

# Adaptation of *Poa alpina* to altitude and land use in the Swiss Alps

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**Abstract** Current land use and climate change are prompting questions about the ability of plants to adapt to such environmental change. Therefore, we experimentally addressed plant performance and quantitative-genetic diversity of the common Alpine Meadow Grass *Poa alpina*. We asked how land use and altitude affect the occurrence of *P. alpina* in the field and whether its common-garden performance suggests adaptation to conditions at plant origin and differences in quantitative genetic diversity among plant origins. Among 216 candidate grassland sites of different land use and altitude from 12 villages in the Swiss Alps, *P. alpina* occurred preferentially in fertilized and grazed sites and at higher elevations. In a common garden at 1,500 m asl, we grew two plants of >600 genotypes representing 78 grassland sites. After 2 years, nearly 90% of all plants had reproduced. In agreement with adaptive advantages of vegetative reproduction at higher altitudes, only 23% of reproductive plants from lower altitudes reproduced via vegetative bulbils, but 55% of plants from higher altitudes. In agreement with adaptive advantages of reproduction in grazed sites, allocation to reproductive biomass was higher in plants from

grazed grasslands than from mown ones. For 53 grasslands, we also investigated broad-sense heritability  $H^2$ , which was significant for all studied traits and twice as high for grazed as for mown grasslands. Moreover, possibly associated with their higher landscape diversity,  $H^2$  was higher for sites of villages of Romanic cultural tradition than for those of Germanic and Walser traditions. We suggest promoting diverse land use regimes to conserve not only landscape and plant species diversity, but also adaptive genetic differentiation and heritable genetic variation.

**Keywords** Alpine grassland · Common garden experiment · Phenotypic plasticity · Quantitative genetic diversity · Reproduction

## Introduction

Plants can be adapted to natural or anthropogenic habitat differentiation (Leimu and Fischer 2008; Stöcklin et al. 2009). However, studies are missing, which simultaneously consider several potential drivers of adaptation. Effects of natural and anthropogenic habitat differentiation on genetic within-species diversity should be especially important and apparent for species that are distributed across a wide altitudinal range and many agricultural land use types such as the Alpine Meadow Grass *Poa alpina* L. (Poaceae). *P. alpina* is among the most important fodder-grass species in the European Alps where it is widespread in mown and grazed mountain grasslands and at natural sites, such as rock fans, snow beds, and riverbeds (Conert 1998).

The heterogeneous landscape of the Alps is characterized by pronounced natural, especially altitudinal, gradients (Theurillat et al. 2003), co-shaped by different cultural and agricultural traditions of human land use for thousands of

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years (Ellenberg 1996; Bätzing 2003). In the Swiss Alps, the old cultural traditions Romanic, Germanic, and Walser, as well as recent land use changes affect vegetation diversity and composition (Maurer et al. 2006; Rudmann-Maurer et al. 2008). Land use changes are particularly important, as in the Alps human land use is undergoing large socio-economically motivated change (Bätzing 1991, 1993, 2003) involving both abandonment of land and intensification of agriculture (Olsson et al. 2000; Fischer and Wipf 2002). In contrast to their effects on between-species diversity and despite the presumably strong selection factors that natural and anthropogenic drivers constitute, their effects on within-species diversity so far received little attention.

Selection by different types of land use over hundreds of years is likely to have caused adaptive variation of growth and reproduction of *P. alpina*. Compared with natural and grazed sites, vegetative growth is likely to be favored under high levels of competition in mown grasslands with their dense homogeneous swards (Abrahamson 1980). Alternatively, in very dense vegetation, such as that in abandoned sites, selection may favor reproduction as means of producing propagules for escape (Abrahamson 1980; Fischer and van Kleunen 2001). Higher allocation to reproduction may have evolved in grazed grassland, where gaps in the vegetation favor recruitment more than homogeneous mown grassland does.

*Poa alpina* occurs in two reproductive forms. Seminaliferous plants produce seeds, while pseudoviviparous plants produce bulbils vegetatively, which develop into little plantlets on the parental plant (Pierce et al. 2000). Vegetative reproduction has been suggested to be of adaptive advantage at higher altitudes, where climatic conditions do not favour seedling establishment (Körner 2003).

While it is likely that long-term selection has led to genetic differentiation, phenotypic variation can additionally be shaped by plastic responses to land use. Moreover, plasticity can be adaptive in heterogeneous environments, where we expect plants to be more plastic, e.g. in response to disturbance brought about by land use, than plants from more uniform conditions (Fischer and van Kleunen 2001). Consequently, as grazed grasslands may be more heterogeneous than mown ones due to heterogeneous impacts by grazing animals, we expect higher plasticity in plants from grazed sites, particularly for reproductive characters. To some degree, also the mode of reproduction appears to be phenotypically plastic in *Poa alpina*, as was reported from experiments where plants turned pseudoviviparous at short day conditions and cold temperatures (Schwarzenbach 1953; Heide 1989).

While current adaptation reflects past processes, heritable quantitative-genetic variation within populations indicates their potential to adapt to future conditions. However, heritable variation and the relative importance of its drivers are

not even known for many widespread plant species. Heritable genetic variation is especially important for traits closely associated with fitness. Under stabilizing selection, such traits are likely to have low heritabilities (Stearns 1980). Nevertheless, in heterogeneous environments substantial heritabilities of fitness-relevant traits may be maintained.

We consider the relationship between land use and heritable genetic variation of especially high interest in the Alps, because land use is undergoing major changes there and many formerly mown sites are converted to grazing (Bätzing 2003). If, as hypothesized above, allocation to reproduction is higher for genotypes from grazed sites and if the frequency of sexually reproducing plants is higher at lower altitudes, we suggest that heritable variation should also be higher among genotypes from grazed sites than from mown ones, and among genotypes from grasslands at lower altitudes. Higher heritable variation could be maintained in grazed sites than in mown sites because of the spatially more heterogeneous selection by grazing animals.

In the Swiss Alps, three many-centuries-old cultural traditions are still apparent in language, culture and landscape, the Romanic, Germanic and Walser traditions (Bätzing 2003). In the valleys of Romanic regions, more diverse types of land use are still found than in the valleys of the other cultural traditions (Maurer et al. 2006). If plants disperse between differently used grassland sites, the higher land use diversity in Romanic regions may suggest that not only microsatellite variation (Maurer et al. 2005; Rudmann-Maurer et al. 2007) but also heritable genetic variation of *P. alpina* is higher in Romanic regions.

Moreover, higher species diversity of the surrounding community may increase heritable variation in *P. alpina*, if it increases the diversity of available niches (Odat et al. 2004, 2010; Vellend and Geber 2005). So far, however, to the best of our knowledge, relationships between plant species diversity and quantitative genetic diversity have not been reported.

A powerful tool to partition phenotypic variation into genetic and environmental components is provided by experimentation in the common garden, where plant growth, plant response to simulated land use, interactions between plant origin and simulated land use, and quantitative genetic diversity can be studied under uniform conditions (Silverton and Charlesworth 2001).

We studied the effects of altitude and land use on the occurrence of *P. alpina* in 216 grassland sites. Then we addressed its growth, reproduction, and its response to an experimental clipping treatment in a common garden experiment. For the experiment, we used clonally derived plants representing more than 600 genotypes from 78 natural, mown, grazed, or abandoned grassland sites. These sites represent different altitudes and land use types around 12 Swiss villages along an east-west gradient of about

170 km. To account for potential regional and cultural differences, we had selected four villages of each of the three main cultural traditions in the Swiss Alps, Romanic, Germanic, and Walser (Fischer et al. 2008). The experiment also served for estimating broad-sense heritability of several vegetative and reproductive characters of *P. alpina* and to relate it to plant species diversity and microsatellite diversity of *Poa alpina* known for all sites from previous studies (Maurer et al. 2005, 2006; Rudmann-Maurer et al. 2007).

We asked the following specific questions: (a) in the field, how does the occurrence of *P. alpina* depend on altitude and land use? In the experiment, (b) do plants from higher altitudes rather reproduce via bulbils than via seeds, (c) do plants from mown sites allocate more to vegetative growth and plants from grazed sites more to reproduction, and (d) are plants from grazed grassland more phenotypically plastic in response to experimental clipping than plants from more homogeneous abandoned or mown grassland? Moreover, we asked whether there is (e) broad-sense heritable genetic variation in vegetative and reproductive traits, and whether it is related to (f) altitude, land use, cultural traditions, (g) diversity of surrounding vegetation in sites of plant origin and (h) diversity of microsatellite markers in sites of plant origin?

## Methods

### Species

The Alpine Meadow Grass *Poa alpina* L. (Poaceae) is widespread in upland regions in the Northern hemisphere (Conert 1998). It occurs mainly on rich soils or alluvial plains and indicates high levels of nutrients and moisture, but it occurs also as a pioneer in stony and rocky places on calcareous and siliceous bedrock. In the Swiss Alps, it occurs in natural sites up to 4,200 m asl and in agriculturally used grassland between 550 and 2,500 m asl (Conert, 1998). Due to its high fat and protein content, *P. alpina* is one of the most important fodder grasses in the Alps (Conert, 1998).

The perennial species occurs in seminiferous and pseudoviviparous forms. The former produce seeds while the latter reproduce by proliferation of the spikelet axis and production of bulbils instead of seeds. Some seminiferous plants produce seeds sexually, others via apomixis (Müntzing 1933). Moreover, *P. alpina* constitutes a polyploid complex with common aneuploidy (Müntzing 1980) and highly variable chromosome numbers (Steiner et al. 1997). In Switzerland chromosome numbers ranging from  $2n = 22$ –46 have been reported (Duckert-Henriod and Favarger 1987), whereas more than 60 chromosomes were reported from Scotch plants (Müntzing 1980).

### Occurrence of the species

We studied the occurrence of *P. alpina* in agricultural grassland sites across 12 villages in the Swiss Alps, 4 of each of the 3 cultural traditions (named after the original settling tribes) Romanic, Germanic, and Walser. Each village is part of a separate alpine valley, and the 12 villages are located along an east–west gradient of about 170 km. To concentrate on effects of agricultural land use change, we excluded regions with extreme touristic or other economic development, or conversion to uniform land use, we selected villages that are not very touristic and that have not grown to more than 1,500 inhabitants. At three altitudinal levels per village (valley at about 1,000 m asl, intermediate altitudes at about 1,500 m asl, and alpine at about 2,000 m asl), we had selected grassland sites representing different land use combinations (Fischer et al. 2008). These combinations comprised sites that were fertilized or unfertilized, had traditionally been mown or grazed, and were currently mown, grazed, or abandoned. The unfertilized mown sites were usually mown once a year whereas the fertilized ones were mown between two and four times. In close collaboration with local farmers, we had found 147 out of 432 possible combinations of villages, altitude, and traditional and current land use. At some altitudes in some villages, there were no sites whose current land use differed from the traditional one. In these cases, we selected two sites of the concerned type of traditional land use to increase sample size. In total, we selected 216 grassland sites, between 12 and 24 per village, and screened them for the presence of *P. alpina*.

### Plant material and its origin

For our common garden experiment, we used plants of *P. alpina* from 65 grassland sites where land use had not had changed according to the local farmers. In each site, we sampled eight plants, plus two extra plants for potential replacement, at interdistances of at least 5 m. In addition, we sampled the same number of plants of *P. alpina* from 24 natural sites, two per village. We considered sites as natural, when they were located within or adjacent to natural plant communities such as the *Caricetum curvulae* or the *Caricetum firmae* (Ellenberg 1996), and when they were at least 200 m separated from agriculturally used grassland.

As measure of landscape diversity in a village, we used the mean number of different land use types per village (Maurer et al. 2006; Fischer et al. 2008). As measure of plant species diversity, we used the mean number of plant species of two vegetation records per site (Maurer et al. 2006; Rudmann-Maurer et al. 2008).

## Plant propagation

Because plant samples consisted of several tillers, we isolated single genotypes from each plant sample. To this end, we first separated each field-collected plant into four single tillers, which we planted into the corners of 7 cm × 7 cm pots. As substrate, we used a 1:2 mix of sand and standard potting turf soil. We grew the plants in a greenhouse. After 2 months, in October 2002, we repotted one randomly selected plant grown out of the four single tillers, and discarded the others. Then, after another 5 months, we divided the plants to receive two replicates per genotype and planted them each into new pots. After leaving the plants for 2 weeks in the greenhouse, we transferred them to the university garden of the University of Zurich (450 m asl) for outdoor acclimatization before planting them to the experimental site in the Alps. 4 weeks later, in May 2003, immediately before transferring the plants to the experimental site, we measured initial size as number of tillers, diameter of the thickest tiller, and, if applicable, we recorded the mode of reproduction for each plant. At the same time, we clipped the plants to a standard height of 12 cm above ground to further reduce potential carry-over effects.

## Experimental design

We used the plants to set up a common garden experiment in a formerly agriculturally used field at about 1,500 m asl at Davos in the Swiss Alps in May 2003. In total, we planted 1,380 plants, two plants of each of 690 genotypes. Microsatellite analysis confirmed that genotypes were indeed different from each other (Rudmann-Maurer et al. 2007). We planted in a grid pattern in eight blocks, each consisting of four rows with up to 44 plants. The space available for each plant was 20 cm × 20 cm. For convenient application of a clipping treatment to one of the plants per genotype, we planted block-wise in four blocks per treatment. The other plant per genotype in the remaining four blocks (alternating with the clipping-treatment blocks) served as control. Within blocks, plants were randomly assigned to planting positions in the grid. Monthly weeding prevented other plants—including non-experimental *P. alpina* plants growing from seed or bulbils—from establishing within the experiment.

## Measurements

In the clipping treatment, we harvested vegetative biomass (later on called clipped biomass) by clipping all leaves 5 cm above ground, but leaving out emerging reproductive shoots. In 2003, we clipped twice, in July and in October. In 2004, we clipped and harvested the vegetative biomass of the plants in the clipping treatment once at the end of June.

1 month later, we finished the experiment by harvesting the aboveground vegetative biomass of all plants, including the control plants, at 3 cm above ground (later on called final vegetative biomass, while the three earlier harvest masses combined are called cumulative clipped vegetative biomass). After the harvests, we dried the biomass at 80°C and weighed it.

We also harvested reproductive biomass of each plant for 2 years. In 2003, we harvested monthly from July to October. Of each reproducing plant, we cut off the reproductive shoots 5 cm above ground, counted them, and collected them in paper bags. Moreover, we noted the reproductive mode as seminiferous or pseudoviviparous. The reproductive shoots were only taken when at least a few anthers were visible (then noted as seminiferous), or when bulbils were well developed and about to dehisce (then noted as pseudoviviparous). Less developed shoots were left for the next harvest. For each plant, we harvested all reproductive biomass into the same paper bag to cumulatively receive the total amount of reproductive biomass. After drying the reproductive biomass at 80°C, we weighed it and summed up the number of shoots. In 2004, we harvested reproductive biomass at the end of June and at the time of final harvest.

## Statistical analysis: plant performance

We analyzed the effects of land use and altitude on the occurrence of *P. alpina* in the field by logistic regression based on binomial distribution. The full hierarchical mixed model included the factors culture (denoting the three cultural traditions), village (nested in culture), altitude, fertilization, abandonment, current land use, and all two-way interactions.

For the analyses of the common-garden experiment, 75 plants were excluded due to wrong sampling information. Moreover, independent of the experimental factors (GLM analyses, data not shown), another 75 plants died during the experiment and were not taken into account. Finally, of the originally 1,380 plants, we included 1,230 plants in the analyses, 905 from 57 mown, grazed or abandoned grassland sites and 325 from 21 natural sites.

For the clipping-treatment plants, we analyzed cumulative clipped vegetative biomass, cumulative clipped reproductive biomass, and cumulative number of clipped reproductive shoots. These cumulative numbers did not include the final harvest. The full hierarchical mixed ANOVA model included the factors culture, village (nested in culture), altitude, natural (distinguishing natural from used sites), fertilization, abandonment, and current land use, including all interactions and site (Table 1). From this full model, we selected reduced best models for each variable using Akaike's Information Criterion (AIC)-values (Burnham and Anderson 2002). This model selection procedure

**Table 1** Full ANOVA model and error terms for the analysis of common-garden variation in the performance of 1,230 *Poa alpina* plants from 57 currently or formerly used grassland sites of different altitude and land use and 21 natural grassland sites in 12 villages of three different cultural traditions in the Swiss Alps

Source of variation	MS	F
Culture	ms <sub>cult</sub>	ms <sub>cult</sub> /ms <sub>vill</sub>
Village	ms <sub>vill</sub>	ms <sub>vill</sub> /ms <sub>site</sub>
Altitude	ms <sub>alt</sub>	ms <sub>alt</sub> /ms <sub>site</sub>
Natural	ms <sub>nat</sub>	ms <sub>nat</sub> /ms <sub>site</sub>
Fertilization	ms <sub>fert</sub>	ms <sub>fert</sub> /ms <sub>site</sub>
Current land use	ms <sub>curr</sub>	ms <sub>curr</sub> /ms <sub>site</sub>
Site	ms <sub>site</sub>	ms <sub>site</sub> /ms <sub>genotype</sub>
Genotype	ms <sub>geno</sub>	ms <sub>geno</sub> /ms <sub>residual</sub>
Clipping treatment	ms <sub>clip</sub>	ms <sub>clip</sub> /ms <sub>residual</sub>
Clipping × Culture	ms <sub>clip</sub> × cult	ms <sub>clip</sub> × cult/ms <sub>clip</sub> × vill
Clipping × Village	ms <sub>clip</sub> × vill	ms <sub>clip</sub> × vill/ms <sub>clip</sub> × site
Clipping × Altitude	ms <sub>clip</sub> × alt	ms <sub>clip</sub> × alt/ms <sub>clip</sub> × site
Clipping × Natural	ms <sub>clip</sub> × nat	ms <sub>clip</sub> × nat/ms <sub>clip</sub> × site
Clipping × Fertilization	ms <sub>clip</sub> × fert	ms <sub>clip</sub> × fert/ms <sub>clip</sub> × site
Clipping × Current land use	ms <sub>clip</sub> × curr	ms <sub>clip</sub> × curr/ms <sub>clip</sub> × site
Clipping × Site	ms <sub>clip</sub> × site	ms <sub>clip</sub> × site/ms <sub>residual</sub>
Residual = Clipping × Genotype	ms <sub>residual</sub>	

MS denotes mean squares, F denotes variance ratios

revealed as best model the one comprising the main seven factors culture, village, altitude, natural, fertilization, current land use, site, without any interactions (Table 1).

For all plants, we analyzed cumulative reproductive biomass and cumulative number of reproductive shoots, final vegetative biomass, total vegetative biomass (i.e. sum of final harvest and cumulative clipped biomass), and percentages of reproductive and vegetative biomass (relative to the sum of vegetative and reproductive biomass) with the same model as above, but adding the factors genotype and treatment. Again, we selected reduced best models for each variable starting with the full hierarchical model including all interactions. Finally, the best model included the main seven factors culture, village, altitude, natural, fertilization, current land use, site, and their two-way interactions with clipping treatment (Table 1). Final vegetative biomass and total vegetative biomass were log-transformed, and reproductive biomass and number of reproductive shoots were square root transformed prior to analysis of variance (ANOVA) to meet ANOVA assumptions.

To test variation in whether plants reproduced at all, we used logistic regression based on binomial distribution. To analyze which factors affect the mode of reproduction, we summed the number of reproducing plants per clipping treatment and site and calculated the percentage of semiferously reproducing plants, arcsin transformed it and fitted an ANOVA model including effects of culture, village, altitude, natural, fertilization, current land use, site, treatment, and all interactions of the treatment.

We analyzed all data separately for each year (by summing both harvests of clipped biomass and all harvests of reproductive biomass respectively number of reproductive

shoots per year) and for both years combined. In all analyses, we treated village, site, and genotype as random factors. Including initial tiller diameter, number of tillers, and row and position in the experiment as covariates did not change levels of significance. Therefore, we report the results of models without covariates. We calculated all logistic regressions and ANOVAs with the program GENSTAT (Version 6.1, Lawes Agricultural Trust, 2002).

#### Statistical analysis: quantitative genetic diversity

To concentrate on effects of different land uses we calculated quantitative genetic diversity between genotypes within sites for the 53 mown and grazed sites, i.e. based on measurements of 825 plants representing >400 genotypes. For each site, we calculated broad-sense heritability of the measured quantitative characters separately (final vegetative biomass, total vegetative biomass, reproductive biomass, number of reproductive shoots, total overall biomass, and percentage of reproductive biomass). Moreover, we calculated the mean of the three heritabilities of reproductive characters, of the two heritabilities of vegetative characters, and of all six characters.

For each site, to calculate broad-sense heritability, we estimated variance components (VC) for variation among genotypes and for residual variation with expected mean squares (EMS) analyses of variance including the random factor genotype and the fixed factor treatment. The broad-sense heritability,  $H^2$ , is given by the quotient of the VC due to differences among genotypes ( $s_G^2$ ) and the sum of this VC and the one due to residual variance ( $s_{Res}^2$ ) as  $H^2 = s_G^2 / (s_G^2 + s_{Res}^2)$  (Falconer and MacKay 1996).

**Table 2** Vegetative and reproductive biomass in the common garden, and number of reproductive shoots and their mean  $\pm$  SE and number  $N$  of *Poa alpina* plants originating from grassland sites of different land use in the Swiss Alps, combined over both years of the experiment and for the years 2003 and 2004 separately

Year	Natural (21)		Mown – (8)		Mown + (6)		Grazed – (29)		Grazed + (11)		Abandoned (4)	
	Mean	$N$	Mean	$N$	Mean	$N$	Mean	$N$	Mean	$N$	Mean	$N$
Total biomass (g)	12.87 $\pm$ 0.52	325	14.92 $\pm$ 0.68	128	17.74 $\pm$ 0.9	93	12.97 $\pm$ 0.42	448	15.09 $\pm$ 0.94	172	15.01 $\pm$ 1.15	64
Final vegetative biomass (g)	5.25 $\pm$ 0.32	325	7.93 $\pm$ 0.34	128	9.68 $\pm$ 0.61	93	5.32 $\pm$ 0.24	448	6.02 $\pm$ 0.45	172	5.79 $\pm$ 0.54	64
Clipped vegetative biomass (g)	5.45 $\pm$ 0.28	162	7.05 $\pm$ 0.47	64	7.08 $\pm$ 0.40	46	4.52 $\pm$ 0.22	224	5.51 $\pm$ 0.46	85	4.69 $\pm$ 0.59	32
	0.92 $\pm$ 0.06	162	1.78 $\pm$ 0.18	64	1.78 $\pm$ 0.14	46	1.11 $\pm$ 0.06	224	1.36 $\pm$ 0.14	85	1.15 $\pm$ 0.10	32
	4.53 $\pm$ 0.25	162	5.27 $\pm$ 0.35	64	5.30 $\pm$ 0.34	46	3.41 $\pm$ 0.19	224	4.15 $\pm$ 0.36	85	3.54 $\pm$ 0.54	32
Reproductive biomass (g)	6.50 $\pm$ 0.60	274	3.01 $\pm$ 0.31	108	4.19 $\pm$ 0.57	85	5.13 $\pm$ 0.23	419	5.80 $\pm$ 0.47	151	4.17 $\pm$ 0.30	60
	4.07 $\pm$ 0.42	241	2.66 $\pm$ 0.25	106	3.18 $\pm$ 0.43	85	3.38 $\pm$ 0.17	387	3.91 $\pm$ 0.36	141	2.77 $\pm$ 0.21	60
	3.65 $\pm$ 0.41	174	2.43 $\pm$ 0.54	18	3.41 $\pm$ 0.63	25	2.95 $\pm$ 0.16	286	3.45 $\pm$ 0.30	94	2.73 $\pm$ 0.25	40
Number of reproductive shoots	55.7 $\pm$ 5.1	274	26.3 $\pm$ 2.9	108	24.9 $\pm$ 2.6	85	47.4 $\pm$ 2.1	419	48.8 $\pm$ 3.7	151	40.7 $\pm$ 2.8	60
	41.2 $\pm$ 4.1	241	24.9 $\pm$ 2.6	106	22.0 $\pm$ 2.5	85	36.9 $\pm$ 1.8	387	37.5 $\pm$ 3.1	141	33.4 $\pm$ 2.1	60
	21.7 $\pm$ 2.6	174	11.5 $\pm$ 2.9	18	9.7 $\pm$ 1.5	25	19.5 $\pm$ 1.2	286	22.2 $\pm$ 1.7	94	17.8 $\pm$ 1.9	40

Total biomass is the sum of vegetative and reproductive biomass. Numbers in brackets denote number of sites of plant origin, and fertilized +, unfertilized –, As not every plant reproduced every year, for the reproductive characters numbers and means of 2003 and 2004 do not add up to both years combined

To analyze whether broad-sense heritabilities overall were significantly different from zero, we used two approaches. First, we tested whether variation among genotypes within grassland sites was significant. To this end, we analyzed the reproductive and vegetative characters with ANOVA using a mixed model including the factors site, genotype, treatment, and site  $\times$  clipping treatment interaction. From this analysis, overall  $H^2$  was obtained from the VC for genotypes and the VC residual using the equation above. Second, we obtained mean and standard error of  $H^2$  from all  $H^2$  estimates across sites. We used these data for a  $t$  test of the test statistic mean/SE.

Then, we analyzed effects of land use, altitude, and cultural traditions on broad-sense heritability with an ANOVA model with sequential sums of squares using a hierarchical mixed model including the factors culture, village, altitude, fertilization, current land use, and all two-way interactions. Effects of culture were tested against remaining variation among villages and effects of all other factors against variation due to remaining differences among sites.

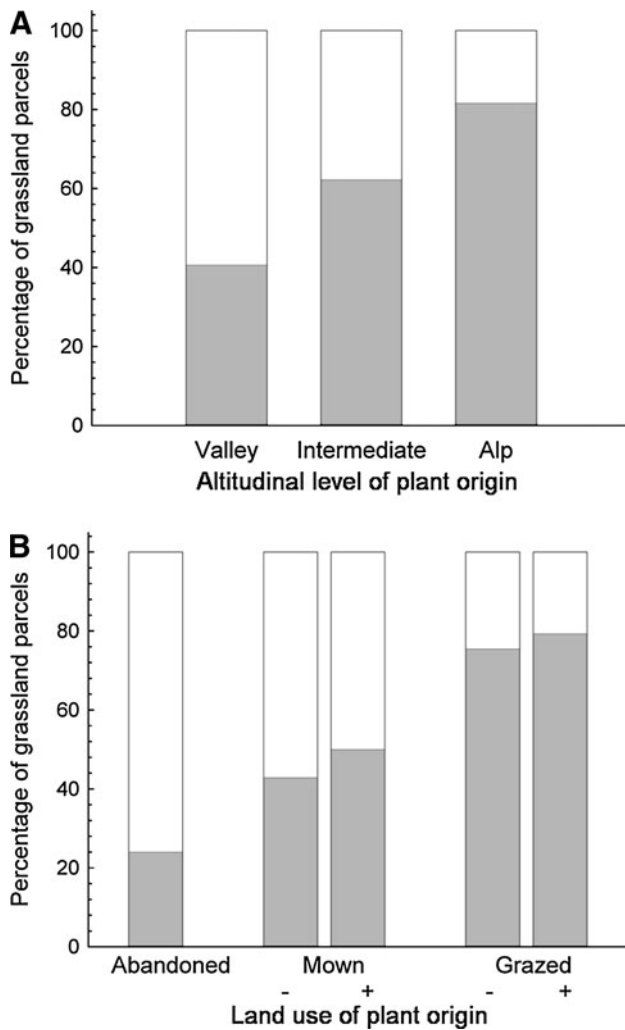
## Results

### Occurrence of *Poa alpina* in the field

*Poa alpina* occurred in sites representing 85 out of the 147 combinations of village, altitude, and land use. It occurred more frequently in sites at higher altitudes than at lower ones ( $N = 147$ ,  $F_{2,130} = 12.57$ ,  $P < 0.001$ , Fig. 1a). Moreover, it occurred more frequently in fertilized sites than in unfertilized ones ( $N = 147$ ,  $F_{1,130} = 12.88$ ,  $P < 0.001$ , Fig. 1b). Finally, *P. alpina* occurred most frequently in grazed sites, followed by mown and abandoned ones ( $N = 147$ ,  $F_{2,130} = 25.87$ ,  $P < 0.001$ , Fig. 1b). In summary, higher altitude, fertilization, and grazing favored the occurrence of *P. alpina*.

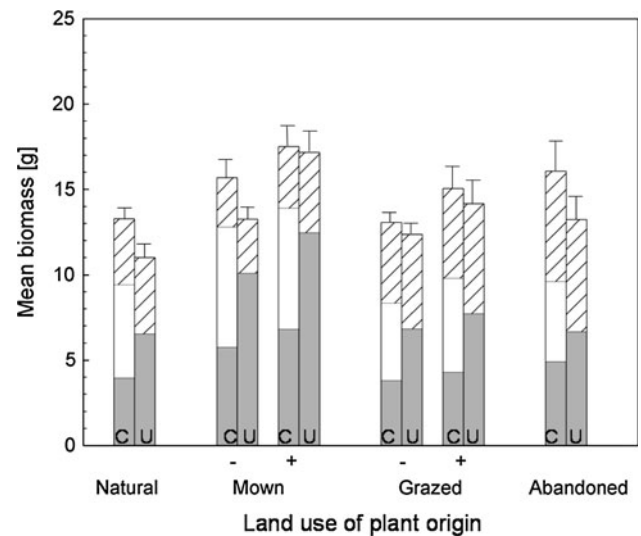
### Vegetative growth of *Poa alpina* in the common garden

In 2003 and 2004 and for both years combined, clipped vegetative biomass was highest for plants from mown sites (ANOVA of combined clipped biomass:  $N = 612$ ,  $F_{2,61} = 5.31$ ,  $P < 0.001$ ; Table 2) and lowest for plants from grazed and abandoned sites. Whereas in 2003 and for both years combined, clipped plants from natural sites produced the second highest vegetative biomass, they produced the least in 2004. While the above-mentioned differences between plants from mown and grazed sites were significant, those between plants from natural, used, and abandoned ones were not. Altitude of origin did not affect vegetative growth in the common garden.



**Fig. 1** Proportion of studied grassland sites in the Swiss Alps in which *Poa alpina* occurred according to **a** three altitudinal levels (valley at about 1,000 m asl, intermediate altitudes at about 1,500 m asl, and alpine at about 2,000 m asl) where the sites were situated, and **b** land use of the sites. Fertilized sites indicated by +, unfertilized by -. *Shaded*, *P. alpina* present; *open*, *P. alpina* absent

At final harvest, control plants yielded more final vegetative biomass than clipped plants ( $N = 1230$ ,  $F_{1,536} = 180.26$ ,  $P < 0.001$ , Fig. 2), although the percentage of total biomass made up by vegetative biomass was higher in clipped plants than in control plants ( $N = 1210$ ,  $F_{1,516} = 130.18$ ,  $P < 0.001$ ). Final vegetative biomass was higher in plants from mown grasslands ( $N = 1230$ ,  $F_{2,61} = 5.74$ ,  $P < 0.01$ , Fig. 2) than in plants from grazed, natural, and abandoned ones. Moreover, at final harvest, plants originating from fertilized sites yielded more final vegetative biomass than those from unfertilized ones did ( $N = 1230$ ,  $F_{1,61} = 4.26$ ,  $P < 0.05$ ). In summary, mowing and fertilization of the site of origin enhanced the common garden yield of final vegetative biomass.



**Fig. 2** Overview of biomass produced in the common garden experiment with 1,230 plants of *Poa alpina* originating from 78 grassland sites of different land use. Final vegetative biomass is indicated by *shaded portions of bars*, cumulative clipped biomass by *open portions of bars*, and reproductive biomass by *hatched portions of bars*. *C* clipped plants, *U* unclipped plants. *Error bars* denote 1 SE of total biomass

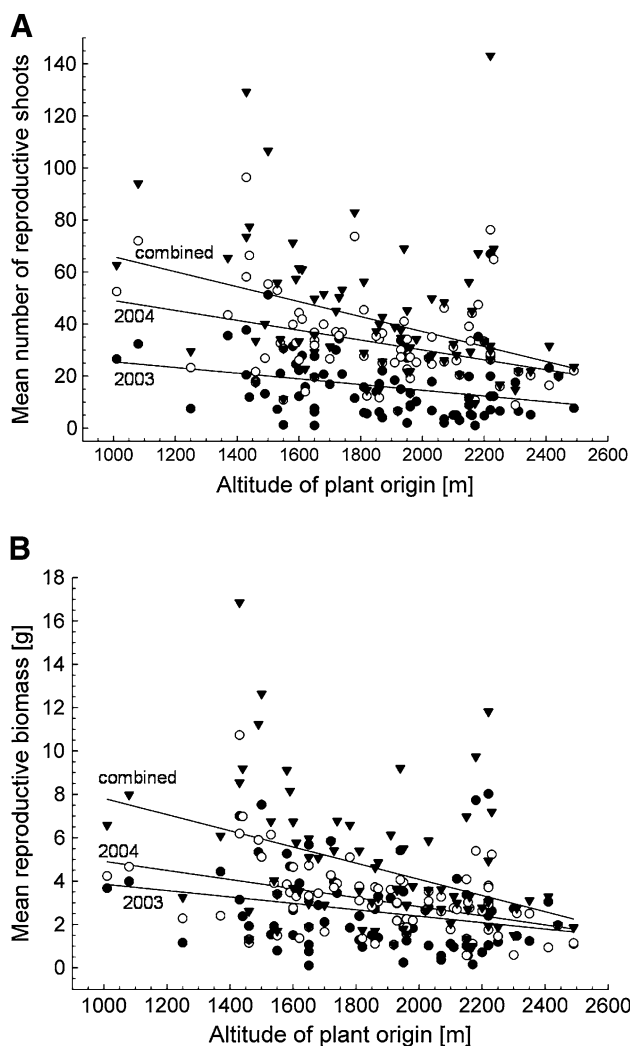
#### Reproduction of *Poa alpina* in the common garden

By the end of the experiment, 89.3% of the 1,230 plants had reproduced. In 2003, 52.2% of all plants reproduced, and in 2004, 82.9% reproduced. Overall, unclipped plants produced more reproductive biomass ( $5.12 \pm 0.23$  g) than clipped ones did ( $4.43 \pm 0.19$  g;  $N = 1097$ ,  $F_{1,61} = 14.43$ ,  $P < 0.001$ ).

In 2003, plants from grazed sites were more likely to reproduce than plants from mown and abandoned ones ( $N = 1230$ ,  $F_{2,61} = 5.80$ ,  $P < 0.01$ ). In 2004 and for the 2 years combined, land use of the site of origin did not affect the likelihood of reproduction.

The number of reproductive shoots was closely positively correlated with reproductive biomass ( $N = 1097$ ,  $R = 0.862$ ,  $P < 0.001$ ). Both the number of reproductive shoots (for both years combined:  $N = 1097$ ,  $F_{1,61} = 12.97$ ,  $P < 0.001$ , Fig. 3a) and reproductive biomass (for both years combined:  $N = 1097$ ,  $F_{1,61} = 13.20$ ,  $P < 0.001$ , Fig. 3b) decreased with increasing altitude of origin. Moreover, the percentage of reproductive biomass decreased with increasing altitude ( $N = 1097$ ,  $F_{1,61} = 25.96$ ,  $P < 0.001$ ).

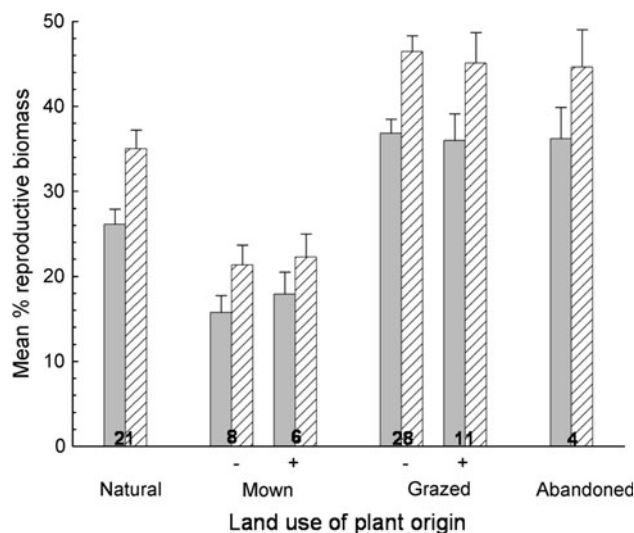
More reproductive shoots were produced by plants from grazed sites than by plants from mown and abandoned ones ( $N = 1097$ ,  $F_{2,61} = 4.81$ ,  $P < 0.05$ ). Land use did not have any effects on the amount of reproductive biomass, whereas it affected the percentage of reproductive biomass. In both treatments, compared with plants from natural sites,



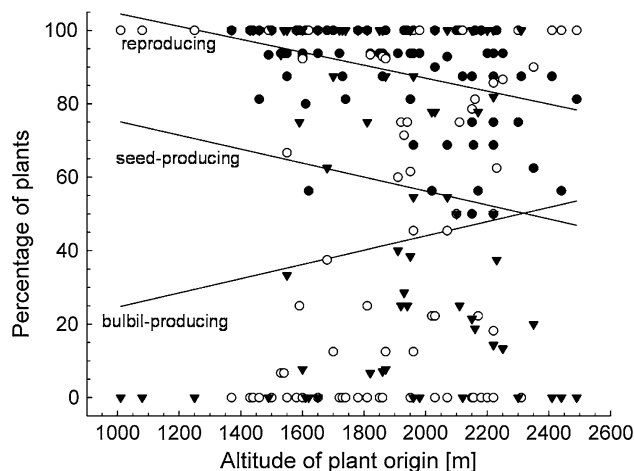
**Fig. 3** **a** Mean number of reproductive shoots, and **b** mean reproductive biomass of *Poa alpina* plants originating from 78 grassland sites at different altitudes grown in the common garden. Filled circles denote plants reproducing in 2003, open circles in 2004, and triangles the combination over both years (i.e. plants reproducing in both or either year)

allocation towards reproduction was significantly increased in plants from grazed sites and decreased in plants from mown ones ( $N = 1210$ ,  $F_{2,61} = 7.53$ ,  $P = 0.001$ , Fig. 4).

In agreement with adaptive advantages of vegetative reproduction at higher altitudes, only 23% of reproductive plants from lower altitudes reproduced via vegetative bulbils, but 55% of plants from higher altitudes ( $N = 156$ ,  $F_{1,61} = 8.37$ ,  $P < 0.01$ , Fig. 5). Land use at plant origin did not affect the mode of reproduction. We recorded only two plants that changed their reproductive mode from one year to another (one from seminiferous to pseudoviviparous, one vice versa). Different reproductive modes between the 2 plants of the same genotype occurred for 6 of the 615 genotypes.



**Fig. 4** Mean percentage of reproductive biomass relative to total biomass of clipping treatment plants (shaded) and control (hatched) plants of *Poa alpina* originating from 78 grassland sites of different land use grown in the common garden. Numbers within bars denote number of sites of origin of the types of land use. Fertilized sites indicated by +, unfertilized ones by -. Error bars denote 1 SE. Note that, compared with the one of plants from natural sites, the percentage of reproductive biomass is reduced for plants from mowed sites and increased for plants from grazed and abandoned sites



**Fig. 5** Proportion of reproducing *Poa alpina* plants and proportion of plants per reproductive mode (filled circles reproducing, open circles reproducing by bulbils, triangles reproducing by seeds) in the common garden in relationship to the altitude of the 78 sites of plant origin

#### Broad-sense heritability of *Poa alpina*

Variation among genotypes within the 53 analyzed sites was significant for all vegetative and reproductive characters (Table 3A). Corresponding estimates of broad-sense heritabilities  $H^2$  were between 0.426 (percentage of reproductive biomass) and 0.647 (final vegetative biomass; Table 3A).



**Table 3** Broad-sense heritability  $H^2$  of reproductive and vegetative characters measured in *Poa alpina* plants from 53 grassland sites of different land use and altitude in the Swiss Alps

	A		B			
	$H^2$	$P$ (genotype)	Mean $H^2$	$\pm$ SE	$t = \text{Mean } H^2/\text{SE}$	$P$ ( $t$ test)
Number of reproductive shoots	0.496	0.000	0.414	0.041	10.011	0.000
Reproductive biomass	0.513	0.000	0.425	0.041	10.342	0.000
% of reproductive biomass	0.647	0.000	0.572	0.046	12.485	0.000
Final vegetative biomass	0.426	0.000	0.363	0.035	10.269	0.000
Total vegetative biomass (clipped and final)	0.466	0.000	0.391	0.041	9.471	0.000
Total biomass (vegetative and reproductive)	0.446	0.000	0.394	0.039	10.065	0.000
Mean reproductive $H^2$			0.470	0.068	6.946	0.003
Mean vegetative $H^2$			0.377	0.014	26.805	0.001
Mean overall $H^2$			0.429	0.029	14.711	0.000

(A) Broad-sense heritability estimated from within-site variance component among genotypes obtained by Analysis of Variance using data of all sites (see “Methods”). (B) Broad-sense heritability estimated as mean across all single-site broad-sense heritabilities. Mean reproductive  $H^2$  denotes mean of broad-sense heritability of three reproductive characters, mean vegetative  $H^2$  denotes mean of broad-sense heritability of two vegetative characters, and mean overall  $H^2$  denotes mean of all six broad-sense heritabilities

In line with the above, our second test also confirmed that all means of the estimates of the single-site broad-sense heritability over all sites were significantly different from zero and were between 0.363 (percentage of reproductive biomass) and 0.572 (final vegetative biomass; Table 3B).

The three heritability estimates for reproductive characters were non-significantly higher than the estimates of the two vegetative characters ( $t$  test,  $df = 3$ ; data of Table 3A:  $t = 1.671$ ,  $P > 0.19$ ; data of Table 3B:  $t = 1.402$ ,  $P > 0.26$ ).

#### Relationships of cultural traditions, land use, and altitude of grassland sites with broad-sense heritability of *Poa alpina*

Broad-sense heritability of total vegetative biomass was higher for sites from Romanic villages than for those from Germanic and Walser villages ( $N = 53$ ,  $F_{2,9} = 5.1$ ,  $P < 0.05$ , Table 4; Fig. 6a). Broad-sense heritabilities were higher for grazed sites than for mown ones. This was especially pronounced for the heritability estimate of percentage of reproductive biomass ( $N = 53$ ,  $F_{1,10} = 15.0$ ,  $P < 0.01$ ), and also for overall mean heritability ( $N = 53$ ,  $F_{1,10} = 6.5$ ,  $P < 0.05$ , Table 4; Fig. 6b). Heritability estimates were independent of altitude and fertilization of grassland sites.

#### Relationships of broad-sense heritability of *Poa alpina* with microsatellite diversity and plant species richness

Broad-sense heritabilities of reproductive and vegetative traits were independent of plant species richness in the sites of origin. Positive relationships of heritability estimates of total overall biomass ( $n = 53$ ,  $r = 0.269$ ,  $P < 0.07$ ) and of

final vegetative biomass ( $n = 53$ ,  $r = 0.234$ ,  $P < 0.09$ ) with mean allelic richness of microsatellite markers per site were only marginally significant, not clearly suggesting positive relationships between selectively neutral and quantitative genetic variation.

## Discussion

### Habitats of *Poa alpina*

The higher likelihood of occurrence of *P. alpina* in grazed sites suggests a preference for more disturbed sites where vegetation gaps facilitate establishment of seedlings (Grubb 1977) or plantlets derived from bulbils. This corresponds to the results that plants in the common garden originating from grazed sites produced more reproductive shoots and higher reproductive biomass than plants from other sites (see below).

The higher likelihood of occurrence of *P. alpina* at higher altitudes corresponds well with its described distribution in subalpine habitats (Conert 1998). Our finding of higher likelihood of occurrence of *P. alpina* in fertilized grasslands also confirms its preference for nutrient-rich habitats, which is also indicated by a high nutrient indicator value attributed to the species (Landolt 1977; Ellenberg et al. 1992).

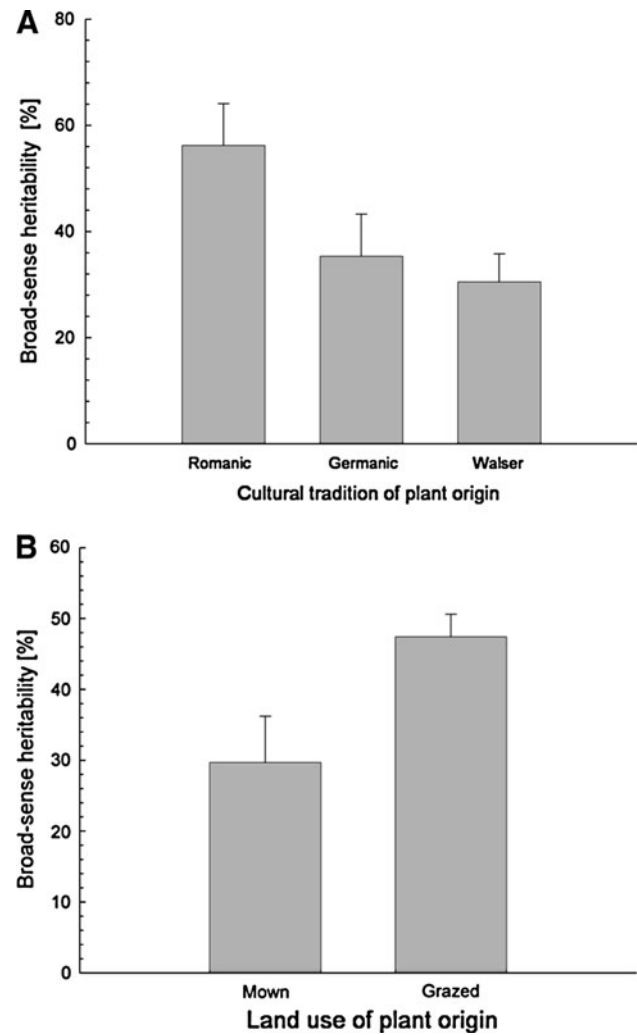
### Evidence for adaptation of vegetative growth

In our experiment, plants from mown grassland sites produced more vegetative biomass than plants from grazed sites did, suggesting divergent selection between mown and grazed sites. We suggest that, as hypothesized, high

**Table 4** Mean broad-sense heritabilities  $H^2$  of different reproductive and vegetative characters of *Poa alpina* plants from 53 grassland sites of different cultural tradition and land use in the Swiss Alps

Mean $H^2 \pm SE$	Reproductive characters					Vegetative characters				
	N sites	Number of reproductive shoots	Reproductive biomass	% of reproductive biomass	Mean reproductive $H^2$	Final vegetative biomass	Total vegetative biomass (clipped and final)	Total biomass (vegetative and reproductive)	Mean overall $H^2$	
Romantic	15	0.405 $\pm$ 0.081	0.492 $\pm$ 0.059	<b>0.742 <math>\pm</math> 0.058</b>	0.546 $\pm$ 0.056	<b>0.495 <math>\pm</math> 0.066</b>	<b>0.562 <math>\pm</math> 0.079</b>	0.448 $\pm$ 0.083	<b>0.524 <math>\pm</math> 0.059</b>	
Germanic	15	0.442 $\pm$ 0.075	0.429 $\pm$ 0.085	<b>0.651 <math>\pm</math> 0.089</b>	0.507 $\pm$ 0.072	<b>0.322 <math>\pm</math> 0.057</b>	<b>0.353 <math>\pm</math> 0.080</b>	0.376 $\pm$ 0.077	<b>0.429 <math>\pm</math> 0.050</b>	
Walser	23	0.400 $\pm$ 0.065	0.376 $\pm$ 0.067	<b>0.408 <math>\pm</math> 0.067</b>	0.401 $\pm$ 0.056	<b>0.304 <math>\pm</math> 0.054</b>	<b>0.305 <math>\pm</math> 0.053</b>	0.371 $\pm$ 0.054	<b>0.365 <math>\pm</math> 0.041</b>	
Mown	13	0.358 $\pm$ 0.094	0.287 $\pm$ 0.091	<b>0.297 <math>\pm</math> 0.098</b>	<b>0.323 <math>\pm</math> 0.088</b>	<b>0.227 <math>\pm</math> 0.071</b>	0.273 $\pm$ 0.073	0.273 $\pm$ 0.063	<b>0.289 <math>\pm</math> 0.059</b>	
Grazed	40	0.43 $\pm$ 0.046	0.466 $\pm$ 0.044	<b>0.661 <math>\pm</math> 0.044</b>	<b>0.519 <math>\pm</math> 0.036</b>	<b>0.407 <math>\pm</math> 0.039</b>	0.430 $\pm$ 0.048	0.434 $\pm$ 0.046	<b>0.471 <math>\pm</math> 0.031</b>	

Significant differences are indicated by *bold numbers*. SE denotes standard error. N denotes the number of sites of plant origin



**Fig. 6** Broad-sense heritability of *Poa alpina*. **a** Relationship between cultural tradition and broad-sense heritability  $H^2$  of total vegetative biomass of *Poa alpina* plants. **b** Relationship between land use and the mean overall broad-sense heritability  $H^2$ . Broad-sense heritabilities were obtained using experimental plants of *Poa alpina* originating from 53 consistently mown or grazed grassland sites of different cultural traditions, land use and altitude in the Swiss Alps. Error bars denote 1 SE

vegetative growth rates are competitively favorable in mown grassland. On the other hand, plants with high vegetative growth rates would be more conspicuous and therefore run higher risks of being consumed in grazed sites, which reduces the potential competitive advantage of fast growth. These differences in common-garden growth of plants from mown and grazed parcels suggest adaptation of *P. alpina* to land use. Similarly, intraspecific variation of the grass *Sesleria albicans* in a common garden was related to habitat quality and land use of its anthropogenic habitats of origin (Reisch and Poschlod 2003).

In our experiment, measures of vegetative plant performance (but not of reproductive performance, see below)

were independent of the altitude of plant origin. The invasive plant *Erigeron annuus* was not adapted to altitude in the Swiss Alps (Trtikova et al. 2010) possibly because time since introduction was too short or due to lack of sufficient initial genetic variation. The alpine forb *Craspedia lamicola* turned out not to be strongly adapted locally in field and garden experiments in Australia (Byars and Hoffmann 2009). In contrast, transplant experiments across three altitudes reported altitudinal adaptation in seedling establishment of the native *Silene ciliata* in Spain (Gimenez-Benavides et al. 2007) and of survival of the native *Poa hiemata* in Australia (Byars et al. 2007). In *Campanula thyrsoides*, specific leaf area was adapted to elevation for populations from a drier region, but not for populations from wetter regions of the Alps (Scheepens et al. 2010). Possibly these different study outcomes reflect differences among species and regions in the strength of altitude-related selection on vegetative traits.

The absence of interacting effects on vegetative growth of clipping treatment and land use at the site of origin indicates that *P. alpina* did not adapt to different land use regimes by differences in plastic response to biomass removal.

If *P. alpina* had adapted to different land use regimes by changing its plastic response to biomass removal, we would have expected to detect a significant interaction between clipping treatment and land use at plant origin in their effect on vegetative growth. No such interaction effect was found, however, indicating that adaptation by way of plasticity change did not occur.

Some previous studies of grassland plants report overcompensation of biomass removal by increased growth (Lennartsson et al. 1998; van Kleunen et al. 2004). Correspondingly, in our experiment previously clipped plants yielded a higher total biomass than previously unclipped plants indicating that compensatory growth plays a role also in *P. alpina*.

#### Evidence for adaptation of reproduction

Lower allocation to reproduction of plants from higher altitudes (Figs. 3, 5) is in line with the hypothesis that harsher conditions (Kikvidze et al. 2011) for seedling and bulbil establishment at higher altitudes cause an adaptive advantage of allocation to vegetative growth. Plant growth and the relative importance of reproductive investment decreased in populations originating from higher altitudes compared to populations originating from lower altitudes in a smaller transplant experiment with *Poa alpina* (Hautier et al. 2009). It corresponds well with the finding that selection for reproductive output was predominant at low altitudes in a three-level between-elevation transplant experiment with *Festuca eskia* (Gonzalo-Turpin and Hazard 2009). Possibly, adaptation to altitude is assisted by

phenology-mediated higher rates of gene flow among sites at similar altitudes than among sites at different elevation, as reported in *Poa hiemata* (Byars et al. 2009).

In general, higher rates of plant establishment are expected in grazed sites due to their spatial heterogeneity and higher density of regeneration gaps (Grubb 1977). Both, the higher likelihood of plants from grazed sites than from mown ones to reproduce in 2003 and their higher biomass allocation to reproduction, are likely to constitute adaptations to take advantage of the increased availability of open sites for establishment created by grazers. They may well explain part of the association of *P. alpina* with grazed habitats. In a common garden study with *Scabiosa columbaria*, plants from populations from mown sites flowered earlier than populations from grazed ones (Reisch and Poschlod 2009) suggesting the avoidance of disturbance by management as potential selection pressure.

As for vegetative performance, the absence of interacting effects on reproduction of clipping treatment and land use at the site of origin indicate that adaptation of reproduction of *P. alpina* to land use does not involve phenotypic plasticity.

Higher rates of reproduction of plants from grazed sites do not only have demographic consequences, but are also likely to increase genetic diversity (Machon et al. 2001) due to increased seedling recruitment and higher numbers of dispersed propagules. In the case of *P. alpina*, genetic diversity measured with microsatellite markers (Rudmann-Maurer et al. 2007) and measured as broad-sense heritabilities of several quantitative traits (Fig. 6b) was indeed higher for grazed sites than it was for mown ones. An alternative explanation for higher genetic diversity among genotypes from grazed sites could be more monotonic selection in more homogeneous mown sites than in more heterogeneous grazed ones. Accordingly, an intensive cutting regime reduced genetic variability for *Festuca pratensis* (Kölliker et al. 1998).

Seed production and establishment of seedlings can be a rather risky mode of propagation at high altitudes (Bliss 1972; Billings 1974; Marcante et al. 2009), which may be even more risky than establishing from bulbils (Winkler et al. 2010). Therefore, the higher percentage of pseudoviviparously reproducing plants from higher altitudes may indicate an adaptation to climatic limitations endangering seed recruitment. The shorter growth periods at higher altitudes are more suitable for pseudoviviparously reproduced offspring, as bulbil-derived plantlets are supported by the maternal plant longer than seeds are and therefore can grow into mature plants much faster than seedlings can (Harmer and Lee 1978).

Apart from being adapted to altitudinal conditions, the mode of reproduction could also respond plastically to changing environments. Previous studies with *P. alpina* reported plastic responses of some, but by far not all, plants

switching from pseudoviviparous to seminiferous reproduction after transplanting pseudoviviparous plants from cold to moderate temperatures (Schwarzenbach 1953; Bachmann 1980). Such switches seem to be the exception, as in our study, only 2 of 1,230 plants (0.16%) switched their reproductive mode between 2003 and 2004, and only 6 of 615 genotypes (0.98%) between the clipped and control replicate plant. Therefore, as far as these test environments were representative for natural variation, the mode of reproduction appears to be largely determined genetically in *P. alpina*.

In abandoned sites with their high levels of standing crop, high reproductive effort is less likely to reflect an adaptation taking advantage of comparatively low competition. Rather, the highest number of reproductive shoots in plants from abandoned sites might reflect an adaptation according to the alternative strategy, where increased production of propagules under high competition enables escape from these local conditions (Abrahamson 1980; Fischer and van Kleunen 2001; van Kleunen et al. 2001).

#### Broad-sense heritability

Heritability can be assessed in several ways. Narrow-sense heritability, which measures the proportion of additive genetic variation relative to total phenotypic variation (Falconer and MacKay 1996), is considered the best predictor of response to selection for sexually reproducing plants. Broad-sense heritability measures the proportion of genotypic variation relative to total phenotypic variation (Falconer and MacKay 1996). In sexually reproducing organisms, it generally overestimates realized response to selection, because variation between genotypes, even in the absence of maternal carry-over effects, may not only include additive genetic variation, but also variation due to dominance or epistasis (Stearns 1992). However, in clonal plants vegetative reproduction contributes largely to offspring reproduction, and therefore broad-sense heritability constitutes a better estimate for realized response to selection in clonal plants than in exclusively sexually reproducing plants (Fischer et al. 2004).

Compared with other species, the observed estimates of broad-sense heritability of vegetative and reproductive characters ranging from 0.363 to 0.572 (Table 1) appear intermediate or even rather high. In *Briza media*, broad-sense heritability of plant size and spikelet size-number ratio ranged between 0.29 and 0.34 (Ellmer et al. 2011). In the grass *Eragrostis tef*, a wide range of broad-sense heritabilities between 0.17 for shoot mass per plant and 0.74 for panicle length were reported (Assefa et al. 2001). Significant broad-sense heritability of 0.198 was reported for fitness-relevant spatial spread in the clonal plant *Ranunculus reptans* (Fischer et al. 2004). Low heritability was also reported

for between-elevation transplants of an Australian herb, *Craspedia lamicola* (Byars and Hoffmann 2009). The observed broad-sense heritabilities suggest that a high potential for further adaptation and evolution has been maintained in *P. alpina* even after hundreds of years of selection by agricultural land use.

The relatively high estimates of broad-sense heritability in *P. alpina* may possibly in part be related to the polyploidy and highly variable chromosome numbers of the species (Müntzing 1980). Since polyploids harbour more alleles at each locus, there are more possibilities for genetic polymorphisms among polyploid plants than among diploid plants. Moreover, if gene flow among plants of different ploidy levels is restricted (Meirmans et al. 2003), high genotypic variation and broad-sense heritability may be maintained. Unfortunately, such relationships between quantitative genetic variation and within-species variation in polyploidy have not been explored yet.

#### Determinants of heritability

The higher frequency of sexual reproduction in plants from lower altitudes was not associated with higher broad-sense heritability in sites at lower altitudes. However, all relationships between broad-sense heritabilities and altitude were non-significantly positive. Possibly, a positive effect of higher frequency of sexual reproducing plants at lower altitudes on broad-sense heritability was masked by a negative one of increased fragmentation of grasslands at lower altitudes. The latter had been brought forward to explain the higher molecular genetic variation within populations of *Primula farinosa* from higher altitudes (Reisch et al. 2005).

The broad-sense heritability estimates of several reproductive and vegetative characters in *P. alpina* were on average twice as high for grazed than for mown sites. These results are even more pronounced than the ones of our microsatellite study of *P. alpina* where the mean number of alleles was also higher in grazed sites than in mown ones (Rudmann-Maurer et al. 2007). The higher heritable genetic variation in grazed sites is in line with the hypothesis that increased allocation to reproduction of plants in grazed sites increases establishment of new genotypes, and thus genetic variation. Moreover, higher allocation to reproduction may also increase gene flow. Because for topographical reasons grazed sites are somewhat more likely to be situated next to other grazed sites than to mown ones, this can also contribute to higher genetic variation within grazed sites. Higher gene flow among grazed sites with *P. alpina* was indeed indicated by the lower microsatellite differentiation among grazed than among mown sites with *P. alpina* (Rudmann-Maurer et al. 2007). An alternative explanation of reduced heritable genetic variation in mown sites could be more spatially homogeneous selection by mowing than by grazing animals.

Accordingly, intensive mowing reduced molecular genetic diversity in *Festuca pratensis* compared to natural populations (Kölliker et al. 1998).

The observed higher heritable genetic variation of *P. alpina* for grassland sites from Romanic regions indicates persisting effects of old cultural traditions on current biodiversity, in this case intraspecific diversity. Most likely this is due to the higher land use diversity especially in the valleys of Romanic villages (Maurer et al. 2006; Fischer et al. 2008). As the current study showed that *P. alpina* from sites of different land use is genetically differentiated (Figs. 2, 3, 4, 5), gene flow among sites of different land use is likely to increase heritable genetic variation within sites. The occurrence of such gene flow is the more likely the more different types of land use occur around a village. As ongoing land use changes are reducing land use differences between villages of different cultural traditions (Bätzing 1991), it may well be that the higher heritable genetic variation for sites in Romanic villages is at least partly due to historical rather than to current gene flow.

Land use turned out to be the most important driver of heritable genetic variation in *P. alpina*. This implies that the ongoing rapid land use change in the Alps, where many mown sites are converted to grazing (Bätzing 2003), will lead to increased heritable genetic variation within grassland sites, at least of *P. alpina*. However, because higher land use diversity also increases quantitative genetic variation between sites, the conservation of quantitative genetic variation requires the conservation of different types of land use, and cannot be achieved by solely maintaining grazed sites.

#### Relationship of heritability with plant species diversity and microsatellite diversity of *Poa alpina*

Our results revealed weak relationships between heritable genetic variation and plant species diversity of the grassland sites. Thus, our study provides little support for the hypothesis that plant community diversity could be positively related to heritable genetic variation, as could possibly have been expected if more diverse niches are available in communities that are more diverse.

Plant species diversity was weakly positively related with molecular genetic diversity in the forest herb *Trillium grandiflorum* (Vellend 2004). In our study, the relationship between heritable genetic variation and molecular genetic diversity was marginally significant. If a positive relationship holds true in *T. grandiflorum*, it may suggest that plant species diversity is also positively correlated with heritable genetic variation in *T. grandiflorum*. However, positive relationships between plant species diversity and molecular genetic variation were absent in *Ranunculus acris* (Odat et al. 2004) and present, but explained by confounding habitat characteristics, in *Plantago lanceolata* (Odat et al.

2010). We suggest to study the relationship between plant species diversity and genetic diversity for more plant species and not only for molecular, but also for heritable, genetic variation.

#### Conclusions

Our study demonstrates that in the heterogeneous landscape of the Alps, *P. alpina* is adapted both to the natural altitudinal gradient and to anthropogenic land use variation. This implies that the ongoing socio-economically motivated change of agricultural land use in grassland of the Swiss Alps and climate change will not only change vegetation composition and diversity, but also adaptive intraspecific diversity of the widespread grass *P. alpina*, and most likely also of other species.

The observed broad-sense heritabilities suggest that a high potential for further adaptation and evolution has been maintained in *P. alpina* even after hundreds of years of selection by agricultural land use. Among the potential drivers of heritable genetic variation in *P. alpina*, land use was most important with heritable genetic variation halved in consistently mown sites compared with grazed ones. Because unfertilized mown grasslands harbor the most species-rich plant communities among our grasslands (Maurer et al. 2006), and because the higher land use diversity in Romanic villages was associated with higher species diversity and higher heritable genetic variation, we suggest maintaining diverse land use regimes to conserve biodiversity not only at the landscape and plant species level, but also at the level of heritable variation within species.

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