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Objekttyp: **Article**

Zeitschrift: **Bulletin of the Geobotanical Institute ETH**

Band (Jahr): **68 (2002)**

PDF erstellt am: **23.07.2024**

Persistenter Link: https://doi.org/10.5169/seals-377845

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Morphological variation of plant populations from differently managed grasslands

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Abstract

1 Morphological traits of plant populations from differently managed grasslands were investigated to test whether genetic differentiation was apparent after 15–30 years of different management. Seeds of three species – *Plantago lanceolata, Lotus corniculatus, Campanula rotundifolia* – were collected in meadows with contrasting cutting frequency and level of fertilization. Plants were grown from these seeds in a growth room for five weeks, and several morphological traits were measured weekly.

2 In *Plantago lanceolata,* plants from intensively managed meadows (fertilized, 2–3 cuts per year) produced longer leaves with a lower tissue density than plants from extensively managed meadows (unfertilized, one cut per year). This might enable plants to place their leaf area higher in the canopy in meadows with dense vegetation. The biomass of the flower stalk increased more rapidly in plants from intensively managed meadows, which is interpreted as an adaptation in flowering time to the earlier cutting of the vegetation.

3 *Campanula rotundifolia* had a lower root/shoot ratio in plants that originate from intensively managed grasslands. This finding is consistent with the hypothesis that increased resource allocation to roots is an adaptation to enhance nutrient acquisition in habitats with low nutrient availability.

4 Within-population variation in morphological traits did not differ consistently between populations from extensive and those from intensive meadows. Thus, our results do not show that genetic variability is reduced by intensive management.

5 This study indicates that genetic adaptation may develop within the relatively short period of 15–30 years as a consequence of changes in management practices.

Keywords: ecotypes, growth rate, selection, morphological variation, life-history

Bulletin of the Geobotanical Institute ETH (2002), **68,** 29–44

Introduction

The plant species composition of grasslands is very sensitive to management and often changes rapidly following a change in management regime. However, some species occur over broad ecological and geographical ranges (Bradshaw 1984). In these species, characters that are relevant to the survival of plants often vary among habitats in response to differences in growth conditions. Such variation in relevant traits may reflect phenotypic plasticity of individuals or genetic adaptation of the population to the habitat or both (van Groenendael 1985, Matthies *et al.* 1995).

A common test to establish whether or not there is a genetic basis for differences in morphological features is to grow plants from different sites under uniform conditions (van Groenendael 1985, Ouborg *et al.* 1991). Genetic differentiation has been found in relation to various habitat characteristics, e.g. soil moisture, nutrient levels, temperature and altitude (see Turkington & Aarssen 1984, Venable 1984 and Kuiper 1985 for references). For the well studied species *Plantago lanceolata* both a high level of phenotypic plasticity and rapid genetic adaptation to the type of grassland habitat have been demonstrated for growth habit, onset of flowering and number of seeds (van Tienderen 1990; van Tienderen & van der Toorn 1991a,b, and references therein). Similarly, populations of *Euphrasia rostkoviana* from different altitudes exhibit differentiation in growth habit and onset of flowering (Zopfi 1998). Such differences can develop rapidly and over a small spatial scale in response to consistent differences in management. For example, Snaydon & Davies (1976) established genetic differentiation in *Anthoxanthum odoratum* at adjacent differently fertilized plots in the Park Grass experiment in growth habit and onset of flowering date. Turkington & Harper (1979) showed that micro-evolution may occur at a very fine spatial scale in response to selective pressures exerted by different neighbouring grass species. Thus, the spatial scale over which differences have been found ranges from hundreds of kilometres to just a few metres (Bradshaw 1984).

Genetic differentiation has often been studied in plants originating from nature reserves with a long continuity of management (Snaydon & Davies 1972 and 1976, Masuda & Washitami 1992) or from strongly contrasting habitats, such as hayfields and pastures (Primack & Antonovics 1981, van Groenendael 1985, Wolff & Van Delden 1987, van Tienderen 1990). Less is known about the degree of genetic differentiation in agricultural grasslands as a response to different management regimes.

In a common-environment experiment, we investigated whether the growth of three species – *Plantago lanceolata, Lotus corniculatus* and *Campanula rotundifolia* – differs between populations from extensively and intensively managed grasslands. Several morphological traits were compared between individuals grown from seeds collected from extensively and intensively managed meadows. Significant differences between offspring from these two types of plant populations would indicate that genetic change has occurred in response to intensification. If such change can be detected, further studies would have to investigate whether this adaptation is reversible in case of a return to extensive management. Re-adaptation might not be possible if genetic diversity within populations has decreased under intensive management. We therefore also examined whether our data provide indications for a decrease in within-population variability as a result of intensification.

Methods

STUDY AREA

Seeds from populations in two differently managed types of grassland were collected in the Schaffhauser Randen in northern Switzerland. This region is an extensive forested area with a number of more or less isolated enclaves of agricultural land on the plateau.

During the last decades most of the unforested area has been used as arable land or as moderately intensive grasslands.

'Extensively' managed meadows are cut only once per year, usually during the first half of July, and are not fertilized. 'Intensively' managed meadows are cut three times per year, in early June, early August and September; they are fertilized mainly with slurry. Extensive meadows have been managed similarly for approximately 100 years, whereas intensive meadows developed from extensive ones in response to changes in agricultural practices 15–30 years ago. The differences in management are reflected in large differences in floristic diversity. On average 38 species of vascular plants were recorded in six 1 m x 1 m quadrats at the extensively used sites compared with 26 species in the intensively used ones (Studer 2000).

For all species two meadows of each management type served as seed sources. Because only one or two of the study species occurred at individual sites, eight meadows were sampled in total (four intensive, four extensive). These meadows were separated by several hundred metres and additionally by patches of forest. Plants from different sites therefore represent different populations.

HABITAT CHARACTERISTICS

Soil fertility of the eight meadows was assessed by means of a bioassay. Six soil samples (2–15 cm depth) were collected at each site, pooled, and sieved. Seedlings of *Lolium perenne* and *Trifolium pratense* were grown in pots filled with this soil ($n = 5$ per species and site) in a heated glasshouse (23/18°C day/night) in January 1999 (Studer 2000 pp. 15 ff.). Additional light was supplied during the day by high-pressure sodium vapour light (400 W). All plants were harvested after 30 days, dried for 48 h at 70 °C, and weighed. The biomass of these individuals was used as an indicator of soil fertility.

Light penetration into the stand was measured in each meadow immediately before the first cut with a Sun Scan probe (Delta-T Devices Ltd., Cambridge, GB) at soil surface and at 20 cm above ground.

STUDY SPECIES AND EXPERIMENTAL LAYOUT

Plantago lanceolata, Lotus corniculatus and *Campanula rotundifolia* were chosen as experimental species because they are common in both extensively and intensively managed grasslands. *Plantago lanceolata* is an outbreeding, self-incompatible, mainly wind-pollinated species (Grime *et al.* 1988) that is commonly found in habitats ranging from open, grazed pastures to dense hayfields (van Tienderen 1989). *Lotus corniculatus* is an insect-pollinated, mainly outbreeding species and is particularly common in limestone pastures and wasteland (Grime *et al.* 1988). *Campanula rotundifolia* is a self-incompatible, insect-pollinated species, which is most abundant in dry grasslands (Grime *et al.* 1988).

Seeds were collected from at least 10 individuals per species at each site. Individuals to sample were chosen so as to be distributed as evenly as possible within sites. Mean seed mass was obtained for each species and site from the dry weight of 100 seeds. The remaining seeds were germinated on moist filter paper under standard conditions recommended by the International Seed Testing Association (ISTA 1999). For *Campanula rotundifolia* a prechilling treatment (7 days at 10 °C) was applied. The freshly germinated seedlings were transplanted into separate sand culture containers consisting of a polyethylene tube with a volume of 500 cm^3 (6.4 cm diameter; 15 cm height, as used by Grime & Hunt 1975). Washed silica sand was used as rooting

Table 1. Number of individuals originating from extensive meadows (ext.) and from intensive meadows (int.) harvested after two, three, four and five weeks for the three investigated plant species.

	2 weeks		3 weeks		4 weeks		5 weeks	
	ext.	int.	ext.	int.	ext.	int.	ext.	int.
Plantago lanceolata	11	14	11	14	9	13	15	14
Lotus corniculatus	12	7	14	7	-	-	14	4
Campanula rotundifolia	11	7	12	6	23	7	14	11

medium. The plants were grown for 35 days in a growth chamber (20/15°C day/night temperature; 90/80% relative humidity; light intensity (day): 32 W m^{-2}). The pots received 20 ml 'Long Ashton' nutrient solution on alternate days (Hewitt 1966).

At least four replicate plant individuals were harvested after two, three, four and five weeks, by immersing the pots in a water bath and removing the sand remaining on roots (Table 1).

For some species low germination and high mortality of seedlings reduced the number of replicates. For *Lotus corniculatus,* only three instead of four harvests were performed, and the number of individuals from the intensive populations was extremely low. For *Campanula rotundifolia,* plants from only one intensive site could be studied.

MORPHOLOGICAL MEASUREMENTS

For each plant, the number of leaves was counted and the fresh weight of the fully turgid plant was measured immediately after harvesting, shoot and root material separately (fresh weight). To determine leaf area, freshly cut leaves were spread out on plain white paper sheets and photocopied. These images were scanned, and leaf area was assessed using an image processing program (Scion-Image, Scion corporation, Frederick, Maryland USA). Shoot length was measured as the maximum length of above-ground plant material immediately after harvesting. In *Plantago lanceolata* both maximum leaf length and the length of the flower stalk (at harvests 3 and 4) were measured. All plant material was dried at 100 °C for 48 h. Cotyledons, other leaves, roots, flower stalks and stems were then weighed separately.

DATA ANALYSIS

To assess whether maternal effects (rather than genetic differentiation) could have caused plant traits to differ in the common environment experiment (Roach & Wulff 1987), mean cotyledon biomass at the first harvest was compared among the three or four populations per species using one-way ANOVA followed by Tukey's honestly significant difference test.

Between-population variation in morphological traits was analysed for each species with two-way factorial ANOVA (fixed factors 'population' and 'harvest'). If populations differed significantly, those from extensive meadows were compared to those from intensive meadows with a-priori contrasts. If the two management types differed significantly, a nested ANOVA was performed to test whether this difference could be generalised to other populations than the four particular ones included in this study. The model included the fixed factors 'management' and 'harvest' and the random factor 'site' (nested within management), so that differences between extensive and intensive meadows were tested against variation among sites with same management.

Within-population variation in morphological traits was quantified as the coefficient of variation (*CV* in %) of traits measured at the last harvest (after five weeks of growth) on all plants originating from the same population. The last harvest was chosen for calculations because differences between populations were strongest then. For traits of *P. lanceolata,* coefficients of variation for populations from extensive and intensive meadows were compared with one-way anova. No test was performed for the two other species, as *CV* were available for only one intensively managed site.

Mean relative growth rate per week was calculated for each plant population with the formula

(ln 5W – ln 2W) / T

where 5W and 2W are mean whole-plant biomass at five and two weeks, respectively, and T is the time interval, three weeks (cf. Fisher 1920). Growth rates were compared among the three species with one-way ANOVA.

To obtain approximately normally distributed residuals, all variables had to be log-transformed, except for the number of leaves, which was square-root transformed. Statistical analyses were performed with the Statistica (StatSoft 1997, version 5.1) and JMP (SAS Institute 1989–97, version 3.2.2) software packages.

Results

HABITAT CHARACTERISTICS

According to our bioassay, soil fertility differed significantly between intensively and extensively managed meadows (ANOVA, $P < 0.001$): the mean biomass of *Lolium perenne* seedlings grown on soil from intensive meadows was fourfold that of seedlings grown on soil from extensive meadows (Fig. 1a). With *Trifolium pratense,* the difference in seedling biomass was smaller, but still obvious and significant (Fig. 1a). The extensively managed meadows also had a more open vegetation structure. This is indicated by significant differences in light conditions at 20 cm height (ANOVA, $F_{1,6} = 10.4$, $P < 0.05$) and at ground

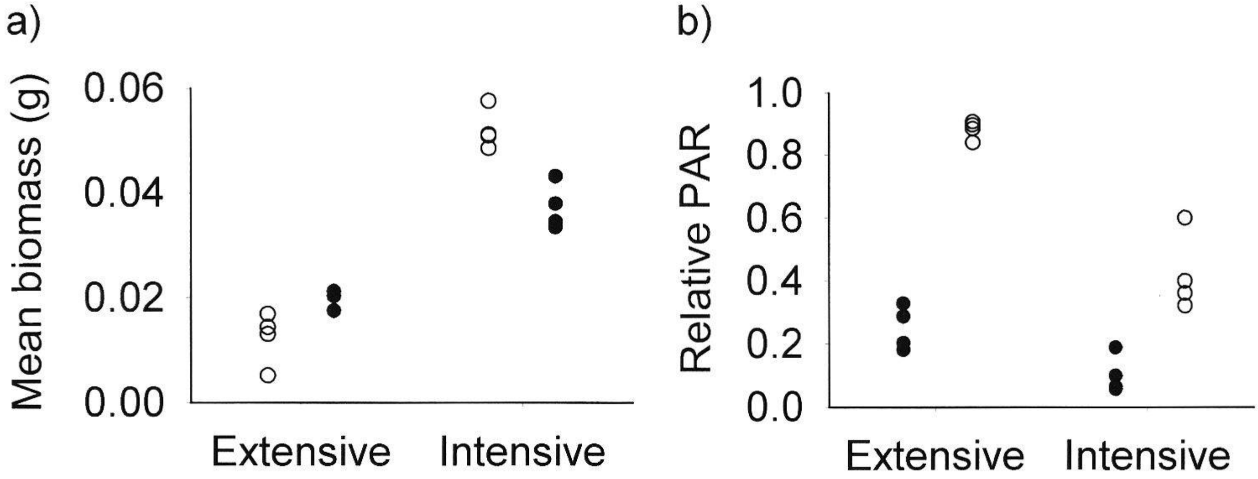

Fig. 1. Habitat conditions of the sites used as seed sources for the experiment: In (a) soil fertility was measured as the biomass of seedlings grown in soil from each site (open circles: Lolium perenne; *filled circles:* Trifolium pratense; *means of five replicates per site and species). In (b) light availability was measured as the proportion of PAR 20 cm above soil surface (open circles) and at soil level (filled circles).*

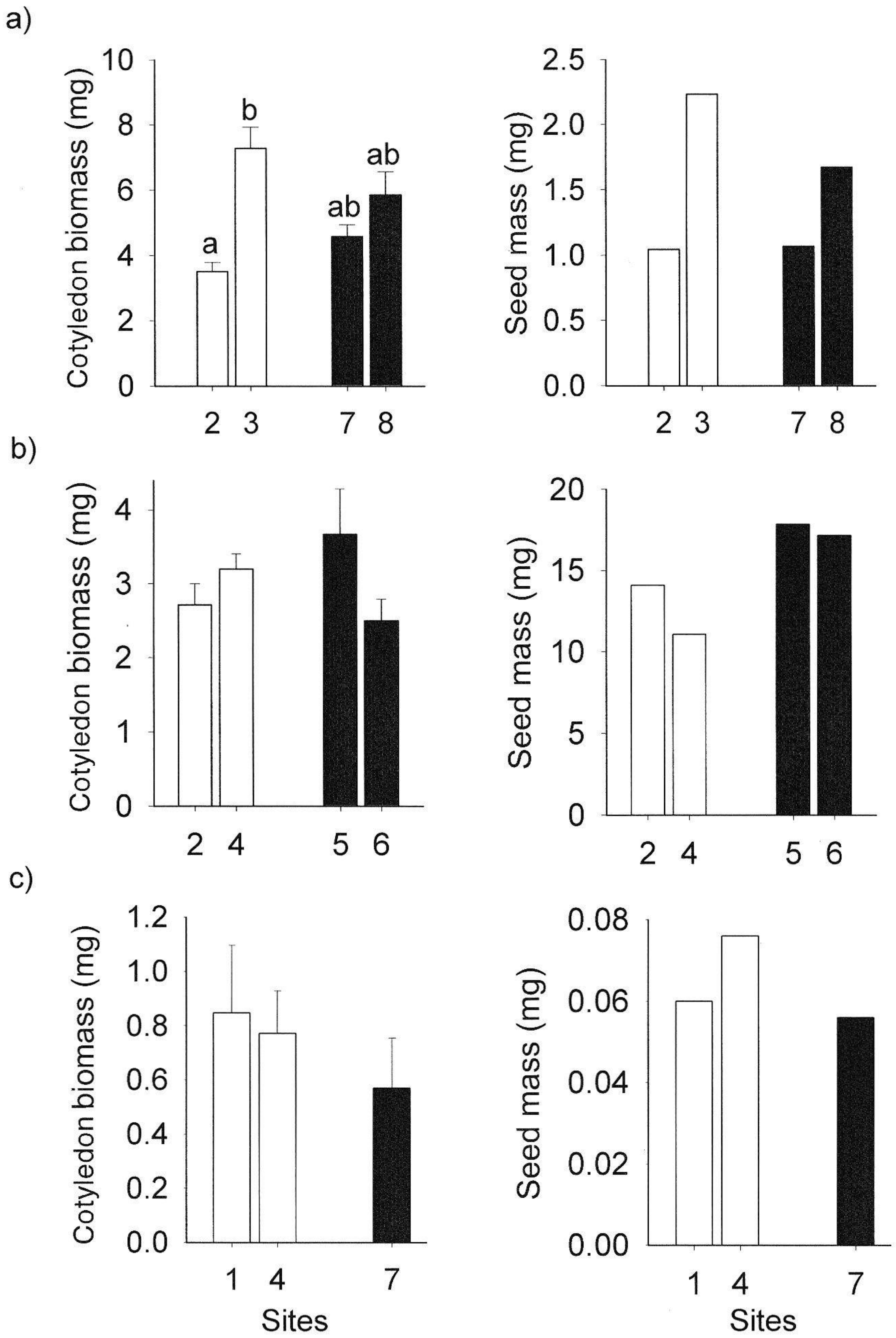

Fig. 2. *Seed mass (mean dry mass of 100 seeds) and cotyledon biomass (two weeks after the start of the experiment) for plant populations from extensively used meadows (open bars) and intensively used meadows (filled bars). Vertical bars denote +1* SE *(not available for seed mass). Significant pairwise differences in cotyledon biomass (Tukey post-hoc test,* $P < 0.05$*) are indicated by different letters.*

Table 2. *Results of two-way* ANOVA *(F-ratios and significance levels) for the effects of population (fixed), harvest (fixed), and their interaction (P * H) on various morphological measures of the three plant species. If the effect of population is significant, the populations from extensive meadows are compared to those from intensive meadows with a-priori contrasts (Ext. vs. Int.; t-values and significance levels are given). Significance levels are:* °, P < *0.10;* *, P < *0.05;* **, P < *0.01;* ***, P < *0.001; no symbol,* P > *0.10.*

	Population	Harvest	P * H	Ext. vs. Int.
(a) *Plantago lanceolata*				
d.f.	3	3	9	1
Leaf number	16.3 ***	132.3 ***	3.6 ***	3.5 ***
Leaf area	10.6 ***	408.8 ***	0.8	–0.7
Leaf length	5.6 **	58.7 ***	0.6	–3.1 **
Shoot dry mass	4.7 **	477.2 ***	0.8	0.6
Root dry mass	4.2 **	362.4 ***	1.0	1.0
Root/shoot ratio	1.2	0.4	1.6	
Fresh mass /dry mass	3.3 *	31.9 ***	2.9 **	–3.1 **
Flower stalk dry mass[1]	8.9 ***	51.2 ***	1.1	–4.5 ***
Flower stalk length[2]	10.5 ***	37.5 ***	3.5 *	–3.9 ***
(b) *Lotus corniculatus*				
d.f.	3	2	6	1
Leaf number	2.4 °	94.6 ***	1.6	0.8
Leaf area	0.8	169.8 ***	1.5	
Shoot length	1.5	233.0 ***	0.5	
Shoot dry mass	1.6	184.7 ***	1.9	
Root dry mass	1.4	18.0 ***	0.4	
Root/shoot ratio	0.2	12.3 ***	3.4 **	
Fresh mass /dry mass	0.4	11.6 ***	2.6 *	
(c) *Campanula rotundifolia*				
d.f.	2	2–3	4–6	1
Leaf number	0.5	66.2 ***	0.2	
Leaf area	0.2	159.5 ***	0.3	
Shoot length	1.2	164.0 ***	5.0 ***	–3.7 ***[3]
Shoot dry mass[1]	0.2	55.4 ***	0.2	
Root dry mass[1]	1.3 *	59.4 ***	0.1	
Root/shoot ratio[1]	5.3 **	3.4 *	1.4	3.0 **
Fresh mass /dry mass[1]	0.3	1.7	1.1	

[1] Only harvests 2,3,4 (values very low and/or inaccurate at harvest 1)

[2] Only harvests 3 and 4

[3] Contrast based on an ANOVA of data from harvests 2,3,4

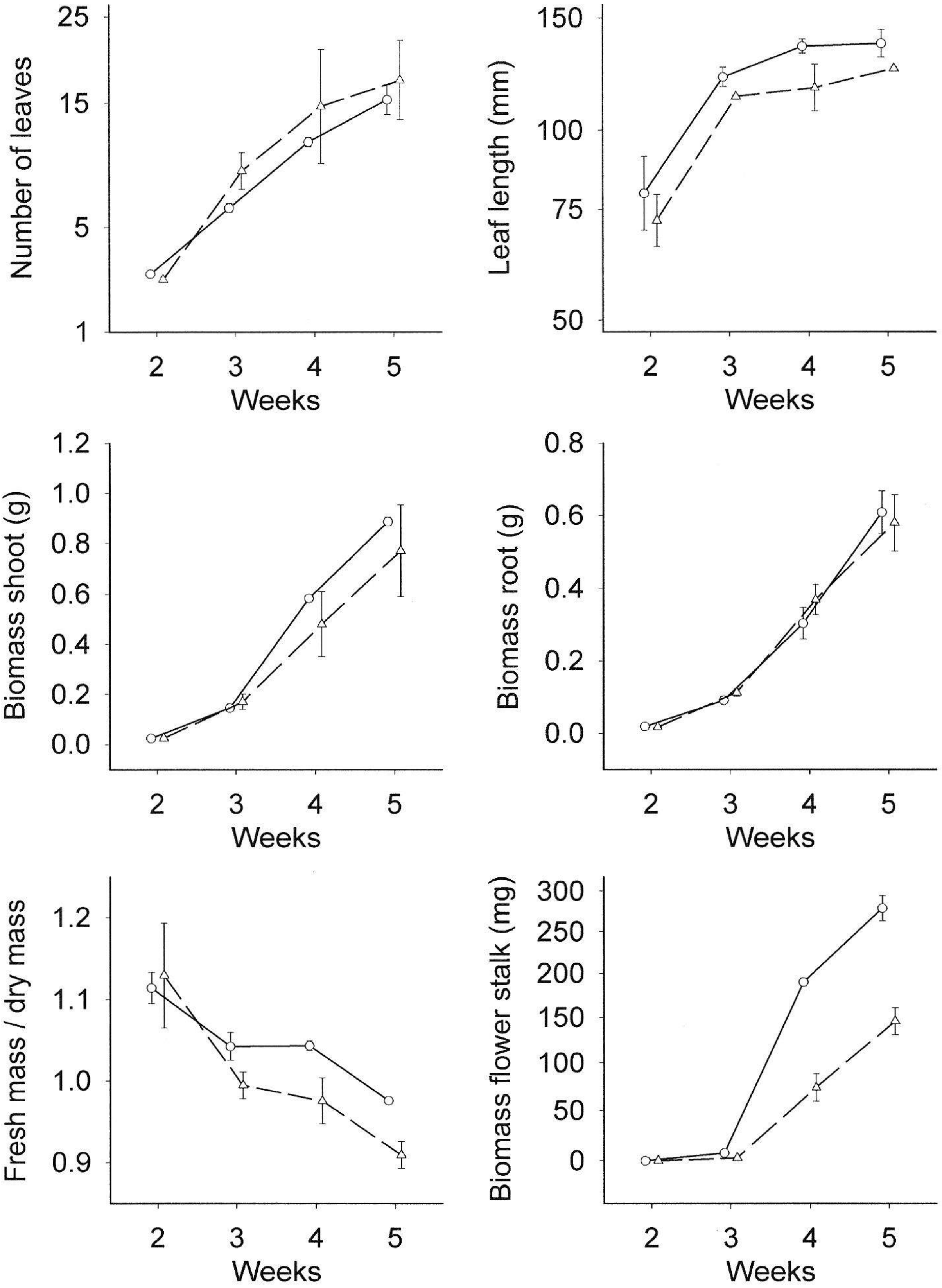

Fig. 3. *Morphological traits of individuals of* Plantago lanceolata *originating from extensively used (triangles, broken line) and intensively used meadows (circles, solid line). Plants were grown in a common growth chamber and harvested at four different dates. Means and* SE *of two sites per management type are shown. Scales were adjusted according to the transformations of the data (see methods section).*

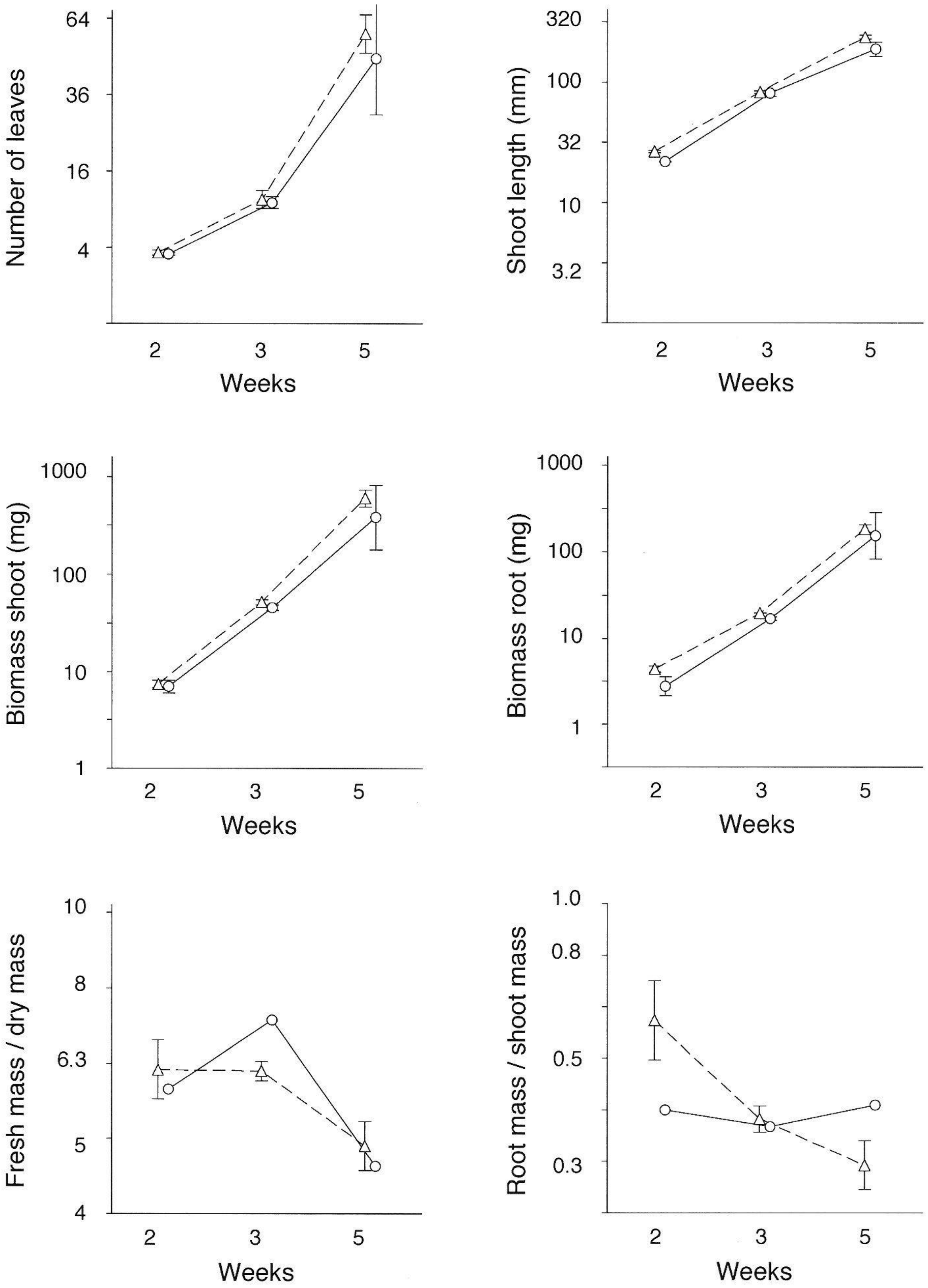

Fig. 4. *Morphological traits of individuals of* Lotus corniculatus *originating from extensively used (triangles, broken line) and intensively used meadows (circles, solid line). Plants were grown in a common growth chamber and harvested at three different dates. Means and* SE *of two sites per management type are shown. Scales were adjusted according to the transformations of the data (see methods section).*

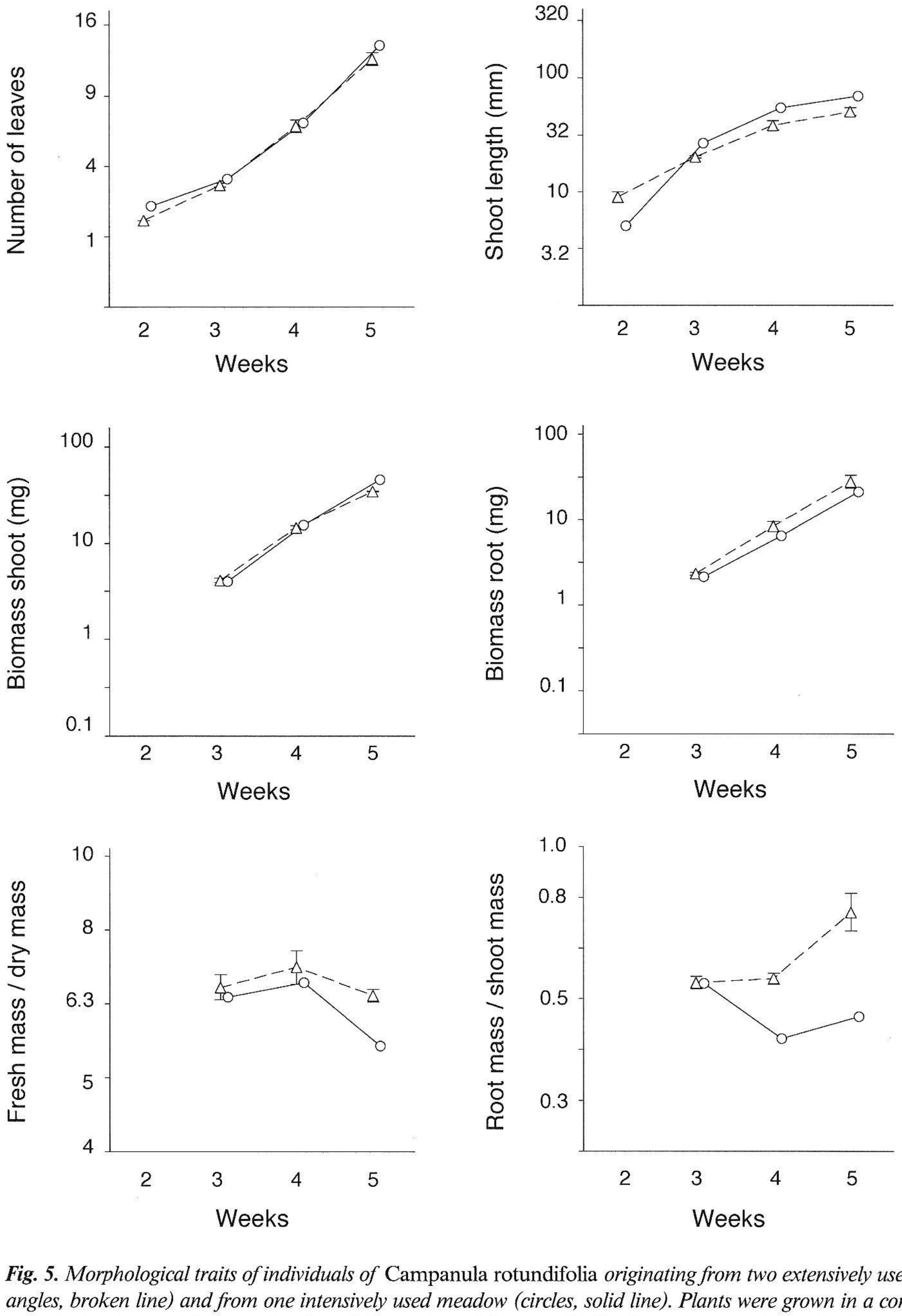

Fig. 5. *Morphological traits of individuals of* Campanula rotundifolia *originating from two extensively used (triangles, broken line) and from one intensively used meadow (circles, solid line). Plants were grown in a common growth chamber and harvested at four different dates. Means and* SE *of two sites are shown for the extensive meadows. Scales were adjusted according to the transformations of the data (see methods section). Biomass data from week 2 are not shown because they could not be determined with sufficient accuracy (very small values).*

level (ANOVA, $F_{1,6} = 52.3$, $P < 0.001$). At both levels the photosynthetically active radiation was more than 50 % lower in intensive than in extensive meadows (Fig. 1b).

MATERNAL EFFECTS

Plantago lanceolata showed considerable between-population variation in mean seed mass and mean cotyledon biomass (Fig. 2a). Cotyledon mass differed significantly between the two extensive populations, whereas the latter did not differ from intensive ones (Fig. 2a). The same pattern was reflected by seed mass. No significant differences in mean cotyledon biomass were found between populations of *Lotus corniculatus* (Fig. 2b) and *Campanula rotundifolia* (Fig. 2c). Seed mass and cotyledon biomass were highly correlated among the four populations of *P. lanceolata* ($r = 0.96$) but uncorrelated in the two other species.

BETWEEN-POPULATION VARIATION IN MORPHOLOGICAL TRAITS

The investigated morphological traits were mostly measures of plant size. These traits all differed significantly among harvests, as plants grew rapidly during the experiment (Table 2). In contrast, differences among harvests were only partly significant for biomass allocation (root/shoot ratio) and tissue structure (fresh mass / dry mass ratio). Population-by-harvest interactions were occasionally significant, either because populations differed more clearly at the later harvests (e.g. if a plant part had not or hardly developed at the first harvest) or due to fluctuations without obvious explanation. The amount and significance of between-population variation in morphological traits strongly differed among the three investigated species:

Table 3. *Within-population variability of morphological traits of plants grown in a common environment, compared between populations from extensively and intensively managed meadows for the three plant species. Within-population variability was quantified as the coefficient of variation (*CV *in %) of traits measured after five weeks of growth on 3–11 plants per population; if two populations per species and management type were investigated, both* CV *are given in the table.*

	Extensive		Intensive	
(a) *Plantago lanceolata*				
Leaf number	19	13	11	15
Leaf area	3	5	3	5
Leaf length	4	3	2	11
Shoot dry mass	42	25	11	27
Root dry mass	42	22	14	38
Root/shoot ratio	11	21	11	20
Fresh/dry mass	8	11	3	5
Flower stalk mass	87	93 *	13	40
(b) *Lotus corniculatus*				
Leaf number	25	11	41	
Leaf area	7	8	20	
Shoot length	3	2	8	
Shoot dry mass	55	19	120	
Root dry mass	85	30	119	
Root/shoot ratio	43	21	12	
Fresh/dry mass	13	6	10	
(c) *Campanula rotundifolia*				
Leaf number	24	23	22	
Leaf area	15	22	23	
Shoot length	6	8	7	
Shoot dry mass	54	72	45	
Root dry mass	90	56	83	
Root/shoot ratio	34	20	45	
Fresh/dry mass	5	8	4	

* Difference significant, $P < 0.05$

Plantago lanceolata

All traits except the root/shoot ratio varied significantly among the four investigated populations (Table 2a). A-priori contrasts revealed significant differences between the populations from extensive and intensive meadows in five traits (Table 2a): plants originating from the extensively managed meadows had on average more but shorter leaves and a lower fresh mass / dry mass ratio (Fig. 3). The length and the biomass of the flower stalk increased faster in the plants from intensive sites (Fig. 3). However, when the generality of these results was tested with a nested analysis of variance, effects of management were only significant for the fresh mass / dry mass ratio ($F_{1,2} = 26.1$, $P < 0.05$) and for the biomass of the flower stalk ($F_{1,2} = 28.2$, $P < 0.05$).

Lotus corniculatus

Of the investigated variables, only the leaf number varied marginally significantly among populations (Table 2b). There was no consistent difference between the populations from extensively and from intensively used meadows (Table 2b, Fig. 4).

Campanula rotundifolia

Shoot length and the root/shoot ratio varied significantly among the three populations investigated in this species (Table 2c). Shoot length was greater in plants from the extensive meadows at the first harvest, whereas at the subsequent three harvests, plant from the intensive meadow had significantly longer shoots (Table 2c, Fig. 5). The root/shoot ratio of individuals originating from the two extensively used sites was significantly higher than that of individuals from the intensively managed meadow (Table 2c, Fig. 5). However, nested ANOVA showed that these effects of management cannot be generalised to other populations than the three ones investigated in this study (effect of management not significant).

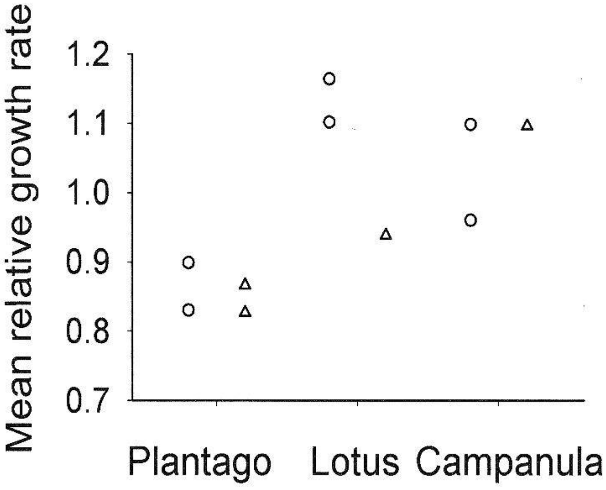

Fig. 6. Mean relative growth rate per week (log scale) of plants from different populations. Circles: populations from extensively used grasslands; triangles: populations from intensively used grasslands.

WITHIN-POPULATION VARIATION IN MORPHOLOGICAL TRAITS

Coefficients of variation of traits measured in individuals from the same population did not differ consistently between populations from extensively and from intensively used meadows (Table 3). In *P. lanceolata,* only the biomass of the flower stalk was significantly more variable in populations from extensively used meadows ($P < 0.05$). For most other traits in *P. lanceolata* and in the two other species, within-population variation differed little between management types, and populations from either extensive or intensive sites could be more variable, depending on the trait considered.

RELATIVE GROWTH RATE (RGR)

Plantago lanceolata had a significantly lower mean relative growth rate than the other two species (one-way ANOVA, $P < 0.05$); its RGR was similar in the four populations (Fig. 6). In contrast the RGR of *Lotus corniculatus* varied considerably between populations from extensively used and those from intensively used meadows. In *Campanula rotundifolia,* mean RGR differed considerably between the two populations from extensive meadows (Fig. 6).

Discussion

Considerable variation in different morphological traits within and between populations was detected in this study. Our sampling design allowed us to distinguish differences between management types from the variability of sites. Indeed, in contrast to several other studies without replication, we sampled two sites of each management type. The considerable variation sometimes found between sites with same management type showed the importance of providing replicate samples in this type of investigation.

Seed size and as a consequence the morphology of the offspring may be influenced by maternal habitat quality. These non-genetic maternal effects are commonly a result of the nutritive role that the seed-producing parent has for the developing seed (Schaal 1984); they may be mediated by seed size (Roach & Wulff 1987; Weiner *et al.* 1997). The high positive correlation between seed mass and cotyledon mass found in this study for *Plantago lanceolata* indicates that the performance of seedlings strongly depended on seed size, as has been shown by other workers (Ouborg & van Treuren 1995, Weiner *et al.* 1997). However, since seed size did not differ greatly between the two management types, seed-size mediated maternal effects could not have produced the differences in morphological traits observed in our experiment between plants from extensive and plants from intensive meadows. The reason may be that seed size is one of the least plastic of plant characters (Harper 1977). Weiner *et al.* (1997) conclude from this low plasticity that maternal effects appear to be small compared to other factors that influence a plant's fitness.

Although we found relatively few significant differences between plants originating from extensively and those originating from intensively used meadows, the differences that were found could be understood as ecologically meaningful adaptations. The more rapid growth of the flower stalk of *Plantago lanceolata* in the more intensively managed meadows points to selection on timing of flowering as a habitat related genetic adaptation to the earlier cutting of the vegetation. Local adaptation in the timing of flowering to the cutting regime has already been shown for this species in several studies (Kuiper 1985, van Tienderen & van der Toorn 1991a and b). Likewise, the production of longer leaves in intensively managed meadows may enable plants to place part of their leaf area higher in the canopy, where light conditions are less unfavourable. Van Tienderen & van der Toorn (1991a) also found differentiation in growth habit (leaf size and form) and in allocation to shoot growth, but these differences were found between a hayfield and a pasture population, habitat types that show greater differences in vegetation structure (vegetation height, light conditions) than differently used hayfields. The lower fresh mass / dry mass ratio in populations from extensively used meadows indicates a higher tissue mass density, which can generally be interpreted as an adaptation to environments with low resource availability (Wahl 2000). High tissue mass density is often associated with slow growth (Poorter 1990), but this relationship was not found here, as plants from extensive sites did not have a reduced growth rate.

In *Campanula rotundifolia* plants that originated from intensively managed grasslands had a lower root/shoot ratio. This indicates a shift of the resource allocation towards the shoot. Greater biomass allocation to roots can enhance the nutrient acquisition and is therefore often found in plants growing in habitats with low nutrient availability. However, it has been shown for several species that this difference between habitats was actually a non-genetic plastic response (Hunt & Nicholls 1986, Poorter 1990, Gedroc *et al.* 1996). The difference found in our study might still reflect a genetically based adaptation to differences in nutrient supply, as genetic differentiation between populations often resembles the plastic responses of plants grown under conditions where the selective factor (light availability; nutrient availability) is varied (van Groenendael 1985, van Hinsberg & van Tienderen 1997).

At the species level there is a tendency in species with a low growth rate to have a competitive advantage in infertile sites; the reverse is true in productive habitats. In particular rapid shoot growth is important to enhance light interception in tall vegetation (Grime & Hunt 1975, Crick & Grime 1987, Poorter 1990). For the three species studied here there was no variation in growth rate due to genetic adaptation to the habitat. *Plantago lanceolata* was the most abundant of the three species in intensively managed grassland, but there was no indication of higher growth rate in this species. However, the erect growth form and the rapid increase in plant height and leaf area in the first two weeks may be an advantage for *Plantago lanceolata* in comparison to the other two species.

The time necessary for the development of genetic differentiation varies widely. Different studies report periods of about 100 years (van Groenendael 1985), about 50 years (Snaydon & Davies 1972) and 30 years (Masuda & Washitami 1992). Our study indicates that adaptation to changed grassland management may develop within 15–30 years for characters such as flower stalk length which are under strong selection.

A loss of genetic variability by strong selection for a specific trait may reduce the capacity for adaptation to future changes in habitat characteristics. Our study did not support the assumption that genetic variability is reduced within populations from intensive meadows. This suggests that the capacity for adaptation to an extensification of grassland management has not been hampered by several decades of intensive use. Obviously, this tentative conclusion should be confirmed by direct investigations, as our study has only included few of the numerous traits that might be subject to selection. Our results are comparable to those of Billeter *et al.* (2002) who found (using allozymes) that up to 35 years of complete abandonment in fen meadows that were previously extensively managed did not erode the genetic diversity of two common plant species.

The results presented here indicate a potential for development of genetic differentiation in a relatively short period in two of the three species studied. Further experiments with a higher level of replication and experiments including transplant and competition experiments to study the influence of the differentiation on plant fitness would be appropriate.

Acknowledgements

We thank Pia Baumann for help with the experiment and Diethart Matthies, Sabine Güsewell and two anonymous reviewers for valuable comments on the manuscript. The study was supported by the Swiss National Science Foundation.

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Reveived 21 January 2002
Revised version accepted 12 July 2002