shoots per plant; (D) mean number of buds per plant.

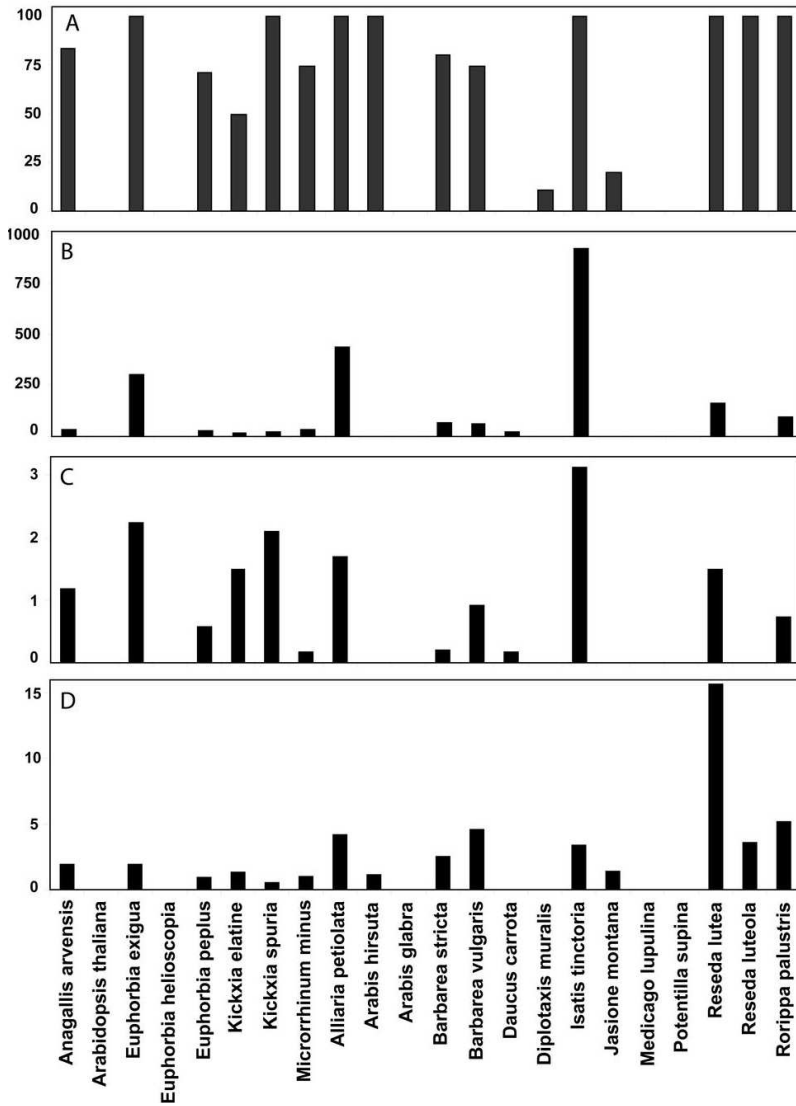


Table 2. Effect of plant size characteristics, developmental stage and damage on the attributes of adventitious sprouting

Response variable	Plant height	Base width	Number of axillary branches	Phenology	Disturbance
No. of adventitious buds and shoots	2.1 (n.s.)	132.5 (<0.001) ↑	43.3 (<0.001) ↑	28.8 (<0.001) ↑	54.5 (<0.001) ↑
No. of adv. shoots/number of adventitious buds and shoots	4.7 (n.s.)	18.1 (<0.001) ↓	2.4 (n.s.)	5.6 (0.018) ↑	74.9 (<0.001) ↑
Presence of adventitious buds or shoots	2.1 (n.s.)	27.1 (<0.001) ↑	15.5 (<0.001) ↑	11.5 (0.003) ↑	63.8 (<0.001) ↑
Cumulative length of adventitious shoots	4.0 (n.s.)	0.9 (n.s.)	10.8 (0.003) ↑	8.3 (0.0012) ↑	8.6 (0.003) ↑
Length of the longest adventitious shoot	0.01 (n.s.)	2.0 (n.s.)	3.8 (n.s.)	8.0 (0.0012) ↑	10.8 (0.002) ↑

Effect of individual predictors (columns) was examined in two separate models for each response variable (rows): one for plant stature parameters (plant height, base width, number of axillary branches), and the other for plant phenological and damage status (phenology, disturbance). The χ^2 statistic value is given first, with the corresponding Type I error estimate for a likelihood-ratio test of the particular model term in parentheses; the symbol (present only for significant predictors) summarizes the direction of the effect: ↑, a positive correlation between the predictor and response values; ↓, a negative correlation.

Table 3. Test of differences among species, between annuals and biennials (life form), and between prostrate and upright annual species (growth form) in the attributes of adventitious sprouting

Response variable	Species	Life form	Growth form
No. of adventitious buds and shoots	390.6 (< 0.001)	0.5 (NS)	12202 (< 0.001) 12187 (< 0.001) smaller for uprights
No. of adv. shoots/number of adventitious buds and shoots	36.5 (< 0.001)	1.9 (NS)	1905 (< 0.001) 1900 (< 0.001) smaller for uprights
Presence of adventitious buds or shoots	403.2 (< 0.001)	0.00 (NS)	3290 (< 0.001) 3290 (< 0.001) probability smaller for uprights
Cumulative length of adventitious shoots	34.6 (< 0.001)	7.1 (0.038) 1.8 (NS) larger for biennials	827 (< 0.001) 825 (< 0.001) longer for uprights
Length of the longest adventitious shoot	45.6 (< 0.001)	9.9 (0.010) 1.2 (NS) larger for biennials	761 (< 0.001) 761 (< 0.001) longer for uprights

Effect of individual predictors (columns) was examined in a separate model for each response variable (rows). The first row for each variable provides the χ^2 statistic and corresponding Type I error estimate for a likelihood-ratio test of the particular model term; the next row provides results from the corresponding model with phylogenetic correction (fitted only for previously significant effects, except for 'Species', where the correction was not appropriate). If any of the two models found a significant effect, then below is described the direction of the effect (for 'Life form' and 'Growth form' predictors).

The annual plant species studied differed in their growth form; some are prostrate whereas others have upright stems. This growth form characteristic influenced significantly all measured characteristics of resprouting: upright annuals had a lower number of adventitious buds and shoots, but shoot length was higher than in the prostrate plants (Table 3).

EFFECT OF ENVIRONMENTAL CHARACTERISTICS

Environmental characteristics were tested with shoot diameter, number of branches, phenology and injury as covariates, i.e. the effect of plant developmental state was removed from the analysis. None of the tested characteristics (light, soil nitrogen, moisture, soil cementation, total cover of the herb layer, temperature and species richness of the community) had any effect on adventitious sprouting. Similar results were obtained when only phenological stage was used as a covariate.

Non-disturbed plants were analysed separately to assess the role of environmental variables on the presence of adventitious bud formation. Again, environmental variables had no effect on adventitious sprouting.

PHYLOGENETIC CORRECTION

The difference between annuals and biennials disappeared when taking into account the phylogenetic relatedness of the species studied. Moreover, the results obtained for environmental variables remained unaffected and non-significant.

DISCUSSION

Adventitious sprouting in short-lived monocarpic herbs was found in natural communities, but its extent differed among species and was generally enhanced by injury. The effect of environmental variables on adventitious sprouting was not significant. Sprouting was more vigorous in large, branched plants and their later phenological phases (i.e. accumulation of disturbance with life span). Biennials tended to produce longer adventitious shoots, but this effect was affected by phylogenetic relatedness within life-history modes and disappeared after phylogenetic correction. Prostrate annuals formed more buds whereas upright annuals had fewer but longer shoots; this indicates that apical dominance was more pronounced in upright forms.

The fact that adventitious sprouting was not observed in all studied plant species should not be considered as proof that they do not have any resprouting ability. However, at least six populations were studied in those species, suggesting that any adventitious sprouting would probably be very rare in the species lacking adventitious sprouting in the present study.

EFFECT OF PLANT CHARACTERISTICS

The results on the effect of plant characteristics on adventitious sprouting are in accordance with the expectations based on experimental studies listed in the Introduction, with the exception of a lack of difference between biennials and annuals. This surprising result may be caused by the presence of carbon storage connected with potential bud bank formation in both life-history modes. Restriction of monocarpic rootsprouters to places affected by human activity and underrepresentation in more pristine communities in comparison with non-sprouters (J. Martínková et al., Institute of Botany ASCR, Czech Republic, unpubl. res.) implies that there are costs of unrealized resprouting when there is a lack of disturbance. These costs may be interpreted as carbohydrate storage in below-ground parts at the expense of growth in aboveground parts. Although differences in the storage economy of root-sprouters versus non-sprouters in monocarpic herbs were not directly tested, the root-sprouting monocarp *Rorippa palustris* builds larger

carbohydrate reserves in comparison with some other annuals (Dina and Klikoff 1974; Clark and Burk 1980; Chiariello and Roughgarden 1984; Sosnová and Klimešová 2009).

Another factor responsible for the lack of difference between adventitious sprouting in annuals and biennials might be the fact that those two life-history modes are rather plastic and many species are characterized by life-history variation (Rauh 1937; Klimešová 2003; Klimešová et al. 2007). Adventitious buds provide a bud bank for production of additional shoots after flowering or over-wintering; many species of short-lived root sprouters can behave as short-lived perennials (MacDonald and Cavers 1974; Klimešová et al. 2007).

The present study compared only surviving plants, and therefore it was not possible to disentangle whether adventitious sprouters were larger because injury and consequent resprouting led to over-compensation and huge growth, or simply because smaller plants were more prone to mortality after injury than larger plants (King et al. 2008). Because successful resprouting of the largest plants is in accordance with experimental studies (Martínková et al. 2004a; M. Sosnová, Institute of Botany ASCR, Czech Republic, unpubl. res.), injury can be considered as the principal factor affecting adventitious sprouting, which is successful in plants exceeding some site- and species-specific size threshold.

The significant effect of later phenological phases on the degree of adventitious sprouting might be explained by the longer time available for accumulation of disturbance events as proposed in the Introduction. This accumulation process, however, did not result in a difference between annuals and biennials. This may be due to the fact that biennial plants occur in less disturbed habitats (Grime 2001) and are less prone to disturbance during the first year of life due to a prostrate growth form (usually a rosette of leaves; Krumbiegel 1999). The accumulation process outweighed the decreasing ability to form adventitious buds on the hypocotyle with plant age in annuals and decreasing resprouting success with advanced phenological phases reported in some biennials (Link and Eggers 1946; Martínková et al. 2004a).

Biennials and upright annuals characterized by strong apical dominance tended to have less numerous but longer adventitious shoots. It is possible that rapid re-establishment of a secondary dominant shoot resumes the role of lateral meristem inhibition (as suggested by [Aarssen 1995](#)). On the other hand, prostrate annuals had more buds and shoots, which indicates lower apical dominance and supports our hypothesis.

EFFECT OF ENVIRONMENTAL CHARACTERISTICS

Contrary to expectation, environmental characteristics such as light, soil nitrogen, moisture, soil cementation, total cover of the herb layer, temperature and species richness of the community were not found to affect adventitious sprouting of plants in the present dataset; only plant size was responsible for the observed variability. Two important points need to be stressed from this result: (1) compensation for lost biomass and fitness seems to be important for resprouting success of adventitious short-lived sprouters rather than survival *per se* as hypothesized in the Introduction, because populations of short-lived monocarps are dependent on seed regeneration contrary to perennial polycarpic species; and (2) benign conditions, especially higher nitrogen availability, were probably counter-balanced by higher competition and thus did not lead to a larger size of target plants and consequently to their enhanced survival and resprouting. Whether the effect of plant size is removed from the analysis or not, the effect of environmental conditions is non-significant, which suggests that the experimentally shown effect of nutrients on resprouting in short-lived adventitious sprouters ([Martínková et al. 2004a, b](#)) or axillary sprouters ([Benner 1988](#); [Huhta et al. 2000a, b](#)) was due to larger plant size. This view is supported also by the fact that, in studies where there are contrasting results for the relationship between nutrient status and resprouting from roots ([Klimeš and Klimešová 1999](#); [Klimešová et al. 2009](#); [Latzel and Klimešová 2009](#)), plant size was controlled for.

CONCLUSIONS

Field assessment suggests that the potential bud bank on the hypocotyle and roots of annual and biennial herbs supports vegetative regeneration of injured plants in natural populations. This result indicates that adventitious bud formation is a functional trait in the studied plant species and should not be considered only as a teratological feature. This finding raises many questions about the ecology and evolution of this trait. For example, what are the consequences of potential bud bank formation for plant distribution and occurrence in different communities or crop cultures with specific types of disturbance? Is there an evolutionary trade-off between the potential bud bank providing persistence after disturbance and seed traits, such as seed dispersion method and longevity of the seed bank? How does adventitious sprouting affect the allometry of annual and biennial species? How does adventitious sprouting contribute to compensation of plant body damage? What are the costs of adventitious bud formation?

That some annuals and biennials possess a potential bud bank implies that this feature should be considered not only in ecological studies, but also in the management of weedy and invasive plants, because mechanical disturbance instead of eradication can lead to vegetative regeneration.

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REFERENCES

Aarssen LW (1995) Hypotheses for the evolution of apical dominance in plants: implications for the interpretation of overcompensation. *Oikos* 74:149–156.

- Beijerinck MW (1887) Wurzelknospen und Nebenwurzeln. Verhandelungen der Koninklijke Akademie van Wetenschappen 25/3:1–150.
- Bellingham PJ, Sparrow AD (2000) Resprouting as a life history strategy in plant communities. *Oikos* 98:409–416.
- Benner BL. 1988. Effect of apex removal and nutrient supplementation on branching and seed production in *Thlaspi arvense* (Brassicaceae). *American Journal of Botany* 75:645–651.
- Boege K, Marquis RJ (2005) Facing herbivory as you grow up: the ontogeny of resistance in plants. *Trends in Ecology and Evolution* 20:441–448.
- Bonser SP, Aarssen LW (1996) Meristem allocation: a new classification theory for adaptive strategies in herbaceous plants. *Oikos* 77:347–352.
- Buhk C, Meyn A, Jentsch A (2007) The challenge of plant regeneration after fire in the Mediterranean Basin: scientific gaps in our knowledge on plant strategies and evolution of traits. *Plant Ecology* 192:1–19.
- Chiariello N, Roughgarden J. (1984) Storage allocation in seasonal races of an annual plant: optimal versus actual allocation. *Ecology* 65:1290–1301.
- Clark DD, Burk JH (1980) Resource allocation patterns of two California-Sonoran desert ephemerals. *Oecologia* 46:86–91.
- Clarke PJ, Knox KJE, Wills KE, Campbell M (2005) Landscape patterns of woody plant response to crown fire: disturbance and productivity influence sprouting ability. *Journal of Ecology* 93:544–555.
- Dina SJ, Klikoff LG (1974) Carbohydrate cycle of *Plantago insularis* var. *fastigiata*, a winter annual from the Sonoran desert. *Botanical Gazette* 135:13–18.
- Duffy NM, Bonser SP, Aarssen LW (1999) Patterns of variation in meristem allocation across genotypes and species in monocarpic Brassicaceae. *Oikos* 84:284–292.
- Desdevises Y, Legendre P, Azouzi L, Morand S (2003) Quantifying phylogenetically-structured environmental variation. *Evolution* 57:2647–2652.
- Eggers V (1946) Influence of carbohydrate and nitrate-nitrogen nutrition on development of hypocotyledonary buds in flax. *Botanical Gazette* 107:385–390.
- Ellenberg H (1986) *Vegetation ecology of central Europe*, 4th edn. Cambridge: Cambridge University Press.
- Ferraro DO, Oesterheld M (2002) Effect of defoliation on grass growth. A quantitative review. *Oikos* 98:125–133.
- Grime JP (2001) *Plant strategies, vegetation processes and ecosystem properties*. Chichester: John Wiley & Sons.
- Hellström K, Rautio P, Huhta AP, Tuomi J (2004) Tolerance of an annual hemiparasite, *Euphrasia stricta* agg., to simulated grazing in relation to the host environment. *Flora* 199 247–255.
- Holm S (1979) A simple sequentially rejective multiple test procedure. *Scandinavian Journal of Statistics* 6:65–70.

- Holm T (1925) On the development of buds upon roots and leaves. *Annals of Botany* 39:867–881.
- Huhta AP, Hellström K, Rautio P, Tuomi J (2000a) A test of the compensatory continuum: fertilization increases and below-ground competition decreases the grazing tolerance of tall wormseed mustard (*Erysimum strictum*). *Evolutionary Ecology* 14:353–372.
- Huhta AP, Lennartsson T, Tuomi J, Rautio P, Laine K (2000b) Tolerance of *Gentianella campestris* in relation to damage intensity: an interplay between apical dominance and herbivory. *Evolutionary Ecology* 14:373–392.
- Huhta AP, Tuomi J, Rautio P (2000c) Cost of apical dominance in two monocarpic herbs, *Erysimum strictum* and *Rhinanthus minor*. *Canadian Journal of Botany* 78:591–599.
- Huhta AP, Hellström K, Rautio P, Tuomi J (2003) Grazing tolerance of *Gentianella amarella* and other monocarpic herbs: why is tolerance highest at low damage levels? *Plant Ecology* 166:49–61.
- Iwasa Y, Kubo T. (1997) Optimal size of storage for recovery after unpredictable disturbances. *Evolutionary Ecology* 11:41–65.
- King GE, Eckhart MV, Mohl CE (2008) Magnitudes and mechanism of shoot-damage compensation in annual species of *Linum* (Linaceae) in Iowa. *American Midland Naturalist* 159:200–213.
- Klimeš L, Klimešová J (1999) Root sprouting in *Rumex acetosella* under different nutrient levels. *Plant Ecology* 141:33–39.
- Klimešová J (2003) Monokarpické rostliny schopné přežít silnou disturbance (Monocarpic plants surviving severe disturbance). *Zprávy České Botanické Společnosti, Praha*, 38, Materiály 19:37–48.
- Klimešová J, de Bello F (2009) (CLO-PLA): the database of clonal and bud bank traits of Central European flora. *Journal of Vegetation Science* 20:511–516.
- Klimešová J, Klimeš L (2003) Resprouting of herbs in disturbed habitats: it is adequately described by Bellingham-Sparow's model? *Oikos* 103:225–229.
- Klimešová J, Klimeš L (2006) CLO-PLA3—the database of clonal and bud bank traits of Central European flora. <http://clopla.butbn.cas.cz>.
- 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, Martínková J (2004) Intermediate growth forms as a model for the study of plants clonality functioning: an example with root sprouters. *Evolutionary Ecology* 18:669–681.
- Klimešová J, Sosnová M, Martínková J (2007) Life-history variation in the short-lived herb *Rorippa palustris*: effects 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 rootsprouting herbs *Rorippa palustris* and *Barbarea vulgaris*. *Weed Research* 48:131–135.
- Klimešová J, Pokorná A, Klimeš L (2009) Establishment growth and bud bank formation in *Epilobium angustifolium*: the effects of nutrient availability, plant injury and environmental heterogeneity. *Botany* 87:195–201.
- Knox KJE, Clarke PJ (2005) Nutrient availability induces contrasting allocation and starch formation in resprouting and obligate seeding shrubs. *Functional Ecology* 19:690–698.
- Krumbiegel A (1998) Growth forms of annual vascular plants in central Europe. *Nordic Journal of Botany* 18:563–576.
- Krumbiegel A (1999) Growth forms of biennial and pluriennial vascular plants in central Europe. *Nordic Journal of Botany* 19:217–226.
- Latzel V, Klimešová J (2009) Fitness of resprouters versus seeders in relation to nutrient availability in two *Plantago species*. *Acta Oecologica* 35:541–547.
- Latzel V, Dospělová L, Klimešová J (2009) Annuals sprouting adventitiously from the hypocotyl: their compensatory growth and implications for weed management. *Biología* 64:923–929.
- Lennartsson T, Tuomi J, Nilsson P (1997) Evidence for an evolutionary history of overcompensation in the grassland biennial *Gentianella campestris* (Gentianaceae). *American Naturalist* 149:1147–1155.
- Lennartsson T, Nilsson P, Tuomi J (1998) Induction of overcompensation in the field gentian, *Gentianella campestris*. *Ecology* 79:1061–1072.
- Link GKK, Eggers V (1946) Mode, site and time of initiation of hypocotyledonary bud primordia in *Linum ussitatissimum*. *Botanical Gazette* 107:441–454.
- van der Maarel E (2007) Transformation of cover-abundance values for appropriate numerical treatment – alternatives to the proposals by Podani. *Journal of Vegetation Science* 18:767–770.
- MacDonald MA, Cavers PB (1974) Cauline rosettes—an asexual means of reproduction and dispersal occurring after seed formation in *Barbarea vulgaris* (yellow rocket). *Canadian Journal of Botany* 52:913–918.
- 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 Oecologica* 25:143–150.
- Martínková J, Klimešová J, Mihulka S. (2006) Vegetative regeneration of biennial *Oenothera* species after a disturbance: field observations and an experimental study. *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 Applied Ecology* 9:44–54.
- McPhee CS, Bonser SP, Aarssen LW (1997) The role of apical dominance in the interpretation of adaptive architecture in prostrate plant species. *Ecoscience* 4:490–500.
- Midgley JJ (1996) Why the world's vegetation is not totally dominated by resprouting plants; because resprouters are shorter than reseeders. *Ecography* 19:92–95.
- Otzen D (1977) Life forms of three *Senecio* species in relation to accumulation and utilization of non-structural carbohydrates. *Acta Botanica Neerlandica* 26:401–409.
- Paige KN (1999) Regrowth following ungulate herbivory in *Ipomopsis aggregata*: geographic evidence for overcompensation. *Oecologia* 118:316–323.
- Penzig O (1921–1922) *Pflanzen Teratologie*, 2nd edn. Berlin: Verlag von Gebrüder Borntraeger.
- Piippo S, Huhta AP, Rautio P, Tuomi J (2005) Resource availability at the rosette stage and apical dominance in the strictly biennial *Erysimum strictum* (Brassicaceae). *Canadian Journal of Botany* 83:405–412.
- Piippo S, Hellstrom K, Huhta AP, Rautio P, Tuomi J. (2009) Delayed flowering as a potential benefit-decreasing cost of compensatory regrowth. *Canadian Journal of Botany* 87:837–844.
- R Development Core Team (2008) *R: A language and environment for statistical computing*. Vienna: R Foundation for Statistical Computing, <http://www.R-project.org>
- Rauh W (1937) Die Bildung von Hypocotyl- und Wurzelsprossen und ihre Bedeutung für die Wuchsformen der Pflanzen. *Nova Acta Leopoldiana* 4(24):395–553.
- Rautio P, Huhta AP, Piippo S (2005) Overcompensation and adaptive plasticity of apical dominance in *Erysimum strictum* (Brassicaceae) in response to simulated browsing and resource availability. *Oikos* 111:179–191.
- Reichardt HW (1857) Beiträge zur Kenntniss hypokotylicher Adventivknospen und Wurzelsprosse bei krautigen Dikotylen. *Verhandlungen der Zoologisch-botanischen Vereins in Wien* 7:235–244.
- Sosnová M, Klimešová J (2009) Storage of carbon in relation to life history mode and resprouting ability in short-lived root-sprouter *Rorippa palustris*. *Acta Oecologica* 5:691–697.
- Stearns SC (1992) *The evolution of life histories*. Oxford: Oxford University Press.
- Vilela A, Cariaga R, Gonzalez-Paleo L, Ravetta D (2008) Trade-offs between reproductive allocation and storage in species of *Oenothera* L. (Onagraceae) native to Argentina. *Acta Oecologica* 33:85–92.
- Wise MJ, Abrahamson WG (2007) Effects of resource availability on tolerance of herbivory: a review and assessment of three opposing models. *American Naturalist* 169:443–454.
- Wittrock VB. (1884) Ueber Wurzelsprossen bei kräutigen Gewächsen, mit besonderer Rücksicht auf ihre verschiedene biologische Bedeutung. *Botanisches Centralblatt* 17(8):227–232, 17(9):257–264.
- Wydler H. (1850) Über subcotyledonare Sprossbildung. *Flora* 8(22):337–338.

STUDY II

Does potential bank increase tolerance of short-lived plant to apical meristem damage?

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ABSTRACT

Plants avoid damage caused by herbivory by protecting themselves by chemical or mechanical protection or they tolerate loss of biomass and resprout from reserve meristems. The resprouting capacity depends on different intrinsic and extrinsic factors. Soil nutrients, availability of dormant axillary meristems and competition with other plants are reported as decisive for tolerance. However, a role of potential bud bank (adventitious meristems) initiated only after injury is not known. Analyzing 389 field populations of 22 short-lived monocarpic herbs in Central Europe we have found that with severity of disturbance the number of resprouting axillary branches decreases and at the same time the number of resprouting adventitious shoots increases. This result implies that potential bud bank initiated only after injury (adventitious buds on roots and/or hypocotyle) can enable a plant to overcome a meristem limitation after severe disturbance.

INTRODUCTION

There are two main ways how a plant responds to damage by herbivory: it either avoids injury by protecting itself by chemical or mechanical protection or it tolerates loss of biomass and resprouts from reserve meristems ([van der Meijden et al. 1988](#); [Herms and Mattson 1992](#); [Leimu and Koricheva 2006](#)). Second mechanism is considered to be especially important in relationship between large herbivores (grazers) and perennial plants, however, due to practical reasons it is often studied in short-lived monocarps where lifelong fecundity could be more easily evaluated than in clonal

polycarpic perennials (e.g. [Lennartson et al. 1997](#); [Piipo et al. 2005](#); [Rautio et al. 2005](#); [Martínková et al. 2008](#)).

Early studies revealed that short-lived monocarpic plant which lost apical meristem due to herbivory is able to some degree compensate or even overcompensate biomass loss and increase fitness in comparison with untouched individuals ([Bergelson and Crawley 1992](#); [Lehtilä and Syrjänen 1995](#); [Lennartson et al. 1997](#)). Such overcompensation was reported in numerous species and decreased with disturbance severity where limitations by meristems became important ([Huhta et al. 2003](#)). Meristems kept in dormant state by apical dominance were considered to have bet hedging strategy: in order to provide plant with insurance for one herbivore attack the buds are dormant to be activated by injury ([Tuomi et al. 1994](#); [Nilsson et al. 1996](#)). However, alternative explanation views overcompensation as a side product of apical dominance which enables height growth at the expense of branching under competition ([Aarssen 1995](#)). Moreover, branching is affected not only by disturbance and competition, it positively correlates with nutrient availability ([Benner 1988](#); [Rautio et al. 2005](#)).

Nutrients, competition and meristems were recognized as principal players in plant response to apical meristem damage. The respective roles of the tree factors have been predicted in set of models (see summary in [Banta et al. 2010](#)) and have been tested in numerous pot experiments ([Benner 1988](#); [Rautio et al. 2005](#); [Boalt and Lehtilä 2007](#); [Banta et al. 2010](#)), with variable results not only for different plant species but also for different populations of one species. One of the reasons for this could be decoupling of a level of environmental factors (nutrient availability and competition) on which examined populations were adapted and the levels in which they were grown in experiments ([Alward and Joern 1993](#)). This drawback could be overcome when plants are studied in field un-manipulated conditions. To test which factor is limiting plant tolerance after apical meristem damage, i.e. nutrients, competition or meristems we studied field populations of 21 short-lived monocarps from Central Europe. We selected species which have not only axillary meristems along a shoot, so far considered as a sole source of meristems for plant tolerance, but also are capable of sprouting from adventitious buds on hypocotyle and/or roots (otherwise meristemless plant

organs). The adventitious sprouting is usually triggered by severe injury to plant body (Klimešová and Martínková 2004, Malíková et al. 2010) therefore we could consider adventitious buds as a reserve fund created by a plant specifically for a case of damage (potential bud bank sensu Klimešová and Klimeš 2007). We can ask, however, whether adventitious sprouting is affected by extrinsic and intrinsic factors similarly as axillary branching. In the preceding study (Malíková et al. 2010) we examined effect of environmental characteristics such as light, soil nitrogen, moisture, soil cementation, total cover of the herb layer, temperature and species richness of the community on adventitious sprouting of short-lived plants. However, only disturbance and plant size were responsible for the observed variability in number and length of adventitious sprouts. Therefore in this study we want to test whether disturbed *versus* undisturbed plants and axillary branching *versus* adventitious sprouting differ in their response to environmental factors such as soil moisture, nutrients, herb cover, light availability and degree of disturbance.

MATERIAL AND METHODS

SAMPLING

22 species of monocarpic short-lived herbs that were reported as being capable of adventitious sprouting from the hypocotyle and/or roots (Klimešová and Klimeš 2006; Klimešová and de Bello 2009) were studied in the field. Populations of annuals and biennials were sampled in different habitats and environmental conditions mainly in the Czech Republic (Central Europe) from 2005 to 2007. The list of studied species, number of sampled populations and individuals is in Table 1, page 16). Measured plant traits were as follows: plant height, number of axillary branches, cumulative length of adventitious shoots, number of adventitious buds and shoots.

A disturbance was assessed as a proportion of main shoot which was removed by disturbance (intensity of disturbance was assessed according to scale: 1 - mild disturbance removing minority of aboveground of biomass, 2 - stronger disturbance removing majority of aboveground parts of plants,

however the axillary branches of stem base are survived, 3 – severe disturbance removing whole aboveground of biomass including cotyledons). Communities where sufficient numbers of individuals of a target species occurred were described using phytosociological relevés (van der Maarel 2007): all species in a relevé were determined and their cover estimated (Braun–Blanquet scale r = 0.05–0.5 %, + = 0.5–2.5 %, 1 = 2.5–7.5 %, 2a = 7.5–15 %, 2m = 15–22.5 %, 2b = 22.5–37.5 %, 3 = 37.5–62.5 %, 4 = 62.5–87.5 %, 5 = 87.5–100 %). Thus, the following community characteristics were also assessed: total vegetation cover and cover of individual species.

Environmental characteristics for the studied populations were assessed using Ellenberg indicator values for light, humidity and nitrogen (Ellenberg 1986). Values of the environmental characteristics for individual populations were calculated as a weighted average of indicator values for individual species, weighted by the estimated species abundance.

DATA ANALYSIS

Our analyses are based on extensive dataset (389 field populations of 22 species) with multiple species, each represented by multiple populations with many individuals. Some of the tested predictors, however, are measured at the level of whole populations (sites) and compared species bear a phylogenetic signal, so statistical models must take both aspects into account.

Because we expected, for the studied environmental characteristics, that the plant response might not have a monotonous character and such a response might substantially deviate from a symmetric second order polynomial shape, we have replaced the (semi-)quantitative estimates of each environmental property by a classification into three groups of approximately identical size, using 0.33 and 0.67 quantiles. This approach provides sufficient resolution for addressed questions and avoids the use of less-commonly adopted approaches of, say, generalized additive models, and resulting descriptors are also very straightforward to include within interaction terms.

We have tested our hypotheses by using linear mixed-effect models or generalized mixed-effect models (assuming quasi-Poisson distribution), depending on the kind of response variable, using population and species

identity as random effects. When comparing the effects of explanatory variables upon disturbed and un-disturbed plants, we have both looked at their independent (marginal) effects within each group, but also fitted a model comparing the response between these two groups using an interaction term including disturbance status. Hypothesis tests used a likelihood-ratio statistics, comparing the difference in model deviances with a χ^2 distribution. All models were fitted using the *lme4* package in R, version 2.8 (R Development Core Team 2008).

To take possible phylogenetic inertia in the traits of compared plant species into account, phylogenetic corrections using the method of Desclaves et al. (2003) were applied, where appropriate. This did not include the plant height and number of branches, where among-species differences were removed, so there was no phylogenetic signal left.

RESULTS

Competition (herb layer cover) light availability and soil conditions affected growth characters of disturbed and undisturbed plants differently (see results for Difference in Tables 1-4) although relationships were seldom significant when evaluating effect of studied factors on undisturbed and disturbed plants separately. Undisturbed plants were higher with increasing herb layer cover (Table 1), had less and shorter adventitious shoots and buds with increasing light conditions and more of them with increasing moisture and soil nutrients (Tables 3, 4). Effect of moisture and nutrients disappear after correcting for phylogeny, indicating that the trend was caused by the same response of closely related species (old specialization).

Disturbed plants were also higher with increasing herb layer cover (Table 1) and moreover, they produced in those conditions also higher number of axillary branches (Table 2) and lower number of adventitious shoots (Table 3). Disturbed plants were further affected by light availability in the same direction as undisturbed plants: they produced less and shorter adventitious shoots under higher light conditions (Table 3, 4). Alike in undisturbed plants this relationship disappeared after phylogenetic correction due to different behavior of whole groups of related species.

Table 1. Effects of environmental characteristics upon plant height. Effects of individual predictors (major columns) were assessed separately for each kind of model (rows) representing, respectively, undisturbed plants, disturbed plants, and a difference in response between disturbed and undisturbed plants. For the first two model kinds, the response of the plant height to increasing values of a predictor is presented graphically using up and down arrows, while the ☼ symbol indicates a significant interaction term further characterized in the text. Test statistic is a likelihood ratio to be compared with χ^2 distribution with 2 degrees of freedom. Type I error estimate (significance) is shown in parentheses for values below 0.1.

	Herb layer cover		Light		Soil moisture		Nutrient availability	
	Effect	Test	Effect	Test	Effect	Test	Effect	Test
Undisturbed	▲	28.7 (<1.0e-6)	-	4.42 (NS)	-	3.32 (NS)	-	3.08 (NS)
Disturbed	▲	7.96 (0.0187)	-	3.95 (NS)	-	1.02 (NS)	-	0.00 (NS)
Difference	-	1.35 (NS)	☼	55.6 (<1.0e-6)	☼	17.4 (0.00016)	☼	5.40 (0.0672)

Table 2. Effects of environmental characteristics upon the number of axillary branches. Effects of individual predictors (major columns) were assessed separately for each kind of model (rows) representing, respectively, undisturbed plants, disturbed plants, and a difference in response between disturbed and undisturbed plants. For the first two model kinds, the response of the number of branches to increasing values of a predictor is presented graphically using up and down arrows, while the ☼ symbol indicates a significant interaction term further characterized in the text. Test statistic is a likelihood ratio to be compared with χ^2 distribution with 2 degrees of freedom. Type I error estimate (significance) is shown in parentheses for values below 0.1.

	Herb layer cover		Light		Soil moisture		Nutrient availability	
	effect	test	effect	test	Effect	test	Effect	Test
Undisturbed	-	1.16 (NS)	-	0.77 (NS)	-	0.05 (NS)	-	2.28 (NS)
Disturbed	▲	6.32 (0.0425)	-	0.22 (NS)	-	0.30 (NS)	-	2.98 (NS)
Difference	-	4.04 (NS)	☼	7.58 (0.0226)	-	4.14 (NS)	☼	12.5 (0.00194)

Table 3. Effects of environmental characteristics upon the number of adventitious buds and shoots. Effects of individual predictors (major columns) were assessed separately for each kind of model (major rows) representing, respectively, undisturbed plants, disturbed plants, and a difference in response between disturbed and undisturbed plants. For the first two model kinds, the response of the number of buds and shoots to increasing values of a predictor is presented graphically using up and down arrows, while the ☼ symbol indicates a significant interaction term further characterized in the text. Test statistic is a likelihood-ratio to be compared with χ^2 distribution with 2 degrees of freedom. Type I error estimate (significance) is shown in parentheses for values below 0.1, and the results shown in *corrected* rows represent models including phylogenetic corrections.

		Herb layer cover		Light		Soil moisture		Nutrient availability	
		effect	Test	effect	test	effect	Test	effect	test
Undisturbed	Corrected	-	2.24 (NS)	▼	9.50 (0.00867)	-	2.40 (NS)	-	0.78 (NS)
	non-corrected	-	0.79 (NS)	▼	26.8 (1.53e-6)	▲	15.8 (0.00037)	▲	17.8 (0.00014)
Disturbed	Corrected	▼	10.8 (0.00454)	-	3.89 (NS)	-	0.62 (NS)	-	0.63 (NS)
	non-corrected	-	1.61 (NS)	▼	10.1 (0.00655)	-	0.93 (NS)	-	1.02 (NS)
Difference	Corrected	☼	79.0 (<1.0e-6)	☼	77.1 (<1.0e-6)	☼	64.8 (<1.0e-6)	-	0.13 (NS)
	non-corrected	☼	79.2 (<1.0e-6)	☼	77.0 (<1.0e-6)	☼	64.9 (<1.0e-6)	-	0.09 (NS)

Table 5. Effect of the severity of disturbance upon the number of axillary branches and of adventitious buds and shoots. The response of the number of axillary branches or of the buds and shoots to increasing severity of disturbance is presented graphically using up and down arrows. Test statistic is a likelihood-ratio to be compared with χ^2 distribution with 1 degree of freedom. Type I error estimate (significance) is shown in parentheses for values below 0.1, and the results shown in *corrected* rows represent models including phylogenetic corrections.

		Disturbance severity	
		effect	Test
Axillary branches	non-corrected	▼	72.7 (<1.0e-6)
	corrected	▲	6.36 (0.0117)
Buds and shoots	non-corrected	▲	6.55 (0.0105)

Table 4. Effects of environmental characteristics upon the cumulative length of adventitious shoots. Effects of individual predictors (major columns) were assessed separately for each kind of model (major rows) representing, respectively, undisturbed plants, disturbed plants, and a difference in response between disturbed and undisturbed plants. For the first two model kinds, the response of the length of shoots to increasing values of a predictor is presented graphically using up and down arrows, while the ☼ symbol indicates a significant interaction term further characterized in the text. Test statistic is a likelihood-ratio to be compared with χ^2 distribution with 2 degrees of freedom. Type I error estimate (significance) is shown in parentheses for values below 0.1, and the results shown in *corrected* rows represent models including phylogenetic corrections.

		Herb layer cover		Light	
		Effect	Test	Effect	Test
Un-disturbed	Corrected	-	1.28 (NS)	▼	5.79 (0.0551)
	non-corrected	-	1.30 (NS)	▼	17.5 (0.00016)
Disturbed	Corrected	-	2.49 (NS)	-	0.56 (NS)
	non-corrected	-	1.34 (NS)	▼	17.0 (0.00021)
Difference	Corrected	☼	33.7 (<1.0e-6)	☼	211.1 (<1.0e-6)
	non-corrected	☼	31.6 (<1.0e-6)	☼	208.2 (<1.0e-6)
		Soil moisture		Nutrient availability	
		Effect	Test	Effect	Test
Un-disturbed	Corrected	-	0.93 (NS)	-	4.37 (NS)
	non-corrected	-	1.36 (NS)	-	2.59 (NS)
Disturbed	Corrected	-	1.21 (NS)	-	1.73 (NS)
	non-corrected	-	0.18 (NS)	-	2.72 (NS)
Difference	Corrected	☼	5.28 (0.071)	☼	15.6 (0.00041)
	non-corrected	☼	6.53 (0.0383)	☼	12.3 (0.00213)

Adventitious sprouting differed from axillary branching by its response to light availability and disturbance severity. Under high light availability, plants produced less and shorter adventitious shoots. Disturbance severity (proportion of main shoot which was lost by disturbance) differently affected resprouting from respective buds: the more severe disturbance the lower number of axillary branches but higher number of adventitious shoots was

recorded in plants from field populations of 22 short-lived monocarps (Table 5).

DISCUSSION

Despite the indication that environmental characteristics affect undisturbed and disturbed plants differently, direct effect was not very pronounced and was usually the same for both plants groups. On the other hand, axillary branching and adventitious sprouting responded uniquely to some environmental factors: while branching did not respond to light, sprouting was reduced by high light availability and branching was decreasing and sprouting increasing as reaction to disturbance severity.

Surprisingly, even some often reported effects, i.e. higher branching of plants in conditions of higher nutrient availability or lower competition (Rautio et al. 2005) were not recorded in our dataset. The reason were not intercorrelations among studied factors, because although high herb layer cover was correlated with soil moisture and nutrients (and not with light!), the relationship was very weak (moisture: $R^2 = 0.018$, $F = 6.55$, d.f. = 357, $p = 0.01$, nutrients: $R^2 = 0.018$, $F = 5.433$, d.f. = 357, $p = 0.02$). On the other hand, adventitious sprouting was supported by high soil nutrients and moisture, but in undisturbed plants only. This result is in contradiction with our previous study (Malíková et al. 2010) where, however, the data were analyzed differently.

In present study, high herb layer cover indicated not only high competitive milieu, but probably also low disturbance. The effect of herb cover layer was with agreement with effect of disturbance severity, both with increasing herb cover and decreasing disturbance severity plants branched more from axillary buds and less resprouted from adventitious buds. This might be caused either by fact that the herb layer cover reflected action of disturbance on community level, proportion of lost main shoot (severity of disturbance) on individual level or that plants in looser vegetation are more prone to disturbance (herbivory). In the first case it would indicate that disturbance in our study was large scale, i.e. rather than affecting only individual plants it affected whole community and caused decreasing of

competition, in second case it would indicate that disturbance was affected by vegetation structure. Although we present our study in a framework of herbivory, the first case would mean that studied plant populations were rather affected by anthropogenic large scale disturbance. Concerning the fact, that weeds of arable land and plants of antropogenous habitats were prevailing in our dataset, first option is highly probable and question whether we could interpret our data in framework of herbivory arose. Anthropogenic influence on vegetation is not comparatively long as influence of herbivores, however, habitats disturbed by human activity are occupied by pre-adapted plants and although disturbance caused by human is very specific, we can always found very similar types of disturbance caused by some natural agent (Shea et al. 2004).

Interesting finding was negative effect of high light environment on number and length of adventitious sprouts consistent for both disturbed and undisturbed plants. This result imply that behavior of adventitious sprouting differ from the pattern usually observed for axillary branching (Aarssen 1995, Rautio et al. 2005). Suppression of number and length of adventitious sprouts by high light conditions probably has something to do with hormonal regulation of adventitious sprouting which is supported by low auxin-cytokinin ratio (Kerstetter and Hake 1997), the conditions which are typical for low apical dominance e.g. in prostrate growth forms (Malíková et al. 2010) or in plants losing their shoot by severe disturbance (Horvath 1998; Klimešová and Martínková 2004).

In the field study, branching and sprouting were limited neither by soil quality nor by competition, however, with increasing severity of disturbance branching (from axillary buds) but not sprouting (from adventitious buds) was limited by availability of dormant meristems. This indicates that reason why tests of tolerance where a role of nutrients and competition are examined give various results might be lack of generality in this relationships when examining the plants in their natural environment (see introduction). On the other hand, the prominent role of dormant meristems and specifically a role of potential bud bank were revealed. This result is in accordance with a model by Tuomi et al. (1994) where authors find out that easy bud activation is selected for in populations with high probability of one herbivore attack. More complicated

bud dormancy, on the other hand, might be favorable when repeated damage is operating or in the case of intense herbivory (Tuomi et al. 1994). In our study, plants damaged only slightly were responding by branching from easily activated axillary buds and severely injured plants with a few axillary buds left resprouted from adventitious buds. Adventitious sprouting needs more intensive stimuli, it takes longer time for development of shoots and shoots are less branched (Bartušková and Klimešová 2010).

Tolerance to disturbance in our studied system was limited only by availability of meristems and this limitation was overcome due to ability of plants to produce adventitious buds - potential bud bank. We have not found any simple relationship between branching or sprouting and availability of nutrients, soil moisture and competition across 22 species and 389 their populations growing in natural conditions, this we believe allows us to conclude that effect of competition and nutrient availability on branching and sprouting (tolerance) after apical meristem damage is not general.

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REFERENCES

- Alward RD, Joern A (1993) Plasticity and overcompensation in grass responses to herbivory. *Oecologia* 95:358-364.
- Aarssen LW (1995) Hypotheses for coevolution of apical dominance in plants: implications for the interpretation of overcompensation. *Oikos* 74(1):149-156.
- Bartušková A, Klimešová J (2010) Reiteration in the short-lived root-sprouting herb *Rorippa palustris*: does the origin of buds matter? *Botany* [in press].
- Banta AJ, Stevens MHH, Pigliucci M (2010) A comprehensive test of the 'limiting resources' framework applied to plant tolerance to apical meristem damage. *Oikos* 119:359-369.
- Benner LB (1988) Effects of apex removal and nutrient supplementation on branching and seed production in *Thlapsi arvense* (Brassicaceae). *Amer. J. Bot.* 75(5):645-651.

- Bergelson J, Juenger T, Crawley MJ (1992) Regrowth following herbivory in *Ipomopsis aggregata*: compensation but not overcompensation. *Am. Nat.* 148:744-755.
- Boalt E, Lehtila K (2007) Tolerance to apical and foliar damage: costs and mechanisms in *Raphanus raphanistrum*. *Oikos* 116:2071-2081.
- Desdevises Y, Legendre P, Azouzi L, Morand S (2003) Quantifying phylogenetically-structured environmental variation. *Evolution* 57:2647-2652.
- Ellenberg H (1986) *Vegetation ecology of central Europe*, 4th edn. Cambridge: Cambridge University Press.
- Hermes DA, Mattson WJ (1992) The dilemma of plants – to grow or defend. *Quarterly Review of Biology* 67:283-335.
- Horvath DP 1998 The role of specific plant organs and polar auxin transport in correlative inhibition of leavy spurge (*Euphorbia esula*) root buds. *Canadian Journal of Botany* 76:1227-1231.
- Huhta AP, Hellstrom K, Rautio P, Tuomi J (2003) Grazing tolerance of *Gentianella amarella* and other monocarpic herbs: why is tolerance highest at low damage levels? *Plant Ecology* 166:49-61.
- Kerstetter R and Hake S (1997) Shoot meristem formation in vegetative development. *The Plant Cell* 9:1001-1010.
- Klimešová J, de Bello F (2009) CLO-PLA: the database of clonal and bud bank traits of Central European flora. *J. Veget. Sci.* 20: 511–516.
- Klimešová J, Klimeš L (2006) CLO-PLA3 – the database of clonal and bud bank traits of Central European flora. <http://clopla.butbn.cas.cz>.
- Klimešová J, Klimeš L 2003 Resprouting of herbs in disturbed habitats: it is adequately described by Bellingham-Sparow's model? *Oikos* 103:225–229.
- Klimešová J, Klimeš L (2007) Bud banks and their role in vegetative regeneration – a literature review and proposal for simple classification and assessment. *Persp. Plant Ecol. Evol. Syst.* 8:115–129.
- Klimešová J, Martínková J (2004) Intermediate growth forms as a model for the study of plants clonality functioning: an example with root sprouters. *Evol. Ecol.* 18:669–681.
- Lehtilä K Syrjänen K (1995) Compensatory responses of two *Melampyrum* species after damage. *Funct. Ecol.* 9:511-517.
- Leimu R, Koricheva J (2006) A meta-analysis of tradeoffs between plant tolerance and resistance to herbivores: combining the evidence from ecological and agricultural studies. *Oikos* 112:1-9.
- Lennartsson Tuomi J, Nilsson P (1997) Evidence for an evolutionary history of overcompensation in the grassland biennial *Gentianella campestris* (Gentianaceae). *Am. Nat.* 149:1147-1155.
- van der Maarel E (2007) Transformation of cover-abundance values for appropriate numerical treatment – alternatives to the proposals by Podani. *J. Veget. Sci.* 18:767–770.

- van der Meijden E, Wijn M, Verkaar H (1988) Defence and regrowth, alternative plant strategies in the struggle against herbivores. *Oikos* 51:355-363.
- Malíková L, Šmilauer P, Klimešová J (2010) Occurrence of adventitious sprouting in short-lived monocarpic herbs: field study on 22 weedy species. *Ann. Bot.* 105(6):905-912.
- Martínková J, Klimešová J, Mihulka S (2008) Compensation of seed production after severe disturbance in the short-lived herb *Barbarea vulgaris*. *Basic Appl. Ecol.* 9:44-54.
- Nilsson P, Tuomi J, Astrom M (1996) Bud dormancy as a bet-hedging strategy. *Am. Nat.* 147:269-281.
- Piippo S, Huhta AP, Rautio P, Tuomi J (2005) Resource availability at the rosette stage and apical dominance in the strictly biennial *Erysimum strictum* (Brassicaceae). *Botany* 83:405–412.
- R Development Core Team (2008) R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing. <http://www.R-project.org>
- Rautio P, Huhta A-P, Piipo S, Tuomi J, Juenger M, Saari M, Aspi J (2005) Overcompensation and adaptive plasticity of apical dominance in *Erysimum strictum* (Brassicaceae) in response to simulated browsing and resource availability. *Oikos* 111:197-191.
- Shea K, Roxburgh SH, Rauschert ESJ (2004) Moving from pattern to process: coexistence mechanisms under intermediate disturbance regimes. *Ecol. Lett.* 7:491–508.
- Tuomi J, Nilsson P, Astrom M (1994) Plant compensatory responses – bud dormancy as an adaptation to herbivory. *Ecology* 75(5):1429-1436.

STUDY III

Compensatory growth of *Euphorbia peplus* regenerating from a bud bank

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ABSTRACT

Tolerance to very severe disturbance by the annual herb *Euphorbia peplus* L. was examined. We explored the role of disturbance timing, competition, and site productivity on the performance of disturbed plants. Ninety-three percent of disturbed plants survived following disturbance 14 d after plant emergence, whereas only 48% of disturbed plants survived disturbance 42 d after emergence. Early disturbed plants compensated for biomass loss and had higher fecundity than undisturbed plants, but this was not the case for plants that were disturbed at later times following emergence. Field assessment revealed that disturbed plants were, in general, of the same height as undisturbed plants, even under competition. Undisturbed plants had very conservative architecture across various conditions (competition and nutrients), whereas disturbed plants had more branched architecture under moderate competition and nutrient availability. Accordingly, we suggest that *E. peplus* utilizes a bet-hedging strategy where adventitious meristems are reserved for regrowth after a severe disturbance event that removes all dormant axillary meristems. Moreover, we propose that the tolerance to disturbance in short-lived species could play an important role in the ecology of disturbed communities. Finally, the tolerance to disturbance could be one of the prerequisites of invasibility of *E. peplus* in non-native ranges. We also speculate about the potential costs and benefits related with the tolerance to disturbance in short-lived species and about a mechanical control of *E. peplus* in invaded ranges.

INTRODUCTION

Highly and frequently disturbed biotopes, like those formed and maintained by humans, are occupied predominately by short-lived monocarpic herbs (Grime 2001). Their population survival relies largely on regeneration from seeds that are produced between disturbance events (Bellingham and Sparrow 2000). Nonetheless, besides avoidance, many short-lived monocarps are able to tolerate disturbance and regenerate from dormant buds (Klimešová and Klimeš 2003). However, bud scarcity, as well as low levels of carbohydrate storage, may constrain the regeneration and compensation for biomass loss (Huhta et al. 2000a, 2000b, 2003). Nevertheless, some short-lived monocarpic herbs are also able to regenerate from their potential bud bank (sensu Klimešová and Klimeš 2007, referred to as a bud bank in the text). The bud bank is formed de novo on otherwise meristemless organs, such as roots or hypocotyls, and may enable vegetative regeneration after very severe disturbance that results in the loss of some or all aboveground organs. This ability is found in 13% of biennial and 2% of annual species of central Europe (Klimešová and Klimeš 2003; Malíková et al. 2010).

Although the ability to regenerate via adventitious sprouting after disturbance is an additive strategy for short-lived species, which might represent an advantage in coping with various stressful conditions (Klimešová and Martínková 2004; Tassin et al. 2007; Theoharides and Dukes 2007), this was not shown for biennial root sprouters (Martínková et al. 2011). Whereas root-sprouting biennials have greater geographical distribution than their nonsprouting congeners, they have a narrower ecological niche (Martínková et al. 2011) because they occupy only disturbed habitats and avoid communities that are less affected by humans (Martínková et al. 2011). This implies that there are costs of root-sprouting strategy associated with bud bank and carbohydrate storage formation, which constrain their competitive ability in undisturbed vegetation. Regarding the higher scarcity of adventitious sprouting in annuals than in biennials or perennials, we can expect even higher costs of resprouting strategy

in annual species. Hence, we assume that the costs of resprouting strategy reflected in lower competitive ability of plants and the decreasing ability of adventitious sprouting with age as possible candidates of constraints of adventitious-sprouting strategy in short-lived species.

Anatomical studies of adventitious-bud formation on the hypocotyl of *Linum usitatissimum* L. (Adams 1924; Crooks 1933; Rauh 1937; Eggers 1946; Link and Eggers 1946; Ishikawa et al. 1997) show that sprouting ability diminishes with aging (Crooks 1933; Rauh 1937; Link and Eggers 1946). Moreover, biennials are able to postpone reproduction to the next season when there has been severe disturbance (Klimešová et al. 2007; Martínková et al. 2008; Piippo et al. 2009), whereas strict annuals are not able to do so, and therefore, a late disturbance might hinder seed ripening despite successful regeneration of plants.

The competitive ability of plants is linked with apical dominance, which is the controlling role of the main shoot in competitive environments, at the expense of lateral branching. Removal of the apical meristem (by herbivory, frost, etc.) releases dormant buds from its control (e.g., Bergelson and Crawley 1992; Aarssen 1995; Lehtilä and Syrjänen 1995; Lennartsson et al. 1997, 1998; Huhta et al. 2000a, 2000b, 2003; Hellström et al. 2004; Latzel et al. 2009a) and results in shorter but more branched morphology of resprouted plants than that of nonsprouted (undisturbed) plants (Midgley 1996). This effect is considered either as a cost of apical dominance (Aarssen 1995; Agrawal 2000) or as a kind of bet-hedging strategy that enables plants to compensate for biomass and seed loss after injury through production of more flowering modules (Crawley 1987; Vail 1992; Tuomi et al. 1994; Nilsson et al. 1996).

To test whether lower competitive ability of resprouted individuals and diminishing ability of adventitious sprouting with aging are constraints of resprouting strategy in short-lived species, we conducted a growth-chamber manipulative experiment and a field survey with *Euphorbia peplus* L. In the manipulative study, we tested whether adventitious sprouting from the hypocotyl is affected by disturbance timing. In the field survey, we assessed individuals of

33 populations for their architecture in relation to their competitive milieu and the productivity of the community. *Euphorbia peplus* was selected as a target species for its common distribution in central European flora. The species is native in Europe, however, it is often introduced and invasive in other regions (e.g., Australia and Pacific offshore islands, [Orchard \(1994\)](#); French Polynesia, [Florence \(1997\)](#); and the USA, [Wagner et al. \(1999\)](#)).

MATERIAL AND METHODS

MANIPULATIVE STUDY

Individuals of four populations of *E. peplus* plants were considered in the manipulative study. Seeds of each population were collected from at least 30 individuals. The seeds of the first and second populations were collected in České Budějovice, Czech Republic; the individuals of the first population were growing between pavement and a house wall with falling facade, and the individuals of the second population were growing in a decorative flower bed. The seeds of the third and fourth populations were collected in Mladá Boleslav, Czech Republic; the individuals of the third population were growing in shrubs in front of a house, and the individuals of the fourth population were growing approximately 40 m from the previous population on the edge of shrubs.

Altogether, 280 individuals of all populations were established on 26 November 2007 in a growth chamber. Forty individuals (10 of each population) were randomly chosen as controls and were, thus, cultivated without any manipulation. One-hundred and twenty individuals (30 of each population) were excised below the cotyledons 14 d after establishment (10 December 2007, further referred to as disturbance 1), and another 120 individuals were excised below the cotyledons 42 d after establishment (7 January 2008, further referred to as disturbance 2). Individuals of the control group were harvested 63 d after sowing, individuals of the first disturbed group were harvested 77 d after sowing (i.e., 63 d after the disturbance event), and individuals of the latest disturbed

group were harvested 105 d after sowing (63 d after disturbance). This approach allowed for the analyses of plants in phenological comparable stages, i.e., in the peak of their growth when their aboveground parts were the same age.

The study was carried out in a growth chamber where the temperature and light conditions were controlled. The mean light and dark temperatures were 22 °C and 20 °C, respectively, and light conditions were maintained at a 14 h light: 10 h dark photoperiod. The light level averaged 180 $\mu\text{mol m}^{-2} \text{s}^{-1}$ photosynthetically active radiation (400–700 nm) in the growth chamber. The mean air humidity was regulated at 70%. Plants were planted in pots (9 cm diameter and 7 cm depth) that were filled with a soil – bare sand mixture of 2:3 (v/v).

At harvest time, the following parameters were recorded: the length of the main shoot (controls) or the longest adventitious shoot (disturbed individuals), number of adventitious shoots, number of the first- and second-order branches of all shoots, number of internodes of all shoots, number of flowers (considered as a fecundity estimate), and aboveground dry biomass (dried at 80 °C for 24 h).

FIELD STUDY

Thirty to fifty individuals of 33 populations of *E. peplus* were sampled in different habitats and environmental conditions in the Czech Republic (central Europe) during 2005–2007. All individuals were assessed for their height, number of branches of the first order, number of adventitious shoots, and presence or absence of fruits. Plants were also assessed for their disturbance history (whether they were injured). Injury was defined as a loss of a part of the primary shoot or the whole primary shoot. Such loss was easily detectable in natural conditions. Each locality was described according to herb layer in a 5 m × 5 m quadrat and was used as an estimate for the degree of competition in the locality. The herb cover was estimated and divided into five categories: 0%–20%, 21%–40%, 41%–60%, 61%–80%, and 81%–100%. The fertility of a site was characterized by using Ellenberg indicator values for nitrogen ([Ellenberg 1986](#))

based on herbaceous species presented on a site. Values of Ellenberg indicator for nitrogen for individual populations were calculated as a weighted average of indicator values of individual species, weighted by the estimated species abundance in a community. Consequently, communities were put into three groups of site fertility (low, moderate, and high nitrogen availability) according to nutrient demand of their resident species. These three groups were used in statistical analyses.

STATISTICAL ANALYSES

Manipulative study

The effect of disturbance on regeneration of treated plants was evaluated by the generalized linear model method with a binomial distribution (regenerating, yes or no). All other analyses were performed using the factorial ANOVA method, and the population was used as a covariate in the model. Created biomass, the main shoot length, number of shoots, number of branches of the first and second order, number of internodes, and number of flowers were used as fixed effects.

Field study

Because individuals of 19 out of 33 populations did not experience a disturbance event or had less than five disturbed individuals recorded, we did not include plants of those populations in the analyses. In addition, because the assessment of individual populations occurred during a broad time period, we did not test the population as a main effect. The potential differences between populations could be attributed to a different time of observation rather than to differences among populations. Thus, disturbance history, competition (forbs canopy cover divided into five categories, 0%–20%, 21%–40%, 41%–60%, 61%–80%, 81%–100%), and fertility of a site (three categories, 0–5, 5–7.5, and 7.5–10

according to Ellenberg 1986) were the main fixed effects, and the time of observation together with the population type were performed as covariates in a factorial ANOVA model.

Statistical analyses were performed in the S Plus software package (Mathsoft 2000).

RESULTS

REGROWTH FOLLOWING DISTURBANCE

Ninety-three percent of plants regenerated when they were disturbed 14 d after sowing compared with 48% that regenerated when plants were disturbed 42 d after sowing (Tables 1 and 2). Individuals disturbed 14 d after sowing compensated for biomass loss but plants disturbed later did not (Tables 1 and 2). Undisturbed plants of the first population formed the longest shoots when compared with disturbed plants, followed by plants that were disturbed 14 d after sowing. Undisturbed individuals developed one main shoot, whereas disturbed individuals formed two adventitious shoots on average (Tables 1 and 2). Disturbed plants developed more branches (both of the first and second order), as well as produced more internodes, compared with undisturbed plants. Plants disturbed 14 d after sowing formed slightly more branches than those disturbed 42 d after sowing, but the number of internodes did not differ (Tables 1 and 2). Plants disturbed 14 d after sowing produced more flowers than either of the two other treatments (Tables 1 and 2).

FIELD STUDY

Disturbed plants were of the same size as undisturbed plants but developed significantly more branches and adventitious shoots (Tables 3 and 4). Competition (leaf cover of a herb community) strongly affected plant height, branching, and number of adventitious shoots; plants were taller in a highly

competitive environment (Tables 3 and 4) and formed more branches and adventitious shoots when they were grown in a moderately competitive environment. Also, nutrient level of a locality significantly affected all observed parameters; the tallest plants with the highest number of branches and adventitious shoots were found in moderately productive sites. Plant height and number of adventitious shoots were also differently affected by the competition and disturbance history of plants (interaction of competition and disturbance is shown in Table 3 and Fig. 1). Individuals were tallest when they were disturbed and grown under either the lowest or highest competition. In moderate competition, undisturbed plants were taller than disturbed ones. Overall, the highest number of adventitious shoots was observed in moderately competitive environments, but disturbed plants developed many more adventitious shoots than undisturbed plants (Table 3 and Fig. 2).

Table 1. Results of the manipulative study: generalized linear model (GLM) and ANOVA analysis of the effect of disturbance on regeneration and growth of *Euphorbia peplus*.

	Df	Regeneration		Biomass		Main shoot length		Shoot number	
		χ^2	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Disturbance history	2 (1)	35.58	0.000	84.37	0.000	19.83	0.000	30.76	0.000
Covariate	3 (3)	15.86	0.001	3.70	0.013	4.26	0.006	3.51	0.016
	Df	Branches 1st order		Branches 2nd order		Internodes		Flowers	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Disturbance history	2	26.86	0.000	53.41	0.000	29.29	0.000	57.40	0.000
Covariate	3	4.19	0.006	4.19	0.006	4.34	0.005	4.02	0.008

Note: The df for regenerative success analysis (using GLM) is presented in parentheses. Statistically significant results are in bold.

Tab 2. Growth characteristics of disturbed and undisturbed *Euphorbia peplus* plants.

		Regeneration (%)	Biomass (g)	Shoot length (cm)	Shoots number
Cumulative dataset	Control	100	0.6±0.03	10.7±0.17	1±0.12
	Injury 1	93±2	0.7±0.02	10.9±0.10	1.9±0.07
	Injury 2	48±5	0.3±0.02	9.9±0.14	2.1±0.10
1 st population	Control	100	0.67±0.05	11.8±0.32	1±0.23
	Injury 1	97±6	0.67±0.02	10.9±0.19	2±0.13
	Injury 2	57±6	0.29±0.04	10.1±0.25	1.8±0.17
2 nd population	Control	100	0.63±0.05	10.2±0.32	1±0.22
	Injury 1	97±6	0.69±0.03	10.6±0.18	2.2±0.13
	Injury 2	37±6	0.36±0.05	9.7±0.30	2.5±0.22
3 rd population	Control	100	0.55±0.05	10.5±0.32	1±0.23
	Injury 1	83±6	0.60±0.03	11.4±0.20	1.6±0.14
	Injury 2	20±6	0.34±0.07	9.9±0.41	1.7±0.29
4 th population	Control	100	0.64±0.05	10.2±0.32	1±0.23
	Injury 1	97±6	0.63±0.03	11.0±0.19	1.9±0.14
	Injury 2	80±6	0.31±0.03	9.8±0.21	2.1±0.15
		Branches 1st order	Branches 2nd order	Internodes	Flowers
Cumulative dataset	Control	8.2±0.68	10.3±0.95	18.8±2.34	126.3±7.81
	Injury 1	13.8±0.41	21.4±0.57	37.7±1.40	168.9±4.67
	Injury 2	11.5±0.56	17.4±0.79	39.1±1.95	86.2±6.49
1 st population	Control	9±1.3	10.6±1.86	19.3±4.60	120.2±15.27
	Injury 1	15.1±0.78	22.3±1.09	38.3±2.70	164.2±8.97
	Injury 2	10.9±1.02	16.8±1.13	36.9±3.52	75.4±11.71
2 nd population	Control	8.1±1.32	10.8±1.86	19±4.60	122±15.27
	Injury 1	15.17±0.77	23.6±1.07	44.1±2.65	186±8.82
	Injury 2	13.8±1.26	21.1±1.78	49.2±4.38	97.6±14.56
3 rd population	Control	8±1.33	10.6±1.86	19.1±4.59	123.6±15.3
	Injury 1	12.6±0.84	19.8±1.18	33.1±2.91	138.6±9.66
	Injury 2	11.2±1.71	17.2±2.41	32.7±5.93	92±19.72
4 th population	Control	7.6±1.33	9.2±1.86	17.6±4.60	139.4±15.27
	Injury 1	11.9±0.79	19.5±1.1	34.3±2.75	182.5±9.13
	Injury 2	10.9±0.86	16.2±1.20	37.5±2.97	87.1±9.86

Note: Mean values and standard errors of mean for the cumulative dataset and for plants of each population are included. Injury 1 plants were disturbed 14 d after establishment and injury 2 plants were disturbed 42 d after establishment.

Table 3. Results of the field survey: ANOVA analysis of the effect of disturbance history and competition on plant performance of *Euphorbia peplus*.

	Df	Shoot length		No. of branches		No. of adventitious shoots	
		F	P	F	P	F	P
Disturbance history (D)	1 (586)	1.193	0.165	34.092	0.000	46.505	0.000
Competition (C)		59.161	0.000	24.974	0.000	5.562	0.000
Nutrients (N)		19.66	0.000	13.952	0.000	11.346	0.000
D x C		2.844	0.023	0.587	0.674	4.135	0.002
D x N		0.638	0.529	7.422	0.001	6.112	0.002
C x N		15.915	0.000	2.187	0.140	0.971	0.324
D x C x N		0.249	0.618	1.570	0.211	0.778	0.378
Covariate		87.856	0.000	4.578	0.000	9.121	0.000

Note: Statistically significant results are in bold. The df for regenerative success analysis (using GLM) is presented in parentheses.

Table 4. Growth characteristics of plants of all populations of *Euphorbia peplus* in relation to disturbance history and competition. Mean values and standard errors of a mean for cumulative dataset.

		Shoot length (cm)	No. of branches	No. of adventitious shoots
Disturbance History	Undisturbed	15.20±0.43	1.37±0.09	0.02±0.02
	Disturbed	15.48±0.82	2.09±0.17	0.16±0.04
Competition	0-20%	12.32±1.74	1.53±0.37	0.00±0.09
	21-40%	13.55±0.75	2.53±0.16	0.19±0.07
	41-60%	12.04±0.58	2.05±0.12	0.24±0.03
	61-80%	19.99±1.01	1.65±0.22	0.00±0.05
	81-100%	18.80±0.61	0.88±0.13	0.00±0.03
Nutrients	3-6	13.78±0.68	1.52±0.14	0.01±0.03
	6.1-7.5	16.38±0.39	1.62±0.08	0.12±0.02
	7.6-9	10.82±1.30	1.47±0.28	0.00±0.07

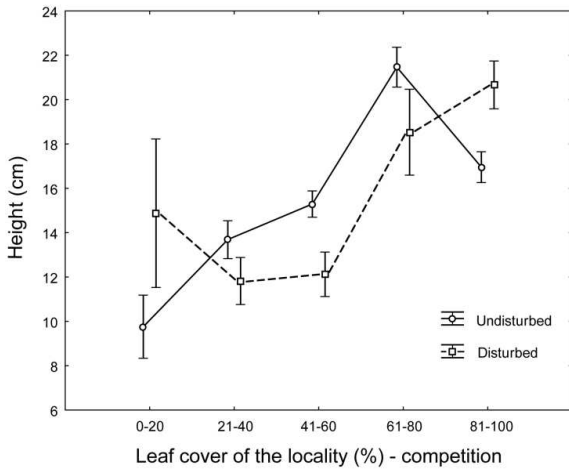


Fig. 1. Height of main or adventitious shoots of *Euphorbia peplus* in relation to disturbance history and competition in the field survey. Means and SE are shown. Statistical results for interaction disturbance and competition: $F = 2.8$, $P = 0.023$, and see also Table 3.

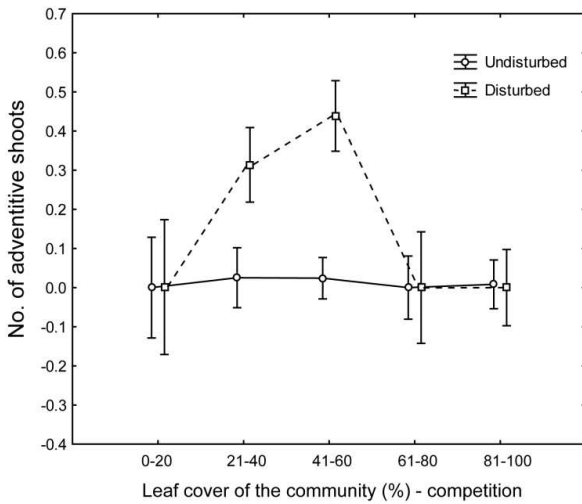


Fig. 2. The number of adventitious shoots of *Euphorbia peplus* in relation to disturbance history and competition in the field survey. Means and SE are shown. Statistical results for interaction disturbance and competition: $F = 4.1$, $P = 0.002$, and see also Table 3.

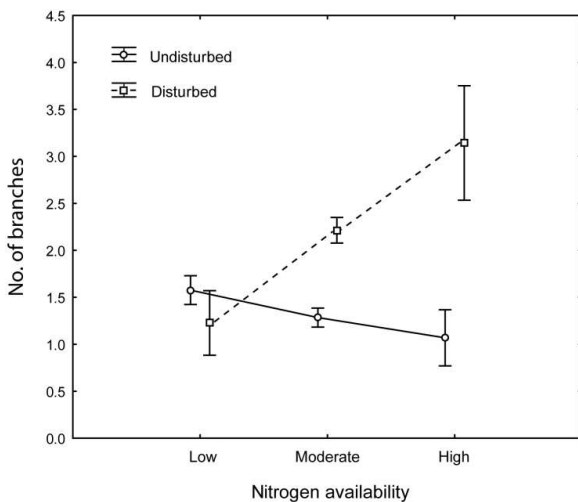


Fig. 3. The number of branches formed by disturbed and undisturbed plants of *Euphorbia peplus* in relation to available nitrogen in localities. Means and SE are shown. Statistical results for interaction disturbance and nutrients: $F = 7.4$, $P = 0.001$, and see also Table 3.

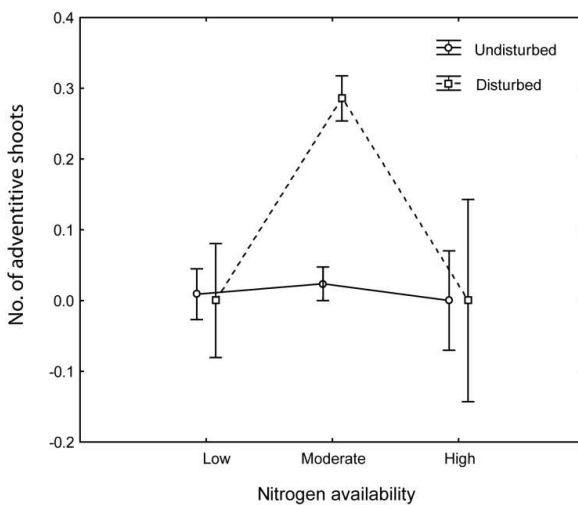


Fig. 4. The number of adventitious shoots of *Euphorbia peplus* formed by disturbed and undisturbed plants in relation to available nitrogen in localities. Means and SE are shown. Statistical results for interaction disturbance and nutrients: $F = 6.1$, $P = 0.002$, and see also Table 3.

The performance of disturbed and undisturbed plants also differed in relation to the nitrogen availability of the locality (interaction of disturbance and nutrients is shown in Table 3). The number of branches slightly decreased with increasing nitrogen availability in the case of undisturbed individuals, whereas the number of branches increased with increasing nitrogen availability in the case of disturbed plants (see Fig. 3). The higher number of adventitious shoots was observed for disturbed plants that were found in moderately fertile sites, but the number of adventitious shoots was not affected by the nitrogen availability if plants were undisturbed (Fig. 4).

DISCUSSION

In the manipulative experiment, we confirmed that injury timing is important for successful regeneration from adventitious meristems, compensation for biomass, and seed production. Plants injured early in ontogeny were able to compensate for biomass loss and fecundity, whereas plants injured later were less successful in regeneration and compensation.

In the field survey, the higher herb cover used as an estimate of competitive milieu in a community led to reduced branching of both injured and uninjured individuals. Disturbed plants were, on average, of the same size as undisturbed plants. The maximum branching intensity was found in conditions of intermediate competition and nutrients, which indicates that sites with low competitive pressures were probably characterized by abiotic stress that reduced both the cover of herbs and the branching of target plants.

Our study showed that central European populations of the annual herb *E. pepplus* are able to overcome severe disturbance, particularly if injured in an early ontogenetic phase. The field survey confirmed that vegetative regeneration after disturbance occurs in natural populations of *E. pepplus*. Nonetheless, because we only had snapshot data from natural populations, we were only able to observe successfully regenerated individuals. This prevents an accurate evaluation of how common or successful vegetative regeneration is in natural populations. For

example, the better performance of disturbed over undisturbed plants in the most competitive environment might be due to the fact that only the largest individuals in benign microsites were able to survive up to the time of our census. Less successful plants may have died or the largest plants in the population may have succumbed to other factors. Despite the above mentioned limitations, the regenerated robust plants imply that the resprouting strategy might provide a selective advantage.

TIMING OF DISTURBANCE AND CONSTRAINS OF RESPROUTING STRATEGY

Phylogenetic analyses revealed that sprouting is not restricted to certain families but is distributed within and between species in the same clades and is widespread across clades (Ojeda 1998; Bond and Midgley 2003; Vesk and Westoby 2004a). As experimental studies are usually in agreement that adventitious sprouting is a beneficial strategy in disturbed biotopes (Martínková et al. 2004a, 2004b, 2006, 2008; Klimešová et al. 2007, 2008; Latzel et al. 2008), the relatively low distribution of this strategy among short-lived forbs points out some ecological and (or) physiological limitations of the strategy (Martínková et al. 2011; see also Introduction). Our study shows that the advantage of adventitious sprouting is expressed particularly if disturbance occurs in juvenile stages of plants. Indeed, the later the disturbance, the worse the regenerative success and regrowth. The worse regeneration suggests costs of resprouting in the case of late disturbance, even when adventitious budding represents lower upfront costs in comparison with axillary buds since adventitious buds are usually formed only after injury (Vesk and Westoby 2004b). When disturbance comes at the time of plant flowering, carbon storage may already be used for generative structures (Sosnová and Klimešová 2009), and moreover, there are anatomical constrains of epidermal bud formation later in development (Link and Eggers 1946). Consequently, we suggest that regeneration from adventitious buds should be preferred in biotopes where disturbance occurs shortly after plant

emergence, i.e., in arable lands or river banks. The resprouting from preformed buds (i.e., axillary buds) should be, therefore, preferred in habitats where disturbance is not so strong and occurs in later plant phenological stages, e.g., grasslands, forests, and the like.

Other constraints of resprouting strategy might occur if seed production is considered. Although our study demonstrates that disturbed individuals of *E. peplus* produced ripened seeds before the end of the growing season, we did not evaluate differences in the amount of seeds between disturbed and undisturbed plants. Hence, it is possible that the final fitness of vegetatively regenerated plants could be lower than undisturbed plants owing to a high risk of suboptimal weather at the end of the growing season.

In addition, the higher production of seeds of disturbed plants does not inevitably imply better performance (fitness) of vegetatively regenerated individuals over intact plants, as the seed quality might differ. For example, although we did not find any indication that such was the case, lower seed weight of resprouted plants could result in lower germination of progeny or a reduction in their establishing success (Huhta et al. 2000a, 2000b; Martínková et al. 2008). Maternal effects due to disturbance could also result in different offspring performance of plants with different disturbance histories (Latzel et al. 2009b, 2010).

COMPETITIVE ABILITY AND COSTS OF APICAL DOMINANCE OR BETHEDGING STRATEGY

The equal size and biomass of disturbed and undisturbed plants in conditions without competition (manipulative study) illustrate that plants of *E. peplus* are potentially able to successfully overcome severe disturbance and even compensate for biomass loss. The field study showed that competition slightly negatively affects the height of disturbed plants with respect to competitive levels, but as a whole there were no significant differences between disturbed and undisturbed plants. The height of disturbed and undisturbed plants

increased in response to increasing competition of a site (see Fig. 1). Undisturbed plants showed very conservative architecture in variably competitive and fertile sites, but this was not the case for disturbed individuals. Disturbed plants produced the most adventitious shoots in moderate environments (i.e., moderate competition and nitrogen availability; see Figs. 2 and 3). In such conditions they also performed better than undisturbed plants with regard to flower and branch number. The observed architectural pattern is more in accordance with the bet-hedging strategy (Crawley 1987; Whitham et al. 1991; Vail 1992; Tuomi et al. 1994; Nilsson et al. 1996) than with the hypothesis of cost of apical dominance (Aarssen 1995; Agrawal 2000). Although our conclusion is constrained by the fact that we observed only an outcome and not a whole process of plant regeneration for supporting the cost of apical dominance hypothesis, we would expect higher branching of intact plants in less competitive environments.

Rautio et al. (2005) showed that the monocarpic herb *Erysimum strictum* Gaertn., Mey, & Scherb. compensates for biomass loss better in unfavourable conditions: in low nutrient levels and in the presence of competition. On the other hand, Huhta et al. (2000a) documented with the same species that the best compensation for biomass loss was under fertile conditions and without competition. In our study, the higher branching of disturbed plants was observed under the highest nitrogen availability. Moreover, disturbed plants produced the most adventitious shoots in nutrient moderate environments where the competition was relatively high. Such a discrepancy illustrates that the ability to tolerate disturbance in monocarpic herbs is not only species but also context specific, which Banta et al. (2010) also reported for different provenances of *Arabidopsis* populations. Moreover, it has been documented that tolerance to disturbance is affected not only by ambient conditions but also by disturbance history of populations (Latzel et al. 2009b, 2010).

ECOLOGICAL CONSEQUENCES OF ADVENTITIOUS SPROUTING IN ANNUALS

Studies on monocarpic species have documented compensatory growth after the loss of maximally 50% of their aboveground biomass (e.g., [Escarré et al. 1996](#); [Lennartsson et al. 1997](#); [Huhta et al. 2000a, 2000b](#)). In our study, we demonstrated that annuals could compensate for nearly 100% of aboveground biomass loss owing to adventitious sprouting. This is an important aspect that should be taken into account in disturbed communities. In addition to *E. peplus*, some other common annuals, such as *Anagallis arvensis* L., *Euphorbia exigua* L., or *Microrrhinum minus* (L.) Fourr., resprout readily from hypocotyls ([Latzel et al. 2009a](#); [Malíková et al. 2010](#)). Resprouted individuals can grow faster than individuals regenerated from seeds ([Klimešová et al. 2008](#); [Latzel et al. 2008](#); [Latzel and Klimešová 2009](#)). Although the seed bank is often richer than the bud bank, resprouted individuals are able to suppress seedlings, which should have a strong impact on community-development dynamics after severe disturbance ([Latzel et al. 2008](#)).

THE CONTROL OF INVASIVE PLANT SPECIES

Although adventitious sprouting in biennial herbs was not confirmed as a prerequisite for their invasiveness ([Martínková et al. 2011](#)), it does not preclude the possibility that resprouting ability is responsible for the success of *E. peplus* in disturbed communities of invaded ranges. Invasive species are notably those that have higher values than noninvasive species for traits associated with high performance, namely physiology, leaf-area allocation, shoot allocation, growth rate, size, and fitness ([van Kleunen et al. 2010](#)). Our study shows that resprouting of *E. peplus* is associated with higher or similar performance and fitness than nonsprouting individuals. It is probable that the resprouting capacity of *E. peplus* could be one of its important traits facilitating successful spread to non-native, disturbed areas.

Consequently, the resprouting ability of *E. peplus* and other invasive species should be considered in management of their control. Although herbicides are the most common tool used to control invasive species (Geyer et al. 2002), other techniques, such as mowing, burning, and clipping, could also be successful (Ailstock et al. 2001; Major et al. 2003). Nonetheless, the mechanical control could fail if the focused species is able to successfully regenerate without significant effect on its fitness as shown in this study. Therefore, we propose that mechanical control of *E. peplus* and other invasive species able to regenerate vegetatively should be applied in their later phenological stages when the resprouting capacity and fitness of regenerated individuals is limited.

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REFERENCES

- Aarssen LW (1995) Hypotheses for coevolution of apical dominance in plants: implications for the interpretation of overcompensation. *Oikos*, 74(1):149–156.
- Adams J (1924) Adventitious shoots on hypocotyl of flax and tomato. *Bot. Gaz.* 78(1–4):461–462.
- Agrawal AA 2000 Overcompensation of plants in response to herbivory and the by-product benefits of mutualism. *Trends Plant Sci.* 5(7):309–313.
- Ailstock MS, Norman CM, Bushman PJ (2001) Common reed *Phragmites australis*: control and effects upon biodiversity in freshwater non-tidal wetlands. *Restor. Ecol.* 9(1):49–59.
- Banta JA, Stevens MHH, Pigliucci M (2010) A comprehensive test of the 'limiting resources' framework applied to plant tolerance to apical meristem damage. *Oikos*, 119(2):359–369.
- Bellingham PJ, Sparrow AD (2000) Resprouting as a life history strategy in woody plant communities. *Oikos*, 89(2):409–416.

- Bergelson J, Crawley J (1992) Herbivory and *Ipomopsis aggregata*: the disadvantages to being eaten. *Am. Nat.* 139(4):870–882
- Bond WJ, Midgley JJ (2003) The evolutionary ecology of sprouting. *Int. J. Plant Sci.* 164(3):103–114.
- Crawley MJ (1987) Benevolent herbivores? *Trends Ecol. Evol.* 2(6):167–168.
- Crooks DM (1933) Histological and regenerative studies on the flax seedling. *Bot. Gaz.* 95(2):209–239.
- Eggers V (1946) Influence of carbohydrate and nitrate–nitrogen nutrition on development of hypocotyledonary buds in flax. *Bot. Gaz.* 107(3):385–390.
- Ellenberg H (1986) *Vegetation ecology of central Europe*. 4th ed. Cambridge University Press, Cambridge, UK.
- Escarré J, Lepart J, and Sentuc JJ (1996) Effects of simulated herbivory in three old field compositae with different inflorescence architectures. *Oecologia (Berl.)*, 105(4):501–508.
- Florence J (1997) *Flore de la Polynésie française*, Vol. 1. Editions de l'Orstom, Institut français de recherche scientifique pour le développement en coopération, Collection faune et flore tropicales, Paris.
- Geyer WA, Fick WH, Carlisle J (2002) Weed management on military storage gravel lots. *Trans. Kans. Acad. Sci.* 105(1–2):66–71
- Grime JP 2001 *Plant strategies, vegetation process, and ecosystem properties*. 2nd ed. Wiley, Chichester, UK.
- Hellström K, Rautio P, Huhta AP, Tuomi J (2004) Tolerance of annual hemiparasite, *Euphrasia stricta* agg., to simulated grazing in relation to the host environment. *Flora* 199(3):247–255.
- Huhta AP, Hellström K, Rautio P, Tuomi J (2000a) A test of the compensatory continuum: fertilization increases and below-ground competition decreases the grazing tolerance of tall wormseed mustard (*Erysimum strictum*). *Evol. Ecol.* 14(4–6):353–372.
- Huhta AP, Lennartsson T, Tuomi J, Rautio P, Laine K (2000b) Tolerance of *Gentianella campestris* in relation to damage intensity: an interplay between apical dominance and herbivory. *Evol. Ecol.* 14(4–6):373–392.
- Huhta AP, Hellström K, Rautio P, Tuomi J (2003) Grazing tolerance of *Gentianella amarella* and other monocarpic herbs: why is tolerance highest at low damage levels? *Plant Ecol.* 166(1):49–61.
- Ishikawa K, Kamada H, Harada H (1997) Another evidence for inhibitory effect of auxin in adventitious bud formation of decapitated flax (*Linum usitatissimum* L.) seedlings. *J. Plant Res.* 110(4):387–392
- Klimesšová J, Klimesš L (2003) Resprouting of herbs in disturbed habitats: is it adequately described by Billingham–Sparrow's model? *Oikos*, 103(1):225–229.

- Klimesšová J, Klimeš L (2007) Bud banks and their role in vegetative regeneration: a literature review and proposal for simple classification and assessment. *Perspect. Plant Ecol. Evol. Syst.* 8(3):115–129.
- Klimesšová J, Martínková J (2004) Intermediate growth forms as a model for the study of plant clonality functioning: an example with root sprouters. *Evol. Ecol.* 18(5–6):669–681.
- Klimesšová J, Sosnová M, Martínková J (2007) Life-history variation in the short-lived herb *Rorippa palustris*: effect of germination date and injury timing. *Plant Ecol.* 189(2):237–246.
- Klimesšová 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 Res.* 48(2):131–135.
- Latzel V, Klimesšová J (2009) Fitness of resprouters versus seeders in relation to nutrient availability in two *Plantago* species. *Acta Oecol.* 35(4):541–547.
- Latzel V, Mihulka S, Klimesšová J (2008) Plant traits and regeneration of urban plant communities after disturbance: does the bud bank play any role? *Appl. Veg. Sci.* 11(3):387–394.
- Latzel V, Dospělová L, Klimesšová J (2009a) Annuals sprouting adventitiously from the hypocotyl: their compensatory growth and implications for weed management. *Biologia*, 64(5):923–929.
- Latzel V, Hájek T, Klimesšová J, Gómez S (2009b) Nutrients and disturbance history in two *Plantago* species: maternal effects as a clue for observed dichotomy between resprouting and seeding strategies. *Oikos*, 118(11):1669–1678.
- Latzel V, Klimesšová J, Hájek T, Gómez S, Šmilauer P (2010) Maternal effects alter progeny's response to disturbance and nutrients in two *Plantago* species. *Oikos*, 119(11):1700–1710.
- Lehtilä K, Syrjänen K (1995) Compensatory responses of two *Melampyrum* species after damage. *Funct. Ecol.* 9(3):511–517.
- Lennartsson T, Tuomi J, Nilsson P (1997) Evidence for an evolutionary history of overcompensation in the grassland biennial *Gentianella campestris* (Gentianaceae). *Am. Nat.* 149(6):1147–1155.
- Lennartsson T, Nilsson P, Tuomi J (1998) Induction of overcompensation in the field gentian, *Gentianella campestris*. *Ecology*, 79(3):1061–1072.
- Link GKK, Eggers V (1946) Mode, site, and time of initiation of hypocotyl edonary bud primordia in *Linum usitatissimum* L. *Bot. Gaz.* 107(4):441–454.
- Major W, Grue C, Grassley J, Conquest LL (2003) Mechanical and chemical control of smooth cordgrass in Willapa Bay, Washington. *J. Aquat. Plant Manage* 41:6–12.
- Malíková L, Šmilauer P, Klimesšová J (2010) Occurrence of adventitious sprouting in short-lived monocarpic herbs: a field study of 22 weedy species. *Ann. Bot. (Lond.)* 105(6):905–912.

- Martínková J, Klimešová J, Mihulka S (2004a) Resprouting after disturbance: an experimental study with short-lived monocarpic herbs. *Folia Geobot.* 39(1):1–12.
- Martínková J, Kočvarová M, Klimešová J (2004b) Resprouting after disturbance in short-lived herb *Rorippa palustris* (Brassicaceae): an experiment with juveniles. *Acta Oecol.* 25(3):143–150.
- Martínková J, Klimešová J, Mihulka S (2006) Vegetative regeneration of biennial *Oenothera* species after disturbance: field observations and experiment. *Flora*, 201(4):287–297.
- Martínková J, Klimešová J, Mihulka S 2008 Compensation of seed production after severe injury in the short-lived herb *Barbarea vulgaris*. *Basic Appl. Ecol.* 9(1):44–54.
- Martínková J, Klimeš L, Klimešová J (2011) Multiple regenerative strategies of short-lived species: an effect on geographical distribution, preference of human-made habitats and invasive status. *Folia Geobot.* [In press.]
- Mathsoft Inc. (2000) S-PLUS 2000 Guide to statistics. Mathsoft, Seattle, Washington.
- Midgley JJ (1996) Why the world's vegetation is not totally dominated by resprouting plants; because resprouters are shorter than seeders. *Ecography*, 19(1):92–95.
- Nilsson P, Tuomi J, Astrom M (1996) Bud dormancy as a bethedging strategy. *Am. Nat.* 147(2):269–281.
- Ojeda F (1998) Biogeography of seeder and resprouter *Erica* species in the Cape Floristic region—where are the resprouters? *Biol. J. Linn. Soc.* 63(3):331–347.
- Orchard AE (1994) *Flora of Australia. Oceanic islands 1.* Australian Government Publishing Service, Canberra, Australia.
- Piippo S, Hellstrom K, Huhta AP, Rautio P, Tuomi J (2009) Delayed flowering as a potential benefit-decreasing cost of compensatory regrowth. *Botany*, 87(9):837–844.
- Rauh W. (1937) Die Bildung von Hypocotyl und Wurzelsprossen und ihre Bedeutung für die Wuchsormen der Pflanzen. *Nova Acta Leopold.* 4:395–553.
- Rautio P, Huhta AP, Piippo S, Tuomi J, Juenger T, Saari M, Aspi J (2005) Overcompensation and adaptive plasticity of apical dominance in *Erysimum strictum* (Brassicaceae) in response to simulated browsing and resource availability. *Oikos*, 111(1):179–191.
- Sosnová M, Klimešová J (2009) Life-history variation in the short-lived herb *Rorippa palustris*: the role of carbon storage. *Acta Oecol.* 35(5):691–697.
- Tassin J, Riviere JN, Clergeau P (2007) Reproductive versus vegetative recruitment of the invasive tree *Schinus terebinthifolius*: implications for restoration on Reunion Island. *Restor. Ecol.* 15(3):412–419.
- Theoharides KA, Duker JS (2007) Plant invasion across space and time: factors affecting nonindigenous species success during four stages of invasion. *New Phytol.* 176(2):256–273.

- Tuomi J, Nilsson P, Astrom M (1994) Plants compensatory responses - bud dormancy as an adaptation to herbivory. *Ecology*, 75(5):1429–1436.
- Vail SG (1992) Selection for overcompensatory plant-responses to herbivory - a mechanism for the evolution of plant-herbivore mutualism. *Am. Nat.* 139(1):1–8.
- van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol. Lett.* 13(2):235–245.
- Vesk PA, Westoby M (2004a) Sprouting ability across diverse disturbances and vegetation types worldwide. *J. Ecol.* 92(2):310–320.
- Vesk PA, Westoby M (2004b) Funding the bud bank: a review of the costs of buds. *Oikos*, 106(1):200–208.
- Wagner WL, Herbst DR, Sohmer SH (1999) *Manual of the flowering plants of Hawaii*. Revised ed. Bernice P. Bishop Museum special publication, University of Hawai'i Press and Bishop Museum Press, Honolulu, Hawaii.
- Whitham TG, Maschinski J, Larson KC, Paige KN (1991) Plant responses to herbivory: the continuum from negative to positive and underlying physiological mechanisms. In *Plant–animal interactions: evolutionary ecology in tropical and temperate regions*. Edited by P.W. Price, T.M. Lewinsohn, G.W. Fernandes, and W.W. Benson. Wiley, New York. pp. 227–256.

STUDY IV

The invasive annual herb *Euphorbia geniculata* is able to regenerate after severe disturbance by adventitious sprouting

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ABSTRACT

Euphorbia geniculata, an annual weed of arable land native to America and invasive in subtropical and tropical regions, is able to regenerate from seeds and is also able to produce adventitious buds on the hypocotyl. Whether sprouting from adventitious buds represents a mechanism for surviving severe disturbance, however, is not known. The significance of such sprouting was investigated with field survey and a pot experiment. Among 897 plants in 25 field populations surveyed in Indonesia, only a few exhibited sprouting from adventitious buds. When seeds were collected from 12 of the populations and used in a pot experiment, however, the seedlings were able to survive severe disturbance by sprouting from adventitious buds on the hypocotyl and were able to set seeds, although they produced less vegetative and generative (flowers and fruits) biomass than control plants. The response to severe disturbance in the pot experiment was affected by population origin. This variation among populations in response to disturbance may be subject to natural selection, and such selection could increase invasibility and decrease sensitivity to mechanical control.

INTRODUCTION

Invasions of ecosystems by introduced species is one of the most serious threats to natural biodiversity (Heywood 1989). Moreover, alien plants are able to change ecosystem function and structure, and influence survival and reproduction of indigenous species (Vitousek et al. 1987; Cronk and Fuller 1995; Pyšek and Richardson 2007).

Many studies have investigated the general characteristics of invasive species (di Castri 1990; Sykora 1990; Richardson et al. 1994; Rejmánek 1995; Chytrý et al. 2005; Pyšek and Richardson 2007; Mihulka et al. 2006; van Kleunen et al. 2010), and some have described traits that facilitate rapid spread into new areas. These traits include: successful germination under various environmental conditions, high competitive ability, a short lifespan, vegetative reproduction, rapid growth, high fecundity, high genetic plasticity and phenotypic variability, polyploidy, the ability to hybridize, apomixy, and a reduced volume of nuclear DNA. According to this list, various types of regeneration contribute to the invasibility of plants. In addition, invasion is realized not only by successful spread but also by the successful overcoming of disturbances because most invasion events have been recorded from anthropogenic biotopes, i.e., from highly and unpredictably disturbed habitats (Grime 1979; Silvertown and Lovett-Doust 1993; Dietz and Edwards 2006).

Annual species are better adapted than perennial species to disturbed habitats because they are able to set seeds between two disturbance events. However, they might fail to found a new population if disturbance comes early in the lifespan (before flowering and fruiting). In our previous work (Malíková et al. 2010), we found that a small percentage of annual species are able to overcome this limitation by resprouting from the hypocotyl or root buds and thereby completing their life cycle. Except for a few anecdotal reports, however, information about the role of resprouting in the ecology of annuals comes mainly from Central Europe (Latzel et al. 2009, 2011; Malíková et al. 2010). Although Vernon (1984) and Kigel et al. (1992) observed the formation of adventitious

buds on the hypocotyl of the tropical invasive weed *Euphorbia geniculata*, the role of these buds in the plant's life history and tolerance to severe disturbance has not been studied. Our knowledge of the ecology of invasion processes (Pyšek et al. 2008) in tropical regions of the Old World is poor, and *E. geniculata* represents an interesting model species.

In Central European monocarpic weeds, the combination of two regenerative strategies (seed production and resprouting from the bud bank) provides an advantage in recurrently disturbed habitats (Martínková et al. 2011) even though the resprouting strategy is not a prerequisite for invasibility (Martínková et al. 2011). Differences in resprouting abilities were found not only at the interspecific level but also at the intraspecific level, i.e., between populations of one species (Latzel et al. 2009; 2011). Such variability among populations in resprouting capacity and also in the ability to produce biomass and/or offspring after damage might be a basis for natural selection in response to a new weeding technique (Neve et al. 2009) or to new conditions in an invasive range (Blossey and Notzold 1995). Consequently, an understanding of the significance of resprouting ability for species as well as for populations should increase our understanding of processes leading to successful invasions.

Here we used *E. geniculata* as a model to increase our knowledge of the biology of tropical invasive weeds and the role of adventitious sprouting from the hypocotyl. We aimed to answer the following questions:

(1) Are severely disturbed plants able to resprout and complete their life cycle?

(2) Can plants resprouting from the adventitious buds on the hypocotyl be found in nature?

(3) Do populations differ in their ability to resprout or in the fitness of resprouting individuals?

METHODS

BACKGROUND ON *E. GENICULATA*

Euphorbia geniculata Ortega (1979) is robust annual herb with a branched stem up to 2 m high and with cyathia that form dense terminal cymes. The fruit capsule contains three seeds about 2 mm long (Wagner et al. 1999). Reproduction is exclusively by seeds, which are shed by an explosive mechanism (Waterhouse 1997).

Although native to an area the extends from the southern United States to Argentina and the West Indies (Wagner et al. 1999), *E. geniculata* has recently spread throughout the tropical and subtropical regions of the world, including most of tropical Africa and the Indian Ocean islands, the Mediterranean region, and South Africa (Wagner et al. 1999). Throughout its range, it occurs in disturbed biotops (crop fields, pastures, and waste lands) (Holm et al. 1997) up to 1800 m a.s.l.

FIELD SURVEY

A field survey was conducted from 2007 to 2009 in Indonesia (Bali, Java, Sumatra, and the Nias islands). Anthropogenic locations were surveyed for the occurrence of *E. geniculata*. When a *E. geniculata* population containing at least 30 individuals was found, data were collected on two levels: (i) the plant population and (ii) the individual plant.

(i) At the population level, we assessed total cover of herbaceous vegetation and soil compaction , which was subjectively assessed (low, medium, or high) by inserting a pencil into the soil. Seeds of *E. geniculata* were collected in all populations that contained at least 10 plants with ripen seeds.

(ii) At the individual level, we assessed growth characteristics (shoot height, width of shoot base, number of axillary branches, number of adventitious buds and shoots, length of the longest adventitious shoot) and signs of main

shoot disturbance. Based on signs of shoot disturbance, plants were categorized as disturbed or non-disturbed. Phenological stage was recorded according to development of the most advanced shoot (sterile - 1, prolongation of stem - 2, buds - 3, flowering - 4, fruiting - 5).

During the field study, a total of 897 individuals of *E. geniculata* from 25 populations were measured (supplementary material Table 6).

Table 6. List of localities where populations of *Euphorbia geniculata* were studied in field. The localities of populations studied in the pot experiment are in bold.

Local-ity or popu-lation	Location	Habitat	Herb cover (%)	Soil com-paction ^a	No. of distur-bed indi-viduals	No. of resprou-ting indi-viduals
1	North of Bali, southwest of Singaraja, northwest part of Pemaron village, edge of Jenderal Achmad Yani street	Regularly mowed ditch beside asphalt road	95	2	1	0
2	North of Bali, southwest of Pemaron village, edge of Seririt-Singaraja street	Anthropogenic habitat near road	75	2	0	0
3	North of Bali, west part of Singaraja, 100 m west of bus-station Banyuasri	Anthropogenic habitat on waste soil near road	90	2	5	0
4	North part of Bali, South part of areal of Ganesha University, Singaraja	Dry ditch beside road	100	2	7	2
5	North part of Bali, South areal of Ganesha University, Singaraja	Anthropogenic habitat between asphalt road and wall of building	90	2	1	0
6	North part of Bali, 0.5 km north of Air Sanah village	Undergrowth of coconut and banana plantain	70 (40)	2	16	0
7	South of Bali, Denpasar town, Banjar Sawah, Pulau Bungin street	Ditch beside asphalt road and rice field	80	2	0	0
8	North of Bali, Tukad Mungga village, west of Singaraja town, 40 m of Happy beach	Anthropogenic habitat – waste land	100	2	0	0
9	North of Bali, Tukad Mungga village, west of Singaraja town, 30 m of Happy beach	Anthropogenic habitat – loamy	100	2	0	0
10	North part of Nias, Sorage village	Anthropogenic habitat beside	85	2	4	0

		cottage on the beach				
11	North of Nias, Zorave village	Anthropogenic habitat beside cottage on the beach	100	2	5	1
12	West of Sumatra, Bukit Tinggi, 500 m north of Koto Baru village, beside path to Merapi Volcano	Edge of field, on nutrient-rich soil	60	2	2	0
13	South of Bali, northeast of Denpasar, Sukawati village, east part of Raya Celuk street	Mowed part of anthropogenic habitat in wasted yard of wasted house	95	2	32	0
14	South of Bali, northeast of Denpasar, Sukawati village, east part of Raya Celuk street	Anthropogenic habitat in wasted yard of wasted house	75	2	0	0
15	South of Bali, Denpasar town, Hayam Wuruk street, areal of Honda shop on crossroad with Kamboja street	As a weed in small ornamental flower-bed	70	2	0	0
16	North of Bali, Kalibukbuk village, near beach	Sandy anthropogenic habitat	30	1	1	0
17	North part of Bali, the centre of Kaliasem village	Shaded anthropogenic habitat	50	1.5	1	1
18	South part of Bali, Kuta village, beside Honda shop, Imam Bonjol street	Cemetery	95 (20)	2	9	0
19	South part of Bali, Denpasar town, Hayam Wuruk street	Anthropogenic habitat in front of golf area	75 (40)	2	0	0
20	South part of Bali, Denpasar town, Hayam Wuruk street beside Radio Bali	Anthropogenic habitat between garden and pathway	70	2	16	2
21	South part of Bali, west edge of Sanur village	Arable field with <i>Zea mays</i>	60	2	3	0
22	South of Bali, Kuta village, Imam Bonjol street	Back-yard	95	2	1	0
23	South of Bali, southwest of Jimabran village, south part of Dreamland area	Anthropogenic habitat on calcareous intermittent soil, close to beach	40	1	1	0
24	North of Java, Bojonegoro town, 100 m west of railway station	Sandy anthropogenic habitat in the ditch along	50	1	5	0

		railway				
25	West part of Bali, 3 km northeast of Gilimanuk on the border of Bali Barat National Park	Dry anthropogenic habitat on the edge of arable field along main road	40	2	0	0

^a Resistance to penetration was rated on a scale from 1–3 (from low to high resistance).

POT EXPERIMENT

A pot experiment was performed in a growth chamber at the Institute of Botany ASCR in Třeboň, Czech Republic. The conditions were: day/night temperatures 30/25 °C, humidity 90–95 %, photoperiod 12/12 h, and average daily light intensity 151.5 $\mu\text{m}^{-2}\text{s}^{-1}\text{mol}$.

Seeds collected from 12 populations in the field study (Table 6) were germinated on pure sand in Petri dishes and then planted in pots (13×13×13 cm³) containing a mixture of pure washed sand and standard garden soil (pH 5.0–7.0, N 150–400 mg/l, P₂O₅ 100–300 mg/l, K₂O 100–300 mg/l, AGRO CS a.s. Česká Skalice, CZ) at a ratio of 2:1 (v:v). Plants were watered regularly, and each pot was fertilized 22 days after planting with one-half of a fertilizer tablet containing 0.06 g of N, 0.03 g of P, and 0.035 g of K.

Altogether, 228 plants originating from 12 populations were used for the pot experiment. Of these plants, 117 (9–10 per population) were injured by clipping when they were 10 days old and in the vegetative stage. The remaining plants (111, 9–10 per population) were left intact as a control. Clipping involved removal of all aboveground biomass, all stems together with axillary buds, leaving only the hypocotyl. Clipping resulted in growth of the adventitious buds on the hypocotyl. When plants were 1.5 and 3.0 months old, the same growth parameters that were recorded in the field were measured. At harvest, 3 months after the experiment was started, the aboveground biomass of each plant was separated into leaves, stems, hypocotyl, and reproductive organs, which were dried at 80 °C for 48 h and weighed.

DATA ANALYSIS

The field data for disturbed and non-disturbed plants were compared with *t*-tests. In the pot experiment, parameters that were measured non-destructively were analysed by repeated measures analysis of variance (ANOVA) in which the two dates of measurement (1.5 and 3.0 months) were compared. Plant biomass data at the end of the experiment were analysed with two-way ANOVAs. Identity of the population and disturbance were used as explanatory variables in both kinds of ANOVAs (this was not the case for field data where population origin could not be studied due to small number of resprouting individuals). To assess the effect of population origin on growth characteristics, the relationship between average number of adventitious buds among natural populations and the number of buds observed in the pot experiment was assessed by Spearman rank correlation; data from disturbed and control plants were analysed separately. All analyses were performed with Statistica 8.0 ([StatSoft, Inc.; 2010](#)).

RESULTS

FIELD STUDY

Of the 897 *E. geniculata* plants evaluated in the field, 88 had adventitious buds and only six had adventitious shoots. In two of the 25 populations, all plants were devoid of adventitious buds and shoots. Disturbed plants tended to be shorter and have more adventitious shoots than non-disturbed plants but the small number of adventitious shoots. The numbers of adventitious buds and axillary branches were not affected by disturbance (Table 1). Because only a small number of plants exhibited resprouting, we did not test the effect of population on resprouting capacity in natural populations.

Table 1 Growth parameters (means \pm SD) of non-disturbed and disturbed plants in field populations of *Euphorbia geniculata* in Indonesia, and evaluation of differences by *t*-test (d.f.= 895).

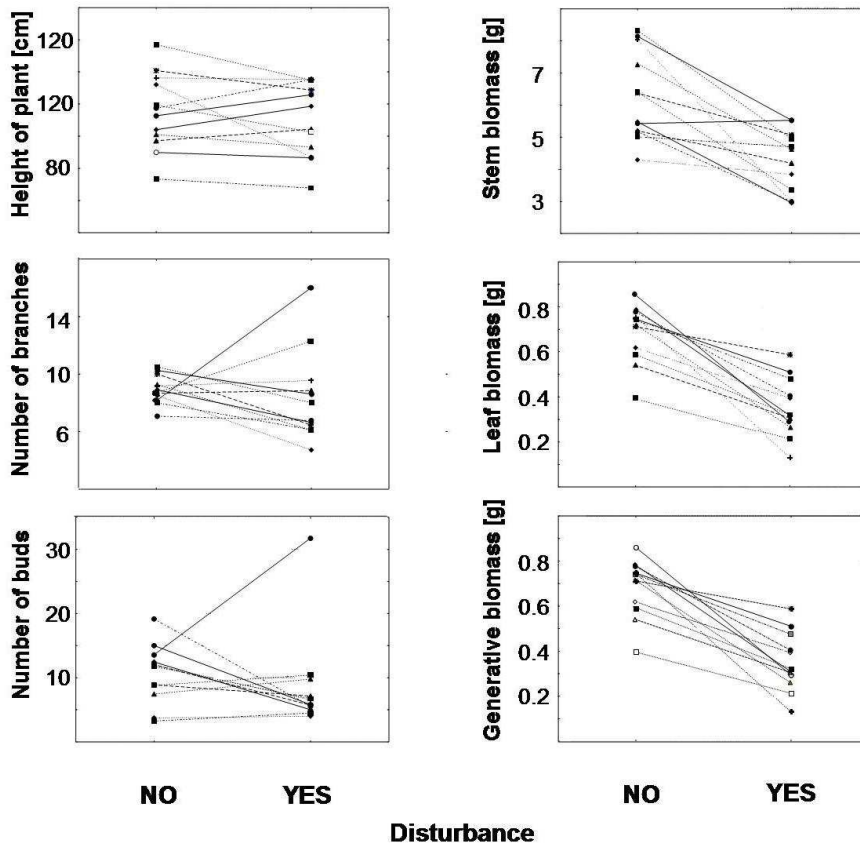
Parameter	Non-disturbed (n=782)	Disturbed (n=110)	t	P
Plant height	42.58 \pm 24.36	37.79 \pm 19.62	1.76	0.078
Width of shoot base	3.21 \pm 1.71	3.98 \pm 2.15	4.35	<10⁻⁴
No. of branches	4.94 \pm 7.23	4.06 \pm 4.36	1.26	0.209
No. of adventitious buds	0.17 \pm 0.74	0.49 \pm 1.44	2.51	0.012

POT EXPERIMENT

All but one plant subjected to severe disturbance (clipping) in the pot experiment survived and regenerated by resprouting from adventitious buds on the hypocotyl. Non-disturbed plants did not produce any adventitious shoot. At harvest, the mortality of disturbed and non-disturbed plants was similar: 1.8% and 2.6%, respectively.

Population origin affected all but one of the characteristics (stem biomass) and often affected the response of plants to disturbance and seasonal development (Fig. 1, Table 2, 3, 4). Disturbance also affected all measured characteristics except leaf biomass (Table 3, 4) and number of adventitious buds (Table 2). The number of adventitious buds varied considerably among plants (0–119) and was affected by population origin and increased with age (Fig. 1, Table 2, 3).

Fig. 1 - Growth parameters of non-disturbed and disturbed plants from 12 populations of *Euphorbia geniculata* at the end of the pot experiment. Each line represents seedlings originating from one population.



Although height was similar for disturbed and non-disturbed plants at the end of the experiment (Fig. 1), the biomass of flowers, fruits, and stems was lower for disturbed plants than for non-disturbed plants (Table 4). Aboveground biomass (without hypocotyl) of disturbed plants was 70.9% of that of non-disturbed plants. The biomass of fruits and flowers of disturbed plants was 52–72% of that of non-disturbed plants.

Table 2 - Effect of population origin, disturbance, and plant age on growth parameters of *Euphorbia geniculata* in the pot experiment as indicated by F values from repeated measures ANOVA. Degrees of freedom were 11 for population, 1 for disturbance, 1 for age, and 203 for error. P = population, D = disturbance, A = Age. Statistical significance: * - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$.

Source of variance	Plant height	Phenology (stages 1-5)	No. of adventitious buds	No. of adventitious shoots	No. of branches
Population	7.26 ***	9.18 ***	5.19 ***	7.70 ***	3.64
Disturbance	36.49 ***	147.26 ***	2.51	1257.81 ***	6.85**
Age	1853.45 ***	694.59 ***	17.14 ***	2.94	12.74
P × D	0.87	4.31 ***	3.72 ***	7.70 ***	3.45***
P × A	7.02 ***	4.04 ***	0.61	0.61	0.81
D × A	18.22 ***	89.22 ***	0.29	2.94	3.01
P × D × A	2.29 *	2.21 *	0.96	0.61	0.93

Table 3 - Growth parameters of *Euphorbia geniculata* in the middle (age 1.5 months) and at the end (age 3.0 months) of the pot experiment.

Parameter	Age (months)	Disturbed (mean ± SD)	Non-disturbed (mean ± SD)
Plant height (cm)	1.5	39.86 ± 8.50	52.69 ± 9.78
	3	95.36 ± 18.80	98.27 ± 15.79
Number of branches	1.5	6.60 ± 3.75	8.27 ± 2.22
	3	8.32 ± 6.95	8.82 ± 2.28
Phenology (stages 1-5)	1.5	2.9 ± 0.78	3.82 ± 0.51
	3	4.31 ± 0.34	4.49 ± 0.15
Number of adventitious buds	1.5	7.09 ± 8.04	8.54 ± 7.57
	3	8.73 ± 10.97	11.16 ± 12.64
Number of adventitious shoots	1.5	1.97 ± 0.77	0 ± 0
	3	1.88 ± 0.77	0 ± 0
Generative biomass (g)	3	0.35 ± 0.27	0.68 ± 0.33
Leaf biomass (g)	3	1.51 ± 2.40	2.11 ± 0.81
Stem biomass (g)	3	4.18 ± 2.40	6.14 ± 3.16

Table 4 - Effect of population origin and disturbance on biomass of *Euphorbia geniculata* in the pot experiment as indicated by F values from two-way ANOVAs. P = population, D = disturbance. Degrees of freedom were 11 for population, 1 for disturbance, and 204 for error. Statistical significance: * - $p < 0.05$, ** - $p < 0.01$, *** - $p < 0.001$.

Source of variance	Flowers and fruits	Leaves	Stems
Population	2.58 **	2.02 *	1.81
Disturbance	72.74 ***	1.93	28.39 ***
P × D	1.48	1.96 *	1.51

RELATIONSHIP BETWEEN PERFORMANCE OF POPULATIONS IN THE FIELD AND IN THE POT EXPERIMENT

The mean number of adventitious buds per plant in 12 field populations was not correlated with the mean number of adventitious buds per plant on seedlings derived from those 12 populations in the pot experiment ($r = -0.18$, $p = 0.578$). This was true for both disturbed and non-disturbed plants.

DISCUSSION

We were able to confirm the resprouting ability of *Euphorbia geniculata* under field conditions in Indonesia. Even though the number of resprouting individuals was so low that we could not study the effect of population origin, the occurrence of adventitious shoots was attributable to plant injury. When we explored the resprouting ability of about half of the populations studied in field in the pot experiment, we determined that severely disturbed plants were able to complete their life cycle and set seeds even though their biomass remained smaller than that of non-disturbed control plants. Moreover, the growth parameters of disturbed and non-disturbed plants in the pot experiment were population specific.

Our study revealed that a short-lived invasive species from the tropics is able to cope with severe disturbance in a manner similar to that of some short-lived species from the temperate zone (King et al. 2008; Malíková et al. 2010; Latzel et al. 2009; 2011). That we found only a few resprouting individuals of *E. geniculata* in the field might be due to the scarcity of disturbance events in the studied populations because disturbance is the main factor triggering adventitious sprouting in this species.

The reduced biomass and seed production of disturbed vs. non-disturbed plants is at least partially caused by a delay in biomass accumulation and phenology in the disturbed plants in (Table 5). This could be a serious problem in areas with a seasonal climate where disturbed plants that resprout may not have sufficient time to set viable seeds (Martínková et al. 2008). On the other hand, there is less danger of suboptimal conditions at the end of growing season in tropical ranges. Had our experiments continued longer than 3 months, the biomass and seed production of the disturbed plants may have eventually “caught up” with those of the non-disturbed plants.

Table 5 – Relative growth of six species of severely disturbed and non-disturbed annual herbs under experimental conditions. The severely disturbed plants resprouted from the hypocotyl. Relative growth is expressed as the ratio between average values for disturbed/non-disturbed plants. # and ## indicate that the data are from Latzel et al. (2009) and the current study, respectively.

Parameter	<i>Microrrhinum minus</i> #	<i>Euphorbia peplus</i> #	<i>Anagallis arvensis</i> #	<i>Kickxia elatine</i> #	<i>Kickxia spárka</i> #	<i>Euphorbia geniculata</i> ##
No. of branches	0.7	0.4	0.6	0.4	0.3	0.9
Aboveground vegetative biomass	1.0	0.3	0.5	0.5	0.3	0.7
Generative biomass	1.1	0.6	0.2	0.4	0.3	0.5
Plant height	0.9	1.2	0.4	1.0	0.5	0.7

The ability to form adventitious buds and shoots on the hypocotyl and/or roots has also been reported for several congeners of *E. geniculata* (Rauh 1937),

and some of these congeners are well recognized for being “weedy”. For example, the annual *Euphorbia peplus* (Latzel et al. 2011) and the perennial *Euphorbia esula* (Horvath et al. 2003) are invasive weeds of arable land in North America. Our results along with the cited examples support the idea that the ability to resprout from adventitious buds on roots and/or the hypocotyl might be important for the spread of these species on disturbed biotopes.

Adventitiously sprouting invasive species might be difficult to eradicate by cutting or uprooting (Klimešová 2011, pers.com.). It follows that some root- and hypocotyl-sprouting invaders, e.g., *Alliaria officinalis* (Pardini et al. 2008; 2009), *Cinchona pubescens* (Jäger and Kowarik 2010), and *Rosa rugosa* (Kollman et al. 2009), could be difficult to manage. In some species of short-lived plants, control has been successful when aimed at a sensitive ontogenetical stage, usually the stage just before seed production (Pardini 2009; Latzel et al. 2010; 2011). However, mechanical control at this stage was poor in the case of other species (Klimešová et al. 2007).

Genetically based differences in sprouting ability among populations of *E. geniculata* could be subject to natural selection triggered by changes in disturbance regime (Thrall et al. 2011). Contemporary evolution of local genotypes may increase the rate of biological invasion (Blossey and Notzold 1995) or the tolerance to weeding (Neve et al. 2009), and has been reported for an increasing number of plants (e.g., Heap 2009; Colautti and Barrett 2010; Buswell et al. 2011).

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REFERENCES

- Blossey B, Notzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants – a hypothesis. *J. Ecol.* 83:887-889.
- Buswell JM, Moles AT, Hartley S (2011). Is rapid evolution common in introduced plant species? *J. Ecol.* 99:214-224.
- Chytrý M, Pyšek P, Tichý L, Knollová I, Danihelka J (2005) Invasions of the Czech Republic by alien plants: a quantitative assessment across habitats. *Preslia* 77:339–354.
- Colautti RI, Barrett SCH (2010) Natural selection and genetic constraints on flowering phenology in an invasive plant. *Int. J. Plant Sci.* 171:960-971.
- Cronk QCB, Fuller JL (1995) *Plant Invaders: the Threat to Natural Communities*. Chapman and Hall, London.
- di Castri F (1990) On Invading Species and Invaded Ecosystems: the Interplay of Historical Change and Biological Necessity. In: di Castri F., Hansen A. J. and Debussche [eds.]: *Biological Invasions in the Europe and Mediterranean Basin*. Kluwer Academic Publishers, Dordrecht, pp 3-16.
- Dietz H, Edwards PJ (2006) Recognition that casual processes change during plant invasions helps explain conflicts in evidence. *Ecology* 87:1359-1367.
- Grime (1979) *Plant strategies and vegetations processes*. John Willey & Son, Chichester.
- Heap I (2009) The international survey of herbicide resistant weeds. Available at: <http://www.weedscience.com>.
- Heywood VH (1989) Patterns, Extents and Modes of Invasions by Terrestrial Plants. In: Drake JA, Mooney HA, di Castri F, Groves RH, Kruger FJ, Rejmánek M et Williamson M [eds.]: *Biological Invasions: A Global Perspective*. John Willey and Sons, Chichester, pp 31-60.
- Holm L, Doll J, Holm E, Pancho J, Herberger J (1997) *World weeds: natural histories and distribution*. John Wiley and Sons, Chichester.
- Horvath PD, Anderson VJ, Chao SW, Foley EM (2003) Knowing when to grow: signals regulating bud dormancy. *Trends Plant Sci.* 8:534-540.
- Jäger H, Kowarik I (2010) Resilience of native plant community following manual control of invasive *Cinchona pubescens* in Galapagos. *Restor. Ecol.* 18(S1):103-112.
- Kigel J, Lior E, Zamir L, Rubin B (1992) Biology of reproduction in the summer annual weed *Euphorbia geniculata* Ortega. *Weed Res.* 32:317-328.
- King GE, Eckhart MV, Mohl CE (2008) Magnitudes and Mechanism of Shoot-damaged Compensation in Annual Species of *Linum* (Linaceae) in Iowa. *Am Midl. Nat.* 159:200-213.
- van Kleunen M, Weber E, Fischer M (2010) A meta-analysis of trait differences between invasive and non-invasive plant species. *Ecol. Lett.* 13(2): 235–245.

- Klimešová J, Sosnová M et Martínková J (2007) Life-history variation in the short-lived herb *Rorippa palustris*: effects of germination date and injury timing. *Plant Ecol.* 189: 237-246
- Kollmann J, Brink-Jensen K, Sally I Frandsen SI, Hansen MK (2009) Uprooting and burial of invasive alien plants: A new tool in coastal restoration? *Restor. Ecol.* 19(3):371-378.
- Latzel V, Dospělová L, Klimešová J (2009) Annuals sprouting adventitiously from the hypocotyl: their compensatory growth and implications for weed management. *Biologia* 64(5):923-929.
- Latzel V, Malíková L, Klimešová J (2011) Compensatory growth of *Euphorbia peplus* regenerating from a bud bank. *Botany* 89(5):313-321.
- Malíková L, Šmilauer P, Klimešová J (2010) Occurrence of adventitious sprouting in short-lived monocarpic herbs: a field study of 22 weedy species. *Ann. Bot.* 105:905-912.
- Martínková J, Klimeš L, Klimešová J (2011) Multiple regenerative strategies of short-lived species: an effect on geographical distribution, preference of human-made habitats and invasive status. *Folia Geobot.* 46:181-189.
- Mihulka S, Pyšek P, Martínková J, Jarošík V (2006): Invasiveness of *Oenothera* congeners alien to Europe: Jack of all trades, master of invasion? *Persp. Plant Ecol. Evol. System.* 8:83-96.
- Neve P, Vila-Aiub M, Roux F (2009) Evolutionary thinking in agricultural weed management. *New Phytolog.* 184:783-793.
- Pardini EA, Teller BJ, Knight TM (2008) Consequences of density dependence for management of a stage-structured invasive plant (*Alliaria petiolata*). *Am. Midl. Nat.* 160:310-322.
- Pardini AE, Drake MJ, Chase MJ, Knight MT (2009) Complex population dynamics and control of the invasive biennial *Alliaria petiolata* (garlic mustard). *Ecol. Appl.* 19(2):387-397.
- Pyšek P, Richardson DM (2007) Traits associated with invasiveness in alien plants: Where do we stand? *Biolog. Invas.* 19(3):97-125.
- Pyšek P, Richardson DM, Pergl J, Jarošík V, Sixtová Z, Weber E (2008) Geographical and taxonomic biases in invasion ecology. *Trends Ecol. Evol.* 23:237-244.
- Rauh W (1937) Die Bildung von Hypocotyl- und Wurzelsprossen und ihre Bedeutung für die Wuchsformen der Pflanzen. *Nova Acta Leopold.* 4(24):395-553.
- Rejmánek M (1995) What Makes a Species Invasive? In: Pyšek P, Prach K, Rejmánek M et Wade PM [eds.] *Plant invasions: General aspects and special problems*, SPB Academic Publ., Amsterdam, pp 3-13.
- Richardson DM, Williams P, Hobbs RJ (1994) Pine Invasions in the Southern Hemisphere: Determinants of Spread and Invasibility. *J. Biogeogr.* 21:511-527.
- Silvertown JW, Lovett-Doust J (1993) *Introduction to Plant Population Biology*. Blackwell Scientific Publications, London.
- StatSoft, Inc. (2010) *STATISTICA for Windows (Computer program manual)*. Version 9.1. Available at: <http://www.statsoft.com>

- Sykora KV (1990) History of Impact of Man on the Distribution of Plant Species. In: di Castri F, Hansen AJ, Dbusche M [eds]: Biological Invasion in Europe and the Mediterranean Basin, Kluwer Academic Publishers, Dordrecht, pp 37-50.
- Thrall PH, Oakeshott JG, Fitt G., Southerton S, Burdon JJ, Sheppard A, Russel RJ, Zalucki M, Heino M, Denison RF (2011) Evolution in agriculture: the application of evolutionary approaches to the management of biotic interactions in agro-ecosystems. *Evol. Appl.* 4:200-215.
- Vernon B, Langston BV, Harger RT, Johnsey SP (1984) Potential for Adventitious Regeneration of Selected Weed Species. *Weed Sci.* 32:360-363.
- Vitousek PM, Walker LR, Whitaker LD, Mueller-Dombois D, Matson PA (1987) Biological Invasion by *Myrica faia* Alters Ecosystem Development in Hawaii. *Science*, 238:802-804.
- Wagner WL, Herbst DR, Sohmer SH (1999) Colocasia. In: *Manual of the Flowering Plants of Hawaii*. University of Hawaii Press, Honolulu, Hawaii, pp 1356-1357.
- Waterhouse DF (1997) The major invertebrate pests and weeds of agriculture and plantation forestry in the Southern and Western Pacific. The Australian Centre for International Agricultural Research, Canberra, pp 93.

CHAPTER III

GENERAL CONCLUSIONS

1. Adventitious sprouting in natural populations was confirmed in majority of studied species of Central European flora and in one American species invasive in Indonesia. For five European species (*Euphorbia helioscopia*, *Arabidopsis thaliana*, *Arabis glabra*, *Medicago lupulina*, and *Potentilla supina*) adventitious bud formation and sprouting was not found out and for American species (*Euphorbia geniculata*) was found only rarely (**STUDY I, IV**).

2. Plant size (large plant height, high number of branches, late phenology) supported adventitious sprouting but only disturbance from studied environmental factors (nutrient level, moisture, illumination) affected (positively) regeneration by adventitious sprouting in studied species (**STUDY I**).

3. Adventitious sprouting was not found to be more often in biennial than in annuals (**STUDY I**)

4. Occurrence of adventitious sprouting in plants with reduced apical dominance differed: upright annuals had a lower number of adventitious buds and shoots, but shoot length was higher than in the prostrate plants (**STUDY I**)

5. With increasing severity of disturbance the number of resprouting axillary branches decreased and at the same time the number of resprouting adventitious shoots increased (**STUDY II**).

6. Adventitious sprouting differed among species and populations in field as well as in experiment (**STUDY III and IV**).

The results imply that potential bud bank initiated only after injury can enable a plant to overcome a meristem limitation after severe disturbance, although degree of tolerance is species and population specific.

PERSPECTIVES

Adventitious sprouting seems to be a response to particular weed management with crop cultivation during process of natural selection. Plant individuals with certain characteristics supported by local conditions produce more surviving offspring than individuals with other characteristics, leads to genetic differentiation among populations. Although selection is regarded as the chief engine of evolutionary change, scientists have only recently begun measure its action in the real time (Kingsolver and Pfennig 2008, Thompson 2009).

Short-term evolution of local genotypes may increase a rate of biological invasion (Blossey and Notzold 1995) or a tolerance to weeding (Neve et al. 2009), and has been reported for increasing number of plants (e.g. Heap 2009; Colautti and Barrett 2010, Buswell et al. 2011).

Although the frequency of weeds decreased with usage of herbicides and some of them become rare in Czech Republic, their role could increase in future with organic farming (Latzel et al. 2009). Similarly management of invasive species might be hindered by their resprouting capacity.

REFERENCES

- Blossey B, Notzold R (1995) Evolution of increased competitive ability in invasive nonindigenous plants – a hypothesis. *Journal of Ecology* 83: 887-889.
- Buswell JM Moles AT, Hartley S (2011) Is rapid evolution common in introduced plant species? *Journal of Ecology* 99:214-224.
- Colautti RI Barrett SCH (2010) Natural selection and genetic constraints on flowering phenology in an invasive plant. *International Journal of Plant Sciences* 171:960-971.
- Heap I (2009) The international survey of herbicide resistant weeds. Available at: <http://www.weedscience.com>
- Kingsolver JG and Pfennig DW (2008) Patterns and power of phenotypic selection in nature. *Bioscience* 57:561-572.
- Latzel V, Dospělová L, Klimešová J (2009) Annuals sprouting adventitiously from the hypocotyl: their compensatory growth and implications for weed management. *Biologia* 64(5):923-929, Section Botany.

Neve P, Vila-Aiub M, Roux F (2009) Evolutionary thinking in agricultural weed management. *New Phytologist*, 184:783-793.

Thompson NJ (2009) Which ecologically important traits are most likely to evolve rapidly? *Oikos* 118:1281-1283.