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Within population genetic differentiation in traits affecting clonal growth: *Festuca rubra* in a mountain grassland

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Abstract

Festuca rubra, a clonal grass of mountain grasslands, possesses a considerable variability in traits related to spatial spreading (rhizome production, length and branching; tussock architecture). Since these traits highly influence the success of the species in a spatially heterogeneous system of grasslands, a combined field and growth chamber approach was adopted to determine the within-population variation in these parameters. Clones were sampled in a mountain grassland (The Krkonoše Mts., Czech Republic); the environment (mean neighbour density) of individual clones varied highly. Before the clones were collected, shoot demography and tussock architecture within these clones were recorded in the field for four seasons. Their clone identity was determined using DNA RAPD. Vegetatively propagated plants from these clones were cultivated in a common garden experiment to demonstrate variation in tussock growth and architecture. Their response to change in red/far red light ratio was determined in the growth chamber.

Highly significant variation among clones was found in almost all parameters. In the common garden, the clones differed in tussock growth (mean tillering rate), architecture (mean shoot angle, mean tussock density) and proportion of flowering shoots. In the growth chamber, both the aboveground parameters and parameters of the rhizome system were strongly affected by red/far red ratio; among-clone

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variation was also almost always significant. The genotype × environment interaction was significant for tillering rate and rhizome architecture. The structure of the rhizome system (which is the major component of clonal spread in space) is a complex result of several components whose inter-clone variations differ: (i) genetically determined mean rhizome system size, (ii) overall plasticity in rhizome system size (with no significant genetic variation in plasticity), and (iii) genetically determined plasticity in rhizome architecture. Because of the variation in plasticity in rhizome architecture, some clones seemed to possess the ability to exploit a favourable habitat patch by producing short branches when there; whereas the remaining clones appeared to possess only a simple escape mechanism from unfavourable patches.

Environmental variation in the light levels in the studied grassland is fine grained; horizontal growth rates of *F. rubra* are sufficient to make genets experience different patches in their lifetime. The high variation in both genotype means and plasticities is likely to be due to selection early in genet life in an environment which is heterogeneous at a fine scale.

Introduction

Most plant communities show pronounced horizontal spatial structure; this horizontal structure brings about heterogeneity in many parameters essential for plant growth, such as light (Silvertown et al., 1989; Tang et al., 1992; Baldocchi and Collineau, 1994) or nutrients (Jackson and Caldwell, 1993; Robertson and Gross, 1994). Any species occurring in such heterogeneous environments is thus exposed to varying selection intensity at the population level (Bell and Lechowicz, 1991; Bell et al., 1991; Stratton, 1994, 1995).

In non-clonal plants, individuals are likely to experience same microenvironment over their lifetime. In contrast, individual genets of clonal plants possess dispersal ability by means of vegetative growth (Eriksson and Jerling, 1990; Schmid, 1990). Vegetative growth enables individual genets to change their spatial position and, as a result of this, their environment. Clonal growth thus translates spatial environmental variation into temporal variation; consequently the selection intensity individual genets experience may vary through the lifetime of the genet. The importance of this effect depends both on the spatial grain of the environment and on the rate of the vegetative growth of the plant (Schmid, 1990); their ratio determines whether an environment is perceived as fine-grained or coarse-grained by the plant. In spite of considerable spatial mobility of clonal plants, the interaction between species vegetative spread and environmental heterogeneity has scarcely been studied (Bell and Lechowicz, 1994; Hutchings and De Kroon, 1994). Spatially explicit models have shown that changing any of these parameters has large effect on the ecological dynamics of such clonally growing system (Cain, 1994; Oborny, 1994). This may have important consequences for both maintenance of genetic polymorphisms (Hedrick, 1986, 1995; van Tienderen, 1991) and selection for generalist or specialist strategies (Gomulkiewicz and Kirkpatrick, 1992; Schlichting

and Pigliucci, 1995). Depending on the species vegetative spreading and the heterogeneity of the environment, selection may favour either an array of specialist genotypes or a plastic generalist genotype (Scheiner, 1993; Bell and Lechowicz, 1994; Schlichting and Pigliucci, 1995).

Clonal dispersal is, however, not entirely blind. To some degree, it may provide an "escape mechanism" from an unfavourable patch (de Kroon and Knops, 1990; Hutchings and de Kroon, 1984) given the plant is able to modify its rate of the clonal growth depending on its environment. The ecological role of this plasticity in growth-related traits has attracted considerable attention in past few years and its role is becoming gradually clear (Hutchings and de Kroon, 1994; Cain, 1994; Oborny, 1994). It has been shown that the importance of the mechanism of active response to the environment is much weaker than thought a decade earlier. First, detailed analyses persuasively demonstrated rather low efficiency of realistic types of morphological response to the environment (Cain, 1994; Oborny, 1994). Second, many cases assumed to result from morphological plastic response turned out to be programmed growth behaviour, partly because the plastic response had not been studied using adequate techniques (Hutchings and de Kroon, 1994; and see discussion in de Kroon et al., 1994).

At any rate, both the rate of clonal growth and the plastic response to the environment do influence the success of a clonal species within a heterogeneous habitat (Cain, 1994; Oborny, 1994) and the time individual genets spend in habitat patches. Consequently, the traits which underlie the differential potential of individual genets to spread through space are subject to selection. The relatively low frequency of sexual reproduction should not matter, since clonal plants are known to possess high levels of genetic variation demonstrable by isozyme or DNA markers (Ellstrand and Roose, 1987; Widén et al., 1994).

Despite considerable progress in understanding the ecological implications of clonal growth (see references above), very little is known about genetic variation for relevant traits in any single species (but see Cheplick, 1995). For some grassland species, there is an indication of the existence of differentiated types in response to different neighbouring plants (Solangaarachchi and Harper, 1987; Turkington, 1989; Skálová and Krahulec, 1992), but the ability of these differentiated types to spread through space is unclear.

To study the genetic differentiation in these traits, we selected a species known to be variable in its clonal growth (*Festuca rubra*) in a spatially heterogeneous habitat (grassland). The horizontal spatial variation in grasslands is quite pronounced at the fine scale (Mahdi and Law, 1987). Though the variation is typically exhibited by many environmental parameters, we studied response to the red/far red ratio of the incident light only. The red/far red ratio is the most important cue plants use to sense their light environment (Casal et al., 1985; Deregibus et al., 1985); it has pronounced morphogenetic effects (Casal et al., 1985; Deregibus et al., 1985) and plays an important role in plant interactions (Schmitt and Wulff, 1993; Ballaré et al., 1994). It is also known to vary within grassland stands in relation to the canopy structure (Silvertown et al., 1989; Tang and Washitani, 1995). In terms of horizontal growth, low light conditions have been shown to induce faster escape growth

(Hutchings and de Kroon, 1994; Svensson et al., 1994; Dong and de Kroon, 1995). In spite of these pronounced effects, the fine scale horizontal heterogeneity in the red/far red ratio has not yet been addressed in the genetic context (Schmitt and Wulff, 1993).

The particular grassland where the clones were sampled shows a fine scale heterogeneity in vegetation structure (Herben et al., 1995) and in red/far red ratio (Skálová et al., unpubl. data). In this system, we aimed to determine differentiation in traits affecting clonal growth between clones of *Festuca rubra*. The study addresses particularly (i) the among-clone variation in traits which influence spatial spread, and (ii) the plasticity of these traits in response to variation in light levels (change of the red/far red ratio). It combines field observation of clones within their natural habitat, common garden cultivation, and response to two red/far red regimes at the levels comparable to within-habitat variation. The whole study relies on previous research in the same grassland, which assessed spatial grain of the community, its light conditions and spatial spreading rates of *F. rubra* (Herben et al., 1993a, b, 1995; Krahulec et al., in press; Suzuki et al., unpubl. data).

Methods

The species

F. rubra L. is a common perennial grass species of temperate meadows in Europe. It is a taxon known for its variability at several levels (Markgraf-Dannenberg, 1980). *F. rubra* s.l. is now divided into more than 20 species and subspecies in Europe alone (Markgraf-Dannenberg, 1980). Further differentiation exists on ecotypic and clonal levels: local functional differentiation has been demonstrated with respect to various factors (Rhebergen and Nelissen, 1985; and references therein, Skálová and Krahulec, 1992). The species is ecologically very flexible, owing to a combination of genetic variation and plastic variation (Grime et al., 1988). The variability in the type of clonal growth concerns flexibility in formation of underground rhizomes and the ability to form shoots in two different ways, viz. intravaginally (i.e., within the sheath of the mother tiller and parallel to it) and extravaginally (outside the sheath and with large angle between the mother and daughter tillers). Tussocks with rhizomes or composed predominantly of extravaginal shoots are much looser (Krahulec et al., in press). The type of the shoot formation and the degree of the rhizome formation are both under genetic and environmental control in the hexaploid type *Festuca rubra* subsp. *rubra* (*F. rubra* s.s.; Krahulec et al., in press), to which the plants in the studied area belong.

Study site

The clones were collected in a grassland in the Krkonoše Mountains, in the North of the Czech Republic (Severka settlement, 50° 41′42″ N, longitude 15° 42′25″ E,

c. 1100 m a.s.l.). The whole area has a harsh climate; mean temperature in the warmest month (July) was 13.6 °C (1988), 13.7 °C (1989) at the nearby climatic station (Pec pod Sněžkou, *c.* 900 m a.s.l.). The snow disappears and vegetation season begins as late as in mid May and ends in the beginning of October. Before the study began, the grassland under study was mown once a year in late July; this management had been maintained over at least several decades (pers. comm. of the owner). The grassland is rather species poor, with only five common species: *Anthoxanthum alpinum*, *Deschampsia flexuosa*, *Festuca rubra*, *Nardus stricta* and *Polygonum bistorta*.

Clone sampling

Sixteen tussocks of *Festuca rubra* subsp. *rubra* were selected using a stratified random approach in a homogeneous area of 12 × 3 m. The tussocks were selected with *a priori* requirements that (i) there be no *F. rubra* in their close surroundings (up to 7 cm) to prevent uncertainty in identifying newly emerged shoots, and (ii) they have a workable number of shoots (not exceeding 25).

In July 1987, the vegetation immediately surrounding the tussocks was recorded. The recording was made in the grid of cells of 3.3 × 3.3 cm in size established over each tussock. The grid was made large enough so that the tussock was surrounded by one row of cells containing no *F. rubra* shoots. The number of shoots of all grasses within each cell was counted by species. Mean *F. rubra* density in the tussocks was 4.41 shoots/10 cm^2 (s.d. 1.86, range 1.2–8.3); mean density of all grass species in the tussocks was 16.0 shoots/10 cm^2 (s.d. 6.17, range 5.4–27.2).

Shoot demography in the field

In the selected tussocks, the demography of all shoots was observed for over four growing seasons. Three censuses were carried out each year before clipping (late May to mid-July) and two to four censuses after clipping (August to October). The dates of the censuses were: 4 June, 25 June, 14 July, 5 August, 29 August, 14 September, 10 November 1987; 24 May, 23 June, 9 July, 3 August, 5 September, 12 October 1988; 19 May, 15 June, 8 July, 7 September, 4 October 1989; 10 May, 15 June, 10 July 1990. Each year in mid July, the tussocks and the surrounding vegetation were clipped to a height of 2.5 cm to simulate the traditional mowing.

All shoots within the tussocks were tagged with coloured plastic rings. In mid July (the third census), flowering shoots were recorded separately. For all newly emerged shoots, intravaginal and extravaginal origin was distinguished. The life span of shoots and their ultimate fate (whether they died from flowering or from other causes) were recorded. A detailed description of the study site and sampling techniques is given in Herben et al. (1993a).

Clone identity

After the field observations ended, all tussocks were taken to the laboratory, the soil and surrounding vegetation were carefully removed and the physical connections between the clusters of shoots were established. All the physically connected shoots were supposed to be of clonal origin and are further referred to as shoot clusters. Plants from the clusters with more than 5 shoots in the field site were kept and propagated vegetatively in the experimental garden of the Institute of Botany in Průhonice.

The genetic identity of these shoot clusters was determined using the DNA RAPD analysis. Total DNA was extracted according to the modified method of Milligan (1992). A modified version of the PCR RAPD procedure of Williams et al. (1990) and Levitan and Grosberg (1993) was used. Amplification was carried out with two primers, OPA-1 and OPA-10 (Operon Technologies Inc., Alameda, California, USA), for each sampled shoot. Amplification products were analysed by electrophoresis in 8% polyacrylamide gels and DNA bands were detected by silver staining (Tegelström, 1992). If two shoots exhibited the identical band patterns, both were assumed to belong to the same genet.

After the clones were identified by the DNA RAPD, the clone identity of shoots recorded in the field was determined whenever possible, using the information both (i) on physical connection within shoot clusters, and (ii) on the mother/daughter relationship determined earlier during the field recordings. The clones were coded using original field codes of tussocks (1 to 19, 11 and 12 were not used) with a third number indicating the clone within the tussock in the field (several tussocks turned out to be composed of several genets).

For logistic reasons, a subsample of the original tussocks was used in the following experimental assays. The subsample used only those clones for which sufficient data were available from the field (after clone identification had been made). Seventeen clones (selected randomly out of those with shoot number >5 in the field data set) were used in the common garden cultivation; twelve clones (selected randomly from the previous 17) were used in the growth chamber experiment.

Common garden cultivation

Fifteen single shoots of each clone were planted into the open garden soil on July 1, 1992. Over the cultivation period of one year, these shoots gave rise to tussocks of 20–200 shoots. The number of shoots per tussock were counted on 28th July 1992 (initial number), on 11th November 1992, on 26th April 1993, and in the end of June 1993. To account for the different initial size of the tussocks due to contingencies of planting and establishment, the number of shoots within the tussock after the rooting was used as a covariate in the ANOVA's. In April 1993 the longest diameter of each tussock and the longest diameter perpendicular to it were measured and the tussock basal area was calculated assuming elliptical shape.

In June 1993, the angles from vertical of the flowering shoots in the tussocks were measured; the angle of the flowering shoot is a good measure of the architecture of the whole tussock being strongly correlated with the angle of all the shoots (Krahulec et al., in press). In July 1993, the number of flowering shoots in all the tussocks were counted.

Red/far red ratio response of the clones

The vegetatively propagated shoots of twelve selected shoot clusters were used for a red/far red ratio response experiment. The plants were grown in two growth chambers (Conviron S 10 H, Winnipeg, Canada) with identical regime except for light levels. The 16/8 light/darkness regime was used. Light intensity was 4600 Lx (measured by Light Intensity Photometer Lux PU 150, Metra Blansko) in both, treated and control plants. Control plants were grown under red/far red = 1.6, treated plants under red/far red = 0.6 (red and far red measured separately by Plant Growth Photometer IL 150; International Light Inc., Newbury Port, Massachusetts). These R/FR ratios roughly correspond to the range of variation encountered by plants in the original habitat (Skálová, Krahulec, unpubl. data). Temperature was 20 °C during the light period, 15 °C during the dark time. Mean air humidity was 60%.

The experiment was begun in December 1993. Single *F. rubra* shoots were rooted under hydroponic culture conditions for a week; then they were planted into plastic 125 ml (5 × 5 × 5 cm) pots in a soil-perlite mixture (1:1). Ten shoots of each clone were grown, one shoot per pot and watered twice a week. Censuses were made on 14th, 33rd, 43rd, 57th, 71st and 85th days of cultivation; total number of shoots and shoot height were recorded at each census. Newly formed shoots were recorded when a leaf tip of the first leaf longer than 1 cm was visible in the axilla of the subtending leaf. Height of shoots was measured as a distance from the tussock base to the top of the longest shoot leaf. In every tussock the longest shoot was measured. An earlier pilot study showed that the longest shoot height provides reliable representation of the mean height of shoot in the tussock (see also Skálová and Krahulec, 1992).

Rhizome structure

After the termination of the growth chamber experiment, five randomly selected plants of each clone were carefully excavated from the substratum and the parameters of their underground rhizome system were determined. The following parameters were used: (i) total number of nodes in the whole rhizome system, (ii) total number of rooting nodes in the whole rhizome system, (iii) number of terminal rhizome buds (growing buds), (iv) length of the longest rhizome, (v) length of the longest rhizome internode, (vi) total length of the rhizome system (sum of lengths of all the rhizomes). All the parameters are expressed per pot, i.e., per plant arisen

from one initially planted shoot. Clone 181 was not included into the rhizome analysis because of insufficient number of replicates surviving till the termination of the study.

Data analysis

Data were analyzed using the analyses of variance. Except for single classification ANOVA's, maximum likelihood approach to the analysis of variance was adopted following Dixon (1992) and Potvin (1993). It may provide a weaker test, but it is less sensitive to unbalanced designs (Fry, 1992; Potvin, 1993). In this approach, the specified full statistical model is fitted numerically by the maximum likelihood technique; the individual terms of this statistical model are tested by the difference in fit between the full model and model in which the tested effect is set to zero. The significance of the difference in fit is assessed by the log likelihood ratio statistic (Sokal and Rohlf, 1981) with a number of degrees of freedom equal to the number of mathematically independent parameters set to zero when excluding the term (number of levels – 1 for fixed effects, 1 for random effects, see Dixon, 1992, p. 1319). The computations were done with the BMDP package (program 3V, Dixon 1992). Unconstrained maximum likelihood estimates (option ML) were used.

Clone was always treated as a random factor sampled from an underlying normal distribution with a mean of zero. Therefore mixed model ANOVA was used whenever two classification ANOVA's involving clone × treatment interactions were needed. The treatments were treated as fixed effects. In a similar manner, the unbalanced nested data on flowering shoot angle in the garden experiment (there were many tussocks of each clone, many angle data points from one tussock), were also tested by the same procedure. Tussock code was used as a nested random factor within clone in this analysis. Data from the growth chamber were analyzed by the Repeated Measurements ANOVA; this was attained by adding time and treatment*subject (i.e. experimental plant) interaction to the model (von Ende, 1991; cf. also Dixon, 1992, p. 1136).

The data structure of the rhizome parameters from the plants exposed to different light levels was summarized by the (centred) principal component analysis of the correlation matrix of the six rhizome parameters; each plant was taken as a separate case with these six parameters as variables. The effects of the clone and treatment on the component scores of individual plants were tested during a mixed model ANOVA in a similar manner to the untransformed parameters.

The life span of the shoots in the field was estimated using the Kaplan-Meier technique, which is able to account for the truncated data due to some shoots surviving past the end of the observations (Dixon, 1992). The differences in shoot life span among the clones in the field were tested using generalized Savage (Mantel-Cox) and generalized Wilcoxon (Breslow) statistics (Dixon, 1992). The Mantel-Cox statistic weights all cases equally; the Breslow statistic puts more weight on the cases with short life span. Two clones (143 and 161) were deleted from this testing because of the low number of observations.

Results

Clone identity

Two pairs of tussocks (tussocks 2 and 3, 7 and 8) turned out to be genetically identical; tussocks 2 and 3 by identifying the underground connections, and tussocks 7 and 8 using the DNA RAPD. The distances between the centres of these two tussocks pairs in the field were 10 cm and 15 cm, respectively. These two clones are further coded 21 and 72. All other tussocks were genetically different from each other (DNA PCR data not shown). Genetically different shoot clusters were found in two tussocks (clones 62, 63, 66 and 67 in the tussock 6, and clones 101 and 102 in the tussock 10).

Demographical differences among the clones in the field

Large differences were found among individual clones in the field. They differed significantly in the proportion of extravaginal shoots (0–40% out of all newly born shoots), and the proportion of flowering shoots (0–40%). The difference in the overall tillering rate was not significant, though few clones (63, 181, 62, 161) seemed to deviate from the rest (Fig. 1). Shoot lifespan did not differ significantly between the clones in the field when tested by the Mantel-Cox statistic (16.4, d.f. = 13, $P = 0.227$) and only marginally when tested by the Breslow statistic (20.7, d.f. = 13, $P = 0.078$). Since the Breslow statistic weights the shorter-lived shoots more heavily, these contribute more to the among-clone difference in the shoot survival.

Common garden experiment

The clones taken into common garden for cultivation differed significantly in all the parameters measured (tillering rate, tussock density, flowering and tussock architecture; Tab. 1; Fig. 2). In some parameters (clone growth rate and mean tussock density), the response of individual clones was symmetrically distributed around the grand mean; for flowering shoots angle and number of flowering shoots the distributions were rather skewed, with some clones exceeding the values of the less differentiated rest (clones 21, 91, 143, 191 for flowering; 143, 171 for flowering shoot angle).

Aboveground response to the red/far red ratio in the growth chamber

Lowered red/far red ratio of the incident light strongly reduced the shoot number in the plants. This effect was highly significant (Tab. 2). Differences between clones were also significant in all censuses except the first two ones. There was a significant effect of clone on the mean shoot number between the 33rd and 57th day of the

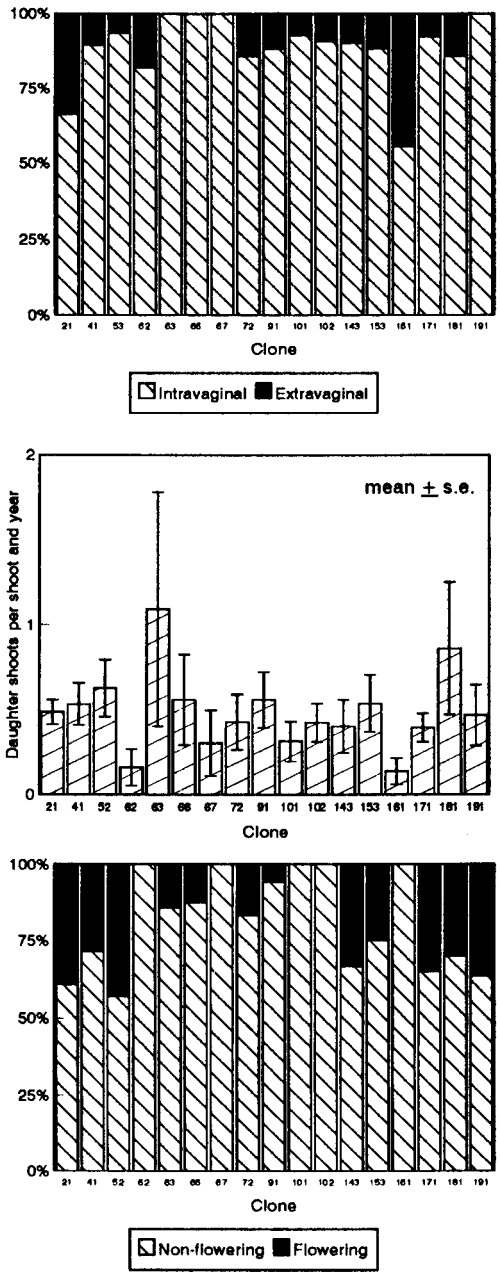

Fig. 1. Variation between the *F. rubra* clones in the field. Upper plot: proportion of extravaginal shoots out of all shoots born during the observation; chi-square = 62.7, d.f. = 16, $P < 0.001$. Middle plot: Mean number of daughter shoots per shoot (per year) s.e.; ANCOVA: F (clone) = 1.2, d.f. = 16,621, $P = 0.202$; F (covariate – life span) = 276.4, d.f. = 16,621, $P < 0.001$. Bottom plot: proportion of flowering shoots out of all shoots dying during the observations, chi-square = 36.0, d.f. = 16, $P < 0.01$. Bars indicate standard errors.

Table 1a. Effect of clone identity on shoot number in tussocks from the common garden experiment. Repeated measures ANOVA is used to test the effect of time. Shoot number after one month of cultivation (end of July 1992) is used as a covariate.

Source of variation	d.f nom., den.	F	Significance
Clone	16,210	2.27	0.005
Covariate: Init. number of shoots	1,210	7.53	0.007
Time	348	202.27	<0.001
Time × Clone	48,633	2.16	<0.001

Table 1b. Effect of clone identity on number of flowering shoots in July 1993 from the common garden experiment. The shoot number in April 1993 (after 269 days cultivation) is used as a covariate.

Source of variation	d.f nom., den.	F	Significance
Clone	16,219	5.806	<0.001
Covariate: Number of shoots	1,219	911.122	<0.001

Table 1c. Effect of clone identity on tussock area from the common garden experiment in April 1993 (after 269 days cultivation). Shoot number is used as a covariate.

Source of variation	d.f. nom., den.	F	Significance
Clone	16,224	3.731	<0.001
Covariate: Number of shoots	1,224	563.135	<0.001

Table 1d. Effect of clone identity on the vertical angle of flowering shoots from the common garden experiment. Individual tussock is taken as a nested random factor. The maximum likelihood estimation of the effects and LR tests were used. The test of an effect is the difference in the likelihood of the two models differing in the presence of the particular effect being tested (Dixon, 1992).

Source of variation	log likelihood ratio	d.f.	*P*
Clone	27.4	1	<0.001
Tussock	1.3	1	0.261

experiment, when the interaction between clone and red/far red ratio was significant (marginally significant on the 43rd day). The difference between the two light treatments was most obvious from the 33rd day to the 57th day of the cultivation; later some clones began to slow down the tillering in the high red/far red treatment and the differences between the treatments diminished (Fig. 3).

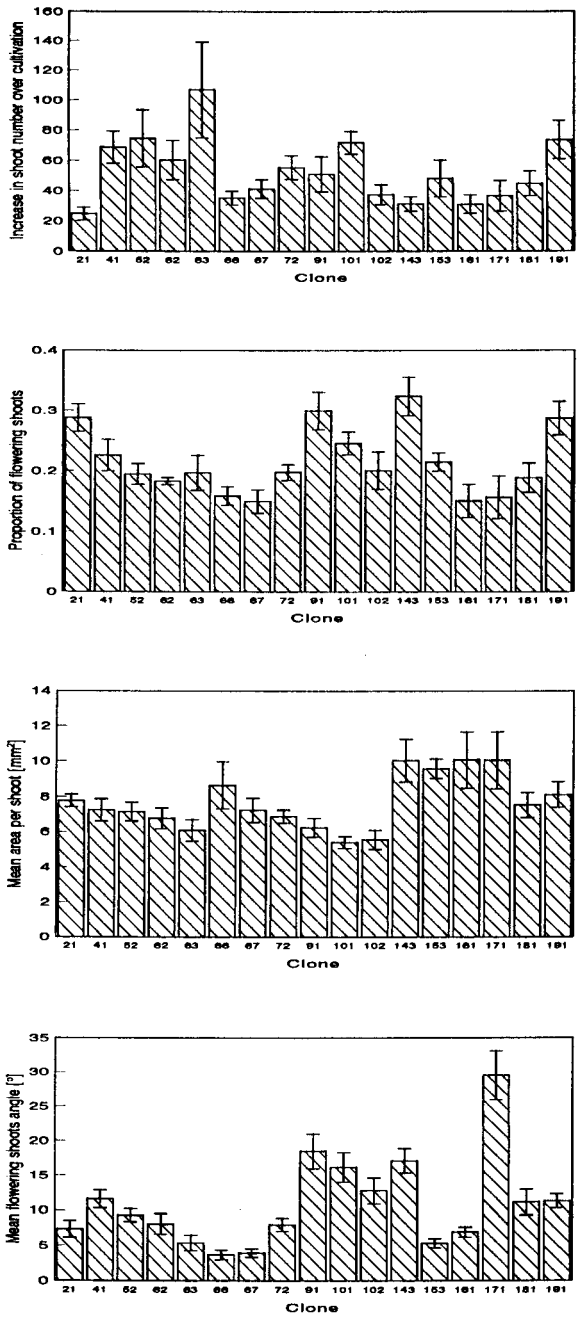

Fig. 2. Variation between the *F. rubra* clones in the common garden. For the significance tests see Table 1. Increase of the shoot number over cultivation is expressed relative to the shoot number in the tussocks after rooting in the garden. Bars indicate standard errors.

Red/far red levels had much weaker effect on the shoot length; this effect appeared earlier in the experiment (14th to 43rd day) and disappeared later. Clones again differed significantly (in all censuses), but clone × light interaction was never significant (Tab. 2)

Rhizome response to the red/far red ratio in the growth chamber

The red/far red ratio had a strong effect on the structure of the rhizome system; all parameters except the total number of rooting nodes were significantly influenced by the light regime (Tab. 3). Clones also differed significantly in most of the traits; the treatment × clone interaction was significant only for the total number of rooting nodes.

The variation in the rhizome system parameters is successfully summarized by the PCA: the first axis accounts for 76.6% and the second axis for further 14.5% of the total variation (Tab. 4). All rhizome parameters have high and positive loadings on the first PCA axis; this axis thus could be interpreted as expressing the overall size of the rhizome system. The second axis has positive loadings of all length parameters, whereas negative loadings for number of nodes (both all and rooting) and number of rhizome terminal buds. The plants with high scores on this axis are those with long, but sparsely branched and little rooting rhizomes; the plants with low scores have short and branched rhizomes with many roots. This axis thus captures density of nodes and relative number of branches. In contrast to the first axis, this axis expresses the "architecture" of the rhizome system.

Since the interpretation of these axes is rather straightforward and they summarize a high proportion of the total rhizome system variation (over 91%), the plant scores at these axes could be used as summary parameters of the rhizome system. Under the low red/far red ratio the rhizome system is larger; this is highly significant using ANOVA of the PCA axis 1 score (Tab. 3, Fig. 4). This effect does not show a significant interaction with clone. In contrast, the architecture response

Table 2. Mixed model analyses of variance with repeated measures of the effect of clone identity on the tillering from the growth chamber experiment. The test of an effect is the difference in the log likelihood ratio (LR) of the two models differing in the presence of the particular effect being tested (Dixon, 1992). Three measurements of each plant are included into the analysis (33rd, 57th and 85th days). Significant G × E interactions are shown in bold.

Dependent variable Effect	d.f	Shoot number		Shoot length	
		LR	*P*	LR	*P*
Red/far red	1	19.67	<0.001	2.80	0.094
Time	2	52.23	<0.001	78.21	<0.001
Clone	1	5.36	0.021	9.88	0.002
Red/far red × clone	1	**4.64**	**0.031**	0.59	0.433
Time × clone	1	187.35	<0.001	14.01	<0.001

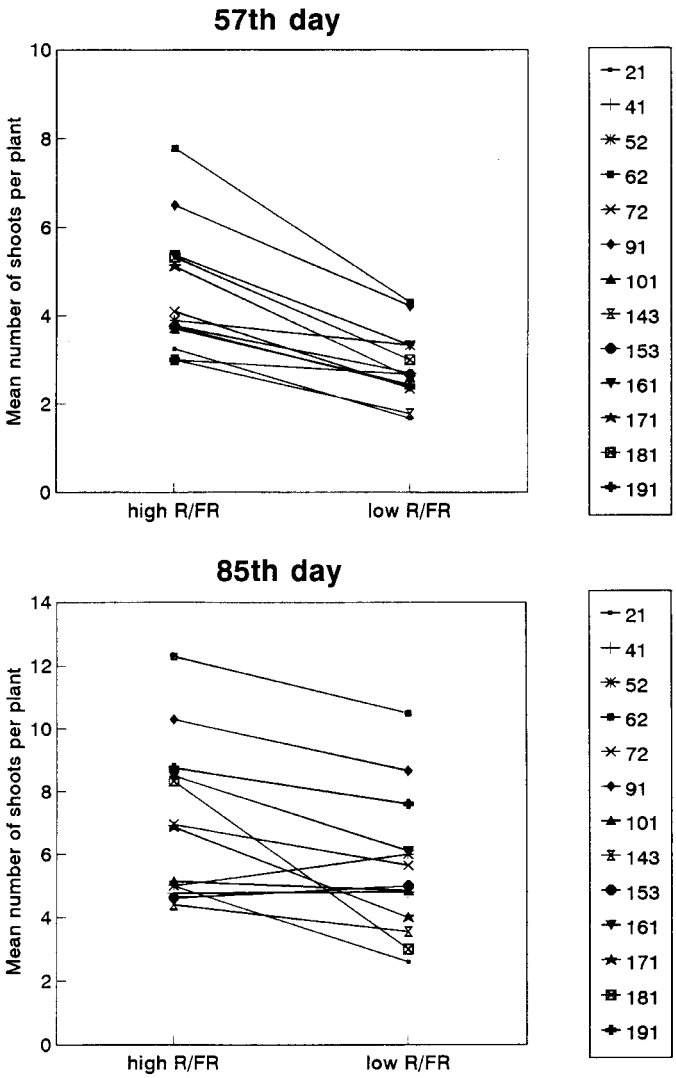

Fig. 3. Norm of reaction diagrams of the tillering response of the *F. rubra* clones to change in the red/far red ratio at two censuses. For the tests of significance see Table 2.

showed a highly significant clone × red/far red ratio interaction (Tab. 3). Clearly, some clones are able to change their architecture in response to environment (relative elongation of the rhizome system; namely 62, 91, 143, 171; Fig. 4), whereas others are not. Clone 52 actually showed a reverse response.

Table 3. Mixed model analyses of variance of the effect of clone identity on the rhizome system in the growth chamber experiment. PCA scores refer to the PCA of the six rhizome parameters (cf. Tab. 4). The test of an effect is the difference in the log likelihood ratio (LR) of the two models differing in the presence of the particular effect being tested (BMDP, program 3V, Dixon, 1992). Note: the tests of the PCA component scores are not independent of the tests of untransformed variables. Significant G × E interactions are shown in bold.

	Effects					
Degrees of freedom	Red/far red 1		Clone 1		Interaction 1	
	LR	*P*	LR	*P*	LR	*P*
Number of nodes	9.17	0.002	11.54	0.001	0.65	0.419
Number of rooting nodes	0.09	0.760	3.66	0.056	**6.53**	**0.011**
Number of rhizomes	4.35	0.037	15.12	<0.001	0.07	0.789
Length of the longest rhizome	13.33	<0.001	4.18	0.041	1.59	0.207
Length of the longest internode	16.30	<0.001	7.14	0.008	0.00	1.000
Total rhizome length	12.37	<0.001	5.56	0.018	1.89	0.168
PCA score 1	13.55	<0.001	13.92	<0.001	0.00	0.976
PCA score 2	8.37	0.004	0.00	0.998	**11.01**	**0.001**

Relation between the clone parameters

No correlations (Spearman correlation coefficient) of any pair of the above parameters (field, common garden and growth chamber) were statistically significant at the Bonferroni corrected significance level $P = 0.05$. Since many correlations are involved and multiple comparisons used, the Bonferroni correction is necessary. However, some of the relations are rather strong (they would be significant at the uncorrected $P = 0.05$ level); all of them are readily interpretable. For example, the strength of the response to red/far red ratio in the growth chamber was inversely related to the shoot number in the tussock in the common garden ($R = -0.62$).

Table 4. Loading of the first two PCA axes of the six rhizome parameters.

Variance explained	Axis 1 76.5%	Axis 2 14.5%
Number of nodes	0.443	−0.166
Number of rooting nodes	0.336	−0.662
Number of rhizomes	0.417	−0.362
Length of the longest rhizome	0.394	0.378
Length of the longest node	0.414	0.429
Total rhizome length	0.436	0.276

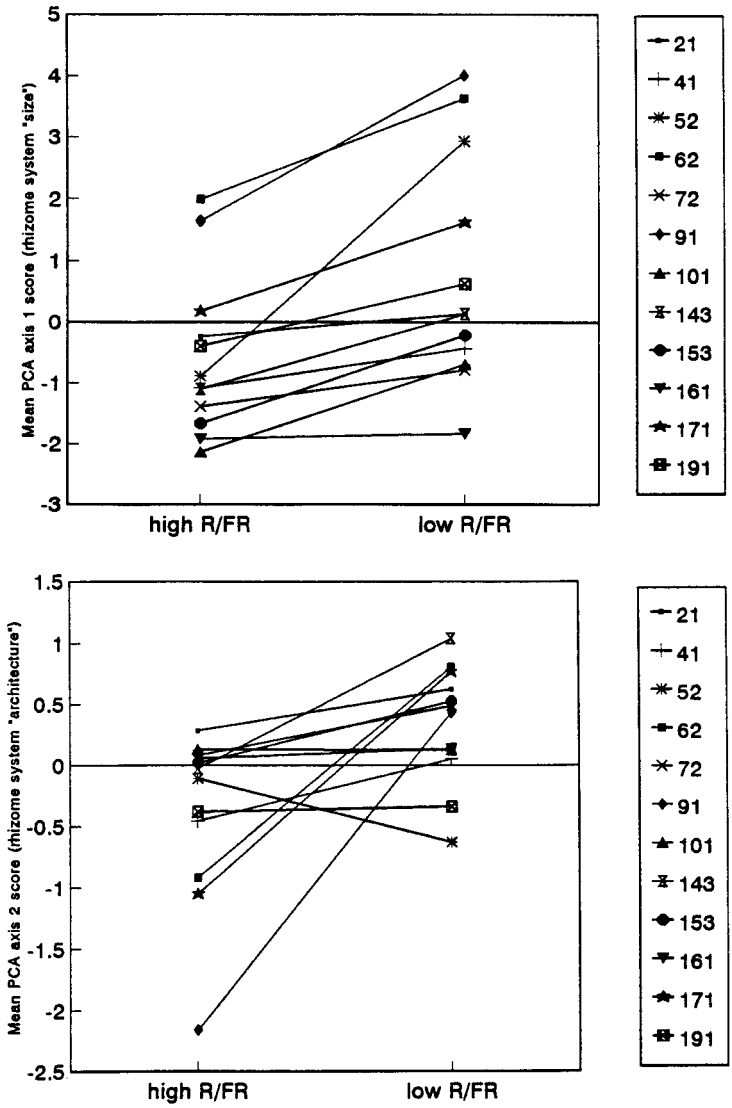

Fig. 4. Norm of reaction diagrams of the rhizome system response of the *F. rubra* clones to change in the red/far red ratio on 85th day of cultivation. Upper plot: first PCA axis (accounting for 76.5% of the total variance) which expresses the overall "size" of the rhizome system. Lower plot: second PCA axis (accounting for 14.5% of the total variance) which expresses the "architecture" of the rhizome system. For the tests of significance see Table 3.

Second, the density of *F. rubra* in the field was strongly inversely related to the mean area per shoot in the common garden experiment ($R = -0.61$).

Discussion

Response to the red/far red ratio

In grasses, the red/far red ratio has been shown to influence primarily tillering rate and leaf length (Casal et al. 1985; see also Murphy and Briske, 1994; Schmitt and Wulff, 1993). There are few reports of its effects on horizontal growth response in any plant species (e.g., in *Lycopodium annotinum*; Svensson et al., 1994). The recorded experiment shows that the red/far red ratio may also elicit a strong underground response in the horizontal direction, which may further affect both the spatial mobility of the plant and its clonal architecture. In *Festuca rubra*, a grass species with more or less unright shoots, the rhizome system seems to provide a means to "escape" horizontally from an unfavourable (shaded) site. We are not aware of any other study demonstrating the effect of the red/far red ratio on the underground structures. Similar experiments using neutral shade did not show any significant response by rhizome systems in several species (Dong and Pierdominici, 1995), though some response was detected in rhizomes of a clonal grass, *Cynodon dactylon* (Dong and de Kroon, 1994).

The strong response in the overall rhizome system size to the light regime corresponds well with the results of a removal experiment carried out at the same locality. That experiment showed that *F. rubra* strongly decreased its spatial mobility following the removal of the dominant *Deschampsia flexuosa* (Herben et al., 1994). This indicates a shift from guerrilla-type (long inter-ramet distances; see Lovett Doust, 1981; Schmid, 1990) to phalanx-type growth (short inter-ramet distances) in the field, though it is not obvious whether all genets present in the experiment responded in a similar fashion.

Variation among the clones

Both the common garden experiment and the red/far red ratio response of the plants in the growth chamber showed that the *F. rubra* clones from the studied grasslands are highly variable in many ecologically relevant traits, including those relating to clonal growth. The traits of the above-ground tussock architecture (mean area per shoot and mean shoot angle) varied strongly among clones in one environment. The ability to form large tussocks in the garden experiment seems to be related to low response to red/far red ratio change. The non-sensitive clones in the experiment (Fig. 3) are probably not limited by the internal shading within the tussock and their tussocks thus may become denser (for data from similar systems,

see Colvill and Marshall, 1984; Skálová and Krahulec, 1992; Murphy and Briske, 1994).

Rhizome systems traits also exhibited a large variation among clones within one habitat (Fig. 4). This indicates that both clones with guerrilla-type and phalanx-type growth were present within the clone population. Plasticity in the environmentally induced overall size of the rhizome system was clone-independent. This rather contrasts with the finding of Cheplick (1995) who identified inter-clonal variation in plasticity to nutrition in overall rhizome biomass in a perennial grass, *Amphibromus scabrivalvis*. In contrast, the architecture of the rhizome system, as summarized by the principal component analysis (2nd axis), had a strong inter-clone variation in plasticity. Only some clones (namely 62, 91, 143, 171) were able to restructure the architecture of their rhizome systems in response to changed light conditions by changing the branching rates and internode lengths. Rhizome system size and structure are thus a complex result of several components whose inter-clone variations differ: (i) genetically determined mean rhizome system size, (ii) overall plasticity in rhizome system size (with no significant genetic variation in plasticity), and (iii) superimposed genetically determined plasticity in rhizome architecture.

This complex structure has important implications for the foraging and escape abilities of genets. Clones able to restructure their rhizome systems by producing more nodes and branching more in high light patches while maintaining their rhizomes small may be able to exploit high light patches in the field. This behaviour falls into a broad category of foraging (Hutchings and de Kroon, 1994). Other clones, possessing only general response in rhizome size, can escape from low light patches to some extent, but may be very ineffective in exploiting high light ones. The ability to forage and escape is thus variable within this species, being difficult to detect by single-clone experiments (cf. Hutchings and de Kroon, 1994; de Kroon et al., 1994).

Environmental heterogeneity in the grassland

To assess the potential role of the among-clone variation in spatial spreading, it is necessary to take an account of the grain of spatial heterogeneity in the grassland they come from. It is rather fine-scale: the spatial autocorrelation of density of any species approaches zero at a distance of 10 cm (Herben et al., 1995). The autocorrelation of biomass does not reach beyond 6.6 cm (Skálová et al., unpubl. data). On the other hand, the difference between neighbouring patches is quite pronounced: the fine scale tiller density may vary from several tillers per 10 cm^2 up to fifty. The sixfold variation in the density of the vegetation immediately surrounding the clones is well in line with this variation.

There is similar fine scale heterogeneity in the light conditions (see aslo Silvertown et al., 1989; Tang et al., 1992; Tang and Washitani, 1995). Unpublished data from the field site (Skálová et al., unpubl. data) show that the ratio between the red/far red at the soil level and above the canopy (i.e., effect of filtering through the canopy) varies between 0 to 1.5 (values higher than 1 are due to reflection). The

distribution is highly skewed, with 25% quartile of 0.333, median of 0.416, and 75% quartile of 0.685. The two red/far red levels used in the growth chamber experiment cover the main part of the red/far red ratio range in the field. The two levels of the red/far red ratio used were 1.6 and 0.6. The value of 1.6 is approximately the red/far red ratio of the light above the canopy; then the value of 0.6 corresponds to the reduction in the ratio by filtering of 0.375, i.e., approximately the lower quartile of the field values.

Importantly, this red/far red fine scale heterogeneity is correlated with the vegetation parameters. First, the grain of variation in the red/far red is similar to that of the species density of biomass, the spatial autocorrelation of the red/far red reduction vanishing at distances of 6–9 cm. Second, there is also a direct correlation: the cross-correlation between biomass within the 3.3×3.3 cm cell and the red/far red reduction is significant up to a horizontal distance to 3 cm (Skálová et al., in prep.).

Potential role of fine scale environmental heterogeneity

In the studied grassland, *F. rubra* ramets move approximately 1 cm/year (Herben et al., 1993b; Suzuki et al., unpubl. data; Krahulec, unpubl. data). In an environment showing heterogeneity at the scale of several centimetres, this rate of spreading is large enough for a genet to experience different microenvironments over several years or decades of its lifetime. Its environment is thus perceived as fine grained. In this respect clonal *F. rubra* differs from non-clonal plants studied until now (*Impatiens pallida*, Bell et al., 1991; *Erigeron annuus*, Stratton, 1994, 1995). The horizontal growth of clonal plants may be thought of as translating spatial variation into temporal variation (Hedrick, 1986), i.e, projecting the rate of clonal growth over the spatial autocorrelation of environmental variables.

It is important to note that movement of genets through a community does not imply that all individuals have an equal chance to experience a particular environment, as is assumed by many evolutionary models (e.g., Gomulkiewicz and Kirkpatrick, 1992). Owing to the constraint of the clonal plant morphology (Bell, 1986), the environmental variation encountered by a genet is determined by explicit spatial positions of different environmental patches. The sequence of microhabitats experienced by a plant then differs both among genets and among parts within a genet. This depends not only on the grain of heterogeneity and global frequencies of individual habitat patches, but also on the actual *geometrical arrangement* of different patches (i.e., local patch occurrence). The role of this spatially constrained process is largely unknown and may require theoretical exploration (for a different context, see Molofsky, 1994; Stone and Ezrati, 1996).

At any rate, the fine grained system as described above is likely to favour a generalist strategy (van Tienderen, 1991; Schlichting and Pigliucci, 1995). Still there is a substantial amount of inter-clone variation. Having in mind the horizontal growth rates, it is rather unlikely that the variation in clonal morphology of *F. rubra* is due to microhabitat specialization. First, there is no evidence that clones

with particular traits are associated with different micro-environments; unfortunately owing to many tests done in parallel the statistical power is rather low. Second, the conditions for the temporal variation to maintain genetic polymorphisms are rather restrictive (Maynard Smith and Hoekstra, 1980; Hedrick, 1986, 1995).

However, there is genetic variation in plasticity in addition to genetic variation within one environment, both in tussock size and rhizome system architecture. Given the fine grain of the environment and the rates of clonal growth of the species, it is quite likely that selection operates on reaction norms (Schlichting and Pigliucci, 1995), affecting thus variation in environmental means. The polymorphism in plasticity then might indicate that the selective advantage of the ability to change rhizome architecture has not been strong enough to eliminate genotypes not having this ability. Maintenance of heterogeneity in both traits (variation in means and plasticity) are connected with each other through the large environmental variation within a genet's lifetime.

The maintenance of inter-clone variation (both in environmental means and plasticities) may also be due to other factors, such as an unknown role of gene flow, pleiotropic effects, relatively temporary nature of the system (which still may be showing transient dynamics), and, particularly, selection at the seedling stage. The selective environment is likely to differ between established and young clones. Analyzing the clone size distribution of *F. rubra*, Suzuki et al. (unpubl. data) concluded that the seedling establishment is common in the studied grasslands (in the range of 10–25 seedlings m^{-2} yr^{-1}, but with a substantial proportion drying before reaching maturity). This is probably the critical moment in the genet lifetime where selection in a microenvironment could act most strongly and its effect could account for a great deal of the observed genetic variation; once the genet becomes large, it may escape local selective forces through clonal growth (Eriksson and Jerling, 1990).

Behaviour in the field and plasticity in culture

The tremendous variation in behaviour in the field (Fig. 1) is due to a combination of both plastic response to the highly varying environment and the genetic makeup of these clones. The data presented here indicate that field and experimental parameters of the clones may co-vary to some degree, but their low correlation is due to the variation in the field conditions (Bell et al., 1991). In some clones, however, their makeup is clearly strong enough to override the environmental variation in the field: the fastest growing clone in culture (63) also showed the highest tillering rate in the grassland. The same is true for the mean shoot density in the field and in culture (Figs 1, 2). To relate the experimentally determined genotype reaction norms to the field behaviour of the population would require planting several replicates of the clones back into the field, sampling thus many different microenvironments with one genotype.

Implications for the taxonomy of the species

Taxonomic/biosystematic studies of the *Festuca rubra* group show that in some (micro-)species there do not seem to be any plastic components for the production of rhizomes and extravaginal shoots (Markgraf-Dannenberg, 1980; Krahulec, 1994; Krahulec et al., in press). In these species the rhizomes and extravaginal shoots are either always present (e.g., in *F. rubra* ssp. *juncea*) or are very short and rare (e.g., in *F. nigrescens*). *Festuca rubra* ssp. *rubra* is generally reported to be variable for the production of rhizomes and extravaginal shoots. However, no information has been available to determine the relative contributions of plastic and genetic (both within populations and among populations) components to the overall variability in *Festuca rubra* ssp. *rubra*. The current data show that both plastic and genetic (in terms of the correlated variation among environments; Fry, 1992) variations are present within one population, and in some traits, the clones differ in their plasticities as well. This may make any taxonomic treatment of the group rather intractable without cultivation experiments. No information of this sort is, however, available on other species from the *F. rubra* complex.

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References

Baldocchi, D. and S. Collineau. 1994. The physical nature of solar radiation in heterogeneous canopies: spatial and temporal aspects, pp 21–72. *In* M. M. Caldwell and R. W. Pearcy (Eds.), Exploitation of environmental heterogeneity by plants. Academic, San Diego.

Ballaré, C. L., A. L. Scopel, E. T. Jordan and R. D. Vierstra. 1994. Signaling among neighboring plants and the development of size inequalities in plant populations. Proc. Natl. Acad. Sci. USA 91: 10094–10098.

Bell, A. D. 1986. The simulation of branching patterns in modular organisms. Phil. Trans. Roy. Soc. London 313B: 143–159.

Bell, G. and M. J. Lechowicz. 1991. The ecology and genetics of fitness in forest plants. I. Environmental heterogeneity measured by explant trials. J. Ecol. 79: 663–685.

Bell, G. and M. J. Lechowicz. 1994. Spatial heterogeneity at small scales and how plants respond to it, pp 391–414. *In* M. M. Caldwell and R. W. Pearcy (Eds.), Exploitation of environmental heterogeneity by plants. Academic, San Diego.

Bell, G., M. J. Lechowicz and D. J. Schoen. 1991. The ecology and genetics of fitness in forest plants. III. Environmental variance in natural populations of *Impatiens pallida*. J. Ecol. 79: 697–713.

Cain, M. L. 1994. Consequences of foraging in clonal plant species. Ecology 75: 933–944.

Casal, J. J., V. A. Deregibus and R. A. Sanchez. 1985. Variation in tiller dynamics and morphology in *Lolium multiflorum* Lam.: vegetative and reproductive plants as affected by differences in red far-red irradiation. Ann. Bot. 56: 59–65.

Cheplick, G. P. 1995. Genotypic variation and plasticity of clonal growth in relation to nutrient availability in *Amphibromus scabrivalvis*. J. Ecol. 83: 459–468.

Colvill, K. E. and C. Marshall. 1984. Tiller dynamics and assimilate partitioning in *Lolium perenne* with particular reference to flowering. Ann. Appl. Biol. 104: 543–557.

de Kroon, H. and J. Knops. 1990. Habitat exploration through morphological plasticity in two chalk grassland perennials. Oikos 59: 39–49.

de Kroon, H. and F. Schieving. 1990. Resource partitioning in relation to clonal growth strategy, pp. 113–130. *In* J. van Groenendael and H. de Kroon (Eds.), Clonal growth in plants: regulation and function. SPB Academic Publishing, The Hague.

de Kroon, H., J. F. Stuefer, M. Dong and H. J. During. 1994. On plastic and non-plastic variation in clonal morphology and its ecological significance. Folia Geobot. Phytotax. 29: 123–138.

Deregibus, V. A., R. A. Sánchez, J. J. Casal and M. J. Trlica. 1985. Tillering response to enrichment of red light beneath the canopy of humid natural grassland. J. Appl. Ecol. 22: 199–206.

Dixon, W. J. 1992. BMDP statistical software manual. University of California Press, Berkeley.

Dong, M. and H. de Kroon. 1994. Plasticity in morphology and biomass allocation in *Cynodon dactylon*, a grass forming stolons and rhizomes. Oikos 70: 99–106.

Dong, M. and M. G. Pierdominici. 1995. Morphology and growth of stolons and rhizomes in three clonal grasses, as affected by different light supply. Vegetatio 116: 25–32.

Ellstrand, N. C. and M. L. Roose. 1987. Patterns of genotypic diversity in clonal plant species. Amer. J. Bot. 74: 123–131.

Eriksson, O. and L. Jerling. 1990. Hierarchical selection and risk spreading in clonal plants, pp. 79–94. *In* J. van Groenendael and H. de Kroon (Eds.). Clonal growth in plants: regulation and function. SPB Acad. Publ., The Hague.

Fry, J. D. 1992. The mixed model analysis of variance applied to quantitative genetics: biological meaning of the parameters. Evolution 46: 540–550.

Gomulkiewicz, R. and M. Kirkpatrick. 1992. Quantitative genetics and the evolution of reaction norms. Evolution 46: 390–411.

Grime, J. P., J. G. Hodgson and R. Hunt. 1988. Comparative plant ecology: a functional approach to common British species. Unwin Hyman, London.

Hedrick, P. W. 1986. Genetic polymorphism in heterogeneous environments. Ann. Rev. Ecol. Syst. 17: 535–566.

Hedrick, P. W. 1995. Genetic polymorphism in a temporally varying environment: effects of delayed germination of diapause. Heredity 75: 164–170.

Herben, T., F. Krahulec, V. Hadincová, M. Kovářová and H. Skálová. 1993a. Tiller demography of *Festuca rubra* in a mountain grassland: seasonal development, life span, and flowering. Preslia (Praha) 65: 341–353.

Herben, T., F. Krahulec, V. Hadincová and M. Kovářová. 1993b. Small scale spatial dynamics of plant species in a grassland community during six years. J. Veget. Sci. 4: 171–178.

Herben, T., F. Krahulec, V. Hadincová and S. Pecháčková. 1994. Is a grassland community composed of coexisting species with high and low spatial mobility? Folia Geobot. Phytotax. 29: 459–468.

Herben, T., H. J. During and F. Krahulec. 1995. Spatiotemporal dynamics in mountain grasslands: species autocorrelations in space and time. Folia Geobot. Phytotax. 30: 185–196.

Hutchings, M. J. and H. de Kroon. 1994. Foraging in plants: the role of morphological plasticity in resource acquisition. Adv. Ecol. Res. 25: 159–238.

Jackson, R. B. and M. M. Caldwell. 1993. Geostatistical patterns of soil heterogeneity around individual plants. J. Ecol. 81: 682–692.

Krahulec, F. 1994. Clonal behaviour in closely related plants. Folia Geobot. Phytotax. 29: 277–289.

Krahulec, F. et al. Comparative ecology of closely related taxa of *Festuca rubra* group 1. Tillering and tussock architecture. Nordic J. Bot. in press.

Levitan, D. R. and R. K. Grosberg. 1993. The analysis of paternity and maternity in the marine hydrozoan *Hydractinia symbiolongicarpus* using randomly amplified polymorphic DNA (RAPD) markers. Molecular Ecology 2: 315–326.

Lovett Doust, L. 1981. Population dynamics and local specialization in a clonal plant *Ranunculus repens*. I. The dynamics of ramets in contrasting habitats. J. Ecol. 69: 743–755.

Mahdi, A. and R. Law. 1987. On the spatial organisation of plant species in a limestone grassland community. J. Ecol. 75: 459–476.

Markgraf-Dannenberg, I. 1980. *Festuca*, pp. 125–154. *In* T. G. Tutin et al. (Eds.), Flora Europaea 5, CUP, Cambridge.

Maynard Smith, J. and R. Hoekstra. 1980. Polymorphism in varied environments: how robust are the models? Genet. Res., Cambridge 35: 45–57.

Milligan, B. G. 1992. Plant DNA isolation, pp. 59–88. *In* Molecular genetic analysis of populations: a practical approach. Oxford University Press, Oxford.

Molofsky, J. 1994. Population dynamics and pattern formation in theoretical populations. Ecology 75: 30–39.

Murphy, J. S. and D. D. Briske. 1994. Density dependent regulation of ramet recruitment by the red:far red ratio of solar radiation: a field evaluation with the bunchgrass *Schizachyrium scoparium*. Oecologia 97: 462–469.

Oborny, B. 1994. Growth rules in clonal plants and predictability of the environment: a simulation study. J. Ecol. 82: 341–351.

Palmer, M. W. and E. van der Maarel. 1995. Variance in species richness, species association and niche limitation. Oikos 73: 203–213.

Potvin, C. 1993. ANOVA: experiments in controlled environments, pp 46–68. *In* S. M. Scheiner and J. Gurevitch (Eds.), Design and analysis of ecological experiments, Chapman and Hall, London.

Rhebergen, L. J. and H. J. M. Nelissen. 1985. Ecotypic differentiation within *Festuca rubra* occurring in a heterogeneous coastal environment. Vegetatio 61: 197–202.

Robertson, G. P. and K. L. Gross. 1994. Assessing the heterogeneity of the belowground resources: quantifying pattern and scale, pp 237–254. *In* M. M. Caldwell and R. W. Pearcy (Eds.), Exploitation of environmental heterogeneity by plants. Academic, San Diego.

Scheiner, S. M. 1993. Genetics and evolution of phenotypic plasticity. Annual Rev. Ecol. Syst. 24: 35–68.

Schlichting, C. D. and M. Pigliucci. 1995. Gene regulation, quantitative genetics and the evolution of the reaction norms. Evol. Ecol. 9: 154–168.

Schmid, B. 1990. Some ecological and evolutionary consequences of modular organization and clonal growth in plants. Evol. Trends Plants 4: 25–34.

Schmitt, J. and R. D. Wulff. 1993. Light spectral quality, phytochrome, and plant competition. Trends Ecol. Evol. 8: 47–51.

Silvertown, J. W., S. D. Prince and B. A. Smith. 1989. A field portable instrument for mapping the microenvironment within grass canopies. Funct. Ecol. 2: 263–268.

Skálová, H. and F. Krahulec. 1992. The response of three *Festuca rubra* clones to changes in light quality and plant density. Funct. Ecol. 6: 282–290.

Slade, A. J. and M. J. Hutchings. 1987. The effects of nutrient availability on foraging in the clonal herb *Glechoma hederacea*. J. Ecol. 75: 95–112.

Sokal, R. R. and F. J. Rohlf. 1981. Biometry. 2nd ed. W.H. Freeman, San Francisco.

Solangaarachchi, S. M. and J. L. Harper. 1987. The effects of the canopy filtered light on the growth of the white clover *Trifolium repens*. Oecologia 72: 372–376.

Stone, L. and S. Ezrati. 1996. Chaos, cycles and spatiotemporal dynamics in plant ecology. J. Ecol. 84: 279–291.

Stratton, D. A. 1994. Genotype-by-environment interactions by fitness of *Erigeron annuus* show fine-scale selective heterogeneity. Evolution 48: 1607–1628.

Stratton, D. A. 1995. Spatial scale of variation in fitness of *Erigeron annuus*. Amer. Natur. 146: 608–624.

Svensson, B. M., B. Floderus and T. V. Callaghan. 1994. *Lycopodium annotinum* and light quality: growth responses under canopies of two *Vaccinium* species. Folia Geobot. Phytotax. 29: 159–166.

Tang. Y. and I. Washitani. 1995. Characteristics of small-scale heterogeneity in light availability within a *Miscanthus sinensis* canopy. Ecol. Res. 10: 189–197.

Tang Y., I. Washitani and H. Iwaki. 1992. Effects of microsite light availability on the survival and growth of oak seedlings within a grassland. Bot. Mag. 105: 281–288.

Tegelström, H. 1992. Detection of mitochondrial DNA fragments, pp. 89–113. *In* Molecular genetic analysis of populations: a practical approach. Oxford University Press, Oxford.

Turkington, R. 1989. The growth, distribution and neighbour relationship of *Trifolium repens* in a permanent pasture. VI. Conditioning effects of neighbours. J. Ecol. 77: 734–746.

van Tienderen, P. H. 1991. Evolution of generalists and specialists in spatially heterogeneous environments. Evolution 45: 1317–1331.

Via, S. 1994. The evolution of phenotypic plasticity: what do we really know? pp 35–57. *In* L. A. Real (Ed.), Ecological genetics. Princeton UP, Princeton.

Via, S., R. Gomulkiewicz, G. De Jong, S. M. Scheiner, C. D. Schlichting and P. H. van Tienderen. 1995. Adaptive phenotypic plasticity: consensus and controversy. Trends Ecol. Evol. 10: 212–216.

von Ende, C. N. 1993. Repeated-measures analysis: growth and other time-dependent measures, pp 113–138. *In* S. M. Scheiner and J. Gurevitch (Eds.), Design and analysis of ecological experiments. Chapman and Hall, London.

Widén, B., N. Cronberg and M. Widén. 1994. Genotypic diversity, molecular markers and spatial distribution of genets in clonal plants. Folia Geobot. Phytotax. 29: 245–263.

Williams, J. G. K., A. R. Kubilk, K. J. Livak, J. A. Rafalski and S. V. Tingey. 1990. DNA polymorphisms amplified by arbitrary primers are useful as genetic markers. Nucleic Acids Research 18: 6531–6535.

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