Local Distribution Pattern of *Brachypodium pinnatum* (Poaceae) – Field Experiments in Xeric Loess Grassland in N. Hungary

By
Gábor Endrezzi*), Ágnes Zold-Balogh**) and Tibor Kálapos***)

With 6 Figures

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Summary

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In surviving fragments of the natural forest-steppe vegetation on the Hungarian Great Plain the perennial rhizomatous grass *Brachypodium pinnatum* (L.) Beauv. (Poaceae) successfully occupies full sun to shade microhabitats on slopes facing N or E, but remarkably avoids adjacent grasslands on hilltops exposed to S or W. To test whether the hot and dry microclimate of the latter exceeds the tolerance limits for this broad-leaved species originally typical in the understorey of xerothermic oak forests, a field experiment was conducted when *B. pinnatum* plants were transplanted to soil monoliths from a xero-mesic grassland on the NE slope to an adjacent xeric grassland on the SW slope (transition) or within the same xerothermic zone. The response of shoot phenology, leaf photochemistry and VA mycorrhizal colonization of the roots were examined. In spring shoot development was faster on the SW slope,

*) G. Endrezzi, Ass.-Prof. Dr. T. Kálapos, Department of Plant Taxonomy and Ecology, L. Kétős University, Pázmány P. s. I/C, Budapest, H-1117. Corresponding author, e-mail: kalaposta@unszmu.edu.hu

**) Á. Zold-Balogh, Department of Plant Physiology, L. Kétős University, Pázmány P. s. I/C, Budapest, H-1117

***) The authors dedicate this article to the memory of Pál Juráz-Nagy, professor of Ecology, who was born 70 years ago.
but final shoot weight and foliage area remained below that on the NE slope. During the summer drought 80% of the shoots on the SW slope died back, while senescence was only 20% on the NE side. Leaf photosynthesis suffered photodamage in summer on the SW slope, but not on the NE one. Autumn rains triggered a vigorous development of new shoots on the SW slope, while not on the NE side. The frequency of VAM-infected roots and of vesicles remained invariant during the vegetation period, while the proportion of arbuscules showed a consistent seasonal trend paralleling host plant physiological activity being high during the spring and autumn, while greatly depressed during the hot and dry summer. The decline in summer was more marked on the SW slope, witnessing a mass shoot dieback, and the production of new shoots here were associated with a steepful enhancement of arbuscule frequency compared to that on the NE side. These results show that the growth of developed B. pseudonodosum plants suffer substantial reduction and even damage on the SW slope, confirming the original hypothesis that the physical environment thesis is not conducive for this grass and thus may explain its local distribution pattern.

Zusammenfassung


Introduction

Under the semiarid climate of the Hungarian Great Rain and neighbouring foothills the rhizomatous perennial grass *Brachypodium pinnatum* (L.) Beauv. was originally a characteristic forest understorey species in open xerothermic oakwoods once typical of loess areas in the forest steppe vegetation zone (ZÖLÖNYI 1137, ZÖLÖNYI & FÖKETE 1954). In historic times most of these oakwoods have been felled, but *B. pinnatum* usually persisted in place and even became dominant in the developing xero-mesic grassland maintained by grazing or cutting. Where management has been abandoned, forest regeneration commenced soon by the colonization of shrubs. In the resulting vegetation mosaic *B. pinnatum* successfully occupies a range of microhabitats from shadoe to full sun mostly on slopes facing N to E, but rarely turns up on slopes facing S or SW. Although this grass has an invasive character under the humid oceanic climate of Western Europe and thus may threaten biodiversity in species-rich calcareous grasslands (BORBÍN & WILLEMS 1987, BORBÍN 1991, HUSZÁR & JORM 1999, BUCELAND & al. 2001), in the semiarid areas of Hungary it does not appear to possess such an aggressive behaviour. Instead, grasslands dominated by *B. pinnatum* support high species diversity by preserving numerous elements of the former oakwood, and thus have a great nature conservation value (VIRÁGH & BARTHA 1998, FÖKETE & al. 1998).

The growth and physiology of *B. pinnatum* in warm and dry habitats have been studied little until now. In a previous study conducted in the same landscape as this report we showed a remarkable plasticity of leaf photochemistry and shoot morphology to habitat light conditions ranging from shade to full sun, and observed a greater tolerance of low light than that of high radiation load and water stress (MÓRÉN & al. 2003).

Mycorrhizal fungi affect plant communities indirectly by influencing the pattern and strength of plant competitive interactions (SMITH & al. 1999). For example, in tallgrass prairie it was found that if the dominant species are highly mycorrhizal responsive, then the suppression of mycorrhizal fungi (e.g. by application of fungicide) will result in higher plant diversity (SMITH & al. 1999). *B. pinnatum* is almost completely dependent on the presence of AMP (arbuscular mycorrhizal fungi) to be successful (VAN EZEM HAZÉN & al. 1998, 2003), but we have little knowledge how physical environment affects the mycorrhizal association of this species.

We assumed that the apparent exclusion of *B. pinnatum* from slopes facing S or W in semiarid loess grasslands on the Hungarian Great Plain and adjacent foothills is at least partly explained by the inability of this
grass to tolerate the relatively hot and dry habitat conditions there. To test this assumption a field transplant experiment was set up.

**Study Area**

Two, ecologically highly similar localities were chosen for this study. One of the sites (site G) is situated 25 km East of Budapest, at the border of the Godolloi Hills at an altitude of 206-209 m a.s.l. (Fig. 1). The climate of the area is intermediate between the continental climate of the Hungarian Great Plain and the subcontinental climate of the hilly regions of the Hungarian Central Range. Mean annual temperature is 9 °C, yearly precipitation is about 600 mm (Fig. 2). Chernozem soil covers the loess sediments typically (Fekete & al., 2008). The other site (site M) is located 30 km West of Budapest at the Northern edge of the Mecsek region (Hungarian Great Plain) 169 m a.s.l.; climatic and soil conditions are very close to that of site G. Both sites were set up in small fluvial erosional valleys with steep slopes facing NE and SW. In this landscape environmental conditions, vegetation development and present plant cover depends on slope aspect. Slopes facing N or NE were originally covered with open, xerothermic *Quercus pubescens* oakwoods with the broadleaved perennial grass *Brachypodium pinnatum* in the understorey. However, most of these forests were clearcut in the early
1900s. Today, a mosaic of small groups of remaining oaks with B. pinnatum in the herb layer, spreading patches of Carex monogyna shrubs and a series of grassland communities occur in the NE-facing slopes. (At site M oak trees are absent). Slopes facing S or SW have conspicuously warmer and drier microclimate and are dominated by steppe type grasses, like Cynodon dactylon, Festuca rapida. Steppe capillaries, forming a xeric grassland community, trees or shrubs are usually absent. The forest understorey grass B. pinnatum is typically absent from SW slopes.

**Fig. 2. Climate diagram of Gödöllő after KAKAS 1967: Klíma Atlas van Ungarn. II. Tabellen. Akadémiai Kiadó Budapest.**

**Material and Methods**

**Field Transplantation Experiment**

To test the plasticity of certain plant traits for B. pinnatum and root colonization by AM fungi a field transplantation experiment was set up at both study sites. Ten soil monoliths (squares) of about 30 x 30 x 30 cm with B. pinnatum plants were transplanted from the steppe type B. pinnatum grassland on the NE-facing slope to the xeric grassland on the SW-facing slope on 23 October 2001. Further 10 monoliths of the same type were similarly transplanted in situ on the NE slope and were used as control monoliths. Observations and measurements on transplanted individuals started on 21 April 2002. Root morphology, leaf phenology and photosynthetic measurements were conducted at site G (Fig. 1), while mycorrhizal colonization was followed at site M. (The destructive nature of sampling for mycorrhizal colonization measurements made necessary to conduct these on a different set of transplanted individuals.)

**Microclimate**

Volumetric soil water content in the top 6 cm of soil was measured near shoots chosen for phenological and photosynthetic measurements from April to October 2002 on the same days when shoot morphology and phenology data were collected by using a Delta-T ThetaProbe ML2 Soil Moisture Sensor (Macaulay Land Use Research Institute, Aberdeen and Delta-T Devices, Cambridge, UK). Solar radiation load on slopes with different aspect was estimated during the growing season (from 16 April...
to [7 September] by measuring substrate soil temperature (in 3-4 cm depth) by using Hobo [Hobo] Temp/Humidity sensors and data loggers (Onset Computer, Bourne, MA, USA) equipped with waterproof sealing. Temperature data gathered this way are proportional to the incoming solar radiation since soil surface was kept bare above the sensor all year round (Ensminger 1989).

Shoot Morphology and Leaf Phenology

On 21 April 2002 twenty B. pinnatula shoots were chosen at site G (for phenological observations and labelled at stem base with a small ring of plastic tape). These shoots were examined fortnightly until 1 July, and then in every three weeks until 6 October. All but one labelled shoots remained vegetative, and the one that produced an inflorescence was omitted from the measurements. Following the method described by Muir et al. 2003, the number of leaves and phenological stages of each leaf blade per shoot were recorded on each day of data collection. Three different phenological stages were distinguished for leaves: 1) newly emerged leaves with rolled blade; 2) leaves unfolded but not yet fully expanded; and 3) fully expanded leaves with exposed ligule. Length, width (measured at 1-1.5 cm distance from the attachment of leaf blade and sheath) of not fully and fully-expanded leaves, and the length of the senescent part of each leaf blade were also measured. Leaf surface area was calculated from leaf length and width data by using an empirical relationship between these two variables and leaf area measured with an LI-3000A leaf area meter (LI-COR Inc., Lincoln, Nebraska). Total leaf area per shoot was calculated by summation the area of a single fully and not fully-expanded leaves per shoot (surface area of folded leaves was neglected). Number of living shoots, number of leaves per shoot, total leaf area per shoot, percentage of photosynthetically active leaf area of total leaf area per shoot and senescence percentage of total leaf area were averaged for the labelled shoots on both experiments. Leaf longevity was estimated for the period from the folded stage until the full senescence of 3-7 leaves per shoot and averaged for the two sites (18th and 20th leaf were already developed on the first day of data collection).

Chlorophyll a Fluorescence Induction

Chlorophyll a fluorescence induction measurements were performed by using a pulse-modulated chlorophyll fluorometer (Hansatech Fluorescence Monitoring System FMS2, Hansatech Instruments, King’s Lynn, UK) on the youngest fully developed leaves of one shoot per month in June and July 2002 and also in July 2003. First, leaves were incubated at standard high light intensity (1000 μmol photons m⁻² s⁻¹) for 5 minutes then light-inoculated fluorescence parameters (PSII quantum efficiency, Fₚₚₚₛₛ; effective quantum yield of PSII, Fₚₚₛₛ) were measured. Right after this procedure the same leaf was kept in dark for 30 minutes and the maximum photochemical efficiency (Fₚ'/Fₚ) was determined using a saturating light pulse (0.5 s, ca. 4000 μmol photons m⁻² s⁻¹). Fₚ'/Fₚ was measured once in early morning before sunrise, then again at midday (between 12:00 and 14:00 h).

Mycorrhizal Colonization

To assess the extent and seasonal course of AM colonization for B. pinnatula root samples were collected three times in 2002 (May, August and October) from 5 control and 5 transplanted plants. Roots were first cleaned with 0.5% KOH and then stained...
with Trypan blue in order to stain fungal structures within the roots (Pimentel & Pimentel, 1976). Five each plant sample 30 root segments of 1 cm length were dissected on a glass slide for microscopic measurements (thus altogether 5 glass slides with 30 root segments on each slide were examined for each of the two treatments and sampling date). Colonization of roots by AM fungi, frequency of arbuscules and vesicles were estimated by using the method described by Taylor et al. (1986). To estimate the colonization of roots the following categories were used: (i) none, (ii) few, (iii) mild, (iv) moderate, (v) heavy colonization. The frequency of arbuscules and vesicles were estimated inside the colonized region of the roots and were divided into 4 categories: A0 = no arbuscules, A1 = less than 30%, A2 = 31-79%, A3 = more than 11% (Va, Vb, Vc, Vd in the case of vesicles). Frequency (%) and intensity (M%) of mycorrhizal colonization, arbuscules (A%) and vesicle (%) content of the roots in the colonized region were calculated from the estimated structures by using the following formulae after Taylor et al. (1986): 

\[ M\% = \frac{N\times 100}{A} \quad \text{and} \quad A\% = \frac{N\times 100}{A} \]

where M is the number of roots in a slide (20 in each case) and N refers to the number of non-mycorrhizal roots. M% = (85 \times nA + 70 \times nB + 50 \times nC + 10 \times nD) \times 100 \quad \text{where} \quad nA = \frac{N - nB - nC - nD}{4}

Frequency of vesicles in the colonized region (%V) was calculated as

\[ V\% = \frac{N\times 100}{A} \]

where \( nB \) and \( nC \) are the number of roots with A% frequency of arbuscules in the colonized region. The results were analyzed by using analysis of variance (ANOVA). Differences among mean values were assessed by the Tukey’s multiple comparison test at the 0.05 probability level. The significance level of differences among means was assessed by using Fisher’s exact test. The data were analyzed by using the Statistical Analysis System (SAS, Inc., USA).

### Statistical Analysis

Means of shoot morphological, leaf phenology, non-photosynthetic partitioning (NPP) and P50 quantum yield (Fv/Fm) data were compared by using unpaired t-test. When data did not meet the assumption of normal distribution (checked by using Kolmogorov-Smirnov test) and due to unequal variance in samples, non-parametric test was performed. In the case of unequal variance in samples but normal distribution unpaired t-test was used with Welch correction. One-way ANOVA with Tukey post hoc test was performed to analyze the effect of different light sources or measure of maximum photosynthetic efficiency (Fv/Fm). Two-way ANOVA with mean squares based on grouping variables was used to check significant difference (LSD test) to analyze significant differences among means of calculated mycorrhizal parameters by using the Statistica 6.0 program package (StatSoft Inc., Tulsa, USA). Since arbuscule content of colonized root area (%) data did not meet the assumption of homocedasticity Kruskal-Wallis test with Dunn’s post hoc test was applied. Furthermore, those data were analyzed by using the Bonferroni test for unequal variances and the significance level was adjusted by using Dunn’s post hoc test. Finally, the data was analyzed by using GraphPad InStat Software (San Diego, USA).
**Results**

**Microclimate**

Both years of measurements (2002 and 2003) were warmer than average with a particularly hot summer. Monthly mean temperatures exceeded long term averages by 1.7–2 °C in spring and summer. In 2003 the period between May and August was the hottest one measured in the past 100 years, while annual precipitation (470 mm) remained 100 mm less than in 2002 (weather data from the website of the Hungarian Meteorological Service, www.meteo.hu). Our microclimate measurements indicated significantly (4-7%) higher volumetric soil water content on the NE-facing slope than on the SW-facing one on each day of data collection in 2003.

![Subsurface soil temperature below bare ground on the two slopes during 3 bright summer days in 2003 (12/06–14/06). Temperature data gathered this way are proportional to the incoming solar radiation since soil surface was kept bare above the sensor all the year round.](image)

(data not shown). The SW-facing slope received markedly higher solar radiation load than the NE-facing one as indicated by continuously recorded subsurface soil temperature below bare ground which was 3.5 °C higher in average throughout the whole period (April to September) and could stay higher for 20 hours a day on clear summer days for the exposed to SW than to that of the NE. The NE slope received solar radiation of high angle of incidence sufficient to warm the topsoil similar to the SW slope only for a few hours in the morning (Fig. 3).

**Shoot Morphology and Leaf Phenology**

Shoots of *B. pinnata* emerged in mid April and developed 3–3 leaves by the first date of data collection. On the SW-facing slope plants started their physiological development 1-2 weeks earlier than on the other side, most probably due to a warmer microclimate. In spring and early summer the number of living shoots decreased slightly at the same degree on both
Fig. 4. Shoot morphology and leaf phenology for transplanted (SW) and control (NE) B. pinaxum plants in the two microhabitats of site G in 2002. Data is indicated on
the horizontal axis (day/month). Statistically significant differences between treat-
ment means (or medians for non-parametric data) within the same date of data col-
lection are indicated with asterisks above the horizontal axis (P < 0.05). (Sample size
increased from 20 to 5 by the end of the growing season.) - a. Percentage of living
shoots (%), where "new" refers to newly sprouted shoots in late summer and autumn.
- b. Number of (not fully and fully expanded) green leaves per shoot. - c. Green
(photosynthetically active) leaf area per shoot (cm²). - d. Shoot height. - e. Percent
part of total leaf area per shoot (%). Unpaired t-test or Mann-Whitney non-par-
metric test was performed on means (or medians) of treatment within the same date.

Slope (Fig. 4a). In July, with the beginning of the hot and dry summer, mortality of shoots on the SW side increased considerably resulting in 75–
80% dieback by August. Meanwhile, on the NE slope 80% of the shoots were
still alive in September suggesting more severe stress on the SW side. Au-
tumn rains triggered abundant sprouting of new shoots on the SW slope, whereas on the NE slope only one new shoot emerged in September. Resi-
mated average leaf longevity was 86 and 69 days on the NE and SW slope, respectively. Until the end of summer the number of leaves per shoot (only green leaves were taken into account, dead ones were neglected) was similar on both slopes (Fig. 4b). However, leaf longevity on the SW slope was significantly lower, shoots on this side produced more leaves (by 0.5 in average) than on the NE side. Number of leaves per shoot from spring till late summer did not differ probably due to this phenomenon (Fig. 4b). On the last three dates of data collection the number of leaves on the SW side exceeded significantly that of the NE side plants. Shoots reached their greatest leaf area in mid June (70-89 cm² on the NE slope and 50-60 cm² on the SW slope in average). In spring the proportion of green (photosynthetically active) leaf area per shoot was similar in both exposures (in one case it was higher on the SW slope) indicating that senescence did not occur yet (Fig. 4c, 4d). This changed rapidly and green leaf area per shoot on the NE slope surpassed that of the SW side shoots in summer (Fig. 4c). In autumn green leaf area per shoot was similar again in both exposures, most probably because new shoots emerged with fully green leaves (Fig. 4a, 4c). Total leaf area showed the same tendency as green leaf area (data not shown). Shoot height on the NE slope was higher than on the SW slope all the year round except in the first two and the last rate of data collection (Fig. 4d). By mid summer leaf senescence increased on both slopes, but more rapidly on the SW side. Leaves of the new shoot generation sprouting in response to late summer rains on SW slope almost lacked senescent parts whereas leaves on NE slope were dying back continuously (Fig. 4e). Three years after the transplantation only three mesoliths out of the original ten were still alive on the SW slope, while on the NE slope none died (data not shown).

Chlorophyll a Fluorescence Induction

Maximum photochemical efficiency of PSII (Fv/Fm) in June 2002 and July 2003 was not significantly lower than the optimal value of 0.83 measured for most plants (MAXWELL & JOHNSON 2000), and depression at midday was common (Fig. 5a). Compared to this a general reduction of Fv/Fm occurred in July 2002 when daily change was not more than 10% and minimum did not fall below 0.7 on the NE slope, while on the SW side the significant diurnal drop reached 28% with a minimum value of 0.5. The highest values of effective quantum yield of PSII (Fv/Fm) were measured in June 2002 (Fig. 5b). In July 2002 and 2004 Fv/Fm was similar on the same exposure, however in July 2001 it was significantly lower on the SW than on the NE slope (in contrast to values measured in June 2002 and 4b, 5b, 4c and 5c). Non-photochemical quenching (NPQ) showed an opposite tendency: highest values were measured in July 2003, when NPQ was the lowest. In July 2002 NPQ decreased significantly on the SW slope compared to the NE side (Fig. 5c).
Fig. 5. Photochemical responses (chlorophyll fluorescence induction parameters) for transplanted (SW) and control (NE) *B. pinnata* plants in the two microhabitats of site C in 2002 and 2003. Statistically significant differences among treatment means (or medians for non-parametric data of 15 replicates) are indicated by letters above columns. Different letters indicate significant differences (P < 0.05). - a. Maximum photochemical efficiency of PSII (Fv/Fm) (dark-adapted chlorophyll fluorescence parameter). - b. Effective quantum yield of PSII (ΦPSII). - c. Non-photochemical fluorescence quenching (NPQ). In tests for differences among treatments of Fv/Fm, Kruskal-Wallis test and Dunn test were used, in the other cases one-way ANOVA were used.

Mycorrhizal Colonization

Almost all roots were colonized by VAM fungi over the year, although mycorrhizal intensity exhibited relatively low values indicating that roots were colonized by *fungi* not in their full length. Remarkable change occurred in the frequency of arbuscules during seasons (Fig. 6). In summer strong decrease appeared in % and % on both slopes with more conspicuous change on the SW slope. All the mycorrhizal parameters followed a similar seasonal trend on both slopes: only frequency of arbuscules showed notable change. Frequency of vesicles remained low in all samples regardless the exposure or season (Fig. 6). Seasonal and microclimatical variation did not have an effect on the frequency of colonization and the frequency of vesicles. In two cases samples showed significant differences in respect of colonization intensity: in summer, more strongly colonized roots were found on the SW slope; and % was higher in autumn than in the other analyzed seasons on the NE side (Fig. 6). The more-
strongly colonized roots are found, the higher the index of mycorrhizal colonization intensity (M%) will be. Since one of the assumptions of two-way ANOVA were not fulfilled (homoscedasticity), a Kruskal-Wallis test was performed or arbuscule frequency data (α%), but no significant difference appeared (Fig. 6), therefore further analysis were carried out. By regressing the seasonal variation, significant difference was revealed between roots from different exposures. Although it was not analyzed, most probably autumn data contributed to this phenomenon. On the other hand, frequency of arbuscules was lower in summer than in spring or autumn when data in each season were treated as individuals regardless the exposure of the slopes they were collected from.

Fig. 6. Mycorrhizal colonization parameters for transplanted (SW) and control (NE) B. pubescens roots in the two exposures of site ID 2 in 2002. Samples were taken in spring (May), summer (August) and autumn (October). Statistically significant differences among treatment means (or medians for non-parametric data) of 5 replicates are indicated with lowercase letters next to symbols. Different letters indicate significant differences (P<0.05). S%, frequency of mycorrhizal colonization; β%, intensity of mycorrhizal colonization; α%, arbuscule content; χ%, vesicle content. For explanation of mycorrhizal parameters see the Material and Methods section. On M% data two-way ANOVA was performed. On α% data Kruskal-Wallis test and Dunn's test was used. Means of treatments in the case of S% and χ% did not differ significantly (data not shown).

Discussion

The field transplant experiment in this study indicated that the physical environment may play an important role in the exclusion of B. pubescens from South-facing slopes despite its conspicuous appearance in adjacent hillsides exposed to the N or E in the loess forest steppe landscape mosaic of the Pungarian Great Plain. Its stress-tolerant competitor strategy (Gnizar & al. 1963) enables this grass to survive the removal of the forest overstorey in its original forest habitat and to persist in places even reaching a dominant position in subsequent secondary grasslands maintained by grazing or cutting (Poch & al. 1998, 2000; Nikolen & Bartha 1998). The high phenotypic plasticity of physiology and morphology observed for a number of succes-
sional intermediate plant species (ABRAMS & MOSTOLLER 1995, BAZZAZ 1978, 1996, BAZZAZ & CARLSON 1982, KALACOV & CRITCHON 2003, KATO & al. 2000, KLAUSEN & al. 2001, MÜNCHEN & HEITZ 1997, BÖLEN & al. 1997, STRATIS-DHERENDETTI & BAZZAZ 1991, ZANGOREK & BAZZAZ 1983) and for this species as well (MOZES & al. 2003) also explains the wide ecological distribution of this grass. However, the species appears to approach the limits of its environmental tolerance when subjected to high radiation load as it was indicated by its reduced photosynthetic activity (MOZES & al. 2003) and growth (PEEKET & al. 1996, VIREGH & BÁTHÓ 1998) in the unshaded grassland compared to the half-shaded shrub microhabitat in its typical biotope in Hungary. The hot and dry microclimate of South-facing slopes in this heath-covered landscape seems to impose intolerable stress on this broad-leaved perennial grass at least in drier-than-average years when our experiment was conducted. This limitation was observed for fully developed plants since these were transplanted in soil monoliths to the new environment. (The physical stress itself associated with transplantation could not cause the observed changes since control plants also received the same treatment on the original stand). Thus, in this environment not only the supposedly more vulnerable establishment process, but the persistence of established individuals is also limited. At the northern edge of its distribution in Northern and upland Britain B. pinetorum is restricted to S-facing slopes (GRIME & al. 1988), where the plant finds similar abiotic conditions like on the N-facing slopes in the southern edge of its distribution. Species that live in different macroclimate occur in those habitats where the microclimate ensures similar abiotic conditions (WALTER 1953).

Seasonal shoot development began earlier on the S-facing slope compared to the N-facing one probably due to the warmer microclimate of the former. However, the reduction of photosynthetic leaf area occurred earlier and in a greater extent on the slope with SW aspect. Consequently, total leaf area and the area of photosynthetically active (green) leaves was lower on the SW slope. Similarly, the lower shoot height on SW slope relative to the NE one may be attributed to the greater water stress limitation on shoot growth in the former microhabitat. Under “average” weather conditions leaf photochemistry was well-protected from radiation damage as chlorophyll fluorescence induction measurements revealed. The severe drought in July 2002 coupled with high radiation load on the S-facing slope, however, resulted in the photosdamage of leaves indicated by decreased capacity for photochemical reactions (Fv/Fm, Fv/Phi) and also for non-photochemical quenching of excess energy (NPQ). Summer drought caused the dieback of the majority of B. pinetorum shoots on the S-facing slope, while on the N-facing one only one fifth senesced. Autumn rains, however, elicited vigorous development of new shoots on the S-facing side producing new foliage area comparable to that surviving from spring
growth on the N-facing side. The rhizomes of *B. pinnatum* support a rich bud bank (VA KNOP & KNOP 1990, or KNOP & SCHURING 1990, MOLNÁR 2003) which provides a high regeneration potential for lost shoots. This trail may also contribute to the plant’s persistence in the habitat, but unfavourable conditions in consecutive years may lead to the depletion of rhizome carbohydrate reserves and of the bud bank, and ultimately contribute to the decline of *B. pinnatum*.

Little is known yet on the way how physical environment affects mycorrhizal properties of *B. pinnatum*. In their database CRANE & al. 1998 reports that VA mycorrhiza is common in this species, but gives no further reference or details. VAN DEN HEuDEN & al. 1998, 2003 examined the effect of mycorrhizal fungal diversity on plant coexistence and plant diversity. In this study we showed a high frequency and extent of VA mycorrhizal colonization in the roots of *B. pinnatum*. Since VA mycorrhiza is known to enhance plant nutrient acquisition, particularly that of immobile phosphorus (BRUNSDEN 1991, HEDGE & VAN BUUREN 1995, Port 1994) this observation supports the high P utilization capacity determined for *B. pinnatum* in its natural habitat (ROBINSEN 1991), but moderate P uptake efficiency under artificial experimental garden conditions (BAYER & LAMBERS 1995) where root mycorrhizal associations may not develop to such an extent as in the natural habitat. A marked seasonal trend was detected in the relative amount of fungal arbusculuses in root cells paralleling the temporal pattern of host plant physiological activity. In the grassland studies, summer is the dry season, while spring and autumn are relatively humid. The greater-than-average summer drought in 2002 reduced the amount of arbusculuses (structures for material transfer between host and fungus), that was more marked on the S-facing slope than on the N-facing one. This reduction of arbusculuse frequency may affect not only P acquisition of the plant, but its water uptake in addition as arbuscular symbiosis may elicit host plant responses to moderate moisture deficit by increasing water uptake (AL-KABAKI & AL-RAMADAN 1997, DAVIES & al. 1992, AUGE & al. 1992). Enhanced plant magnesium associated with the growth of new shoot generation on the S-facing slope in late summer was coupled with an increased intensity of mycorrhizal infection (M%) of roots. The amount of fungal vesicles remained invariably low throughout the vegetation period. In a South American semiarid mountain grassland and in coastal dunes in California marked seasonal change was observed in mycorrhizal colonization with a peak in the frequency of both arbusculuses and vesicles in the rainy season and a minimum during the dry season (LOJO & al. 2003, SOTOZUCK & al. 1996). Similarly, a marked seasonal course of arbusculuse frequency with a summer minimum was observed for several vascular species inhabiting a peat bog community under semiarid climate in Hungary (GOLD-BALOGH & al. 2003).
In conclusion, the results of our field transplant experiment support the original assumption that the lost and dry environment on south-facing slopes is not conducive for B. pratensis. Shoot growth, leaf photosynthesis, and root colonization by VAM suffered marked reduction on the south-facing slope, while not on the north-facing one during a drier than average vegetation period. Even the rich bud bank on its rhizomes B. pratensis replaced the shoots lost during the summer drought, but repeated occurrence of such losses in consecutive years will soon deplete the reserves of perennating organs and ultimately lead to the death of plants.

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