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Comparative synphysiological studies on *Brachypodium pinnatum* dominated forest- and steppe-type grasslands

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ABSTRACT The lack of community-level, synphysiological investigations inspired us to plan a study on *Brachypodium pinnatum* grasslands, well-known objects of local long-term coenological and dynamical examinations in Hungary. After removing every species but B. pinnatum, CO_2 gas exchange responses by the grass stands indicated the difference in the degree of water-stress between the two investigated habitats. However, in intact community measurements these responses are masked by the presence of other species, by the change of species coexistence patterns and by different light conditions. We conclude that to understand the physiological performance of a dominant species in a plant community and also the photosynthetic behaviour of the whole community, considering the coenological aspect and examining the intensity of photosynthesis at a level of organization higher than the population level are essential.
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KEY WORDS

synphysiology
WUE
LAI
light-use efficiency
Brachypodium pinnatum
grasslands

Studies of plant physiology have concerned two spatial-scales, so far. First, conclusions are related to the scale of an "average plant" from infraindividual (leaf, shoot, root) aut-ecophysiological investigations. Second, on macro- (land-scape) scale the production, as the final issue of vegetation's physiological activity was estimated by remote sensing.

There has been little attempt to investigate the medium scale, at the level of the supraindividual organization (*i. e.* stand, community). Little is known about stand-level gas exchange properties (*i.e.* spatial or temporal variability, regulation, community-dependent characteristics), transpiration and water-use efficiency (WUE), especially in temperate non-forested vegetation types. Recent results, data and hypotheses of synphysiology have suggested that communities have a kind of supraindividual organization from the point of view of physiological activity, different from that of individuals. So differences between species and individuals are balanced or dissolved at the spatial scale of community.

B. pinnatum grasslands are typical in low precipitation areas of Hungary after clearing of the oak forest. *B. pinnatum* plays a central role in the course of secondary succession following deforestation. This species was the dominant component of the sparse underground layer of ancient oak steppe woodlands. Clones of *B. pinnatum* survived forest cut and the vegetation developed into species rich xeromesophilous *B.* communities. These grasslands can persist for centuries after forest felling and slowly change into more xeric type of *Festuca rupicola* dominated grasslands, typical of loess vegetation of the area (Zólyomi and Fekete 1994).

Past investigations revealed that the behaviour of the *B. pinnatum* species shows much plasticity over the different climatic regions (Bobbink and Willems 1987; Fekete et al. 1998). Recent studies suggest that morphological (leaf thickness and bulk tissue density) and physiological plasticity (PSII quantum yield and its components) can explain the clonal expansion of *B. pinnatum* and enable the species to be successful both in sun and shade microhabitats (Kalapos and Mojzes 2002).

It is already well known (Csintalan et al. 1991; Czóbel et al. 2000) that any conclusion drawn from individual level measurements, *e.g.* from leaves or shoots on stand level photosynthetical function cannot be sufficiently successful. Thus the main purposes of this study are:

1) to compare the synphysiological activity of *B. pinnatum* dominated forest- and steppe type stands adapted to different light conditions and having different coenological structure and dynamic state, and

2) to reveal the photosynthetic performance by *B. pinnatum* species in habitats with differing water supply.

Material and Methods

Study area

The study site is situated 25 km east of Budapest, at the border of the Gödöllő Hills. The area is part of a forest-steppe region with loess soil. The vegetation is a mosaic of forest fragments and grassland patches on the NE-facing slopes of the 2 km long valley (Fekete et al. 1998).

Two typical patches (Forest-type and Forest-steppe meadow as Steppe-type) of *B. pinnatum* (a C3 grass) grass-lands were selected for the present study. Forest-type of *B. pinnatum* community occurs along the edge of *Crataegus monogyna* shrubby area. Coverage of *B. pinnatum* amounts to 80%, the stand is dense with an average shoot-number of 1295. The average height of the sward is about 60 cm. The thickness of the litter layer is 10-15 cm. The steppe-type of *B. pinnatum* community contains mixture of mesic and xeric species with many codominants dicots and broad-leaved grasses. Total cover of *B. pinnatum* is only ca. 20%, the average shoot-number is 658. The number of steppe species

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is relatively high giving 40% of the total species number, and their cover is considerable (35-55%). The average height is 38-40 cm, the litter thickness is 5-10 cm. This patch-type is spatially well structured with highly complex multispecies coalitions (Virágh and Bartha 1998).

Field sampling and coenological survey

Three physiognomically uniform stands of each community-type, occurring close together in space were choosen. Ten plots of the steppe-type and seven plots of the forest-type were sampled. Percentage cover of each species was recorded in all plots. Shoots of *B. pinnatum* were also counted at the time of the synphysiological measures. To analyse the gas exchange characteristics of *B. pinnatum* population of the multi-species community we removed all species except the target one.

Physiological methods

We measured CO_2-exchange, transpiration, air temperature, relative humidity and vapour pressure, and calculated stomatal conductance by using a portable closed-loop IRGA gas exchange system (LI-COR 6200) sampling the air in a plexi-chamber of 60 cm diameter and 70 cm height with three replicate measurements in each plot. Canopy CO_2-assimilation rates were corrected by soil respiration (including the after-cut respiration burst) values, the latter measured in the same way as canopy CO_2-exchange on 3 (steppe-type) and 2 (forest-type) plots with a lag of at least 30 minutes after the vegetation was cleared. WUE is given as the ratio of net photosynthesis to transpiration. PPFD values were recorded and leaf-area index (LAI) was estimated using sunfleck ceptometers (Decagon), and canopy-surface temperature was measured with an infrared thermometer (RayngerII.). The photosynthetic light-use efficiency in the intact community plots and in the thinned (*i.e.* containing only *B. pinnatum*) plots was calculated as photosynthesis corrected by soil respiration and divided by LAI and PPFD, and photosynthesis corrected by soil respiration and divided by LAI or shoot-number and PPFD, respectively.

The study was carried out on 12th of June, 2001. At this time the *B. pinnatum* in the steppe-type stands was over the intensive groth period just entering into the start of the senescent phase and apparently suffering from severe drought-stress. In contrast *B. pinnatum* plants in the forest-type were in the fully developed but still green and healthy stage seemingly without the symptoms of any severe stress.

Results and Discussion

Single-species "community"

The environmental abiotic conditions differed significantly at the time of measurements between the two stands, with smaller average values of PPFD and air temperature, and higher average values of relative humidity and vapour pressure in the forest-type. We measured significant differences in shoot numbers, LAI and photosynthetic light-use efficiencies of *B. pinnatum*-shoots and stands between the two types, with significantly higher average values and smaller coefficient of variation in the forest-type. CO_2-assimilation (on 1 m^2 soil and on 1 m^2 leaf area base) and transpiration rates were also higher in the forest-type patch. However, there were no significant differences between the WUE values of the two *B. pinnatum* stands. These responses indicate the difference in the degree of the stress in the two investigated habitats. Decreased photosynthetic performance of the steppe-type grass was an apparent consequence of the prolonged water-stress. However these plants still could maintain a similar WUE as the unstressed ones of the other type reflecting the adaptation of the steppe-type grasses to the limited water-supply. This higher WUE in the stressed plants was achieved at low values of leaf conductances (Fig.

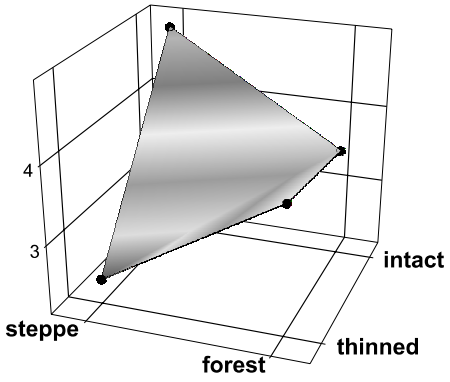

Figure 1. WUE in the intact and thinned stands of the forest and steppe types.

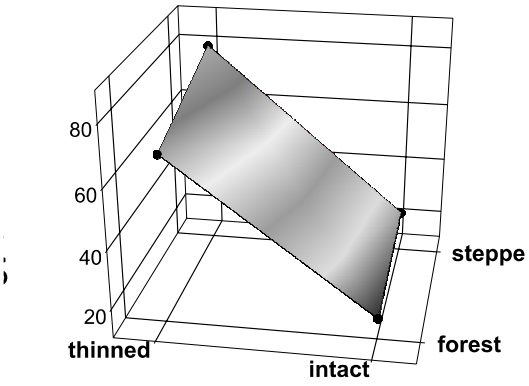

Figure 2. The coefficient of variation in WUE in the intact and thinned stands of the forest and the steppe type.

1). Photosynthesis in the forest-type *B. pinnatum* grasses seemed to benefit of the increased light intensity after the removal of the coexisting plants.

Multi-species community

During the measurements in the intact stands there were no significant differences between the environmental conditions of the two types. LAI, average total cover and cover by *B. pinnatum* were significantly higher, while the average number of species and the ratio of xeric species were significantly lower in the forest-type as compared to those in the steppe-type. We measured significantly higher CO_2-assimilation, photosynthetic light-use efficiency (referred to both 1 m^2 soil area and 1 m^2 leaf area) and WUE in the steppe-type. These photosynthesis responses can also be considered as responses of differently light-adapted plant-canopies as the canopy adapted to higher light intensities displays higher CO_2-assimilation rates and WUE. The coefficient of variation of the physiological responses (as WUE, Fig. 2) in the single-species (thinned) *B. pinnatum* canopy were higher than in the multi-species grassland canopy suggesting more pronounced supraindividual regulation of the two intact communities.

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