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A Contribution to the Ecology of the Genus *Stipa* II. Water Relations of Plants and Habitat on the Hill of Křížová hora Near the Town of Moravský Krumlov

Příspěvek k ekologii kavylů
II. Vodní režim rostlin a stanoviště na Křížové hoře u Moravského Krumlova

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Abstract — The present paper deals with the water relations and the microclimatic differences in the covers of *Stipa pulcherrima*, *S. stenophylla*, *S. joannis*, and *S. capillata* in one locality. The author studies the physiological properties of the plants by means of a field experiment. She compares tufts growing on a naturally dry substrate with tufts artificially supplied with water and studies their daily transpiration curve, the water content in their leaves, the variations in the water saturation deficit, and the content of carbohydrates. *Bromus erectus*, artificially transplanted to this biotope, is used as a control plant. The most drought-resistant plant is *S. pulcherrima*, then *S. joannis* and the least resistant species was *S. stenophylla*. *S. capillata* suffered from drought most of all, although it is usually enough drought-resistant. The author explains this by the insufficient development of xerophytic properties in the relatively humid Central European climate and by the low degree of adaptation of this species to the dry period which took place. The established properties of the plants fully correspond to the properties of the biotopes, in which they naturally occur in Czechoslovakia.

Itroduction and Problems

In order to find the causal explanation of the natural distribution of the genus *Stipa* in this country we carried out a detailed analysis of one typical locality in a rocky amphitheatre near the town of Moravský Krumlov. It is situated in a block of Perm conglomerates which, from the point of view of soil chemistry, is quite homogenous and was described in the preceding paper (Úlehlová 1964). On the whole, the terrain in the locality is very uneven and rugged; its upper part is covered by forest and its central part is bare to rocky, so that it displays a wide range of microclimatic differences. In the area of the Krumlov rocky amphitheatre we found a natural grouping of the following species of the genus *Stipa*: *Stipa pulcherrima* C. Koch (*S.p.*), *Stipa joannis* Čelak. (*S.j.*), *Stipa stenophylla* Čerň. (*S.s.*), *Stipa capillata* L. (*S.c.*); their distribution in the locality is more or less determined by microclimatic differences. We tried, first, to establish these differences; secondly, to find some coincidence in the occurrence of the species of the genus *Stipa* and of microclimatic characteristics which we supposed to be representative of the habitat (even on such a small scale) and of the differentiation of the species under consideration (so as these characteristics appear in larger areas); and, thirdly, to find an explanation for the relations thus established in the physiological properties of the plants.

Material and Methods

On 16th to 18th July 1963 we performed a series of measurements in the steppe locality of "Křížová hora" near the town of Moravský Krumlov in SW Moravia. We established the distribution of the various species of the genus *Stipa* and in places in which some of the species predominated small microclimatic stations were installed. In addition to the common microclimatic data we followed the dynamics of the soil moisture in the depth of 5—10 cm. The selected tufts of the feather grasses were marked and the following data were collected:

1. Their transpiration during the period of 24 hours, in the intervals of 1 hour, by a rapid

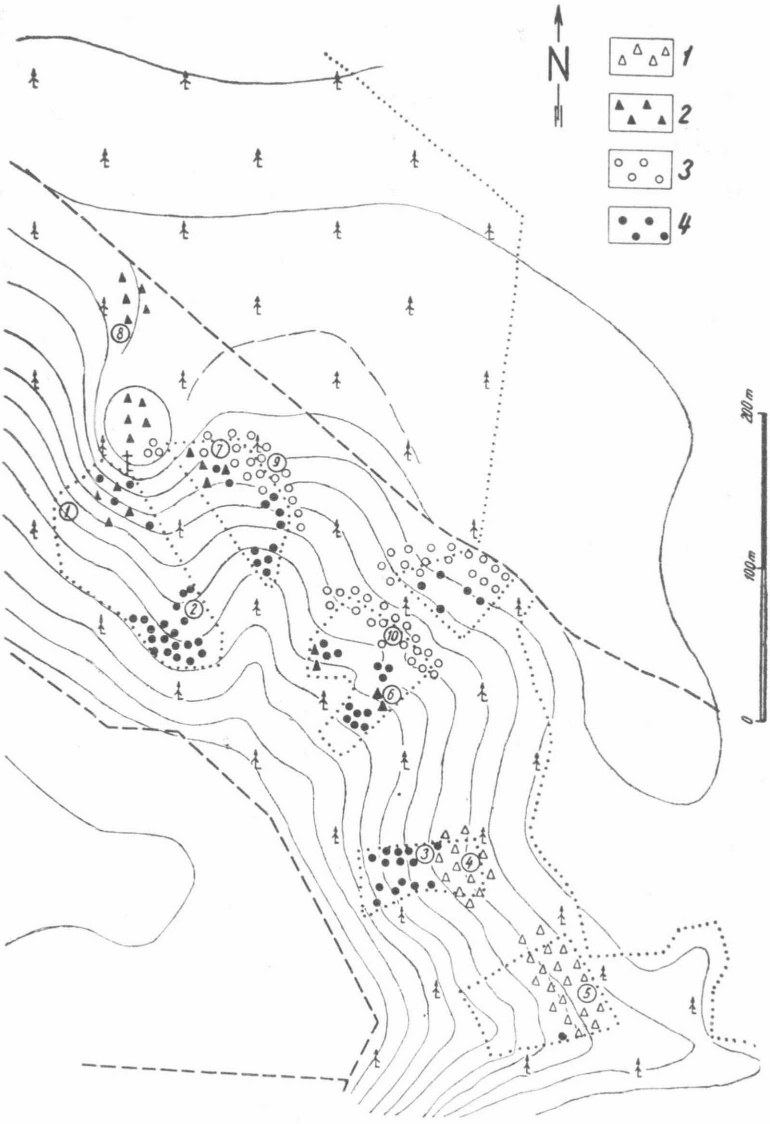


Fig. 1. — Sketch of the locality on the hill of Křížová hora near the town of Moravský Krumlov. The numbers denote the small microclimatic stations. 1. *S. pulcherrima* 2. *S. joannis* 3. *S. stenophylla* 4. *S. capillata*

weighing of the cut leaves on a torsion balance and their expositio, for 3 minutes, in their original stand (on July 18th).

2. The variations of the water saturation deficit of their leaves durng the period of 24 hours, in the intervals of 6 hours. The measurement was carried out by applying water-saturated poly-

Table 1

Content of glycids in the leaves expressed in per cent. of the dry weight

Species	20,00	4,00	12,00	20,00 o'clock
Stipa joannis	0.31	0.30	0.55	5.22
Stipa stenophylla	1.07	0.68	1.94	4.90
Stipa pulcherrima	0.62	1.28	1.15	1.09
Stipa capillata dry	5.83	1.45	0.24	1.43
Stipa capillata supplied with water	3.30	0.71	0.44	0.94

urethane foam to the cut sections of the leaves, as was described by ČATSKÝ (1960) and RYCHNOVSKÁ et BARTOŠ (1962) (on July 16th to 17th).

3. The fluctuations in carbohydrate content in the parts above the ground. The samples were collected in the field, weighed, immediately put into test tubes filled with 96% ethanol and subjected to loratabory treatment after a longer period. The dry weight of the samples was established by means of parallel weighing of fresh samples. The carbohydrate content was established colorimetrically by means of the Nelson reagent, the pre-treatment of the sample according to the "Official Methods of Analysis" (1955) (July 16th to 17th).

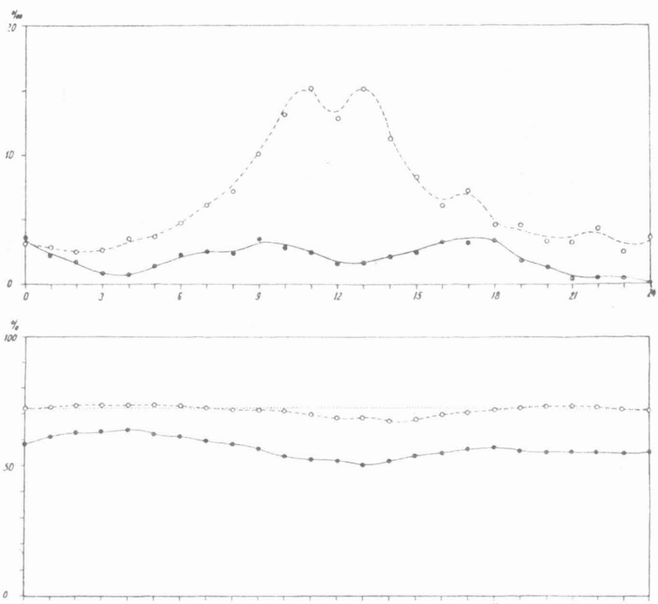


Fig. 2. — Upper graph: Daily variations in transpiration of *Bromus erectus*, expressed in mg./1000 mg. of water content per 1 minute. The full line belongs to plants growing on a naturally dry substrate, the deshed line to plants supplied with water to full capacity on July 18th, 1963. Lower graph: Water content in leaves expressed in per cent. of fresh weight. Full turgidity is expressed by dotted line. All curves were plotted from moving averages of five measurements.

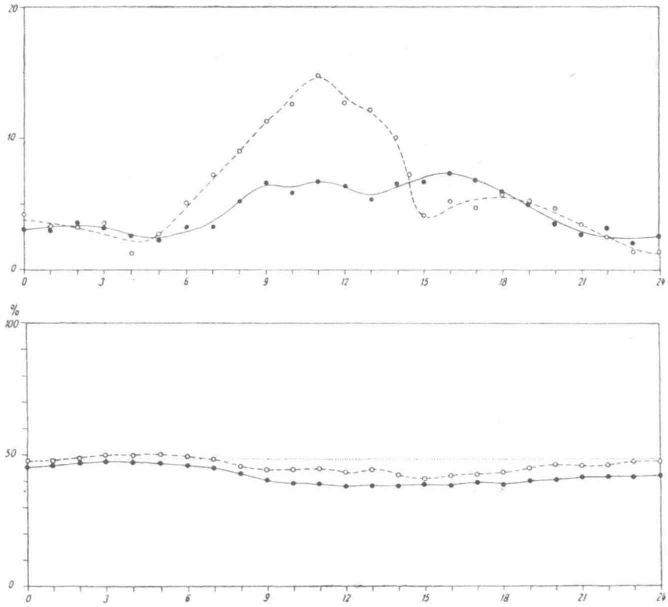


Fig. 3. — Daily variations in transpiration of *Stipa joannis*. Explanation as for Fig. 2.

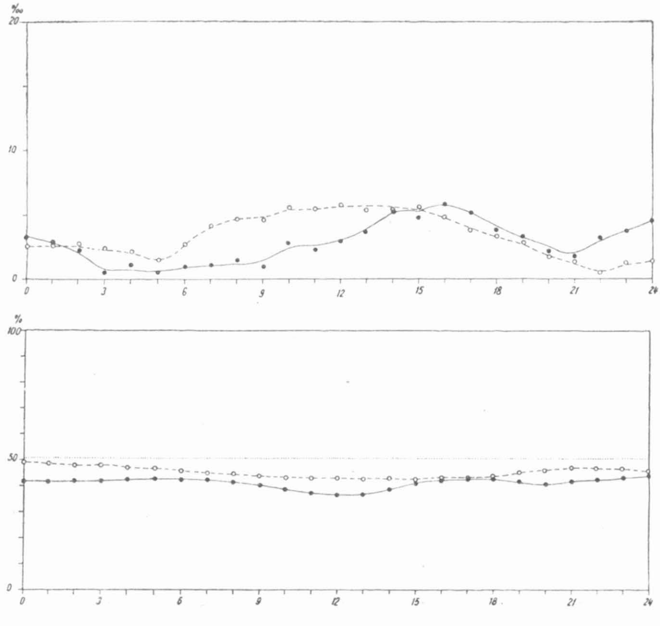


Fig. 4. — Daily variations in transpiration of *Stipa pulcherrima*. Explanation as for Fig. 2.

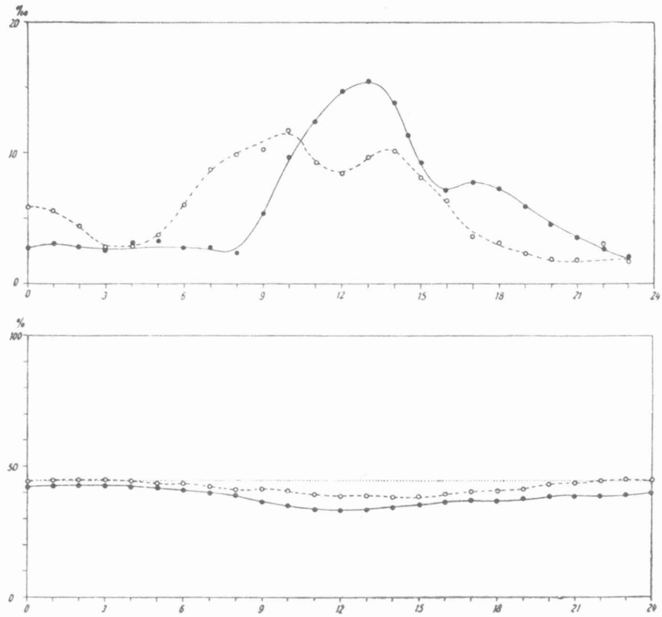


Fig. 5. — Daily variations in transpiration of *Stipa stenophylla*. Explanation as for Fig. 2.

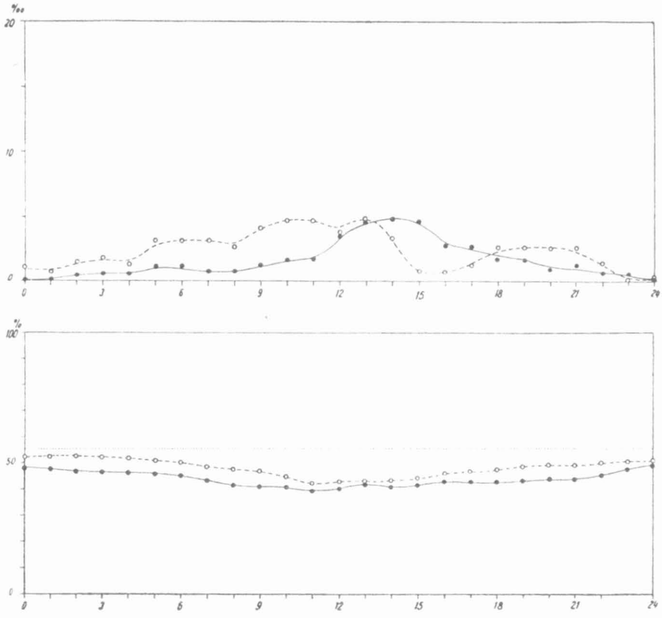


Fig. 6. — Daily variations in transpiration of *Stipa capillata*. Explanation as for Fig. 2.

In addition to the four species of *Stipa* we analysed tufts of *Bromus erectus* HUDS. (*B.e.*), which occur in the more remote forest covering part of the locality under study. In this comparative measurement we made use of tufts of *B.e.* transplanted to the close vicinity of the feather grasses in the spring 1961; the tufts fulfilled all their vegetative functions very well.

All the plants were studied in two experimental varieties:

A. tufts on the naturally dry substrate,

B. tufts artificially supplied with moisture nearly to their maximum capillary capacity.

To complete the data on our experiments, we must add that the research was carried out in the period of high temperatures and after a long spell without any rain, i.e. under conditions of unusual aridity in our area.

The Results of Experiments and Observations

A. Microclimatic Characteristics and Occurrence of Species of the Genus *Stipa*

From the microclimatic point of view the locality under study, (the area of about 500 × 300 m.,) can be divided into several zones. The upper woody plateau is characterized by a deeper soil profile and its temperature and moisture are least of all the zones subject to marked fluctuations. On its S edge there are many places with a dense cover of *S.s.* The area then passes into a rocky slope on which the soil profile is shallow, skeleton-like, and the bare rocky surface protrudes in many places. In the upper half of the slope *S.j.* occurs abundantly together with some scattered tufts of *S.c.* The most arid lower steep slopes are, however, covered by *S.c.* only. *S.p.* is chiefly found on the W and SW slopes declining to a small stream; there it occupies a wide area under the protective screen of low shrubs of *Prunus fruticosa*; solitary plants can also be found in rock cracks and galleries, and on small rocky platforms covered with soil. Some microclimatic characteristics established in the covers of feather grasses are displayed in Table 2. This table shows that *S.p.* and *S.c.* can be found growing under most extreme microclimatic conditions, *S.j.* reveals a wider amplitude from the localities characterized by microclimatic extremes to the more shadowy places with less extreme conditions, and *S.s.* grows in places in which the microclimatic conditions are most balanced of all. Even more extreme microclimatic values were found in the most exposed place, in the cover of *Melica transsilvanica*, in which, however, the feather grasses do not occur.

For the biological evaluation of the humidity relations of the site the phytometric method was also applied: *Teucrium chamaedrys* which grows very abundantly over all the locality was used as the test plant. At noon we collected samples of this plant in the neighbourhood of each small microclimatic station and established its water deficit. The results are also given in Table 1 It follows from these data that the highest water deficit was recorded in the covers of *S.c.*, and *S.p.* The high value for *S.s.* is obviously anomalous considering the terrain and other microclimatic characteristics.

B. Transpirations of Selected Specimens of the Feather Grasses and of *Bromus erectus*

The variations in the curve of transpiration of all the plants under study (both the plants on arid substrate and those artificially supplied by moisture) are given in Figs 2—6. We can see that, under natural conditions of the day chosen, the highest intensity of transpiration (expressed in parts per thousand of the water content in the leaves) was found in *S.s.* and *S.j.*, a lower one in *S.p.* and *S.c.* and the lowest intensity in *B.e.* When one set of the tufts was artificially supplied with water, the course of transpiration was as follows (arranged from the highest to the lowest values): *B.e.*, *S.j.*, *S.s.*, *S.p.*, and *S.c.* It should be noticed that the transpiration of *B.e.* increased fivefold, of *S.j.* twofold, the transpiration of *S.s.* fell to a lower level than that of the dry tufts, and the transpiration of *S.p.* and *S.c.* remained roughly at the same level, the maxima being shifted to the morning hours. The water content in the leaves of the plants under study shows similar results in both variants. The most pronounced differences between the tufts supplied with water and those under natural conditions were found in *B.e.*, while the differences among the feather grasses were not too marked. The condition of full water saturation in the plants growing on a dry substrate was approached by the leaves of *S.j.* and *S.s.* in the early morning hours. The tufts supplied with water reach full saturation in all the species under study with the exception of *S.c.* at least during the night hours. The mean values of the maximum water saturation in experimental conditions described in the following paragraph were taken for the measure of full turgescence.

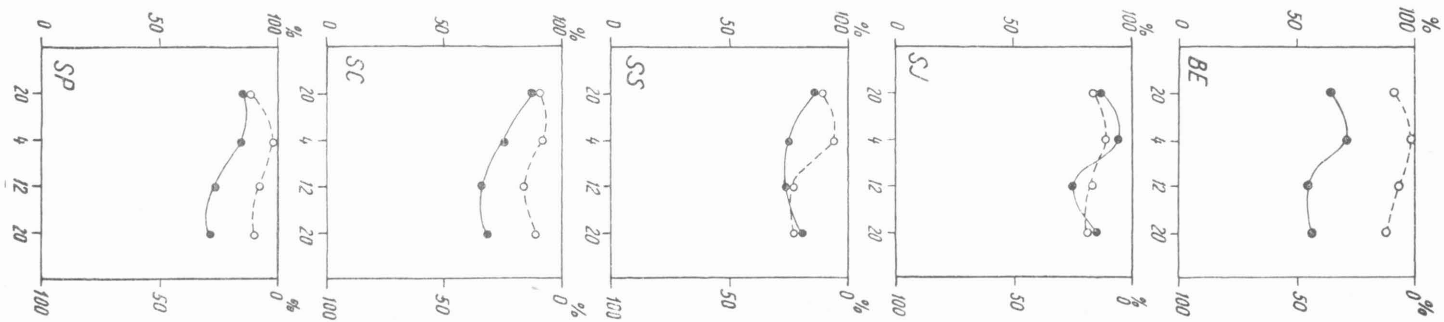
C. The Water Saturation Deficit

The variations of the water saturation deficit, shown in Fig. 7, were followed in both variants. In dry climatic conditions the deficit of *B.e.* is very pronounced. During the night hours the plant gets partly saturated with water but the day losses in the water content are greater than the

Table 2

Microclimatic data on the hill of Křížová hora near the town of Moravský Krumlov

No	Predominant species in the vegetational cover	Maximum air temperature (at 5 cm.)		Maximum soil surface temperature		Maximum soil temperature (at 5 cm.)		Minimum relative air humidity (in per cent.)		Average soil moisture (in per cent. of maximum capillary capacity)	Water saturation deficit of *Teucrium chamaedrys* (in per cent.)
		16. 7.	17. 7.	16. 7.	17. 7.	16. 7.	17. 7.	16. 7.	17. 7.		
1	*Melica transsilvanica* (without the feather-grasses)	39	40	47	52	36	34.5	20	23	12.5	42.7
2	*Stipa capillata*	36	36	40	36	32.5	32	22	24	12.5	48,5
3	*Stipa capillata*	39	43	39	41.5	29	29	26	28	19.6	46.1
4	*Stipa pulcherrima*	41	43	45	47	29	29	27	32	19.9	19.7
5	*Stipa pulcherrima*	37	42	37.5	37.5	29.5	30	22	24	28.5	38.4
6	*Stipa joannis*	36.5	39	53	50.5	32	32	20	26	16.7	35.8
7	*Stipa joannis*	39.5	38.5	38	40	26	26	26	31	71.0	22.8
8	*Stipa joannis*	39.5	38	41	41	20.5	20	27	32	53.0	32.1
9	*Stipa stenophylla*	34.5	34.5	34	34.5	20	20	40	45	86.6	19.0
10	*Stipa stenophylla*	37	34	28.5	29	22	23.5	30	37	41.1	40.7



partial saturation during the night. When supplied with water, however, the plant brings its water turnover within physiological limits. The dry variant of *S.j.* shows loss of water by day and partial saturation by night within a very wide range, which only narrows when the plants are supplied with water; the resulting values, however, remain almost identical. *S.p.* reacts in a similar manner only the difference between the specimens on a dry substrate and those supplied with water is greater. The partial saturation during the night in the dry variant does not fully balance the loss in the water content during the day. The water deficit of *S.s.* and *S.c.* increased even in the night hours under natural conditions. The tufts of *S.c.* supplied with water brought the variations of the deficit during the day within physiological limits. *S.s.* did not balance its water turnover even after it was supplied with water. The water losses by day were always greater than the partial saturation by night.

D. The Production of Carbohydrates

In all feather-grasses supplied with water the production of carbohydrates was measured at 20, 4, 12, and 20 o'clock on July 16th and 17th. In *S.c.* also under natural dry conditions. The results are given in Table 1. Under extremely arid natural conditions *S.c.* showed loss of carbohydrates in the parts above the ground. If supplied with water, all the plants under study showed an increase of carbohydrates in the leaves, with the exception of *S.c.* in which the decrease in the amount of carbohydrates continued.

Discussion

If we want to find the causal explanation of the distribution of the feather grasses in Czechoslovakia, we have to begin with the study of the habitats in their localities studied in the whole area under research. The first systematic research into the soil characteristics is described by ÚLEHLOVÁ in the preceding paper. Dealing with the humidity demands of the plants under study the above-mentioned paper points to the fact that xerophytic properties increase as follows: *S.s.—S.j.—S.p.—S.c.* The same sequence is also reported by MARTINOVSKÝ (1964). While studying the steppe vegetation in Hungary we arrived at the following sequence of resistance to drought as measured by rate of leaf-dessication: *S.s.—S.p.* and *S.j.—S.c.* (KVĚT and RYCHNOVSKÁ 1965). If this sequence of xerophytic properties is right, then their natural distribution in a locality must correspond to it. The locality on the hill of "Křížová hora" proved our hypothesis. During two typical summer days in which our microclimatic measurements were performed, differences in the habitat found were adequate to the humidity demands of the plants under study. The humidity and temperature extremities increased in the covers of *S.s.—S.j.—S.p.—S.c.* The biological test, based on the use of *Teucrium chamaedrys* as a phytometer, corresponded to the water relations of the habitat; only in the case of *S.s.* its high value indicated an exceptional situation in this locality, as the vegetation there requires more mesophytic conditions; the high value is due to the extraordinarily long period of drought. The site of *S.c.* also displays a high level of the water deficit (although this part of the locality suffering from strong exposure is continuously covered with vegetation and some xerophytic adaptation may be supposed to have taken place here) so that this also seems to be a case of exceptionally pronounced aridity and overheating.

Fig. 7. — Daily variation of the relative water saturation deficit in the leaves. The full line belongs to *B.e.*, *S.j.*, *S.s.*, *S.c.*, and *S.p.* growing on a naturally dry substrate, the dashed line to the plants supplied with water on July 16th and 17th, 1963.
The x-axis: time in hours. The y-axis: water content in per cent. of maximum saturation (left side), relative water saturation deficit (right side).

If we compare the physiological properties of the plants under study in the extreme conditions and after supplying the specimens with water we may find out that the reactions of plants explain their distribution to a considerable degree.

Stipa stenophylla stands closest to the mesophytes both in its distribution and in its physiological properties. Thus, for example, the transpiration curve which we measured in the mountains of Bílé Karpaty in 1962 is typical for the mesophytes. Similar conclusions may be drawn from the reversibility of the water deficit in the plant as studied in a previous paper (RYCHNOVSKÁ 1963). In the period of our experiments in the area of „Křížová hora" the manifestation of the physiological activity of the plant were much suppressed by the ever-increasing period of drought. As it cannot be assumed that the feather grasses are able efficiently to regulate the rate of transpiration by means of their stomata but by means of their general xerophytic structure and the furling of the blade, *S.s.* could not — even during the existing period of drought — diminish the rate of transpiration although its water deficit was very pronounced. As *S.s.* does not markedly unfurl its leaves during a humid period, supply of water resulted in no increase of the rate of transpiration — on the contrary, a decrease took place. This decrease is, however, apparent if the rate of transpiration is expressed relative to the water content in the leaves. If the rate of transpiration is reduced to dry weight, the two curves are conform to each other as to their character, the only marked difference being the pronounced shift of the maximum to the morning hours in the case of specimens supplied with water. After supplying the plants with water the curve of the water deficit did not conform to the normal physiological curve but the production of carbohydrates during the day increased considerably. We can conclude from these facts that *S.s.* balanced on the verge of its physiological capacities, as: the photosynthesis was high when supplied with water, but the water relations of the plant had obviously underwent unfavourable changes.

Stipa joannis is the second species in the sequence arranged according to the increasing xerophytic properties. In our experiment it appeared as the most adaptable plant easily surviving the periods of extreme drought. The rate of transpiration, although it was high enough, was obviously reduced by the plant itself, as it increased twofold when water was supplied. The water deficit returns to the initial value during the night hours even in dry periods, and no fundamental change could be observed after supplying the specimens with water. Similar relations can be presupposed as far as the photosynthesis. When supplied with water the photosynthesis appears considerably high.

Stipa pulcherrima grows in extremely dry biotopes, to which it is perfectly adapted, so that the extreme conditions in the period of our measurements did not do any harm to it. The rate of transpiration was low, but it cannot be much higher in any case. Supplying the specimens with water resulted only in the shift of the maximum to the morning hours which can be explained by increased water content in the tissues during that period. The variations of the water deficit return more or less to the same value, even if the partial saturation with water does not fully compensate the day losses. After supplying the plant with water the curve of the water deficit reaches optimum values, the curve of carbohydrates shows only a small variation; no remarkable increase of photosynthesis was found. It seems probably that even under dry conditions the diurnal variation of the photosynthesis is very similar.

Stipa capillata was, contrary to all expectation, damaged by the drought most of all. The rate of transpiration was low and no increase took place after supplying it with water; only the maximum was shifted to the morning hours as in the case of *S.p.* The variations of the water deficit, however, indicated that the deficit was increasing and was not compensated by saturation in the night hours. When the specimens were supplied with water, the curve returned to its normal course within physiological limits, so that the deficiencies of the water relations were reversible. The production of glycides, however, suffered an irreversible change: loss of carbohydrates during the drought was not reverted to production of glycides when the tufts were supplied with water only the rate of decrease of glycides was slowed down. It should be noted here that this species was in an earlier state of its reproductive cycle, as it was just developing its flower-bearing stalks, while the reproductive cycle of the other species had already come to an end. This fact may have influenced the lower resistance towards drought.

Bromus erectus — the control plant — showed a great adaptability of its water relations. This was apparent from the greatest surpression of transpiration and the most pronounced water deficit. When the plant was supplied with water, it reacted much more intensively than the feather grasses; the much increased water turnover was the most characteristic signs of the change.

The above-mentioned facts point to the conclusion that the feather grasses under study—continental plants, occupying marginal localities of their area of distribution and found, in this country, only in arid habitats characterized by microclimatic extremities—are adapted to life there principally by their xerophytic structure and physiological properties. As the Central European climate is not belonging to the purely continental type, but forms a transition to the oceanic climate, these species adapt themselves very easily to the predominant climatic type of various periods. This adaptation is embodied in their anatomy and metabolism and in the more humid years it is so marked that the species react like the mesophytes in many respects. If, however, a genuine continental summer takes place, the feather grasses, not adaptive enough to regulate their physiological processes within wide limits definitely suffer from drought in this country. Thus a paradoxical situation emerges here: these xerophytic continental plants suffer from drought to the same extent as, and even more than, the genuine mesophytes which grow in less extreme localities. A nice example of this paradox is supplied by *S.c.* which, though it appears to be the most xerophytic species, suffered most of all from the extraordinary drought, almost extreme in this country. *Bromus erectus*, which belongs to the oceanic type of vegetation, survived the dry period, but its water turnover was almost equal to zero. Only in humid conditions are its physiological functions normal. The continuous presence of *B.e.* in the locality under study is obviously impossible. On the contrary, the feather grasses settle in similar biotopes quite regularly and are adapted to them; their distribution on the site roughly corresponds both to their humidity demands and to their distribution in various parts of Czechoslovakia, and is adequate to their physiological properties.

Souhrn

Práce se zabývá vodním režimem a mikroklimatickými rozdíly v porostech *Stipa pulcherrima*, *S. stenophylla*, *S. joannis* a *S. capillata* v rámci jedné lokality. Fysiologické vlastnosti studovaných rostlin autorka sleduje na základě terénního pokusu: srovnává přirozeně suché a uměle

zavlažené trsy, při čemž si všímá jejich denní křivky transpirace, obsahu vody v listech, chodu vodního deficitu a obsahu glycidů. Jako srovnávací rostlinu používá *Bromus erectus*, uměle vysazený na tento biotop. Zjišťuje, že nejodolnější vůči suchu je *S. pulcherrima*, dále *S. joannis*, nejméně *S. stenophylla*. *S. capillata* byla relativně nejvíce poškozena suchem, ač je jinak dosti odolná proti suchu, což autorka vysvětluje nedostatečným vývojem xerofilnosti při relativně vlhkém středoevropském klimatu, a malou přizpůsobivostí této rostliny k nastalé periodě sucha. Zjištěné vlastnosti rostlin plně souhlasí s vlastnostmi biotopů, na nichž se přirozeně vyskytují v Československu.

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