

## NOTE / NOTE

## Performance and response to defoliation of *Sanguisorba officinalis* (Rosaceae) seedlings from mown and successional habitats

Martin Musche, Josef Settele, and Walter Durka

**Abstract:** In agricultural habitats, selection may favour plants that show a pronounced ability to tolerate stress induced by specific management methods. However, genetic erosion associated with habitat fragmentation may diminish this ability. To assess the role of mowing as a selection pressure and the impact of fragmentation processes on the ability to tolerate foliage loss, we grew 215 plants of the perennial herb *Sanguisorba officinalis* L. originating from 16 differently sized populations, located in mown meadows and successional fallows, in a common environment, and measured their performance and response to defoliation. Plants from meadows and fallows neither differed in performance characters nor in their ability to compensate for foliage loss. However, independently from the habitat of origin, populations slightly differed in performance. This variation was not due to differences in population size, plant density, or level of genetic variation, indicating its independence from genetic erosion, which may go along with habitat fragmentation. Rather, these differences between populations appear to be the outcome of unknown selection pressures or random genetic drift. Plants from successional fallows retain their potential to cope with mowing, presumably due to the low generation turnover of the perennial species. Selection by mowing may act over time scales larger than those reflected by the developmental stage of the current habitats.

**Key words:** agricultural practice, habitat fragmentation, mowing, plasticity, selection, succession.

**Résumé :** En agriculture, la sélection des habitats peut favoriser les plantes qui montrent une forte tolérance aux stress induits par des méthodes spécifiques d'aménagement. Cependant, l'érosion génétique associée à la fragmentation de l'habitat peut diminuer cette capacité. Afin d'évaluer le rôle de la tonte comme pression sélective et l'impact des processus de fragmentation sur la capacité à tolérer des pertes de feuillage, les auteurs ont cultivé 215 plants de l'herbacée pérenne *Sanguisorba officinalis* L. provenant de 16 populations différant par leurs dimensions et localisées dans des prairies tondues et jachères successives, dans un environnement commun; ils en ont ensuite mesuré la performance et la réaction à la défoliation. Les plantes des prairies et des jachères ne diffèrent, ni par les caractéristiques de performance ni par leur capacité à compenser les pertes de feuillage. Cependant, indépendamment de leur habitat d'origine, la performance des populations a légèrement différé. Cette variation n'est pas due à des différences de dimension de population, à la densité des plantes ou au degré de variation génétique, ce qui indique son indépendance par rapport à l'érosion génétique qui peut accompagner la fragmentation de l'habitat. Ces différences entre les populations semblent plutôt provenir de pressions sélectives inconnues ou d'une dérive génétique aléatoire. Les plantes provenant de jachères successives retiennent leur capacité à tolérer la tonte, possiblement à cause de la faible rotation de génération des espèces pérennes. La sélection par tonte pourrait agir sur des échelles de temps plus grandes que celles rencontrées dans les stades de développement des habitats actuels.

**Mots-clés :** pratique agricole, fragmentation de l'habitat, tonte, plasticité, sélection, succession.

[Traduit par la Rédaction]

### Introduction

Many plant species are distributed across a wide variety of habitats that differ in environmental conditions. Plants growing in contrasting habitats are likely to be exposed to different selection pressures favouring those characters that

maximize fitness in their respective environments. Consequently, divergent selection may cause small scale genetic differentiation depending on the strength of selection pressures and the magnitude of gene flow (Clausen et al. 1947; Linhart and Grant 1996). In agriculturally used ecosystems many plant species are permanently exposed to human activ-

Received 16 November 2009. Accepted 26 April 2010. Published on the NRC Research Press Web site at botany.nrc.ca on 8 July 2010.

M. Musche,<sup>1</sup> J. Settele, and W. Durka. Helmholtz Centre for Environmental Research-UFZ, Department of Community Ecology, Theodor-Lieser-Str. 4, 06120 Halle, Germany.

<sup>1</sup>Corresponding author (e-mail: martin.musche@ufz.de).

ity. In these habitats natural selection may favour plant adaptations to specific management methods, for example rapid development in heavily weeded habitats (Sobey 1987; Theaker and Briggs 1993), tolerance against herbicides (Warwick 1991), or distinct growth forms in response to trampling (Warwick 1980). Repeated defoliation caused by mowing and grazing may select for avoidance of herbivory (Warwick and Briggs 1978; Carman and Briske 1985; McKinney and Fowler 1991) and the ability of regrowth (Aarssen and Turkington 1987; Painter et al. 1989; Damhoureyeh and Hartnett 2002).

Agricultural land often becomes abandoned for economic reasons, and is thereby subject to secondary succession. Successional change however, may alter selection pressures acting on the life history of plants. While agricultural practice is expected to favour those traits that allow plants to endure repeated disturbance, theoretical work predicts selection for enhanced competitive ability in late successional (mature) habitats (Ronce and Olivieri 1997). Such an increase in competitive ability over successional time may be realized by allocating more resources to aboveground biomass (Hartnett et al. 1987), leaf biomass (Houssard and Escarré 1991), vegetative propagation (Houssard and Escarré 1995), or root development (Grace and Wetzel 1981; Houssard and Escarré 1991). Adaptation to local environmental conditions increases plant fitness, but at the same time it may restrict the ability of plants to perform in different environments (van Tienderen and van der Toorn 1991; Joshi et al. 2001). Given the contrasting selection pressures that predominate in mown habitats and successional fallows, one may expect differences among plants regarding their growth form and their response to defoliation.

The ability of a population to cope with man-made environmental stress may also be affected by habitat fragmentation. Small and isolated populations are likely to lose genetic variation, owing to genetic drift, increased inbreeding, and restricted gene flow (Ellstrand and Elam 1993; Young et al. 1996). As a consequence, the accumulation and expression of genetic load may lead to inbreeding depression, and thus negative consequences for individual fitness (Keller and Waller 2002; Reed and Frankham 2003). Thus, the genetic processes that go along with habitat fragmentation are likely to affect plant response to environmental stress and disturbances (e.g., Heschel and Paige 1995; Pluess and Stöcklin 2004). Despite a large number of studies demonstrating reduced fitness in small and genetically less diverse plant populations (reviewed by Leimu et al. 2006), possible interactions between habitat fragmentation and disturbance caused by agricultural practice have rarely been investigated. However, as many plant species of conservation interest grow in agriculturally used habitats, such interactions should be taken into account.

The great burnet, *Sanguisorba officinalis* L. (Rosaceae), is a perennial plant species that in Central Europe occurs in a range of moist grassland and meadow habitats. To evaluate the role of mowing and succession as likely selection pressures causing genetic differentiation, we grew seedlings from frequently managed meadows and successional fallows in the green house and measured their performance and response to experimental defoliation. Additionally we examined whether the effects of habitat fragmentation may affect

seedling performance and response to defoliation. Specifically we addressed the following questions: (i) Are plants from meadows and fallows differentiated in morphological characters that may indicate local adaptation? (ii) Do seedlings from meadows and fallows differ in their response to experimental defoliation? (iii) Do seedlings originating from populations of small size, low density, or low genetic diversity suffer from reduced performance or reduced ability to respond to stress caused by defoliation?

## Materials and methods

### Study species, source populations, and plant material

We studied 16 populations of *S. officinalis* located around the city of Landau (Germany, 49°11'56"N, 8°8'34"E). Half of the sites were located in meadows that are cut at least twice a year, and half were in fallows that have been left unmanaged for at least 10 years (J. Settele, personal observation, 2003). Populations differed in size, plant density, and level of genetic diversity (Table 1). Population size was estimated by counting the number of flowering shoots. Plant density was assessed by calculating the mean number of flowering shoots per square metre, based on counts within 50 squares (2 m × 2 m) per study site. Gene diversity (Lynch and Milligan 1994), which is equivalent to expected heterozygosity (Nei 1987), was used as a measure of intra-population genetic variation. These data were derived from a related study that was based on 69 polymorphic AFLP loci (Musche et al. 2008).

On each site, 20 plants (if available) were sampled at the end of August 2003. Seed families were obtained from the terminal flowerheads. All developed and undamaged seeds were taken and the mean seed mass per seed family was determined. Seeds were stored at 4 °C for 3 months to break dormancy. Afterwards, seeds were sown in Petri dishes filled with a 1:2 mixture (v/v) of sand and potting compost (COMPOSANA Anzuchterde, COMPO GmbH, Münster, Germany). Germination took place in a greenhouse chamber at 12 h (light) – 12 h (dark), and 25 °C.

### Experimental design

For the clipping experiment, a subset of 14 seedling families was drawn from each of the 16 populations, except for population 1, for which only 5 families were available. One seedling per family was selected at random. Altogether, 215 seedlings, each representing one single family were planted in pots (12 cm) and arranged randomly in a greenhouse under natural light conditions. The temperature was allowed to fluctuate between 10 and 30 °C, and plants were watered regularly. To avoid infection by pathogenic fungi, a fungicide (Ortiva, Syngenta Agro GmbH, Maintal, Germany) was applied twice, and aphids were controlled using a systematic insecticide (Neudosan, W. Neudorff GmbH KG, Emmertal, Germany). After 3 months, half of the replicates of each population were clipped 1 cm above the level of the potting medium and half were left as control. After 6 months, all of the plants were harvested and the following performance traits were measured: number of leaves per plant, maximum number of leaflets per leaf, maximum length of leaves, and maximum length of terminal leaflets. The aboveground biomass of plants was measured after drying at 60 °C for 2 d.

**Table 1.** Summary data for the 24 studied populations of *Sanguisorba officinalis*.

Population	Habitat	Population size*	Plant density <sup>†</sup> mean ( $\pm$ SD)	$H_e$ ( $\pm$ SD) <sup>‡</sup>	Seed mass (mg) mean ( $\pm$ SD)
1. Landau Reiterwiesen	Fallow	5	0.06 (0.06)	0.289 (0.020)	1.12 (0.14)
2. Schweighofen	Fallow	120	0.88 (0.52)	0.301 (0.021)	1.41 (0.01)
3. Steinfeld	Fallow	126	2.53 (0.90)	0.303 (0.022)	1.32 (0.15)
4. Landau Kläranlage	Fallow	185	2.95 (1.00)	0.307 (0.021)	1.24 (0.14)
5. Lustadt Ludwigsmühle	Fallow	550	0.62 (0.13)	0.306 (0.020)	0.98 (0.08)
6. Landau Queichheim	Fallow	600	1.44 (0.78)	0.314 (0.019)	1.41 (0.13)
7. Offenbach Strassenrand	Fallow	800	2.38 (0.35)	0.277 (0.021)	1.54 (0.19)
8. Dernbachtal	Meadow	1000	3.05 (0.77)	0.290 (0.021)	1.21 (0.11)
9. Eussertal	Fallow	1100	3.12 (0.69)	0.287 (0.022)	1.44 (0.22)
10. Zeiskam Gärtnerei	Meadow	2100	2.62 (0.53)	0.296 (0.021)	1.50 (0.11)
11. Herxheim	Meadow	2200	2.00 (0.37)	0.311 (0.020)	1.56 (0.14)
12. Lustadt Lachenmühle	Meadow	2600	3.20 (0.45)	0.297 (0.020)	1.35 (0.15)
13. Oberotterbach Ort	Meadow	2800	10.44 (1.85)	0.305 (0.020)	2.04 (0.18)
14. Freckenfeld	Meadow	3100	1.70 (0.45)	0.281 (0.021)	1.73 (0.17)
15. Gräfenhausen	Meadow	4900	19.14 (2.79)	0.315 (0.021)	1.58 (0.15)
16. Neuburg Rheindamm	Meadow	8200	7.57 (1.08)	0.303 (0.021)	1.77 (0.17)

\*Number of flowering individuals.

<sup>†</sup>Number of flowering individuals per square metre.

<sup>‡</sup>Gene diversity (from Musche et al. 2008).

## Data analysis

The influence of defoliation treatment (clipping, control), source habitat (meadow, fallow), and population of origin on seedling performance was analyzed using linear mixed models. Models were fitted using restricted maximum likelihood (REML) available within the procedure MIXED (SAS, version 9.2, SAS Institute Inc., Cary, North Carolina). Habitat, treatment, and the interaction of both factors were included as fixed effects. Population within habitat, and the interaction between population within habitat and treatment were treated as random effects. Mean seed mass of maternal seed families (fixed effect) was included as a covariate to check for possible maternal effects on seedling performance. Fixed effects were tested for significance using *F* tests and random effects were tested using likelihood ratio tests. Full models were reduced stepwise backwards, starting with the least significant highest order interaction term (treatment  $\times$  population (habitat)), followed by the least significant two-way interaction. The covariate was eliminated last, and all main factors were kept in the final models. Differences between reduced and previous models were tested for significance after each step, using likelihood ratio tests. Model simplification was halted if reduced models differed from the previous at  $p < 0.1$ . Defoliation tolerance of each population was estimated as the difference between mean trait values of control plants and clipped plants at final harvest. This estimate was calculated for all investigated traits. Defoliation tolerance between meadows and fallows was compared using *t*-tests. Pearson's correlation coefficients were calculated to investigate the relationship between gene diversity, population size, plant density and the population means of performance traits within each treatment. Similar correlations were calculated to examine the relationship between gene diversity, population size, plant density, and defoliation tolerance.

## Results

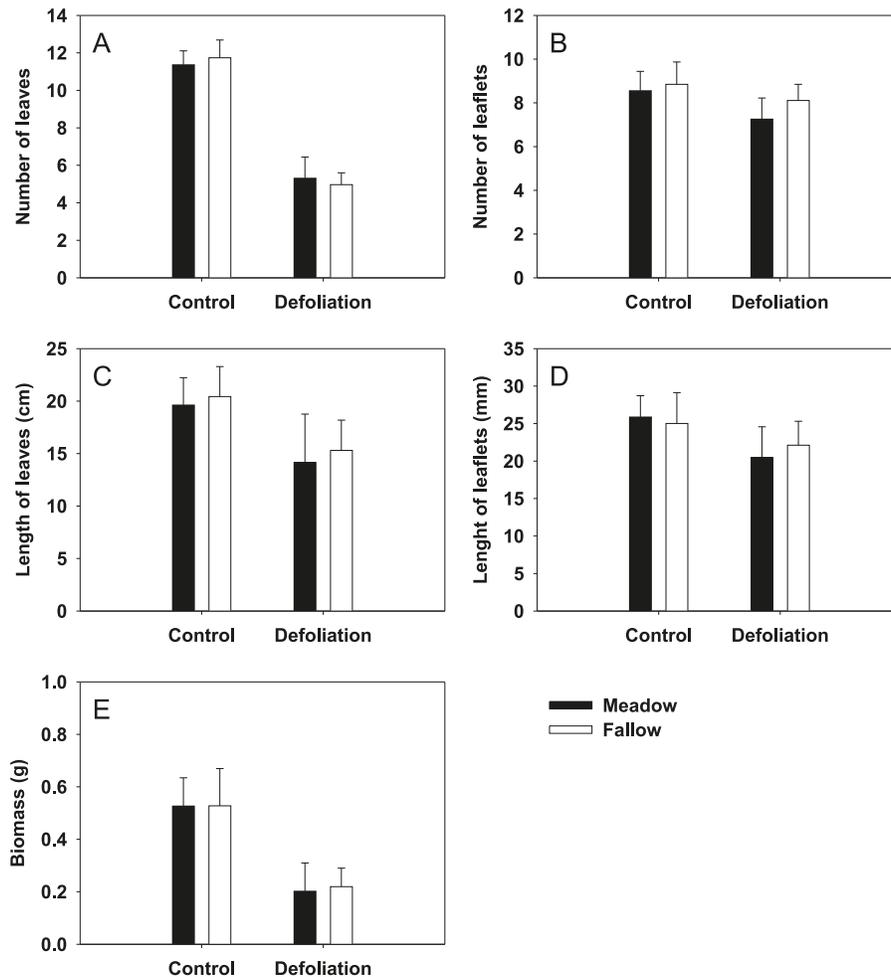
### Performance of seedlings and response to defoliation

In total, 206 of the 215 seedlings planted survived until harvest. Thus, mortality was less than 5% and was therefore not considered in the further analysis. Mean aboveground biomass across all plants was 0.374 g ( $\pm$ 0.271 SD) at final harvest. Mixed model analysis revealed that plants originating from meadows and fallows did not differ in performance (Fig. 1; Table 2), neither in biomass nor in leaf characters. However, populations within habitats differed with respect to the number of leaflets per leaf and the length of leaves (Fig. 2; Table 2), but not in leaf number, length of leaflets, and biomass. Maternal seed mass did not influence any performance trait (Table 2). Defoliation after 8 weeks reduced final dry mass of plants by 65.7% in meadows and 58.3% in fallows. Plants from meadows and fallows responded to defoliation in the same manner ( $P > 0.05$  for treatment  $\times$  habitat in all cases, Fig. 1). Accordingly, there was no significant difference in defoliation tolerance between habitat types regarding the number of leaves per plant ( $t = 0.40$ ,  $P = 0.69$ ), number of leaflets per leaf ( $t = 0.53$ ,  $P = 0.60$ ), length of leaves ( $t = -1.17$ ,  $P = 0.26$ ), length of leaflets ( $t = -1.33$ ,  $P = 0.20$ ), and aboveground biomass ( $t = -1.08$ ,  $P = 0.30$ ). Populations did not respond differently to defoliation ( $P > 0.05$  for all interactions between population within habitat and treatment).

### Performance and response in relation to gene diversity, population size, and plant density

Neither gene diversity, nor population size was correlated with any performance trait, regardless of whether plants had been subjected to the defoliation treatment or control. Likewise, there was no relationship between plant density and plant performance ( $P > 0.05$  in all cases), with one exception; offspring originating from denser populations devel-

**Fig. 1.** Habitat means ( $\pm$ SD) for the number of leaves per plant (A), number of leaflets per leaf (B), length of leaves (C), length of leaflets (D), and aboveground biomass (E), of *S. officinalis* from meadows and fallows in relation to treatment. Habitats neither differed in mean trait values nor in their response to defoliation (Table 2).



oped fewer leaflets per leaf ( $r = -0.52$ ,  $P < 0.05$ ). However, this negative correlation could only be found within the control group. The defoliation tolerance of populations did not correlate with genetic variation ( $P > 0.05$  in all cases).

## Discussion

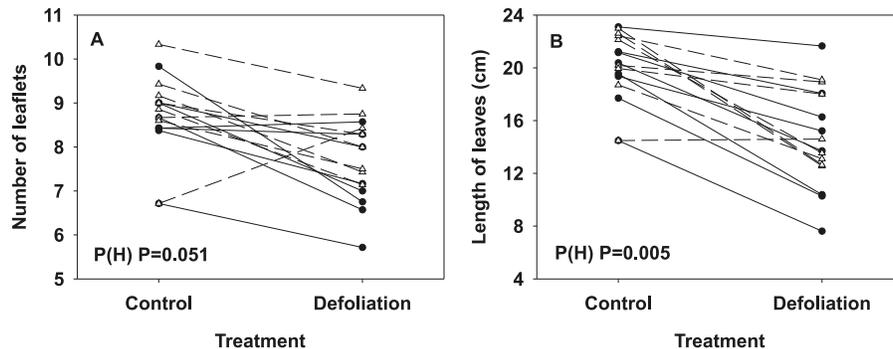
The loss of plant tissue because of herbivory is a major driver of plant evolution, which fostered numerous adaptations to resist and (or) to tolerate tissue loss (Strauss and Agrawal 1999; Núñez-Farfán et al. 2007). Mechanisms of resistance and tolerance include the development of specific plant architectures (e.g., Wise and Abrahamson 2008) and the compensation of lost tissue (Rosenthal and Kotanen 1994), respectively. Like herbivory, repeated mowing on agricultural grasslands may exert selection pressure facilitating the evolution of distinct plant architectures (Carman and Briske 1985; McKinney and Fowler 1991) or enhanced compensation ability (Aarssen and Turkington 1987; Painter et al. 1989; Damhoureyeh and Hartnett 2002). Once the selection regime is relaxed, e.g., by cessation of mowing on successional fallows, previous adaptations are expected to get lost. The fact that we did not find genetic differentiation among *S. officinalis* plants from sites with different mowing

history may be explained by several non-mutually-exclusive factors. First, adaptations may persist for long periods of time after the source of selection is removed (Lahti et al. 2009), especially, when the benefits of a trait outweigh the costs. Second, selection requires a certain time to be effective, and the long generation time of perennial plants has been suggested to decelerate population differentiation (Linhart and Grant 1996; but see Detling and Painter 1983; Jaramillo and Detling 1988). Although it is assumed that all meadows in our study area have a long history of intensive defoliation, the age of the fallows cannot be ascertained accurately. Certainly, these fallows, which have developed from former meadows, have been out of use for at least 10 years. Regarding the perennial life form of *S. officinalis*, this time span might have been too short to generate population differentiation. Third, in heterogeneous environments selection is predicted to favor phenotypic plasticity rather than adaptation to a particular environment (Scheiner 1993; Schlichting and Pigliucci 1995). Such a mechanism was hypothesized by Tomás et al. (2000), who did not find population differentiation in relation to grazing history in a perennial grass. The ability to adjust phenotype in response frequently changing management practices, e.g., mowing, grazing, or abandonment, may facilitate plant survival and

**Table 2.** Stepwise backward reduced linear mixed models analyzing the effects of the defoliation treatment, maternal seed mass, source habitat, and population of origin on performance traits.

Trait	Effect type	Source	df	$F/\chi^2$	$P$
No. of leaves	Fixed	Treatment	1,189	288.97	<0.001
	Fixed	Habitat	1,14	0.10	0.750
	Random	Population (habitat)	1	0.00	0.999
No. of leaflets	Fixed	Treatment	1,189	15.15	<b>&lt;0.001</b>
	Fixed	Habitat	1,14	2.48	0.137
	Random	Population (habitat)	1	3.80	<b>0.051</b>
Length of leaves	Fixed	Treatment	1,189	40.70	<b>&lt;0.001</b>
	Fixed	Habitat	1,14	0.73	0.408
	Random	Population (habitat)	1	7.80	<b>0.005</b>
Length of leaflets	Fixed	Treatment	1,14	12.62	<b>0.003</b>
	Fixed	Habitat	1,14	0.43	0.523
	Fixed	Treatment×habitat	1,14	0.61	0.450
	Random	Population (habitat)	1	0.70	0.403
	Random	Treatment×population (habitat)	1	3.30	<b>0.069</b>
Biomass	Fixed	Treatment	1,188	114.8	<b>&lt;0.001</b>
	Fixed	Habitat	1,14	1.00	0.335
	Random	Population (habitat)	1	0.10	0.752
	Fixed	Seed weight	1,188	2.8	<b>0.096</b>

**Note:**  $F$ -values for fixed effects and  $\chi^2$ -values from likelihood ratio tests for random effects are shown.  $P$  values < 0.1 are indicated in bold font.

**Fig. 2.** Population means for the number of leaflets per leaf (A) and length of leaves (B) of *S. officinalis* seedlings and the response of populations to defoliation.  $P$  values are shown for significant differences in mean trait values between populations. P(H), population(habitat); filled circles and open triangles denote populations located in meadows and fallows, respectively. For detailed results see Table 2.

persistence in areas subject to anthropogenic activity. However, as we did not include further treatments in our experiment, we cannot assess the role of phenotypic plasticity. Finally, gene flow is considered to counteract selection and to prevent genetic differentiation (Lenormand 2002; Levin and Kerster 1974). It seems likely that gene flow contributed to the low degree of differentiation observed in this study, as a related study revealed low differentiation among all study populations ( $F_{ST} = 0.008$ ), the absence of isolation by distance, and the maintenance of high genetic variation in small populations (Musche et al. 2008). The commonness of the species in the study area, its outcrossing breeding system, and its generalist and highly mobile pollinators are likely to maintain gene flow at a sufficiently high level to counteract pronounced population differentiation.

Habitat fragmentation is considered to affect plant fitness adversely as the probability to lose genetic variation by drift and inbreeding is higher in small and isolated populations (Ellstrand and Elam 1993; Young et al. 1996). However, the growth of *S. officinalis* was almost independent of popu-

lation size, plant density, and gene diversity. One possible explanation may lie in the fact that genetic drift acts slowly on populations of long-lived perennials (Loveless and Hamrick 1984). In such plant species, recent fragmentation processes are unlikely to have immediate effects on the level of genetic variation, and thus, genetic load, would be expressed slowly. Further, gene flow can compensate for the loss of genetic variation in small populations and thereby prevent inbreeding depression. Although our study populations vary in their level of intrapopulation genetic variation, this variation could not be attributed to actual population sizes (Musche et al. 2008). This may be an indication for both low drift and high gene flow. Lastly, inbreeding depression as related to habitat fragmentation may not affect all plant traits and life cycle stages equally. It has been suggested that inbreeding depression in predominantly outcrossing plant species mainly acts on the reproductive stages (Oostermeijer et al. 1994; Husband and Schemske 1996), whereas the early development may be more affected by parental effects (Roach and Wulff 1987; Schmid and Dolt 1994).

Although maternal seed mass did not significantly explain variation in any performance measure, such parental carry-over effects cannot be excluded.

Genetic erosion in the course of habitat fragmentation may also affect the ability to cope with stress. Consequently, environmental stress has the potential to shape the relationship between genetic variation and fitness (Pluess and Stöcklin 2004). Therefore, we expected that plants from small and genetically less diverse populations may be particularly vulnerable to biomass removal, as for example demonstrated for *Ipomopsis aggregata* (Heschel and Paige 1995), although these results have been doubted for statistical reasons (Ouborg and Groenendaal 1996). However, population size, density, and genetic diversity of *S. officinalis* populations did not influence the response of seedlings to defoliation. Thus, our results are in line with other studies on perennial plants that did not find effects of habitat fragmentation on the ability to respond to stress (Galeuchet et al. 2005; Paschke et al. 2005) and support the findings of a previous study that indicates a minor importance of fragmentation processes for the fitness of *S. officinalis* in the study area (Musche et al. 2008).

This study revealed that *S. officinalis* from mown meadows and successional fallows were not differentiated with respect to performance characters and response to defoliation. We conclude that offspring from successional fallows retain the ability to cope with defoliation, facilitating successful establishment under conditions of repeated mowing. The slight population differentiation, which was not due to habitat type and almost independent from measures of genetic variation, indicates either genetic drift or an evolutionary response to unknown selection pressures associated with environmental heterogeneity. We only investigated the performance and response of juvenile life stages, and thus missed any potential selection on later stages of the life cycle. Further studies are required to examine whether plant performance and response to defoliation might differ between juvenile plants and plants at the reproductive stage.

## Acknowledgements

We thank Christian Anton, Harald Auge, Ina Geier, Martina Herrmann, Stefan Klotz, Holger Loritz, and Verena Schmidt for their support, and two anonymous reviewers for their helpful comments on a previous version of the manuscript. Research has been conducted within the project CLIMIT (Climat Change Impacts on Insects and their Mitigation) funded by the German Federal Ministry of Education and Research through the FP6 BiodivERsA Eranet and the FP5 EU project MacMan (EVK2-CT-2001-00126).

## References

- Aarssen, L.W., and Turkington, R. 1987. Responses to defoliation in *Holcus lanatus*, *Lolium perenne*, and *Trifolium repens* from three different aged pastures. *Can. J. Bot.* **65**(7): 1364–1370. doi:10.1139/b87-188.
- Carman, J.G., and Briske, D.D. 1985. Morphologic and allozymic variation between long-term grazed and non-grazed populations of the bunchgrass *Schizachyrium scoparium* var *frequens*. *Oecologia* (Berl.), **66**(3): 332–337. doi:10.1007/BF00378294.
- Clausen, J., Keck, D.D., and Hiesey, W.M. 1947. Heredity of geographically and ecologically isolated races. *Am. Nat.* **81**(797): 114–133. doi:10.1086/281507. PMID:20297036.
- Damhoureyeh, S.A., and Hartnett, D.C. 2002. Variation in grazing tolerance among three tallgrass prairie plant species. *Am. J. Bot.* **89**(10): 1634–1643. doi:10.3732/ajb.89.10.1634.
- Detling, J.K., and Painter, E.L. 1983. Defoliation responses of western wheatgrass populations with diverse histories of prairie dog grazing. *Oecologia* (Berl.), **57**(1-2): 65–71. doi:10.1007/BF00379563.
- Ellstrand, N.C., and Elam, D.R. 1993. Population genetic consequences of small population size — implications for plant conservation. *Annu. Rev. Ecol. Syst.* **24**(1): 217–242. doi:10.1146/annurev.es.24.110193.001245.
- Galeuchet, D.J., Perret, C., and Fischer, M. 2005. Performance of *Lychnis flos-cuculi* from fragmented populations under experimental biotic interactions. *Ecology*, **86**(4): 1002–1011. doi:10.1890/03-0762.
- Grace, J.B., and Wetzel, R.G. 1981. Phenotypic and genotypic components of growth and reproduction in *Typha latifolia* — experimental studies in marshes of differing successional maturity. *Ecology*, **62**(3): 789–801. doi:10.2307/1937746.
- Hartnett, D.C., Hartnett, B.B., and Bazzaz, F.A. 1987. Persistence of *Ambrosia trifida* populations in old fields and responses to successional changes. *Am. J. Bot.* **74**(8): 1239–1248. doi:10.2307/2444159.
- Heschel, M.S., and Paige, K.N. 1995. Inbreeding depression, environmental stress, and population size variation in scarlet gilia (*Ipomopsis aggregata*). *Conserv. Biol.* **9**(1): 126–133. doi:10.1046/j.1523-1739.1995.09010126.x.
- Houssard, C., and Escarré, J. 1991. The effects of seed weight on growth and competitive ability of *Rumex acetosella* from two successional old-fields. *Oecologia* (Berl.), **86**(2): 236–242. doi:10.1007/BF00317536.
- Houssard, C., and Escarré, J. 1995. Variation and covariation among life history traits in *Rumex acetosella* from a successional old field gradient. *Oecologia* (Berl.), **102**: 70–80.
- Husband, B.C., and Schemske, D.W. 1996. Evolution of the magnitude and timing of inbreeding depression in plants. *Evolution*, **50**(1): 54–70. doi:10.2307/2410780.
- Jaramillo, V.J., and Detling, J.K. 1988. Grazing history, defoliation, and competition — effects on shortgrass production and nitrogen accumulation. *Ecology*, **69**(5): 1599–1608. doi:10.2307/1941657.
- Joshi, J., Schmid, B., Caldeira, M.C., Dimitrakopoulos, P.G., Good, J., Harris, R., Hector, A., Huss-Danell, K., Jumpponen, A., Minns, A., Mulder, C.P.H., Pereira, J.S., Prinz, A., Scherer-Lorenzen, M., Siamantziouras, A.S.D., Terry, A.C., Troumbis, A.Y., and Lawton, J.H. 2001. Local adaptation enhances performance of common plant species. *Ecol. Lett.* **4**(6): 536–544. doi:10.1046/j.1461-0248.2001.00262.x.
- Keller, L.F., and Waller, D.M. 2002. Inbreeding effects in wild populations. *Trends Ecol. Evol.* **17**(5): 230–241. doi:10.1016/S0169-5347(02)02489-8.
- Lahti, D.C., Johnson, N.A., Ajie, B.C., Otto, S.P., Hendry, A.P., Blumstein, D.T., Coss, R.G., Donohue, K., and Foster, S.A. 2009. Relaxed selection in the wild. *Trends Ecol. Evol.* **24**(9): 487–496. doi:10.1016/j.tree.2009.03.010. PMID:19500875.
- Leimu, R., Mutikainen, P., Koricheva, J., and Fischer, M. 2006. How general are positive relationships between plant population size, fitness and genetic variation? *J. Ecol.* **94**(5): 942–952. doi:10.1111/j.1365-2745.2006.01150.x.
- Lenormand, T. 2002. Gene flow and the limits to natural selection. *Trends Ecol. Evol.* **17**(4): 183–189. doi:10.1016/S0169-5347(02)02497-7.

- Levin, D.A., and Kerster, H.W. 1974. Gene flow in seed plants. *Evol. Biol.* **7**: 139–220.
- Linhart, Y.B., and Grant, M.C. 1996. Evolutionary significance of local genetic differentiation in plants. *Annu. Rev. Ecol. Syst.* **27**(1): 237–277. doi:10.1146/annurev.ecolsys.27.1.237.
- Loveless, M.D., and Hamrick, J.L. 1984. Ecological determinants of genetic structure in plant populations. *Annu. Rev. Ecol. Syst.* **15**(1): 65–95. doi:10.1146/annurev.es.15.110184.000433.
- Lynch, M., and Milligan, B.G. 1994. Analysis of population genetic structure with RAPD markers. *Mol. Ecol.* **3**(2): 91–99. doi:10.1111/j.1365-294X.1994.tb00109.x. PMID:8019690.
- McKinney, K.K., and Fowler, N.L. 1991. Genetic adaptations to grazing and mowing in the unpalatable grass *Cenchrus incertus*. *Oecologia (Berl.)*, **88**(2): 238–242. doi:10.1007/BF00320817.
- Musche, M., Settele, J., and Durka, W. 2008. Genetic population structure and reproductive fitness in the plant *Sanguisorba officinalis* in populations supporting colonies of an endangered *Maculinea* butterfly. *Int. J. Plant Sci.* **169**(2): 253–262. doi:10.1086/524112.
- Nei, M. 1987. *Molecular evolutionary genetics*. Columbia University Press, New York, N.Y.
- Núñez-Farfán, J., Fornoni, J., and Valverde, P.L. 2007. The evolution of resistance and tolerance to herbivores. *Annu. Rev. Ecol. Syst.* **38**(1): 541–566. doi:10.1146/annurev.ecolsys.38.091206.095822.
- Oostermeijer, J.G.B., Eijck, M.W., and Nijs, J. 1994. Offspring fitness in relation to population size and genetic variation in the rare perennial plant species *Gentiana pneumonanthe* (Gentianaceae). *Oecologia (Berl.)*, **97**: 289–296.
- Ouborg, N.J., and Groenendaal, J.M. 1996. Demography, genetics, or statistics: comments on a paper by Heschel & Paige. *Conserv. Biol.* **10**(4): 1290–1291. doi:10.1046/j.1523-1739.1996.10041290.x.
- Painter, E.L., Detling, J.K., and Steingraeber, D.A. 1989. Grazing history, defoliation, and frequency dependent competition — effects on two North-American grasses. *Am. J. Bot.* **76**(9): 1368–1379. doi:10.2307/2444561.
- Paschke, M., Bernasconi, G., and Schmid, B. 2005. Effects of inbreeding and pollen donor provenance and diversity on offspring performance under environmental stress in the rare plant *Cochlearia bavarica*. *Basic Appl. Ecol.* **6**(4): 325–338. doi:10.1016/j.baae.2005.02.005.
- Pluess, A.R., and Stöcklin, J. 2004. Genetic diversity and fitness in *Scabiosa columbaria* in the Swiss Jura in relation to population size. *Conserv. Genet.* **5**(2): 145–156. doi:10.1023/B:COGE.0000029999.10808.c2.
- Reed, D.H., and Frankham, R. 2003. Correlation between fitness and genetic diversity. *Conserv. Biol.* **17**(1): 230–237. doi:10.1046/j.1523-1739.2003.01236.x.
- Roach, D.A., and Wulff, R.D. 1987. Maternal effects in plants. *Annu. Rev. Ecol. Syst.* **18**(1): 209–235. doi:10.1146/annurev.es.18.110187.001233.
- Ronce, O., and Olivieri, I. 1997. Evolution of reproductive effort in a metapopulation with local extinctions and ecological succession. *Am. Nat.* **150**(2): 220–249. doi:10.1086/286064. PMID:18811283.
- Rosenthal, J.P., and Kotanen, P.M. 1994. Terrestrial plant tolerance to herbivory. *Trends Ecol. Evol.* **9**(4): 145–148. doi:10.1016/0169-5347(94)90180-5.
- Scheiner, S.M. 1993. Genetics and evolution of phenotypic plasticity. *Annu. Rev. Ecol. Syst.* **24**(1): 35–68. doi:10.1146/annurev.es.24.110193.000343.
- Schlichting, C.D., and Pigliucci, M. 1995. Gene regulation, quantitative genetics, and the evolution of reaction norms. *Evol. Ecol.* **9**(2): 154–168. doi:10.1007/BF01237754.
- Schmid, B., and Dolt, C. 1994. Effects of maternal and paternal environment and genotype on offspring phenotype in *Solidago altissima* L. *Evolution*, **48**(5): 1525–1549. doi:10.2307/2410246.
- Sobey, D.G. 1987. Differences in seed production between *Stellaria media* populations from different habitat types. *Ann. Bot. (Lond.)*, **59**: 543–549.
- Strauss, S.Y., and Agrawal, A.A. 1999. The ecology and evolution of plant tolerance to herbivory. *Trends Ecol. Evol.* **14**(5): 179–185. doi:10.1016/S0169-5347(98)01576-6. PMID:10322530.
- Theaker, A.J., and Briggs, D. 1993. Genecological studies of groundsel (*Senecio vulgaris* L). IV. Rate of development in plants from different habitat types. *New Phytol.* **123**: 185–194.
- Tomás, M.A., Carrera, A.D., and Poverene, M. 2000. Is there any genetic differentiation among populations of *Piptochaetium napostaense* (Speg.) Hack (Poaceae) with different grazing histories? *Plant Ecol.* **147**(2): 227–235. doi:10.1023/A:1009856732262.
- van Tienderen, P.H., and van der Toorn, J. 1991. Genetic differentiation between populations of *Plantago lanceolata*. I. Local adaptation in three contrasting habitats. *J. Ecol.* **79**(1): 27. doi:10.2307/2260782.
- Warwick, S.I. 1980. The genecology of lawn weeds. VII. The Response of different growth forms of *Plantago major* L. and *Poa annua* L. to simulated trampling. *New Phytol.* **85**(3): 461–469. doi:10.1111/j.1469-8137.1980.tb03182.x.
- Warwick, S.I. 1991. Herbicide resistance in weedy plants — physiology and population biology. *Annu. Rev. Ecol. Syst.* **22**(1): 95–114. doi:10.1146/annurev.es.22.110191.000523.
- Warwick, S.I., and Briggs, D. 1978. The genecology of lawn weeds. I. Population differentiation in *Poa annua* L. in a mosaic environment of bowling green lawns and flower beds. *New Phytol.* **81**(3): 711–723. doi:10.1111/j.1469-8137.1978.tb01646.x.
- Wise, M.J., and Abrahamson, W.G. 2008. Ducking as a means of resistance to herbivory in tall goldenrod, *Solidago altissima*. *Ecology*, **89**(12): 3275–3281. doi:10.1890/08-0277.1. PMID:19137934.
- Young, A., Boyle, T., and Brown, T. 1996. The population genetic consequences of habitat fragmentation for plants. *Trends Ecol. Evol.* **11**(10): 413–418. doi:10.1016/0169-5347(96)10045-8.