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

By

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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*) succesfully occupies full sun to shade microhibitats on slopes facing N or E, but remarkably avoids adjacent grasslands on hillsides exposed to S or W. To test whether the hot and dry microclimate of the latter exceeds the tolerance limits for this broadleaved species originally typical in the understorey of xerothermic oak forests, a field experiment was conducted when *B. pinnatum* plants were transplanted in soil monoliths from a xero-mesic grassland on the NE slope to an adjacent xeric grassland on the SW side (treatment) or within the same sward (control). 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,

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***) The authors dedicate this article to the memory of Pál JUHÁSZ-NAGY, professor of Ecology, who was born 70 years ago.

but final shoot height 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 photochemistry suffered photodamage in summer on the SW slope, but not on the NE one. Autum 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 paralelling 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 threefold enhancement of arbuscule frequency compared to that on the NE side. These results show that the growth of developed *B. pinnatum* plants suffer substantial reduction and even damage on the SW slope confirming the original hypothesis that the physical environment there is not conducive for this grass and thus may explain its local distribution pattern.

Zusammenfassung

Endresz G., Zöld-Balogh Á. & Kalapos T. 2005. Lokales Verbreitungsmuster von *Brachypodium pinnatum* (*Poaceae*) – Feldversuche in trockenem Löß-Grasland in N-Ungarn. – Phyton (Horn, Austria) 45 (2): 249 – 265, mit 6 Abbildungen. – Englisch mit deutscher Zusammenfassung.

In Resten der natürlichen Waldsteppen-Vegetation in der Großen Ungarischen Tiefebene besetzt *Brachypodium pinnatum* (L.) Beauv. (*Poaceae*) (perennierend, mit Kriechsprossen) an N- und E-Hängen voll sonnige bis schattige Kleinstandorte, meidet bemerkenswerter Weise aber benachbarte Grasfluren auf S- und W-Hängen. Um zu testen, ob das heiße und trockene Mikroklima an letzteren Standorten die Toleranzgrenze dieses breitblättrigen, ursprünglich im Unterwuchs xerischer Eichenwälder zu findenden Grases, überschreitet, wurde ein Feldversucht durchgeführt: *B. pinnatum* Pflanzen wurden in Boden-Blöcken von trockenen bis mäßig trockenen Rasen eines NE-Hanges in eine benachbarte xerische Grasflur auf dem SW-exponierten Hang (Versuch) und innerhalb desselben Standortes (Kontrolle) verpflanzt. Die Veränderungen von Sproß-Phänologie, Blatt-Photochemie und VA-Mykorrhiza-Entwicklung der Wurzeln wurden untersucht. Im Frühjahr verlief die Sproßentwicklung am SW-Hang rascher, aber zuletzt waren Sproßhöhe und Blattfläche kleiner als am NE-Hang. Während der Sommertrockenheit starben am SW-Hang 80 % der Sprosse zurück, auf der NE-Seite nur 20 %. Die Blatt-Photochemie weist auf Lichtschäden während des Sommers am SW-Hang, nicht aber am NW-Hang. Die Herbstregen lösen eine kräftige Entwicklung neuer Sprosse auf den SW-Hang aus, nicht dagegen am NE-Hang. Die Häufigkeit von Wurzeln mit VAM und Vesikeln blieb während der Vegetationsperiode konstant, während die Zahl der Arbuskeln – entsprechend der physiologischen Aktivität der Pflanzen – im Frühjahr und Herbst hoch, im Sommer dagegen stark herabgesetzt war. Der sommerliche Rückgang war am SW-Hang mit dem starken Absterben der Sprosse ausgeprägter und die Produktion neuer Sprosse war hier, im Vergleich zum NE-Hang mit dreifacher Arbuskel-Frequenz verbunden. Ausgewachsene *B. pinnatum*-Pflanzen erfahren also am SW-Hang ausgesprochene Reduktion des Wachstums oder Schädigung;

dies bestätigt die ursprüngliche Hypothese, daß die physikalischen Umweltfaktoren für dieses Gras nicht förderlich sind und das lokale Verbreitungsmuster erklären.

Introduction

Under the semiarid climate of the Hungarian Great Plain 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 (ZÓLYOMI 1957, ZÓLYOMI & FEKETE 1994). 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 shade 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 (BOBBINK & WILLEMS 1987, BOBBINK 1991, HURST & JOHN 1999, BUCKLAND & 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, FEKETE & 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 radiaton load and water stress (MOJZES & 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, than 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 AMF (arbuscular mycorrhizal fungi) to be successful (VAN DER HEIJDEN & 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 Gödöllő Hills at an altitude of 200–300 m a.s.l. (Fig. 1). The climate of the area is intemediate 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., 2000). The other site (site M) is located 30 km West of Budapest at the Northern edge of the Mezőföld region (Hungarian Great Plain) 180 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

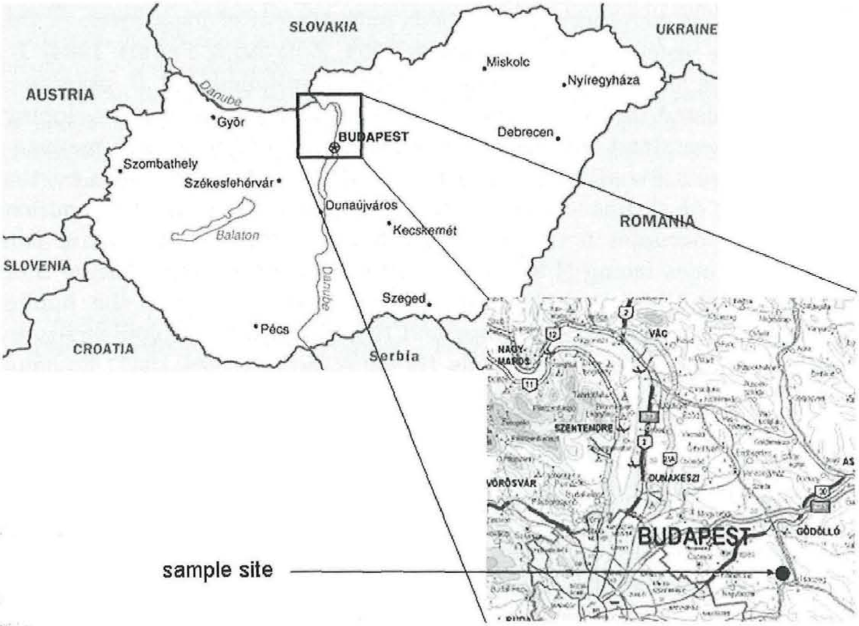

Fig. 1. Map of Hungary with the main sample site G.

1900s. Today, a mosaic of small groups of remaining oaks with *B. pinnatum* in the herb layer, spreading patches of *Crataegus 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 *Chrysopogon gryllus, Festuca rupicola, Stipa capillata*, forming a xeric grassland community, trees or shrubs are usually absent. The forest understorey grass *B. pinnatum* is typically absent from SW slopes.

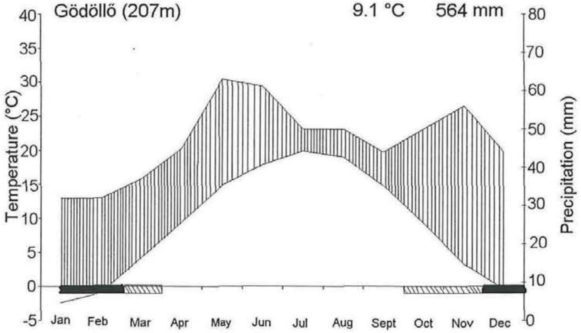

Fig. 2. Climate diagram of Gödöllő after KAKAS 1967: Klima Atlas von Ungarn. II. Tabellen. Akadémiai Kiadó Budapest.

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 25–30 x 25–30 x 25–30 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 ten 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. Shoot morphology, leaf phenology and photochemical measurements were conducted at site G (Fig. 1), while mycorrhizal colonization was followed at site M. (The destructive nature of sampling for micorrhyzal 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 photochemical 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 17 September) by measuring subsurface soil temperature (in 3-4 cm depth) by using HOBO H8 Temp automatic temperature sensor and data logger (Onset Computers, 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 (EHLERINGER 1989).

Shoot Morphology and Leaf Phenology

On 21 April 2002 twenty *B. pinnatum* 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 MOJZES & 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 inrolled 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 summing the area of 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 exposures. 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 slopes (1^{st} and 2^{nd} leaf were already developed on the first date of data collection).

Chlorophyll a Fluorescence Induction

Chlorophyll 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 monolith in June and July 2002 and also in July 2003. First, leaves were incubated to standard high light intensity (1000 µmol photons m^{-2} s^{-1}) for 5 minutes then light-incubated fluorescence parameters (non-photochemical quenching: NPQ, effective quantum yield of PSII: ΦPSII) were measured. Right after this procedure the same leaf was kept in dark for 20 minutes and the maximum photochemical efficiency (Fv/Fm) was determined using a saturating light pulse (0.7 s, ca. 4000 µmol photons m^{-2} s^{-1}). Fv/Fm 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 colonizaton for *B. pinnatum* root samples were collected three times in 2002 (May, August and October) from 5 control and 5 transplanted plants. Roots were first cleared with 10% KOH and then stained with Trypan blue in order to stain fungal structures within the roots (PHILIPS & HAYMAN 1970). From each plant sample 30 root segments of 1 cm length were distributed 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 TROUVELOT & al. 1986. To estimate the colonization of roots the following categories were used: 0) when no mycorrhiza was detected, 1) in traces, 2) less than 10%, 3) 11–50%, 4) 51–90%, 5) more than 90%. Density was regarded 100% when whole length of the root was colonized by any structures of the fungus (hypha, arbuscule or vesicle). Frequency of arbuscules and vesicles were estimated inside the colonized region of the roots and were divided into 4 categories: A_0) no arbuscules, A_1) less than 30%, A_2) 31–70%, A_3) more than 71% (V_0, V_1, V_2, V_3 in the case of vesicles). Frequency (F%) and intensity (M%) of mycorrhizal colonization, arbuscule (a%) and vesicle (v%) content of the roots in the colonized region were calculated from the estimated structures by using the following formulas after TROUVELOT & al. 1986: $F\% = 100 \times (N-n_0) / N$, where N is the number of roots in a slide (30 in each case) and n_0 refers to the number of non-mycorrhizal roots. $M\% = (95 \times n_5 + 70 \times n_4 + 30 \times n_3 + 5 \times n_2 + n_1) / N$, where $n_1 \ldots n_5$ mean the number of roots in the given colonization categories (1...5). $a\% = (100 \times mA_3 + 50 \times mA_2 + 10 \times mA_1) /100$, where $mA_1 = (95 \times n_5A_1 + 70 \times n_4A_1 + 30 \times n_3A_1 + 5 \times n_2A_1 + n_1A_1$ and $n_5A_1 \ldots n_1A_1$ mean the number of roots with A1 frequency of arbuscules in the given colonization categories (1...5). mA_2 and mA_3 were calculated in the same way as mA_1. Frequency of vesicles in the colonized region (v%) was counted with the formulas used for a%. This method of measuring mycorrhizal colonization allows to analyze a relatively large sample within a reasonably short time. However, due to the subjectivity of estimation it is best used to intraspecific comparisons.

Statistical Analysis

Means of shoot morphological, leaf phenological, non-photochemical quenching (NPQ) and PSII quantum yield (ΦPSII) data were compared by using unpaired t-test. When data did not meet the assumption of normal distribution (checked by using Kolmogorov-Smirnov test) a Mann-Whitney non-parametric test was performed. In the case of unequal variance in samples but normal distribution unpaired t-test was executed with Welch correction. One-way ANOVA with Tukey post hoc test was performed to analyze the effect of different slope aspect on means of maximum photochemical efficiency (Fv/Fm). Two-way ANOVA with seasons and exposures as grouping variables was used with least significant difference (LSD) test to analyze significant differences among means of calculated mycorrhizal parameters by using the Statistica 5.0 program package (StatSoft Inc., Tulsa, USA). Since arbuscule content of colonized root area (a%) data did not meet the assumption of homoscedasticity Kruskal-Wallis test with Dunn's post hoc test was applied. Furthermore, these data were analyzed by merging one effect. In the first case, data from different exposures in one season while in the other case, data from different seasons in one exposure were treated as an individual sequence and their significance was analyzed by using Kruskal-Wallis test with Dunn's post hoc test or unpaired t-test with Welch correction depending on the number of the grouping variables. One-way ANOVA, Kruskal-Wallis test and t-test were executed by using the 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.met.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 (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 to 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).

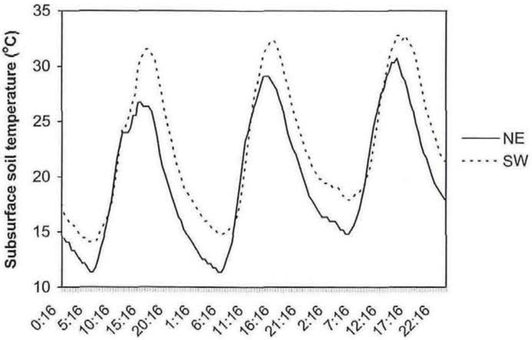

Fig. 3. Subsurface soil temperature below bare ground on the two slopes during 3 bright summer days in 2002 (12/06–14/06). Temperature data gathered this way are proportional to the incoming solar radiation since soil surface was kept bare above the sensor all the year round.

Shoot Morphology and Leaf Phenology

Shoots of *B. pinnatum* emerged in mid April and developed 2–3 leaves by the first date of data collection. On the SW-facing slope plants started their phenological 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

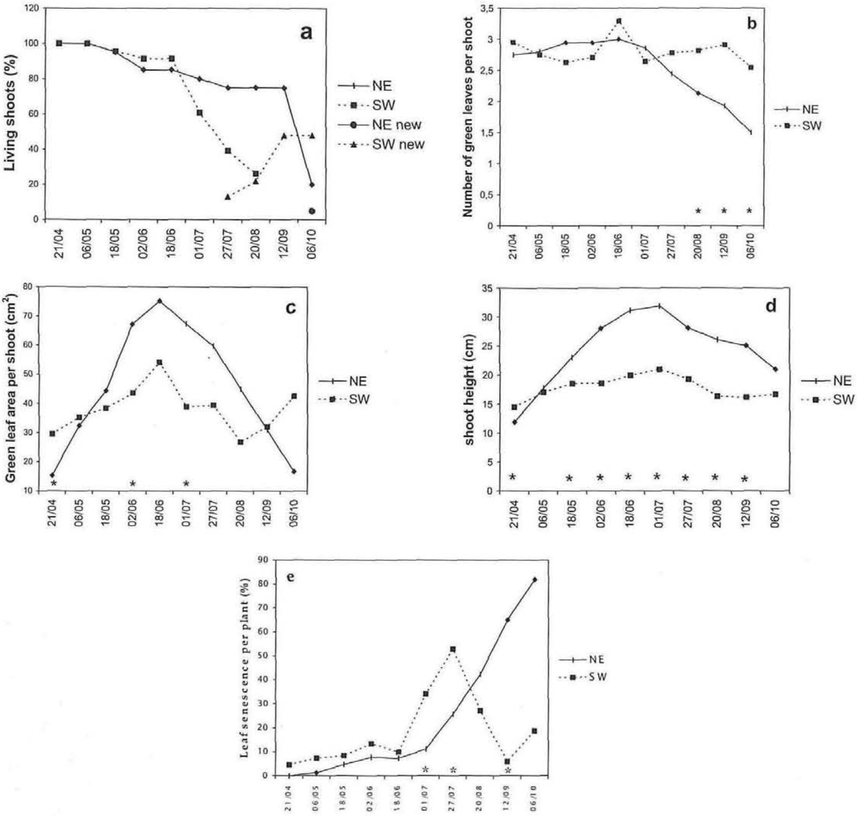

Fig. 4. Shoot morphology and leaf phenology for transplanted (SW) and control (NE) *B. pinnatum* plants in the two microhabitats of site G in 2002. Date is indicated on the horizontal axis (day/month). Statistically significant differences between treatment means (or medians for non-parametric data) within the same date of data collection are indicated with asterisks above the horizontal axis ($P < 0.05$). (Sample size decreased 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 (cm^2). – **d.** Shoot height. – **e.** Senescent part of total leaf area per shoot (%). Unpaired t-test or Mann-Whitney non-parametric test was performed on means (or medians) of treatment within the same date.

slopes (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. Autumn rains triggered abundant sprouting of new shoots on the SW slope, whereas on the NE slope only one new shoot emerged in September. Estimated average leaf longevity was 86 and 60 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 (70–80 cm^2 on the NE slope and 50–60 cm^2 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, 4e). 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 date of data collection (Fig. 4d). By midsummer leaf senescence increased on both slopes, but more rapidly on the SW side. Leaves on 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 continously (Fig. 4e). Three years after the transplantation only three monoliths 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 occured in July 2002 when daily change was not more then 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 (ΦPSII) were measured in June 2002 (Fig. 5b). In July 2002 and 2003 ΦPSII was similar on the same exposures, however in July 2002 it was significantly lower on the SW than on the NE slope in contrast to values measured in June 2002 and in July 2003. Non-photochemical quenching (NPQ) showed an opposite tendency: highest values were measured in July 2003, when ΦPSII was the lowest. In July 2002 NPQ decreased significantly on the SW slope compared to the NE side (Fig. 5c).

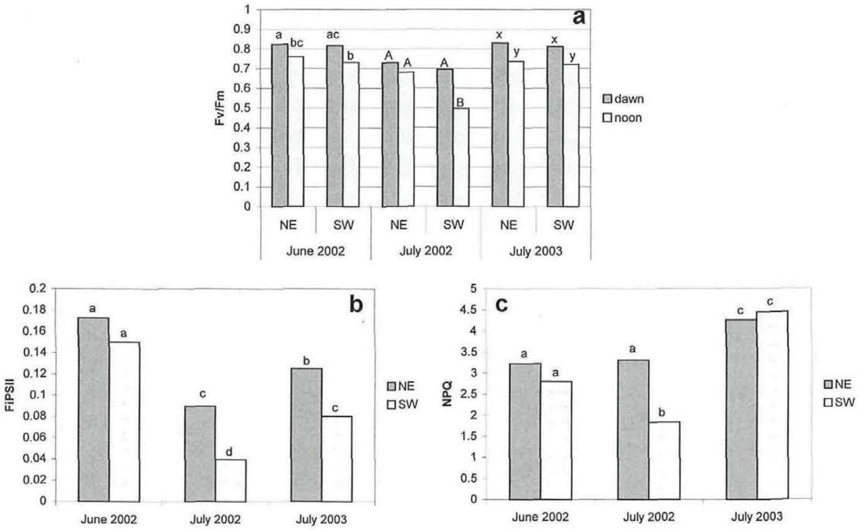

Fig. 5. Photochemical responses (chlorophyll fluorescence induction parameters) for transplanted (SW) and control (NE) *B. pinnatum* plants in the two microhabitats of site G in 2002 and 2003. Statistically significant differences among treatment means (or medians for non-parametric data) of 10 replicates are indicated by letters above columns. Different letters indicate significant differences ($P < 0.05$). – **a.** Maximum photochemical efficiency of PSII (Fv/Fm) (dark-incubated chlorophyll fluorescence parameter). – **b.** Effective quantum yield of PSII (ΦPSII). – **c.** Non-photochemical fluorescence quenching (NPQ). To test for differences among treatments of Fv/Fm Kruskal-Wallis test and Dunn's 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 a% and A% 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 changes. 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 M% 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 (homoscedasciticy) a Kruskal-Wallis test was performed on arbuscule frequency data (a%), but no significant difference appeared (Fig. 6), therefore further analysis were carried out. By merging 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.

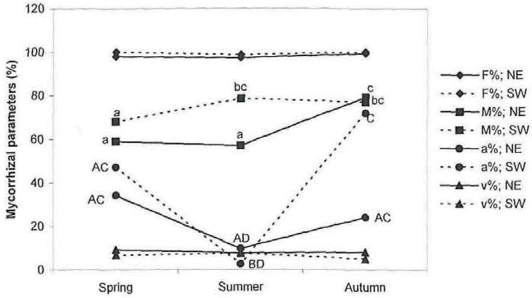

Fig. 6. Mycorrhizal colonization parameters for transplanted (SW) and control (NE) *B. pinnatum* roots in the two exposures of site M in 2002. Samples were taken in spring (May), summer (August) and autumn (October). Statistically significant differences among treatment means (or medians for non-parametric data) of 5 replicates are indicated with lowercase letters next to symbols. Different letters indicate significant differences ($P<0.05$). F%: frequency of mycorrhizal colonization. M%: intensity of mycorrhizal colonization. a%: arbuscule content. v%: vesicle content. For explanation of mycorrhizal parameters see the Material and Methods section. On M% data two-way ANOVA was performed. On a% data Kruskal-Wallis test and Dunn's test was used. Means of treatments in the case of F% and v% 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. pinnatum* from South-facing slopes despite its gregarious appearance in adjacent hillsides exposed to the N or E in the loess forest steppe landscape mosaic of the Hungarian Great Plain. Its stress-tolerant competitor strategy (GRIME & al. 1988) enables this grass to survive the removal of the forest over storey in its original forest habitat and to persist in place even reaching a dominant position in subsequent secondary grasslands maintained by grazing or cutting (FEKETE & al. 1998, 2000, VIRÁGH & BARTHA 1998). The high phenotypic plasticity of physiology and morphology observed for a number of successional intermediate plant species (Abrams & Mostoller 1995, Bazzaz 1979, 1996, Bazzaz & Carlson 1982, Kalapos & Csontos 2003, Kiato & al. 2000, Krause & al. 2001, Murchie & Horton 1997, Roden & al. 1997, Strauss-Debenedetti & Bazzaz 1991, Zangerl & Bazzaz 1983) and for this species as well (Mojzes & 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 (Mojzes & al. 2003) and growth (Fekete & al. 1998, Virágh & Bartha 1998) in the unshaded grasssland compared to the half-shaded shrub microhabitat in its typical biotope in Hungary. The hot and dry microclimate of South-facing slopes in this loess-covered landscape seems to impose untolerable 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. pinnatum* 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 photodamage of leaves indicated by decreased capacity for photochemical reactions (Fv/Fm, ΦPSII) and also for non-photochemical chanelling of excess energy (NPQ). Summer drought caused the dieback of the majority of *B. pinnatum* 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 (DE KROON & KNOPS 1990, DE KROON & SCHIEVING 1990, MOLNÁR 2003) which provides a high regeneration potential for lost shoots. This trait 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 GRIME & al. 1998 reports that VA mycorrhiza is common in this species, but gives no further reference or details. VAN DER HEIJDEN & 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 phosphorous (BRUNDRETT 1991, HARRISON & VAN BUUREN 1995, PATE 1994) this observation supports the high P utilization capacity determined for *B. pinnatum* in its natural habitat (BOBBINK 1991), but moderate P uptake efficiency under artificial experimental garden conditions (RYSER & LAMBERS 1995) where root mycorrhizal associations may not develop in such an extent as in the natural habitat. A marked seasonal trend was detected in the relative amount of fungal arbuscules in root cells paralleling the temporal pattern of host plant physiological activity. In the grassland studied, summer is the dry season, while spring and autumn are relatively humid. The greater-than-average summer drought in 2002 reduced the amount of arbuscules (sructures 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 arbuscule frequency may affect not only P acquisition of the plant, but its water uptake in addition as arbuscular symbiosis may alleviate plant responses to moderate moisture deficit by increasing water uptake (AL-KARAKI & AL-RADDAD 1997, DAVIES & al. 1992, AUGÉ & al. 1992). Enhanced plant metabolism 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 arbuscules and vesicles in the rainy season and a minimum during the dry season (LUGO & al. 2003, SIGÜENZA & al. 1996). Similarly, a marked seasonal course of abruscule frequency with a summer minimum was observed for several vascular species inhabiting a peat bog community under semiarid climate in Hungary (ZÖLD-BALOGH & al. 2003).

In conclusion, the results of our field transplant experiment support the original assumption that the hot and dry environment on south facing slopes is not conducive for *B. pinnatum*. Shoot growth, leaf photochemistry and root colonization by VAM suffered marked reduction on the S-facing slope, while not on the N-facing one during a drier than average vegetation period. From the rich bud bank on its rhizomes *B. pinnatum* 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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