

CONTRIBUTION TO THE ECOLOGY OF THE STEPPE VEGETATION OF THE TIHANY PENINSULA

III. ESTIMATION OF DROUGHT RESISTANCE BASED ON THE SATURATION OF WATER DEFICIT

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Introduction

The evaluation of the water-loss curves obtained with shoots of characteristic steppe plants growing at Kiserdőtető on the Tihany Peninsula has revealed differences in the water-retention capacity of some xerophytic grass species (KVĚT and RYCHNOVSKÁ 1963). These differences seem to be somewhat paradoxical at first sight: curves obtained with shoots of typically continental species, such as *Stipa stenophylla*, *S. pulcherrima*, *S. joannis*, indicate a lower resistance to desiccation than that found in some subboreal-submeridional (*Koeleria gracilis*) to mediterranean-oceanic (*Chrysopogon gryllus*) species. The water-retention capacity of the continental species did not exceed that of some mesophytic grasses such as *Brachypodium silvaticum*. If the shape of the water-loss curves were used as one of the criteria of drought resistance (CETL 1953, SLAVÍK 1958) then, in this particular case, it would contradict the phytogeographical and phytocenological characteristics of the species studied. For this reason, an attempt has been made to apply a different criterion of drought resistance. This criterion, the reversibility of water deficit, has already been successfully applied in an earlier study (RYCHNOVSKÁ 1962).

Materials and method

As in the previous paper of this series, the plants studied were from the steppe community at Kiserdőtető on the Tihany Peninsula (Ti). The performance of the following grass species was investigated:

Stipa capillata
Stipa joannis
Stipa stenophylla
Stipa pulcherrima
Melica ciliata.

Andropogon ischaemum
Chrysopogon gryllus
Agropyrum intermedium
Koeleria gracilis

In order to avoid spurious results even in a short-term investigation of this nature, experiments were also carried out with analogous plant material coming from the drier localities of Csomád (Cs) and Szentendre-Sziget (Se).

With all the species tested there were 2 to 5 replicates in each experiment. The experimental procedure was as follows: Shoots of the species investigated were sampled at the site in the early morning after heavy rain and were trans-

ferred to the laboratory in a polythene bag. On arrival, the leaves were kept in darkness with their bases in water, in a water-saturated atmosphere. After two hours of this treatment the leaves were fully saturated with water and turgid. Separate leaves were then dried in an incubator at 28° to 30° C for periods ranging from 0 to 9 hours to induce different degrees of water deficit. Samples of the leaves to be tested were taken out from the incubator at two-hourly intervals and segments 2.6 mm long were cut from the leaves with 2 razor-blades mounted parallel to each other.

The segments were then placed in a row on a special plexiglass frame. To supply the leaf segments with water polyurethane foam wetted to its full water-capacity was attached to the cut surfaces. This experimental arrangement has already been proved and described in earlier papers (RYCHNOVSKÁ et BARTOŠ 1962, RYCHNOVSKÁ 1963). The saturation of the leaf segments was carried out in darkness at ambient temperature for 2 hours. The water deficit was determined by accurate weighing on analytical balances. The leaf segments placed on the frames were weighed both before and after saturation and finally, they were dried at 105° C to constant weight and their dry weight determined.

The water deficit and its saturation have been expressed as a percentage of the fully turgid state (= 100%) at the beginning of the experiment. The arrangement of the whole experiment was similar to that described in an earlier paper. Plants from the localities Cs and Se were treated in the same way as those from Ti except that the material had been sampled a day before the experiments. To fully saturate these leaves they were left with their bases in water, etc. (see above) overnight, i.e. for 14 hours.

Experimental results

The results are presented in figures 1 to 9. The curves showing the saturation of water deficit plotted against the water deficit induced can be divided into two distinct groups.

1. *Stipa*-type. The first type of curve is characteristic of plants whose leaf segment never reach a higher water content than that of saturated and turgid intact leaves. An increasing water deficit is fully reversible until a certain value is reached, beyond which the wilted segments do not become fully saturated; this effect increases with increasing water deficit of the species tested such a relationship holds for *Stipa stenophylla*, *S. pulcherrima*, *S. joannis*, *S. capillata*, *Melica ciliata*, and *Andropogon ischaemum*.

2. *Chrysopogon*-type. The second type of water-saturation curve is characteristic of plants whose leaf segments cannot increase their water content directly, i.e. if cut from fully turgid leaves immediately placed on the frames and supplied with water through the cut surfaces. However, if a water deficit is induced it is possible to cause the treated segments to take up more water than was lost during drying (see Fig. 5). Between 15 and 50% of water deficit (dependent on species and habitat) this effect reaches a maximum. Further increase in the water deficit seems to cause irreversible changes in the plant tissues with the same consequences as described for the *Stipa*-type. This relationship suggests that in the *Chrysopogon*-type a higher water-holding capacity of the leaf tissues can be induced by water stress. Of the species tested this kind of relationship holds good for *Chrysopogon gryllus*, *Agropyrum inter-*

medium, *Koeleria gracilis*, *Festuca vaginata* and the water-saturation curves are similar for mesophytic grasses such as *Dactylis glomerata* and *Brachypodium silvaticum*.

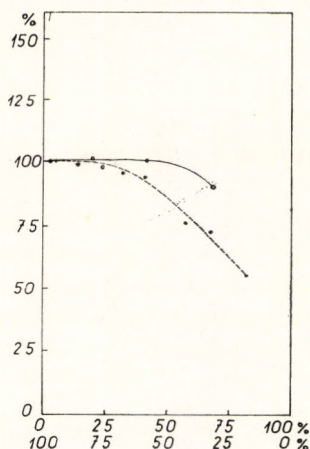


Fig. 1. Water-saturation curves obtained with leaf segments of *Melica ciliata* (—) and *Stipa stenophylla* (---) from the locality Ti. The initial water content of the leaf segments has been taken as 100%. Abscissa: water deficit (upper scale) and the corresponding water content of the leaf segments expressed as percentage of their dry weight (lower scale). Ordinate: water content of the leaf segments after saturation of 2 hours expressed as percentage of the initial water content

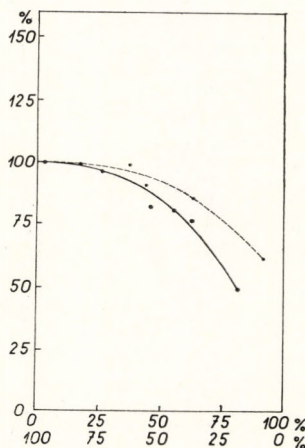


Fig. 2. Water-saturation curves obtained with leaf segments of *Andropogon ischaemum* (---) and *Stipa pulcherrima* (—) from the locality Ti. Explanations as for Fig. 1.

Discussion and conclusions

The aim of this study has been to throw some light upon the water relations of some grass species characteristic of the steppe communities at Kiserdötetö. It is not within the scope of a short-term study to show the sea-

sonal dynamics of any physiological process or its dependence upon varying weather conditions; nor can the ecological significance of the water relations be shown. However, a short-term study can indicate from a certain standpoint some specific characteristics that account for the presence of the plants inves-

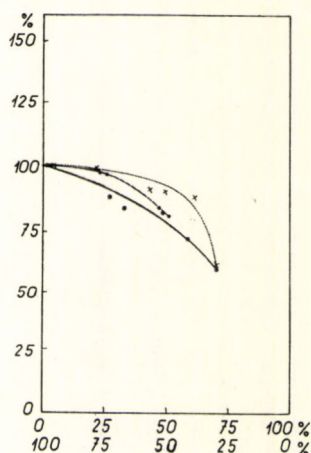


Fig. 3. Water-saturation curves obtained with leaf segments of *Stipa capillata* from the localities Se (...), Cs (---) and Ti (—). Explanations as for Fig. 1.

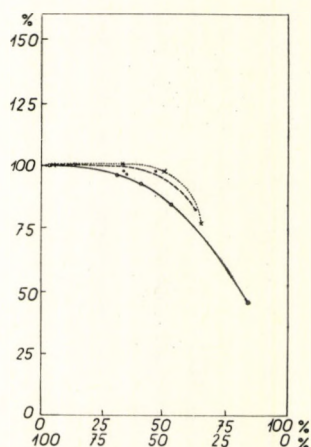


Fig. 4. Water-saturation curves obtained with leaf segments of *Stipa joannis* from the localities Se (...), Cs (---) and Ti (—). Explanations as for Fig. 1.

tigated in the Pannonian steppe communities where, by Central European standards, the environmental conditions appear to be relatively severe.

With the plants studied several mechanisms of drought resistance have been found. It has been found that the water deficit is reversible to a great extent in all the species tested. In those plants having the *Stipa*-type of water-saturation curves a normal water deficit does not cause any particular

changes: the plants can bear the water stress and recover to their original vigour when supplied with sufficient water. All the *Stipa*-species tested, *Andropogon ischaemum* and *Melica ciliata* seem to possess such properties.

The physiological properties of naturally growing plants and their communities reflect the environmental conditions in their habitats; therefore

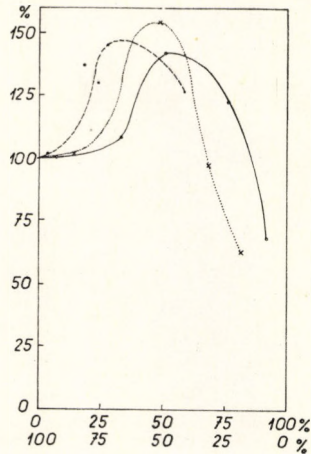


Fig. 5. Water-saturation curves obtained with leaf segments of *Chrysopogon gryllus* from the localities Se (...), Cs (---) and Ti (—). Explanations as for Fig. 1.

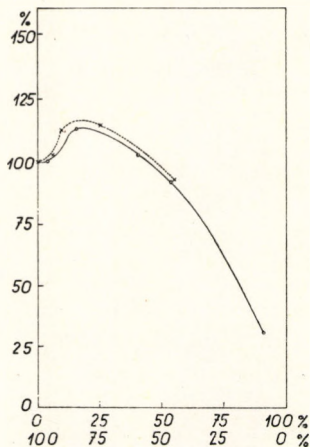


Fig. 6. Water-saturation curves obtained with leaf segments of *Koeleria gracilis* from the localities Se (...) and Ti (—). Explanations as for Fig. 1.

an assumption can be made that the plants with the properties shown by the curves of the *Stipa*-type are adapted to long rainless periods. This kind of drought resistance is advantageous especially in ecotopes which are generally dry throughout most of the growing season. Indirect evidence in favour of this assumption is represented by *Stipa joannis*. The time taken for the water deficit reach the stage where it is only partly reversible was shorter with plants from Tihany, than with those from Csomád and Szentendre-sziget. This fact

seems to be related to total amounts of rainfall from January to July 1962 which were 292 mm, 225 mm (meteorological station at Alsógöd) and 184 mm respectively at the three localities (Ti—Cs—Se).

In the plants characterized by the *Chrysopogon*-type of the water saturation curves the normal water deficit seems to give rise to changes caus-

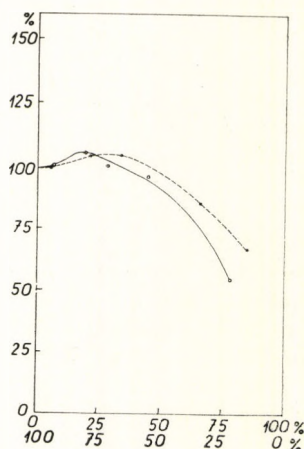


Fig. 7. Water saturation curves obtained with leaf segments of *Agropyrum intermedium* (—) and *Festuca valesiaca* (---) from the locality Ti. Explanations as for Fig. 1.

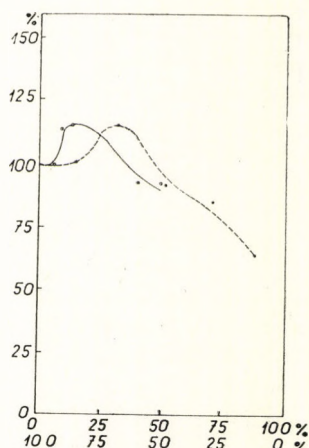


Fig. 8. Water-saturation curves obtained with leaf segments of *Dactylis glomerata* Ti (—) and *Brachypodium silvaticum* (---). Explanations as for Fig. 1.

ing a higher uptake of water if this becomes available. The nature of these changes has not yet been determined, but it is likely to be of a biochemical rather than of a physical nature. This aspect is now being investigated. It seems quite obvious, however, that plants showing the *Chrysopogon*-type of water-saturation curve can make full use of occasional rain, especially if it follows a dry period that has induced a higher water stress in the plants.

It should be noted that the species showing these properties also control their water loss more actively as was shown in the second paper of this series. The form of the water-loss curves with these more reactive xerophytic species may even approach that found with mesophytic grasses. The reversibility of the water deficit and the increase in the water-holding capacity of the leaf tissues which is induced by water stress seems to be an advantage in relatively dry regions with some occasional rainfall during the whole growing season. *Chrysopogon gryllus* is a typical example of plants showing this relationship, but *Koeleria gracilis*, *Koeleria glauca*, *Agropyrum intermedium* and *Festuca valesiaca* also behave in the same way. Similar properties can also be demonstrated for the mesophytic grasses tested such as *Dactylis glomerata* and *Brachypodium silvaticum*. The phytogeographical characteristics of the species studied are in general accord with what is known of their ecological amplitude. The *Stipa*-type water saturation curve appears to characterize rather continental floristic elements (according to the classification by MEUSEL 1942) while the *Chrysopogon*-type seems to characterize species having an oceanic and mesophytic character.

Thus it has again been proved that physiological properties of naturally growing plants are in agreement with their phytogeographical characteristics. In many cases an analysis of these physiological properties can help to explain the distribution of these plants.

Summary

Reversibility of the water deficit in leaves of some characteristic steppe grasses growing at Kiserdötető on the Tihany Peninsula was compared with that found in the same species from Szentendrei-sziget and Csomád. With each species tested a series of different water-deficit values were induced by drying the intact leaves at constant temperature for periods varying from 0 to 9 hours. Segments cut from these water-deficient blades were then saturated with water through both their cut surfaces for 2 hours. The initial water content, the water deficit and the water content after saturation of the segments were determined by weighing. The grass species tested were found to fall into two groups:

1. *Stipa*-type. The leaf segments fully recover from their water deficit by regaining their initial water content, but beyond a certain water deficit, irreversible changes seem to occur in the leaf tissues which prevent the segments from fully saturating their water deficit.

2. *Chrysopogon*-type. Increase in water deficit brings about an increase in the water-holding capacity of the leaf tissues. In general, the water content of the leaf segments after saturation is higher than it was initially. As with the *Stipa*-type, irreversible changes seem to occur, with the same consequences, when the water deficit reaches a certain value.

These findings have been compared with the phytogeographical distribution of the species studied which is supposed to be in accordance with their ecological amplitude. The *Stipa*-type of water deficit saturation seems to be advantageous to plants that have to survive long rainless periods in regions with continental conditions. The *Chrysopogon*-type seems to be favourable to plants in mesophytic conditions, or those having a rather oceanic distribution,

where only short periods of drought have to be survived. The plants of this type can undoubtedly make full use of occasional rainfall, especially if it follows a dry period.

Acknowledgements

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Összefoglalás III.

1. Szerzők jellegzetes füvek levelében előálló vízhiány visszafordíthatóságát vizsgálták Tihanyban (Ti), a Szentendrei-szigeten (Sz) és Csomádon (Cs), jellegzetes pusztai termőhelyeken.

2. Metodikailag a következőképpen jártak el: A vizsgált növények leveleit addig szárították, míg azokban részleges vízhiány állt elő. Ezután a levél lemezt részekre vágták és két órán át mindkét vágási felületen keresztül vízzel telítették. A felszívódás tempóját és az előző deficit fokát súly méréssel regisztrálták.

3. Megállapították, hogy a vizsgált füvek kétféleképpen viselkednek:

a) *Stipa*-típus. Erre az jellemző, hogy a vízdeficit csak bizonyos fokig egyenlítődik ki az eredeti víztartalomra, mert ezen túl irreverzibilis változások lépnek fel. Ez csökkent telítődési képességű szövetekre utal.

b) *Chrysopogon*-típus. Ennek a vízkapacitása egyenletesen nő az emelkedő vízdeficittel. Egy bizonyos határon túl természetesen itt is irreverzibilis károsodás léphet fel, ahol csökken a sejtszövet telítődési képessége.

4. A megfigyelt jelenséget összehasonlították a vizsgált füvek növényföldrajzi elterjedésével, mely elvben megegyezik azok ekológiai amplitúdójával. A *Stipa*-típus kontinentális feltételeknek felel meg és hosszú csapadék nélküli időszakok átvészeléséhez idomult. A *Chrysopogon* ezzel szemben inkább mezofil környezetnek felel meg. Az ilyen típusú növények inkább oceanikus elterjedésűek, melyek csak rövid ideig tartó szárazsághoz képesek alkalmazkodni, mikor is a szórványos esőzést tökéletesen kihasználják, különösen ha a száraz időszak után áll be.

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