Caespitose grasses in dry grassland communities at several organization scales

Horstgräser in Trockenrasen auf mehreren Organisations-Ebenen

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Abstract Several observations from a multi-scale study of two tussock grasses are mentioned. *Festuca pallens* and *Sesleria albicans* are dominants in three studied dry grassland communities phytosociologically belonging to the order *Festucetalia valesiacae*. At this scale the long-lived dominant tussock grasses play a role of matrix species. The species composition of these communities was found to be affected mostly by the intensity of direct solar irradiation, soil depth and slope. At the population scale, a spatial pattern analysis was performed. Individuals of *Sesleria albicans* are uniformly distributed in the *Carici-Seslerietum* community on the northern slopes while isolated tussocks are formed in the most xeric community *Poo-Festucetum* on the southern slopes. The isozyme analysis revealed the substantial genet size of more than one meter which supports the idea of their long life span and of the important role of clonal growth in this species. Nevertheless, the frequency of generative reproduction is very high documented by a high density of different genotypes (almost 50 per m^2).

Spatial pattern of *Festuca pallens* populations was correlated with habitat factors and it seems to be mostly affected by habitat microtopography and competition with *Carex humilis*. The prevailing type of reproduction in this species is the generative one. The following ontogenetical stages could be distinguished in the studied populations: seedling, juvenile, virginile, generative and senile individuals.

General aspects of both tiller and leaf demography of the studied species are discussed. The effect of environmental conditions upon the species' life cycle was evaluated by comparing the demography in different plant communities. At the level of tussocks, the populations differed in size, ontogenetical structure and seed production. Differences at the level of tillers were found in quantitative characteristics such as leaf number, leaf length and stalk length. Tiller life cycle and its life span were not influenced by the external conditions. At the leaf level the studied populations differed also only in quantitative characteristics while the general course of natality and mortality was very similar.

Keywords caespitose grasses, *Festuca pallens*, leaf demography, life cycle, *Sesleria albicans*, spatial pattern, tiller demography, vegetation-environment relationships

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1. Introduction

Dry grassland communities are frequently dominated by caespitose grasses which do not only play an important role as structural components but are also important in spatial pattern formation and community functioning. In this paper the detailed study of two long lived and stress tolerant caespitose grass species – *Festuca pallens*

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and *Sesleria albicans* – will be reviewed with regard to several spatial observation scales and organization levels.

First of all, the plant communities dominated by the studied grasses were analysed in relation to the main environmental factors (community level). Over the last decades numerous studies were devoted to investigation of vegetation-environment relationships in dry grasslands at a larger scale (e. g. Thompson et al. 1996, Ejrnæs & Bruun 2000, Duckworth et al. 2000). In the presented study, these relationships were investigated at a micro scale. The basic idea was to assess the effect of hypothetical main environmental gradient and to determine the partial factors by which it is supported. Simultaneously, the relative importance of individual environmental factors was assessed in different community types and their effect upon cryptogams and phanerogams was compared.

At the level of populations, the spatial pattern of grass populations was studied in plant communities with contrasting habitat conditions. In central Europe *Sesleria albicans* occurs in habitats which strongly differ from each other with regard to habitat quality and land use (Reisch & Poschlod 2003, Reisch et al. 2002, 2003). It can not only change the growth form according to the given environmental conditions but also alternate the prevailing mode of reproduction (Lysák et al. 2000, Urbas & Zobel 2000, Reisch & Poschlod 2003). In the studied grasslands it forms contiguous closed stands composed of mutually overgrown loose tussocks of the N-facing ridges, and dense sharply bounded clumps on the S-facing slopes. The presented study includes results of *Sesleria albicans* isozyme analysis, which was aimed to find the membership of the measured tillers to genets and to estimate the role of both generative reproduction and clonal growth in the total reproduction of the species.

The complete life cycle of caespitose grasses in dry grasslands, mostly steppe communities, was frequently studied by Russian authors (e. g. Gatsuk et al. 1985, Zhukova 1974, 1975, Vorontzova & Zaugolnova 1985). Numerous demographical studies of grasses have been published from various types of temperate grasslands (e. g. Hroudová-Pučelíková 1972, Rychnovská & Úlehlová 1975, Symonides 1979a, b, Herben et al. 1993, Briske & Derner 1998). In the presented paper life cycle of *Festuca pallens* was studied at three hierarchical levels of its structure: individuals (tussocks), tillers and leaves. The aim was to estimate the basic demographical traits of both leaf and tiller life cycles. The majority of published demographical data have been derived from greenhouse and garden experiments and relatively little is known about these traits in natural habitats (van Groenendael & de Kroon 1990, Oborny & Podani 1996). The presented results are based on field observation of the studied grasses in their natural environment. Most measurements were done on permanent plots in Považský Inovec Mts. (western Slovakia) where the grassland communities are subject of phytosociological and ecological research yet since the beginning of this century (Sillinger 1931, Maglocký 1978, 1979, Mucina & Bartha 1999).

2. Materials and methods

2.1. *Studied species*

Festuca pallens Host is a perennial polycarpic caespitose grass with intravaginal tiller production. It has a submediterranean-subatlantic distribution in Europe (Conert 1998a). In the West Carpathians *Festuca pallens* inhabits steep rocks exposed to solar radiation or slopes with soils which are shallow rocky and neutral to alkaline. It is the characteristic species of the *Seslerio-Festucion pallentis* (Conert 1998a) where it belongs to the earliest colonisers and dominants.

Sesleria albicans Kit et Schult. is a perennial polycarpic grass producing both intra- and extravaginal tillers. It has a submediterranean-subatlantic distribution in Europe (Conert 1998b). Its occurrence in the Western Carpathians is concentrated on the montane and subalpine belt over the calcareous bedrock, where it dominates several community types. Occasionally, it enters dry grasslands in lower altitudes and here it was considered to be a relic dealpine species (Ellenberg 1986, Conert 1998b). Recent studies of *Sesleria albicans* genetic pattern gave no evidence for its glacial relic endemism (Reisch et al. 2002).

2.2. *Study site and the studied communities*

The study site is located in the Považský Inovec Mts. (western Slovakia), near the village Lúka nad Váhom (latitude 48° 9' 25'' N, longitude 17° 54' 20'' E). The studied communities were sampled in altitudes of 380–390 m. At the location, the Triassic dolomite supports shallow protorendzina soils. The whole area has a warm climate with a mean annual temperature of 9.2 °C, mean temperature in the warmest month (July) of 19.3 °C and a mean annual precipitation of 625 mm (all data for the nearby located climatic station Piešťany).

Phytosociologically, the studied communities belong to the class *Festuco-Brometea* Br-Bl. et R.Tx. 1943, order *Festucetalia valesiacae* Br-Bl. et R.Tx. 1943 and to three associations: *Carici humilis-Seslerietum calcariae* Sillinger 1930, *Festuco pallentis-Caricetum humilis* Sillinger 1930 corr. Gutermann et Mucina 1993 and *Poo badensis-Festucetum pallentis* Klika 1931 corr. Zolyomi 1966.

The distribution of these communities in the field depends on meso- and microclimate, so that they are sharply separated topographically as well as ecologically. The *Carici-Seslerietum* is always located on the northern slopes. In contrast to this, the *Poo-Festucetum* is located on the warmest and driest southern slopes. The *Festuco-Caricetum* occupies transitional places between the former two communities typically located on the hill plateau.

2.3. Measurements and data analyses

Most of the measurements were done on permanent plots established in 1993 in three plant communities. On each permanent plot (of 2 m^2) two hundred randomly chosen tillers were marked by a coloured plastics with a number. Detailed measurements of tiller and leaf characteristics were performed in three weeks intervals during the growing season in 1993. In spring and in autumn of both 1994 and 1995 the fate of marked tillers and their daughter tillers was recorded. Individuals of *Festuca pallens* were distinguished at the level of ramets, the attempt to define genets was done for *Sesleria albicans* in the *Carici-Seslerietum*, where the isozyme analysis was performed in 1995. Five isozyme systems were observed and interpreted (*MDH*, *MNR*, *6-PGDH*, *SkDH*, *LAP*) and visual control was done by *ADH* (Janišová 2006c).

The life cycle of *Festuca pallens* was studied on permanent plots in two populations within the *Poo-Festucetum* and *Festuco-Caricetum* from 1993 to 1996. Tussocks were mapped and the number of both vegetative and flowering tillers was counted each spring. Simultaneously, the frequency of seedlings was recorded on plots and the fate of seedlings and juvenile plants was followed also in a sowing experiment (Janišová, ined.).

Data for the analysis of vegetation-environment relationship were collected along a transect located in south-north direction across the ridge so that all studied communities were involved. The transect was composed of 50 quadrates of 0.25 m^2 divided into micro quadrates with a size 10 × 10 cm, in which the rooted frequency of vascular plants, bryophytes and lichens was recorded. Nine environmental factors were measured in quadrates including topographic, pedological and biological characteristics (see Janišová 2005 for the details). The analysis was done by canonical correspondence analysis with variation partitioning (Økland & Eilertsen 1994), including statistical testing by Monte-Carlo permutation test performed by CANOCO (ter Braak & Šmilauer, 1998).

For the determination of a spatial pattern in *Festuca pallens* populations several quadrate variance methods (BQV, TTLQV and T3LQV) were used based on data from measurements of frequency across sampling units (Ludwig & Reynolds 1988). In these methods, changes in quadrate size and spacing provide the information on pattern.

3. Results and discussion

3.1. Vegetation-environment relationship (plant community level)

Three main environmental factors were found to be responsible for the differentiation of the studied vegetation types, with the intensity of solar irradiation playing a crucial role among them. The second most important factor was soil depth, and the slope also had a significant effect. The gradient of increasing solar irradiation, pH, and soil skeleton content and decreasing content of both humus and fine soil particles were correlated with the first DCA axis which can be evaluated as a complex environmental factor »xericity«. In the analysis of quadrates from the southern slope (after excluding the role of aspect) data set variation was explained mostly by soil properties: soil depth, humus content and pH. On the northern slope the most important factors were solar irradiation followed by soil depth. The effect of environmental variables upon cryptogams and phanerogams was different. As expected, the vascular plants were controlled by the same factors that were confirmed to be relevant for the whole species set: solar irradiation, soil depth and slope. In cryptogams, solar irradiation obviously played a minor role and soil properties together with the vegetation cover were most important factors affecting their distribution (Janišová 2005).

3.2. *Spatial pattern (population level)*

The mosaic of various plant communities represented the coarse grain in spatial pattern of the studied dry grasslands. The diameter of patches in a mosaic ranged from several meters up to tens of meters. Along the transect different vegetation types changed after 5 to 8 m (Janišová, ined.).

Spatial pattern of *Festuca pallens* populations was found to be affected mostly by habitat microtopography and species interactions. The results showed that the finest grain aggregations corresponding to the morphological pattern of *Festuca pallens* (size of tussocks and their aggregations) had a diameter of 10 to 20 cm in the *Poo-Festucetum*, and up to 40 cm in the *Festuco-Caricetum*. In the *Poo-Festucetum*, clumps with a diameter of 120 to 160 cm were revealed by all the methods used. These aggregations are a consequence of habitat topography (rocky outcrops not inhabited by *Festuca pallens*) and could be interpreted as an environmental pattern. In the *Festuco-Caricetum*, clumps were detected which correspond to gaps in *Festuca pallens* distribution due to the compact tussock structure of *Carex humilis* in this community. These clumps were not very distinct and had an diameter of approx. 1 m.

Individuals of *Sesleria albicans* were uniformly distributed in the *Carici-Seslerietum* community on the northern slopes while isolated tussocks were formed in the most xeric community of the *Poo-Festucetum* on the southern slopes. In total, 98 distinct isozyme profiles were identified on the permanent plot in the *Carici-Seslerietum*. This indicates the important role of generative reproduction in *Sesleria albicans*. Several very remote ramets (more than 1 m) belonging to the same genet indicate an intensive clonal growth and subsequent fragmentation. This suggests, that the vegetative reproduction in *Sesleria* occurs and the genets can reach a long lifetime (cf. Reisch et al. 2002). In the *Poo-Festucetum* with aggregated occurrence of tillers (clumps physiognomically resembling tussocks), the number of identified isozyme profiles was higher than the number of tussocks/clumps. That means that even physiognomically defined tussocks were composed of more genetically distinct individuals (Janišová 2006c).

3.3. *Life cycle (tussock – tiller – leaf level) of* Festuca pallens

Festuca pallens formed short and compact tussocks composed from individual tillers of various tiller generations. Physical separation of clone parts and subsequent vegetative reproduction was not observed. The year-to-year abundance dynamics of both populations were characterised primarily by germination and mortality of seedlings. The proportion of middle-sized tussocks was rather stable. The proportion of seedlings varied between the seasons. Seedlings appeared frequently but their mortality was also rather high. Most tussocks declined in size during the growing season and size of tussocks in autumn reached about 75 % of their size in spring. In both populations, the vegetative tussocks were significantly smaller than the generative ones (Janišová, ined.).

Seedlings and juveniles had the highest annual mortality. The lowest mortality was found in generative and young vegetative tussocks. Flowering was not restricted by the individual size. The smallest flowering individuals had only two tillers. On the other hand, there were some larger individuals which did not flower in any of the four years recorded. The process of annual transformation both from vegetative to generative stage and generative to vegetative stage was accompanied by a significant change in individual size.

The recruitment by seeds is supposed to be a prevailing type of reproduction in *Festuca pallens*. Seeds of *Festuca pallens* germinated mostly in autumn and spring following the seed production. Some seeds could germinate during summer immediately after their ripening. On permanent plots about 2 to 23 newly emerged seedlings were recorded per m^2 each year. The seedling mortality was high due to the summer drought and intensive disturbances. In the appropriate conditions the tillering went on immediately after the germination. During the following growing season young plants produced three to ten tillers each having two to seven leaves. Flowering in *Festuca pallens* seems to be age-restricted. Young plants have not flowered during the first three years of their life (Janišová, ined.).

The growth, development and dynamics of modular organisms such as the studied tussock grasses depend on the life cycle and demography of their structural units – individual tillers. These are in turn dependent on the dynamics of the elementary structural units of grass body – the metamers. Each metamer consists of a blade, sheath, node, internode, axillary bud and adventitious roots.

Tillers of *Festuca pallens* are exclusively intravaginal with a leaf rosette and polycyclic (living for more than three years). The tiller half-life was estimated to be 25–27 months. An approximate maximum life span of orthotropic tiller parts was five or six years. The proportion of flowering tillers in the studied population varied between 3 % and 10 % from season to season. The mortality of tillers due to flowering represented about 50 % of the overall tiller mortality. Flowering was mostly accompanied by an intensive pregenerative tillering. Tillering culminated twice a year – in spring and in autumn. About a quarter of the axillary buds developed into daughter tillers immediately after their formation. The fate of tillers in terms of survival, flowering and daughter tiller production could be predicted by their size. Both components of tiller size – leaf number and leaf length – influenced the fate of tillers although the predictive ability was stronger for leaf number (Janišová 2006b).

Compared to other grasses, *Festuca pallens* had a very low rate of leaf turnover and considerably long-lived leaves (cf. Mitchley 1988, Diemer et al. 1992, Craine et al. 1999). The highest leaf birth rates and the lowest leaf death rates were observed in June. Leaf mortality was uniformly distributed in time without a distinct minimum or maximum. For the surviving tillers the leaf production exceeded the leaf mortality during the whole growing season. The steady net gain of leaves in tillers was not interrupted by the parallel process of tillering. Among the leaf cohorts leaves produced in May had the longest leaf blades. Leaves grew during the whole year. The winter cold and summer drought might slow down the growth rate or interrupt the growth. The growth of a leaf blade took five to eight weeks. Leaf life span was estimated as 150–200 days (time from the leaf appearance at the apex to the complete loss of its green assimilating parts, Janišová 2006a).

3.4. The effect of environmental conditions on the demography and life cycle of Festuca pallens

The effect of environmental factors on the demography and life cycle of *Festuca pallens* and its structural units was followed by the comparison of different plant communities.

At the level of individual tussocks the studied populations differed in size and functional structure as well as in their dynamics in time. The population in the *Poo-Festucetum* contained more individuals of smaller size per area unit whereas the population in the *Festuco-Caricetum* was composed of less individuals of larger size. The annual seed production by an average generative individual was lower in the *Poo-Festucetum* population than in the *Festuco-Caricetum* population. The size of both vegetative and generative tussocks was bigger in the *Festuco-Caricetum* population (Janišová, ined.).

Comparing the two studied populations at the structural level of tillers they differed in the leaf number, leaf length and the height of inflorescences. All these characteristics are quantitative and relevant for the standing crop production. They are supposed to be determined by external habitat conditions. The individual tiller life cycle did not differ between the populations, thus the factors by which it is determined seem to be identical. The following characteristics were similar for both studied populations: survival, fate and life span of tillers, tillering intensity, proportion of axillary buds developing into the daughter tillers (Janišová 2006b). These results support the idea of Serebrjakova (1971) that in the tiller ontogeny the basic processes and structures are fixed internally specifically for each species while the external environmental conditions can only induce the variability in absolute size.

At the level of leaves the populations differed in some quantitative characteristics such as the leaf length of May and June leaf cohorts, maximum length of a leaf blade in a tiller and daily increments during May and

June. The course of leaf natality and mortality was very similar in both studied populations (Janišová 2006a).

Schlüsselwörter Blattdemographie, *Festuca pallens*, Horstgräser, Lebenszyklus, Raummuster, *Sesleria albicans*, Sproßdemographie, Vegetation-Standort-Beziehungen

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