

MORPHOLOGICAL PLASTICITY OF *FESTUCA RUBRA* CLONES FROM THREE NEIGHBOURING COMMUNITIES IN RESPONSE TO RED : FAR-RED LEVELS

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Abstract: Morphological parameters of *Festuca rubra* clones and their response to differences in the red/far red ratio (R : FR) were investigated in a growth chamber experiment. The twenty-four clones tested came from 15 micro-sites in three neighbouring meadow communities in the Krkonoše Mts. (Czech Republic). The community types were characterized by different canopy height and structure, and by different radiation conditions (relative R : FR) within the canopies. Low R : FR treatment resulted in reduced tillering and stimulated shoot elongation in most of the clones. In some clones, low R : FR ratios stimulated extravaginal tillering and rhizome system formation. The origin of the clones (i.e., community type) explained a part of variation in morphological parameters, but did not explain variation in the response to R : FR levels. Evidence for a consistent relationship between clone performance and radiation environment in the micro-sites from where the clones originated was not found. It seems that there is only limited selection of *F. rubra* clones (ecotypes) specialized for particular community types and no selection of clones specialized for particular micro-sites within communities.

Keywords: Ecotypes, Grasses, Norm of reaction, Phenotypic plasticity, R : FR ratio

Nomenclature: KUBÁT et al. (2002)

INTRODUCTION

Low photon flux density and low red : far-red (R : FR) ratios are two important characteristics of the radiation environment in the lower layers of plant canopies. While low photon flux density can be a limiting resource, reductions in the ratio of red (R) to far-red (FR) radiation act as an indicator of the presence of neighbouring plants (SMITH & WHITELAM 1997). In response to decreased R : FR plants show increased stem, petiole and leaf elongation, and decreased branching and tillering (MORGAN & SMITH 1979, CASAL et al. 1985, THOMPSON & HARPER 1988, HUBER 1996, BALLARÉ & SCOPEL 1997).

Plant communities show pronounced gradients in radiation quantity and R : FR (HOLMES & SMITH 1977). Plants capable of intensive vertical elongation of stems and petioles induced by low R : FR in lower canopy layers may thus avoid shade and reach more favourable radiation conditions in upper canopy layers. However, the shade-avoidance elongation is advantageous only for plants that have a chance to overtop their plant neighbours (SCHMITT & DUDLEY 1996 and references herein). Plants from open-site populations or from populations growing for a longer time with short neighbours show thus higher plasticity in response to changes in radiation environment than plants from shaded (i.e., woody) habitats or

populations growing with tall neighbours (DUDLEY & SCHMITT 1995 and WEINIG 2000, respectively). These results were obtained in plants from isolated populations growing under apparently different radiation conditions, but it has not been clear whether the same pattern works at a finer scale, i.e., in different community types or even in sites with different canopy height and density within a community. Genetic differentiation in life history and growth pattern shaped by radiation conditions, canopy structure or management regime found among plant populations over a scale of a few centimetres to hundreds of centimetres (STRATTON 1994, LINHART & GRANT 1996) indicate such a possibility.

Besides the vertical gradient, a pronounced fine-scale horizontal variation in radiation conditions was observed in plant communities (TANG et al. 1988, SILVERTOWN et al. 1989). Plants possess considerable plasticity in horizontal growth in response to the radiation environment, which may enable them to fill canopy gaps or escape dense patches. Plasticity in elongation of horizontally oriented stems and petioles was rather low (compared to vertically oriented organs) and its ecological importance questionable with regard to poorly predictable horizontal radiation pattern (STUEFER 1996, HUBER et al. 1998). Probably due to this reason, plasticity of horizontally growing spacers was not studied in more detail. Different plasticity of branching (tillering) in response to R : FR levels or canopy density found in related taxa (DEREGIBUS et al. 1985, STUEFER & HUBER 1998, MONACO & BRISKE 2001) was not interpreted in relation to canopy density in original communities. Lower plasticity of tillering in response to neutral shading found in grass species dominating dense canopies (EVERSON et al. 1988) indicate that a relationship between plasticity in horizontal growth and radiation conditions in original plant communities may exist.

Clonal plants seem to be suitable for testing closer relationships between the plasticity of vertical and horizontal growth in response to incident radiation, and conditions in the original sites. Due to clonal multiplication the genotypes can persist in suitable sites for a long time. Rapid genetic differentiation (i.e., within several years or generations) shaped by environmental factors was found, however, in clonal plants (LINHART & GRANT 1996 and FISCHER et al. 2004, respectively). Spatial distribution of individual genotypes in a community on a small scale may thus reflect differences between the genotypes and their different abilities to comply with environmental conditions in individual micro-sites (PRATI & SCHMID 2000).

Perennial clonal grass *Festuca rubra* was used to study relationships between morphological plasticity of its clones, and conditions in the sites of clones' origin in a growth-chamber experiment. Clones of the species have been documented to differ both in morphological parameters and growth response to R : FR ratios (SKÁLOVÁ et al. 1997). The species was reported to have different average height in different community types (SKÁLOVÁ et al. 1999). The aim of the study was to investigate (1) whether clones coming from three neighbouring meadow communities with different canopy height and structure, and vertical R : FR profiles in the canopies differ in their above- and below-ground architecture and the response to R : FR levels and (2) whether there is any consistent relationship between the performance of individual clones and relative R : FR in their original micro-sites within the communities.

METHODS

Species and clone sampling

Festuca rubra is a common perennial grass species of temperate grasslands. Both seedling recruitment and clonal spreading occur in the species. Two types of clonal growth were identified (HERBEN et al. 1994): new tillers can either occur “intravaginally” (i.e., within the sheath of the mother tiller), or “extravaginally” (i.e., outside the sheath of the mother tiller, which results in the formation of daughter tussocks placed at a certain distance from the mother tussocks).

The clones were sampled from three community types in a mountain meadow in the Krkonoše Mts., the Czech Republic (the Severka settlement – latitude 50°41'42" N, longitude 15°42'25" E, altitude approx. 1100 m). Community type #1 was a sparse, 30 cm high, species-poor meadow dominated by narrow-leaved grasses (*Avenella flexuosa*, *Festuca rubra*, and *Nardus stricta*). Community type #2 was a 20-year-old degradation phase of community type #1 dominated by *Bistorta major*, with a canopy height of 40 cm. During the community degradation, abundance of *F. rubra* decreased considerably (PECHÁČKOVÁ & KRAHULEC 1995), which indicates the selection of shade tolerant clones. These communities were about 100 m distant. Type #3 was a dense, 40 cm high, species-rich meadow both with grasses and herbs (*Agrostis capillaris*, *Anthoxanthum alpinum*, *Deschampsia cespitosa*, *Avenella flexuosa*, *Festuca rubra* and *Alchemilla* spp., *Geranium sylvaticum*, *Bistorta major*, respectively) situated about 500 m down-hill of the previous types and separated from them by a drive. Only limited pollen and diaspore transfer among the communities is expected.

The community types differed in the extent and partly also in the pattern of the R : FR decrease along a vertical canopy profile: the lowest decrease in R : FR was found in community #1; community #2 was characterized by a sharp decrease in R : FR about 10–15 cm above the soil surface, just under a layer of leaf blades of the dominating herb. A gradual decrease in R : FR ratios along the vertical transect was typical of community #3 with a more homogeneous vertical distribution of the biomass. Canopy structure and R : FR profiles were investigated at five micro-sites in each community type. Vegetation was recorded in imaginary vertical prisms with a base of 30 × 30 cm² using inclined point quadrats. R and FR were measured on vertical transects in the centres of the 30 × 30 cm² plots at distances of 5 cm using Plant Growth Photometer IL 150 (International Light Inc., Newburyport, Massachusetts). For more details on community structure and R : FR profiles see SKÁLOVÁ et al. (1999).

The clones were sampled from the plots (micro-sites) where the aforementioned investigation was carried out (Table 1). The distance between the plots within each community was 3 m at minimum. Two samplings (marked as A and B) were taken from each plot (clones 1–5 came from community type #1, clones 6–10 from #2, clones 11–15 from #3). The distance between A and B in each plot was about 10 cm. Due to average genet diameter of 4.6 cm and genet density of about 900 per 1m² found in the locality (SUZUKI et al. 1999), and the distance between the plants sampled, I assume that they belong to different genotypes.

Experiment

Table 1. Relative R : FR at the canopy bottom (i.e., percentage of the R : FR value above the canopy) in the micro-sites of the clones' origin. For details on R : FR profiles see SKÁLOVÁ et al. (1999).

Community	Site	Relative R : FR	Clones
1	1	73	1B
1	2	91	2B
1	3	84	3A, 3B
1	4	79	4B
1	5	85	5A, 5B
Mean		82.4	
2	6	49	6A, 6B
2	7	50	7A, 7B
2	8	70	8A
2	9	59	9A
2	10	45	10A, 10B
Mean		54.6	
3	11	63	11B
3	12	55	12A, 12B
3	13	48	13A, 13B
3	14	59	14A, 14B
3	15	38	15A, 15B
Mean		52.6	

The collected clones were cultivated in an experimental garden in Průhonice for nine years. Well-developed tillers with three leaves were cut from the 24 surviving clones and rooted in water. After 10 days, 16 tillers of each clone (eight for each R : FR regime) were transplanted individually into 125-ml ($5 \times 5 \times 5$ cm) plastic pots filled with a mixture of common garden soil and perlite (1 : 1).

The plants were grown in two growth chambers (Conviro S 10 H, Winnipeg, Canada) with identical climate regimes except for R : FR levels (16/8h light/darkness, mean humidity of 60%, temperature simulating the summer course in the field: 5am–7am ~ 18 °C, 7am–7pm ~ 20 °C, 7pm–9pm ~ 18 °C, 9pm–5am ~ 15 °C). Control plants were grown under R : FR = 1.58, treated plants under R : FR = 0.59 (R and FR measured

with Plant Growth Photometer IL 150, International Light Inc., Newburyport, Mass., USA). The aim was to achieve the same level of photosynthetically active radiation (PAR) in both treatments. Unfortunately, due to technical reasons PAR was rather low: 90 and 100 $\mu\text{mol.m}^{-2}.\text{s}^{-1}$ for treated and control plants, respectively (measured with LI-170 instrument with quantum sensor (LI-COR Inc., Lincoln, NE, USA). The radiation levels were achieved due to a combination of different sources in the growth chambers (incandescent bulbs and fluorescent lamps, both with 3-level regulation) and a green plastic foil placed under the lamps (for transmission spectrum of the foil see SKÁLOVÁ & KRAHULEC 1992).

The experiment lasted for 4 months. At each census (every two weeks), the number of intravaginal and extravaginal tillers, and shoot height of the plants were recorded. Rhizome architecture was investigated at the end of the experiment and the following parameters were recorded: number of branches from the initial tussock, number of terminal buds, number of branching nodes within the rhizome system (branching frequency), and total rhizome length.

Data analysis

Differences in the response of clones to R : FR levels were tested using ANOVA. Treatment and community type were treated as fixed effects and clone was treated as a random factor nested within community type (d.f. of clone was thus 1). These analyses were done using BMDP (program 3V, DIXON 1992).

To test whether parameters of the sites from which the clones originated (relative R : FR at the canopy bottom) affect the clones' performance and the response to the experimental

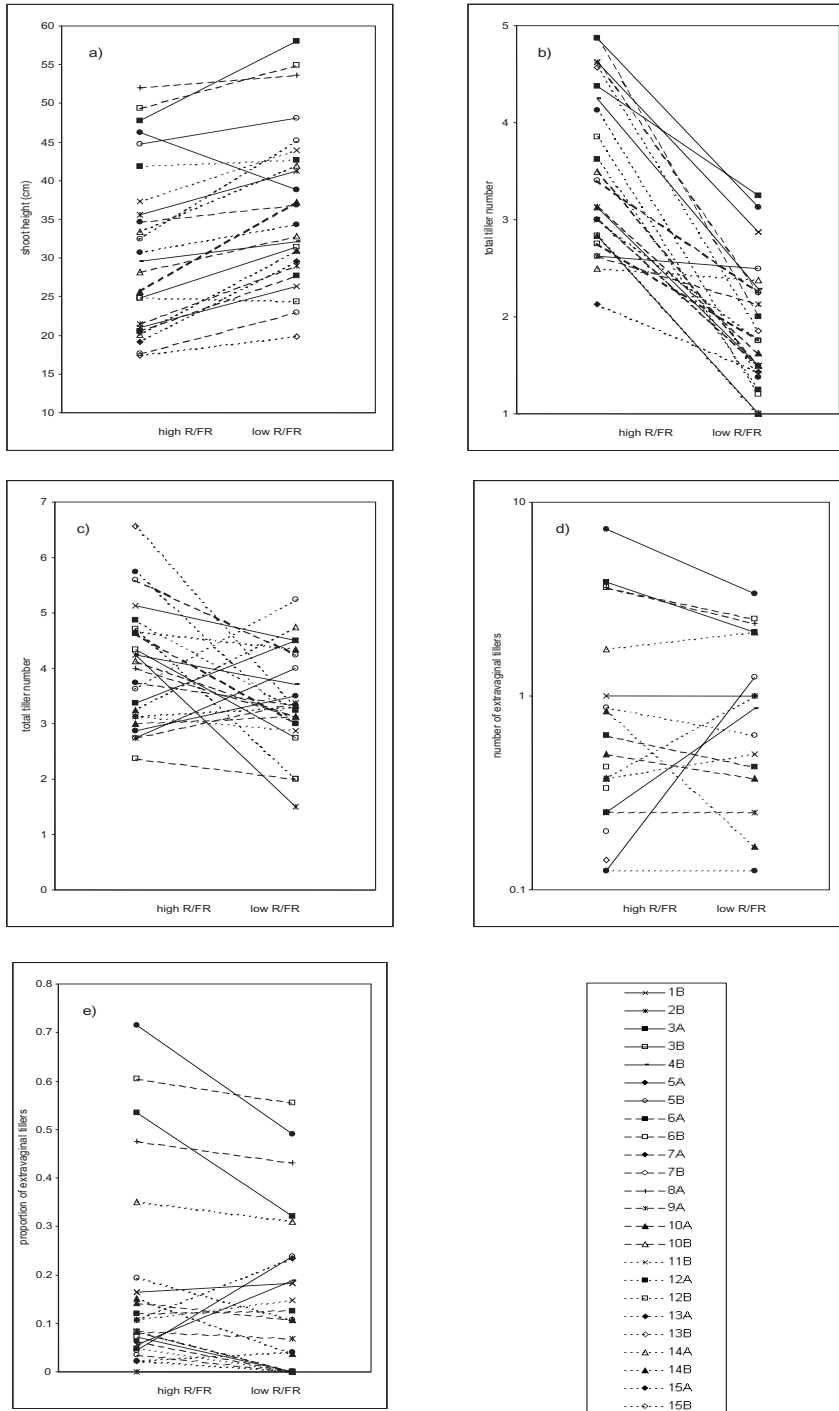


Fig. 1. Norm of reaction diagrams of shoot response of *Festuca rubra* clones to R : FR levels for: (a) average shoot height on day 70 of the experiment, (b) average shoot height per plant on day 70 of the experiment, (c) average total tiller number per plant at the end of the experiment, (d) average number of extravaginal tillers per plant at the end of the experiment, and (e) proportion of extravaginal tillers at the end of the experiment (number of extravaginal tillers/total tiller number). Solid lines – clones from the short, sparse, species-poor community (#1), dashed lines – clones from the degradation phase of the previous community (#2), dotted lines – clones from the dense, taller, species-rich community (#3). For the test of significance see Table 2a,b.

Table 2. Mixed effect model of analyses of variance of the effect of treatment (low R : FR), community type and clone identity on shoot height and tiller number (a) on day 70, and (b) at the end of the experiment. Statistically significant values are shown in bold; LR – Log likelihood ratio; note that clone was treated as a random factor and the d.f. is thus 1.

Dependent variable Effect	d. f.	Shoot height		Total tiller number		Number of intravaginal tillers		Number of extravaginal tillers	
		LR	<i>P</i>	LR	<i>P</i>	LR	<i>P</i>	LR	<i>P</i>
(a)									
Treatment (low R : FR)	1	21.01	<0.001	45.30	<0.001	38.71	<0.001	2.64	0.104
Community type	2	1.36	0.506	5.98	0.050	2.16	0.340	1.09	0.580
Treatment (low R : FR) × community type	2	1.22	0.545	0.78	0.676	2.72	0.257	4.26	0.119
Clone (nested in community type)	1	41.66	<0.001	2.47	0.116	0.92	0.337	3.94	0.047
Treatment (low R : FR) × clone (nested in community type)	1	15.81	<0.001	6.80	0.009	8.13	0.004	0.00	0.999
(b)									
Treatment (low R : FR)	1	29.13	<0.001	7.19	0.007	4.48	0.034	1.09	0.297
Community type	2	1.39	0.499	1.78	0.411	2.80	0.247	4.62	0.099
Treatment (low R : FR) × community type	2	1.97	0.374	0.03	0.984	0.71	0.701	2.01	0.366
Clone (nested in community type)	1	46.60	<0.001	4.54	0.033	0.00	1.000	6.95	0.008
Treatment (low R : FR) × clone (nested in community type)	1	3.27	0.071	24.88	<0.001	15.59	<0.001	0.79	0.374

treatment, a split plot ANOVA model with two error levels (clone level and pot level) was used. Using the clone level is necessary for testing site parameters as these are defined only at this level; any other analysis would inflate the error d.f. Additive effect of R : FR conditions and community type was assumed. The analysis was done using S-plus 2000 (MATHSOFT 2000).

To analyze the response of the rhizome system to the treatments, a two-step analysis was used. First, the presence/absence of the rhizome system in all plants was tested using logistic regression, with treatment, community and clone as independent variables. Second, ANOVA with two error levels as described above was applied to analyze the magnitude of the response in total rhizome length, number of branches from the initial tussocks, branching frequency, number of terminal buds for plants that produced rhizomes.

RESULTS

Morphological parameters of clones and their response to R : FR levels

Between the clones I found significant differences in total tiller number, number of extravaginal tillers, shoot height (Table 2), presence of a rhizome system, total rhizome length, and rhizome structure (Table 3). Shoot responses to low R : FR are summarized in Fig. 1. The low R : FR treatment resulted in increased shoot elongation; clones 5B and 12B had higher plants under high R : FR due to the flowering. Plants grown under low R : FR had a lower tiller number during most of the experiment. In some clones, tiller number recorded in

Table 3. Logistic regression of the effect of treatment (low R : FR), community type and clone identity on rhizome system development (i.e., presence of rhizomes) and differences in rhizome system parameters tested by ANOVA (only plants forming rhizomes included). Significant values are shown in bold.

Dependent variable Effect	Rhizome system development			Rhizome system parameters								
	d. f.			d. f.	Total length		Number of branches		Branching frequency		Number of terminal buds	
		<i>F</i>	<i>P</i>		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Treatment (low R : FR)	1, 353	8.54	0.004	1, 91	30.84	0.000	17.08	0.000	9.16	0.003	25.44	0.000
Community type	2, 351	3.07	0.048	2, 91	22.63	0.000	12.74	0.000	8.16	0.001	17.40	0.000
Treatment (low R : FR) × community type	2, 328	0.33	0.717	2, 91	6.76	0.002	3.60	0.031	2.38	0.098	3.39	0.038
Clone (nested in community type)	21, 330	15.30	0.000	17, 91	7.97	0.000	5.07	0.000	3.74	0.000	8.55	0.000
Treatment (low R : FR) × clone (nested in community type)	21, 307	1.58	0.053	9, 91	7.31	0.000	2.81	0.006	3.87	0.000	6.70	0.000

plants grown under low R : FR at the end of the experiment exceeded that of plants grown under high R : FR. Extravaginal tillering occurred mainly in the second half of the experiment and was often suppressed by low R : FR ratio. However, low R : FR levels increased the number of extravaginal tillers in some clones. Clones showed a different proportion of extravaginal tillers and different ability to switch to extravaginal tillering under different R : FR levels. Similarly as in extravaginal tillering, the development of rhizome systems was usually suppressed by low R : FR ratios (Fig. 2). Several clones did not develop any rhizome system under the low R : FR treatment. There was one clone (13A), in which the rhizome system developed only under low R : FR. Rhizome systems of plants grown under low R : FR levels were smaller and less branched in most of the clones, but some clones showed the opposite behaviour. Most responses to low R : FR were clone specific, i.e., significant clone × treatment interactions were revealed (Tables 2 and 3).

Performance of clones in relation to the original community types

The effect of community type explained only a minor part of variability in the morphological parameters of shoots, but did not explain the response to R : FR levels: effect of community type and community type × treatment interactions were not significant, except the effect of community type on total tiller number on day 70 (Tables 2 a and 4 a, b). In the earlier state of development, clones coming from community type #1 formed tussocks with the highest tiller number and clones from community type #3 with the lowest (Fig. 3). A higher percentage of plants from community type #1 developed rhizome systems under high R : FR (51% compared to 36% of plants from both remaining community types). One and two clones with large and highly branched rhizome systems were found in community types #1 and #2, respectively. Two of them (one from community type #1 and one from community type #2) were also highly responsive to R : FR levels (Fig. 2). The analysis at the plant level (Table 3) revealed a significant effect of community type on rhizome system

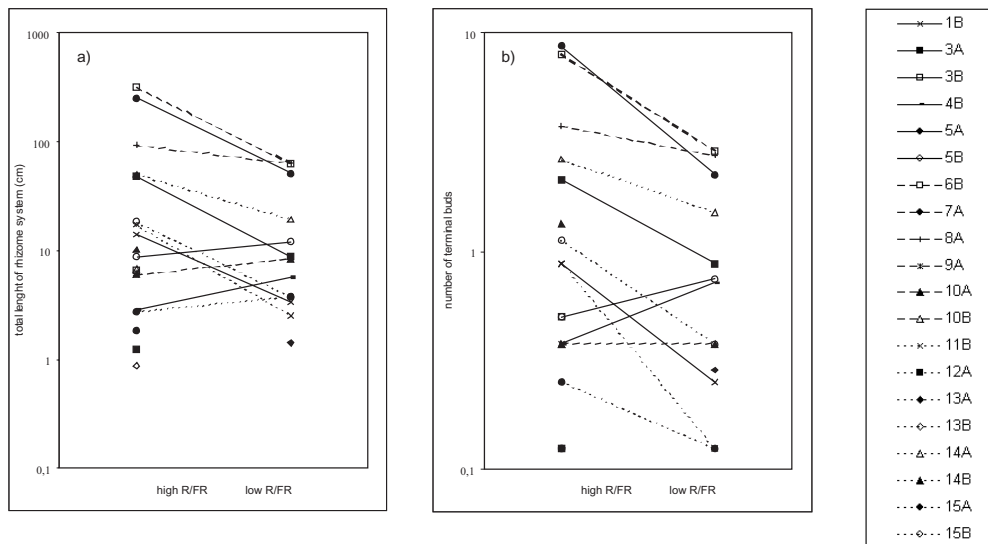


Fig. 2. Norm of reaction diagrams of rhizome system response of *Festuca rubra* clones to R : FR levels for: (a) average total length of rhizome system, and (b) average number of terminal buds per plant. Solid lines – clones from the short, sparse, species-poor community (#1), dashed lines – clones from the degradation phase of the previous community (#2), dotted lines – clones from the dense, taller, species-rich community (#3). Only clones forming a rhizome system involved; absence of lines indicates absence of rhizome systems in plants grown under either regime. For the test of significance see Table 3.

presence and structure, and significant community type \times treatment (low R : FR) interactions in rhizome system parameters. The effects were not significant at the clone level (Table 4c).

Performance of clones in relation to relative R : FR in the original micro-sites within the communities

The analyses done at the clone level (Table 4) did not reveal any evidence for a consistent relationship between the performance of individual clones and the R : FR conditions in the micro-sites of their origin. Morphological parameters and the responses of the clones to the low R : FR treatment (Fig. 4) were completely independent of the radiation conditions in the original micro-sites within the communities.

DISCUSSION

Performance of clones in relation to the original community types

The effect of community type explained a part of variability in morphological parameters of the clones. Clones (ecotypes) coming from the short, sparse, species-poor meadow community (#1) formed tussocks with a higher tiller number in the earlier state of the development. It seems that such clones are able to survive in sparse canopies with better radiation conditions at the canopy bottom only. They might have been out-competed during

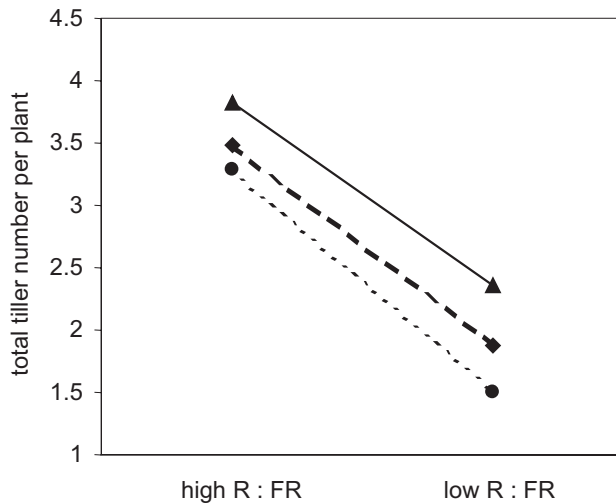


Fig. 3. Norm of reaction diagram of tillering response of *Festuca rubra* coming from 3 community types to R : FR levels on day 70 of the experiment. Solid lines and ▲ – clones from the short, sparse, species-poor community (#1), dashed lines and ◆ – clones from the degradation phase of the previous community (#2), dotted lines and ● – clones from the dense, taller, species-rich community (#3). For the test of significance see Table 2a, and Table 4a.

differences in morphological parameters but only minor differences in the plasticity of *Plantago lanceolata* coming from two grassland habitats with different canopy height and density. It seems that intra-specific differences in plasticity in response to R : FR occur only in plants from communities with really pronounced differences in canopy height as demonstrated by DUDLEY & SCHMITT (1995) and WEINIG (2000).

The effect of community type on shoot height was not revealed. Thus, differences in the height of *F. rubra* plants found in the three community types (SKÁLOVÁ et al. 1999) were probably not due to the occurrence of ecotypes with different height or plasticity. It is considered to be due to the direct effect of the edaphic conditions on plant height, and plant response to the radiation conditions in the canopies.

Performance of clones in relation to relative R : FR in the original micro-sites within the communities

The results indicate that there is only limited selection of clones typical for individual communities. The mountain meadows are characterized by considerable heterogeneity in R : FR (SKÁLOVÁ et al. 1999) and it might thus be possible that there are clones specialized at micro-sites with particular radiation conditions instead of clones specialized at individual community types. However, the analyses presented (Table 4) did not reveal any relationship between performance of individual clones and relative R : FR in their original micro-sites within the communities.

the change of community type #1 into #2. During the expansion of *Bistorta major*, R : FR at the canopy bottom decreased to levels similar to that in community type #3 where such clones were also not found. Clones that developed large rhizome systems came from community types #1 and #2. Absence of such clones in the taller and denser community with better edaphic conditions (#3) may be explained by a lower necessity to search for nutrient-rich patches and the limited chance to find free patches.

Clones coming from the three community types did not differ in plasticity in response to radiation conditions. Similarly, VAN TIENDEREN & VAN HINSBERG (1996) found considerable

Table 4. Effect of community type, radiation conditions (relative R : FR at the canopy bottom) in the micro-sites of the clones' origin and treatment (low R : FR) on the performance of *Festuca rubra*: (a) shoot parameters on day 70, (b) shoot parameters at the end of the experiment, (c) rhizome system parameters at the end of the experiment (only plants forming rhizomes included). Split plot ANOVA model with two error levels was used; additive effect of radiation conditions in the micro-sites and community type was assumed. Significant values are shown in bold.

(a) Dependent variable Effect	d. f.	Shoot height		Total tiller number		Number of intravaginal tillers			
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Pot level									
Treatment (low R : FR)	1,327	84.78	0.000	188.10	0.000	143.62	0.000		
Clone level									
Community type	2, 16	0.61	0.556	4.39	0.030	1.40	0.276		
Treatment (low R : FR)	1, 16	1.81	0.198	2.98	0.104	0.02	0.880		
Relative R : FR in micro-sites of origin	1, 16	3.12	0.097	0.02	0.882	3.39	0.084		
Treatment (low R : FR) × community type	2, 16	0.12	0.884	1.85	0.190	0.86	0.442		
Treatment (low R : FR) × relative R : FR in micro-sites of origin	1, 16	0.00	0.975	0.21	0.650	1.01	0.329		
(b) Dependent variable Effect									
	d. f.	Shoot height		Total tiller number		Number of intravaginal tillers		Number of extravaginal tillers	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Pot level									
Treatment (low R : FR)	1,327	95.14	0.000	22.33	0.000	9.95	0.002	6.24	0.013
Clone level									
Community type	2, 16	0.56	0.581	1.32	0.295	1.90	0.182	1.52	0.249
Treatment (low R : FR)	1, 16	1.29	0.272	4.54	0.049	0.14	0.716	3.76	0.070
Relative R : FR in micro-sites of origin	1, 16	2.89	0.109	0.34	0.568	2.98	0.103	2.04	0.172
Treatment (low R : FR) × community type	2, 16	0.10	0.904	1.27	0.309	2.22	0.141	1.14	0.343
Treatment (low R : FR) × relative R : FR in micro-sites of origin	1, 16	0.03	0.875	0.28	0.605	0.00	0.966	0.25	0.621
(c) Dependent variable Effect									
	d. f.	Total length of rhizome system		Number of branches		Branching frequency		Number of terminal buds	
		<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>	<i>F</i>	<i>P</i>
Pot level									
Treatment (low R : FR)	1,107	23.983	0.000	19.23	0.000	10.57	0.002	21.54	0.000
Clone level									
Community type	2, 16	0.29	0.795	0.37	0.757	0.12	0.897	0.22	0.836
Treatment (low R : FR)	1, 16	0.37	0.653	0.60	0.580	0.89	0.518	0.76	0.544
Relative R : FR in micro-sites of origin	1, 16	0.05	0.858	0.00	0.958	0.02	0.904	0.01	0.928
Treatment (low R : FR) × community type	2, 16	0.00	0.997	0.00	1.000	0.07	0.936	0.02	0.978
Treatment (low R : FR) × relative R : FR in micro-sites of origin	1, 16	0.00	0.93	0.09	0.811	0.01	0.955	0.03	0.889

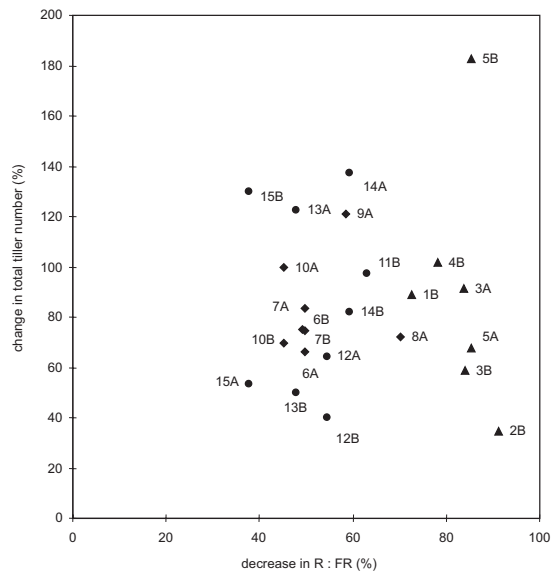


Fig. 4. Relationship between tillering response of *Festuca rubra* clones to R : FR levels (total tiller number at the end of the experiment) and relative R : FR in the micro-sites of the clones' origin. Change in total tiller number per plant (%) refers to the percentage of total tiller number in treated plants in total tiller number in control plants; decrease in R : FR (%) refers to the percentage of the above canopy value recorded at the canopy bottom. ▲ – clones coming from the short, sparse, species-poor community (#1), ◆ – clones from the degradation phase of the previous community (#2), ● – clones from the dense, taller, species-rich community (#3). For the test of significance see Table 4b.

A possible explanation lies in the unstable radiation conditions in the meadows. Radiation conditions are dependent on biomass, structure, and partly also on species composition of a canopy (HOLMES & SMITH 1977). Biomass of the meadows fluctuates substantially from year to year (HERBEN et al. 1990), and there are also considerable changes in species abundance on a fine scale (HERBEN et al. 1993). Clonal grass thus experiences different conditions due to changes in the radiation conditions in particular micro-sites, and also due to its clonal growth. The average yearly shift of 0.8 cm (WILDOVÁ, unpubl. data) is close to the scale of horizontal heterogeneity in the stands (SKÁLOVÁ et al. 1999). In addition, there is a remarkable yearly cycle in canopy height

resulting from the spring-to-fall persistence of the canopy and mowing the meadows. These factors are probably strong enough to prevent the selection of clones with typical morphology and response to R : FR ratio in individual micro-sites. Genetic variation and differences in phenotypic plasticity may be maintained in a heterogeneous environment at a considerably fine scale (PRATI & SCHMID 2000, LENSSEN et al. 2004), but only when there is a pronounced and stable environmental gradient.

Approach limitation

For technical reasons, experimental conditions were not identical with those in the field. The experiment was carried out under a relatively low level of photosynthetically active radiation (PAR), which might slow down the response to low R : FR because growth rate and branch initiation have been reported to be decreased under reduced PAR levels (CORRÉ 1983, DAVIES & THOMAS 1983, EVERSON et al. 1988). Low PAR, however, results in stimulated shoot and petiole elongation in some plants (WARRINGTON et al. 1988, SOLANGAARACHCHI & HARPER 1987). An additive effect of low PAR and R : FR was observed (MÉTHY et al.

1990, BALLARÉ et al. 1991). Poor attention has been paid to doing a systematic study of interactions between response to PAR and R : FR levels, but recent work by MONACO & BRISKE (2000) indicates that shade-avoidance response to low R : FR is not affected by PAR levels.

In contrast to natural habitats where a pronounced R : FR gradient from the top of the canopy towards its bottom occurs (HOLMES & SMITH 1977), the experiment was carried out under relatively homogeneous radiation conditions. Shoot elongation response to simulated vertical radiation gradient (PAR + R : FR) exceeded that to comparable homogeneous radiation conditions (LEEFLANG et al. 1998). A separate effect of low R : FR and the absence of a radiation gradient might cause a weaker response of plants compared to their performance in naturally shaded habitats and might thus mitigate differences between the clones' responses. A consistent relationship between clone performance and radiation environment in the original sites might thus not be revealed.

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