Proceedings IAVS Symposium, pp. 321-324, 2000

Genetic diversity, competitive ability and neighbourhood structure of grassland communities

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Abstract. A dominant plant of temperate nutrient-poor grasslands, *Festuca rubra*, possesses remarkable intraspecific differentiation both within and among localities. This differentiation concerns parameters that determine its spatial mobility and competitive ability, such as growth and tillering rate, sensitivity to red/far red light ratio and rhizome length and branching. An implant experiment in their native habitat showed that clones differing in these parameters also fared differently in the field. Our experiment showed that the response in the demographic parameters to the structure of neighbouring vegetation (species composition, biomass) was rather weak; the difference among clones in these parameters was pronounced. This suggests that the genetic composition of a population may have profound effects on the whole community dynamics.

Keywords: Competitive ability; *Festuca rubra*; Implant; Rhizome.

Introduction

A major part of plant ecology is based on the assumption that species can be represented by a set of quantities that are species-specific. Recent examples are species-specific growth forms (Grime et al. 1988), species-specific competitive effects (Silvertown et al. 1994; Law et al. 1997), Ellenberg indicator values (which express species' preferences to ecological factors; Ellenberg et al. 1991). Using similar logic, single species-specific quantities (means) have been typically used as state variables in plant stands to represent a population (variables such as average canopy height, mean population density, etc.; but see Hara 1993; Pacala & Levin 1997).

The same type of reasoning also affects treatment of the parameters of the environment. Again, mean values of the environment are often used to represent growing conditions of individuals (see e.g. Bell & Lechowicz 1994 for an extensive discussion of that matter).

It is rather obvious that each of these parameters has not only its mean, but also variance around this mean (Table 1). These variances may considerably affect dynamical behaviour of such a system (Hara 1993; Pacala & Levin 1997). For example, each individual experiences different environments since densities of neighbouring plants and correlated abiotic factors vary, both in time and space (Bell & Lechowicz 1994). As a result hereof, (1) different individuals of one species may encounter different neighbours, and (2) an individual plant may encounter different neighbours through its life-span (Mahdi & Law 1987). Performance of an individual in a stand is then a function of these environmental parameters. Along similar lines, species-specific parameters of the response are modified by intraspecific/intrapopulational differentiation.

A critical element is the 'interaction' between variation in the environment and genetic variation in the plant. Such interactions are commonly studied both in evolutionary ecology and in applied research on crops and their results are represented as 'reaction norms' which may or may not show genotype × environment interaction (G × E interaction; Via 1994). Most of the experiments are done with respect to variation in a single factor in the environment, often in culture. The critical issue here is that ecologically relevant experiments have to assess G × E interaction with respect to actual environmental variation that a plant encounters in the field: if within-stand variation is the question, then with respect to microhabitat variation. For example, our earlier experiments have shown that aboveground shoot growth and tillering and growth of the rhizome system in *Festuca rubra* is very plastic in response to spectral light quality and that this plasticity differs among genotypes (Skálová & Krahulec 1992; Skálová et al. 1997). These experiments, however, were done in a growth chamber; though every attempt was made to make the treatment differences to reflect environmental variation in the field, it is never fully possible. Therefore the reaction norm has to be evaluated using actual variation in the neighbour density in the field. To do this, we performed an implant experiment with multiplied genetically identical shoots originating from four clones; these shoots were planted back into the grassland to sample the actual range of microhabitats that occur there. To augment the biomass variation among microsites, half of the microsites were fertilised. Using this experiment it should be possible to tell (1) whether the actual microenvironmental variation is 'sensed' by the plant, and (2) whether this response to the environment is affected by intraspecific genetic differentiation. In addition, we assessed (3) how does the environment structure (presence and quantity of neighbouring plants) vary at the fine scale.

Table 1. Examples of components of plant performance in the stand: means and variances.

	Mean	Variance
Environment	Mean neighbourhood composition	Fine-scale variance in the neighbourhood composition
Plant	Species-specific growth rate	Genotypic/inter-individual variation in the growth rate

Methods

Study site

The study site was located in a mountain grassland in the Krkonoše Mts., northern part of the Czech Republic (Severka settlement, ca. 3 km NW of Pec pod Sněžkou, 50°41' 42" N, 15 °42' 25" E, altitude ca. 1 100 m). The whole area has a harsh climate; the grasslands under study are not natural, but have been maintained by mowing and occasional manuring. The vegetation is rather short, most of the biomass being concentrated below 15 cm in height (Skálová unpubl.).

Experimental design

Four genetically non-identical clones of *Festuca rubra* sampled in 1987 at the study site were multiplied in the experimental garden in Průhonice. The genetic non-identity of these clones was assessed employing DNA RAPD using two primers. In June 1989, twenty individual shoots of each of these clones (each of them with three leaves) were planted into filter paper tubes of 1 cm in diameter and 5 cm long filled with a mixture of compost and peat. In July 1989, these tubes were implanted into an undisturbed grassland at the study site. They were implanted at regular intervals along four rows (with distance between implants 25 cm), with the clones arranged in a Latin square design. The distance between rows was 90 cm. After establishment, the number of shoots in clusters originating from individual implants and the growth and demography of the shoots were monitored till June 1994. All shoots within the clusters were tagged with coloured plastic rings. For all newly formed shoots, their origin, whether intravaginal or extravaginal, was recorded. In autumn 1992 and in spring 1993 half of the plants were fertilized with a mixture of phosphate, potassium, magnesium, calcium and nitrate and ammonia nitrogen (2.5 g/m^2 of each element) in a factorial design with the clones.

Each year in summer (after the July recording), the vegetation surrounding each implant was recorded. To collect information on neighbouring plants, a 10cm × 10cm plot (further referred to as 'plot') was positioned over the implant (with the implant in the centre). All living shoots of each species of grass and the number of leaves of dicots (mainly *Polygonum bistorta*) were counted in these plots. After counting, the plants within each 10cm × 10 cm plot were clipped at a height of 2.5 cm and the dry mass (dried at 70 °C) of the clippings was taken as an estimate of neighbourhood aboveground biomass.

Data analysis

The data were processed to yield the following variables: (a) natality and mortality over time, (b) intravaginal or extravaginal origin of each shoot, (c) within-season growth rate of shoots. These response variables were analysed for their dependence on clone identity, fertilization, neighbouring biomass and species composition. Species composition was summarised by means of partial principal components analysis (using the program CANOCO; ter Braak 1988). Biomass and year were used as covariables to remove correlation between the first PCA score and biomass that appeared if no covariables were used.

The effects of clone, treatment, neighbouring biomass and identity on natality and mortality was tested using generalized linear models using the Poisson distribution of errors and the log link. The number of shoots in each cluster in the summer of the previous year was used as a covariate. The effects of clone, treatment and neighbours on the mode of tiller formation for each newly formed shoot (i.e. intra- vs. extravaginal) were tested using logistic regression. All calculations using generalized linear models were done using the S-PLUS 4 system (Anon. 1997). The effects of independent variables on shoot size and relative growth rate (RGR) were tested by analysis of variance. A nested ANOVA with clone, treatment, biomass and species composition (first PCA score) as fixed factors and cluster as a nested random factor was used. Neighbouring biomass and PCA scores were divided into two classes according to the position of the mean. The maximum likelihood estimation of the ANOVA effects was used (using program BMDP; Dixon 1990). In all analyses, separate runs were done for the period 1991-1992 (before fertilization) and 1993-1994 (after part of the experimental area was fertilized).

Results

Structure of the neighbouring vegetation

There were only four main heterospecific neighbouring species in the surrounding vegetation (mean densities per 10 × 10 cm ± s.d., minimum and maximum): *Deschampsia flexuosa* (60 ±35, 4, 293), *Nardus stricta* (39 ±45, 0, 217),

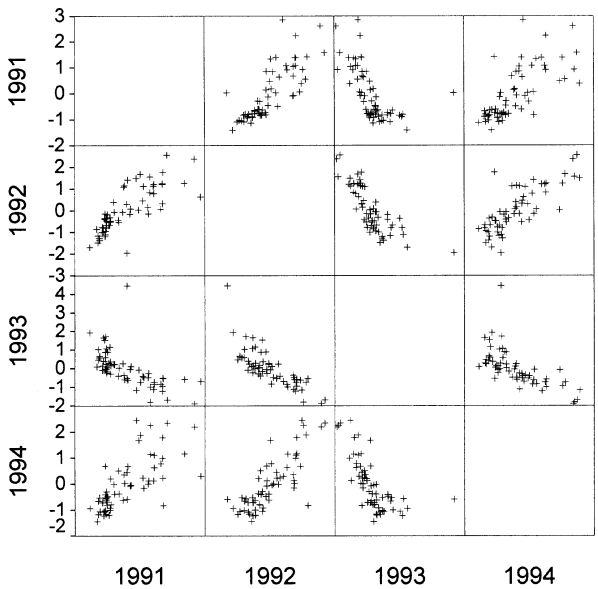

Fig. 1. Matrix plot of the scores on the first principal component axis of composition of neighbouring species recorded in 10 cm× 10 cm plots around *Festuca rubra* implants over four years. Each point refers to one implant. 1991, first principal component axis in 1991; 1992, first principal component axis in 1992, etc. The horizontal axis is scaled exactly the same as the vertical axis.

Anthoxanthum alpinum (20 ±14, 0, 73) and *Polygonum bistorta* (6 ±4, 0, 31). Principal components analysis of the number of shoots of the species present around each *Festuca* shoot cluster revealed strong intercorrelations among these species. The first principal axis accounted for 60.9% of the variation in the neighbouring species composition. The first axis separated neighbourhoods rich in *Nardus* (with negative first axis scores) from those rich in *Deschampsia* and *Polygonum* (with positive first axis scores). There was little change in the species composition over time; the scores of the first axis at individual microsites in different years were closely correlated (Fig. 1).

Total biomass of the vegetation was 2.11 g/10 × 10 cm (± 1.35, minimum 0.20, maximum 7.37). The biomass in individual plots was also correlated over time, but its year-to-year variation was higher than for the species composition and its temporal autocorrelation decays faster than that of the species composition (Fig. 2).

Plant response to the local environment

Total number of shoots, natality and mortality differed markedly between the clones (Table 2). In the first two years of observation (1991-1992), both natality and mortality were affected by the neighbouring species composition; individuals with a high density of *Nardus* in their neighbourhood had consistently lower natalities (results not shown), but the clone × neighbourhood interaction was not significant (i.e. this response was not clone-specific). In the last two years of the experiment (1993-1994), there was no detectable effect of the neighbouring species composition. In this period, natality was affected by neighbouring biomass; interaction clone × fertilization was also significant. In 1993-1994, mortality was not significantly affected by any of the factors.

The difference between clones in the proportion of extravaginal shoots was always significant (marginally significant in 1991-1992) (Table 2). The proportion of extravaginal shoots showed little response to environment. Two tests showed significant species composition (first PCA score) × clone interaction (for all unfertilized shoots and for all shoots in 1993-1994). In both cases a larger proportion of *Nardus* increased the proportion of extravaginal shoots in two clones (8, 20), whereas clones 13 and 19 did not respond to *Nardus* density.

There was no significant effect of the neighbouring species composition summarized by the PCA on the growth rate (Table 2). In contrast, biomass of the neighbours rather consistently affected the size parameters, both directly and in interaction with the clone (Table 2). In implants with high biomass of the neighbours, the spring size was invariably higher; the difference persisted throughout the growing season, but was weaker in summer.

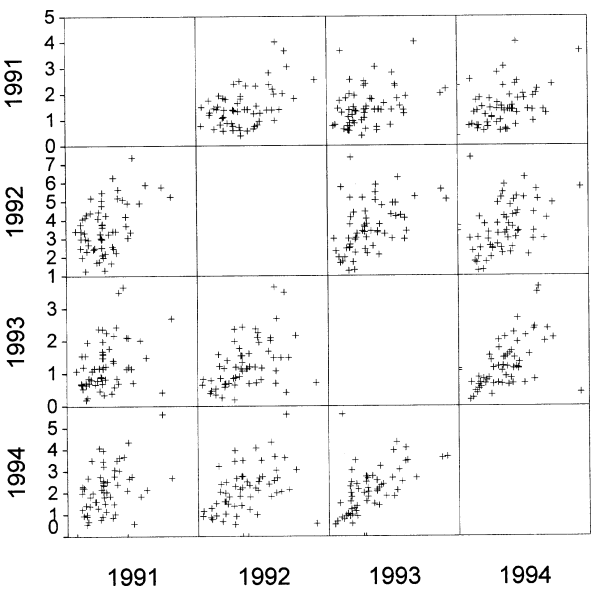

Fig. 2. Matrix plot of aboveground biomass recorded in 10cm × 10 cm plots around *Festuca rubra* implants over four years. Each point refers to one implant. 1991, aboveground biomass in 1991; 1992, aboveground biomass in 1992 etc. The horizontal axis is scaled exactly the same as the vertical axis.

Discussion

The experiment shows that the response in the demographic parameters to the structure of the neighbouring vegetation is rather weak. This is surprising since the variation in neighbouring plant density and correlated light levels changes severalfold across microsites (Skálová et al. unpubl.). This may be due to a large number of contrasting stimuli in the field, including soil heterogeneity, sunfleck movement with the stand etc. This phenomenon has important implications for the notion of plant plasticity. Although the plant is able to a remarkably plastic response to the environment, under field conditions this capacity of plastic

Table 2. Summary of clone-specific responses to micro-environment (implant experiment). The following statistical tests were used to test individual response variables: growth rate: nested ANOVA; shoot formation mode: logistic regression; natality and mortality: GLIM (Poisson errors, log link). Neighbour biomass is expressed per area of 10cm × 10 cm; 'neighbour identity' is the first principal component of shoot counts of individual species at this area. C×B = Clone × Neighbour biomass interaction; C×I = Clone × Neighbour identity interaction. + = $P < 0.1$; * = $P < 0.05$; ** = $P < 0.01$; *** = $P < 0.001$.

	Clone	Neighbour Biomass	C×B	Neighbour Identity	C×I
Shoot growth rate					
1991-1992		*	*		
1993-1994		+	*		
Shoot natality					
1991-1992	**			***	
1993-1994	***	**			
Shoot formation mode (intra- vs extravaginal)					
1991-1992	+	+			
1993-1994	**		+		**
Shoot mortality					
1991-1992				**	
1993-1994	+			+	

response is exploited by the plant to much lesser degree than under many experimental conditions. Obviously, the *potential* of the plastic response measured by a typical experiment is clearly less relevant to the plant's behaviour in the field than we often think.

A similar result has been found in other studies working with field densities (Fowler 1984, 1995; Bullock et al. 1994). In our view, it gives support to the argument of Law et al. (1993) that the field variation in competitive pressure is not pronounced enough to elicit a really consistent demographic response (see also Fowler 1990). In contrast to this, differences between clones were pronounced and concerned many parameters studied. The differences between the clones were strong enough to override the environmental variation in the field and produced consistent responses, e.g. in proportion of extravaginal tillers or overall natality. As a result, the between-clone differences in sizes of shoot clusters resulting from individual implants were gradually building up. The clone specificity in competition has also been shown by other studies (Taylor & Aarssen 1990; Mehrhoff & Turkington 1995; Miller & Fowler 1993).

An independent DNA RAPD study in the experimental grassland (Suzuki et al. 1999) has shown a high number of genotypes coexisting at a fine scale. This is the case in spite of genetic variation in plasticity which means that some genotypes may be better adapted over a range of microenvironments and should ultimately prevail. This indicates that the selective environments in the grassland does not lead to selection of one or a few 'best' genets. Possible (non-exclusive) explanations are (i) weak selective pressure relative to the age of the grassland, or (ii) differential selection at the seedling stage (this is not accounted for by this study).

The variation in plasticity with respect to microenvironmental variation may also have a community-wide effect. In such a case, the overall effect of one species on an other would depend on the genotype composition of the latter; in addition, the effect of the genetic variation will be coupled with the spatial effects due to the spatial distribution of genotypes in different microenvironments.

Acknowledgements. The research reported here was partly sponsored by the GA CR grants 206/98/1533 and 206/99/0899.

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