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Transpiration in Seven Plant Species Colonizing a Fishpond Shore

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Dedicated to Academician S. Prát on the occasion of his 80th birthday

Abstract. In 7 species (*Eleocharis palustris* R. Br., *Juncus bufonius* L., *Gypsophila muralis* L., *Trifolium repens* L., *Agrostis stolonifera* L., *Potentilla anserina* L. and *Achillea millefolium* L.) growing in a gradient of habitats from aquatic to terrestrial, on a sandy fishpond shore in Southern Bohemia, Czechoslovakia, the daily course of transpiration rate and water content was assessed gravimetrically in their cut-off transpiring parts on two typical summer days. Transpiration rate was largely controlled by microclimate but depressions occurred in *Juncus* and in some species growing in the drier habitats. The highest instantaneous transpiration rate and total daily transpiration per unit dry weight, about 100 mg g^{-1} min^{-1} and 50 g g^{-1} d^{-1}, respectively, were recorded in *Achillea* and *Trifolium*. The water turnover rate ranged from 16.1 g g^{-1} (H_2O) d^{-1} in *Juncus* to 10.7 in *Gypsophila*. The estimated daily maximum water saturation deficit was highest in *Eleocharis* (45.7%) and lowest in *Achillea* (15.0%). The adaptational significance of the observed phenomena is discussed.

Plant habitats as well as communities situated on fishpond shores exhibit various kinds of zonation determined by both the rate and extent of changes in the position of water level in the fishpond. During a dry growing season, shores of fishponds filled incompletely with water pass through a limoso-terrestrial sequence of ecophases (Hejný 1957, 1969, 1971), with conditions differentiated from shallow aquatic through marshy and waterlogged to purely terrestrial, in both space and time. Plants colonizing individual zones of such shores have to become adapted to progressively drier conditions. The demands of these plants on water supply are therefore of importance. The adaptation of individual plant species populations to the actual conditions of water supply may be illustrated by comparative measurements of their transpiration and other characteristics of water relations on suitably chosen days. The results reported here form part of the Czechoslovak IBP project nos. PT/5 and PP-P/3, see IBP News nos. 13 and 14.

Material and Methods

The transpiration and other measurements were accomplished on the shore of the Rožboud fishpond (lat. 49°07′ N., long. 14°08′ E., alt. 420 m), on 4th and 5th July 1964. The fishpond

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is situated in the Blanice river valley between the towns of Bavorov and Vodňany, Czechoslovakia, and its surface area is about 0.05 km^2. The water level in this small fishpond depends primarily on the local rainfall, hence it fluctuates widely. In the relatively dry summer of 1964, the water level was low, and the emerged sandy shores (covered with a thin layer of loamy mud only along the actual shoreline) were colonized by a hydrosere of plant communities: their zonation is to be described elsewhere. Seven abundant plant species, typical of the individual zones from the shoreline towards dry land, were selected for the measurements of transpiration. The following were the species and their respective plant parts the transpiration of which was measured; the ranges of sample fresh and dry weight are also given.

1. *Eleocharis palustris* R. BR., growing in shallow water (about 0.1 m deep) along the shoreline: a bunch of 6 fruit-bearing shoots cut off at ground level; fresh and dry weight 112 to 414 and 26 to 99 mg, respectively.
2. *Juncus bufonius* L., growing in a zone flooded with only a few cm of water: a bunch of the apical leaf- and fruit-bearing parts of several small shoots or only one such part of a single larger shoot; fresh and dry weight 95 to 400 and 24 to 100 mg, respectively.
3. *Gypsophila muralis* L., growing together with *Trifolium repens* (4.) and *T. arvense* in sandy soil in a zone with water level situated about 0.2 m below ground level: one whole flowering shoot; fresh and dry weight 36 to 305 and 8 to 79 mg, respectively.
4. *Trifolium repens* L., from the same habitat as (3.): a bunch of 6 mature basal leaf blades with parts of petioles; fresh and dry weight 134 to 354 and 27 to 59 mg, respectively.
5. *Agrostis stolonifera* L., growing somewhat higher up than (3.) or (4.) in sandy loam: 3 medium-sized shoots (10 to 17 cm high) with panicles emerged but not yet unfolded, and with the dead basal leaves stripped off; fresh and dry weight 137 to 406 and 43 to 125 mg, respectively.
6. *Potentilla anserina* L., growing in the same habitat as (5.): one mature and vigorous leaf or an apical part thereof; fresh and dry weight 115 to 392 and 28 to 106 mg, respectively.
7. *Achillea millefolium* L., included as a reference mesophyte, growing on dry land in a narrow strip of grassland separating the fishpond shore from an adjacent field: one mature and vigorous basal leaf; fresh and dry weight 110 to 392 and 18 to 71 mg, respectively.

Estimation of Transpiration Rate and Actual Water Content

The transpiration of this plant material was estimated gravimetrically from the water loss recorded after a 3 minutes' exposure to the local actual microclimate. The measurements were made at hourly intervals from the disappearance of dew at dawn to its reappearance or rain (on 4th July) in the late evening; for the description of the method see SLAVÍK (1974, pp. 253 to 257). The standard site for exposing the samples was situated in the *Gypsophila-Trifolium* zone (3.) and (4.). Prior to their weighing, the samples were placed into a polythene bag, and the manipulation with them being weighed twice in a tent took more or less the same time: the water loss recorded was therefore assumed to have taken place during the 3 minutes' exposure. A torsion balance was used, the accuracy of the weighing was $\pm$ 0.5 mg. The samples were then first air- and later oven-dried (at 105 °C). The water loss during the exposure of each sample was related to its dry weight estimated with an accuracy of 0.1 mg. The initial fresh weight and the dry weight of each sample were used to calculate its actual water content expressed on a dry weight basis. In view of the wide random variation in the actual values of both water content and transpiration rate, their daily courses were evaluated from gliding averages, each calculated from 5 consecutive actual values. These averages were used for estimating the other characteristics of plant water relations employed.

Estimation of Daily Total Transpiration and Water Turnover Rate (WTR)

These estimates were made for the second day of measurement, 5th July 1964, when the weather was more regular than on 4th July. The daily total transpiration [g H_2O g^{-1} dry weight d^{-1}] was calculated, from dawn to dusk (exact time stated with the results in Tab. 3), by adding up the averaged values of transpiration rate per minute recorded each hour, each value multiplied by 60. The water turnover rate (WTR) [g H_2O g^{-1} water content d^{-1}] *i.e.*, the daily total transpiration per 1 g water contained in the plant material, was estimated by relating the total daily transpiration to the daily average water content in the samples.

Estimation of the Daily Maximum Water Saturation Deficit (WSD)

This was estimated as the percentage difference between the highest and lowest averaged water content recorded during the day. For the ways of calculating daily total transpiration, WTR and WSD see, *e.g.*, RYCHNOVSKÁ *et al.* (1972).

Accompanying Microclimatic and Other Measurements

The evaporative power of the air was estimated with Piché-type evaporimeters furnished with discs of green blotting paper 3 cm in diameter. Relative air humidity was measured within the stands of the plants investigated, with an Assmann-type ventilated psychrometer. Air-temperature data were read off the dry-bulb thermometer of the psychrometer; in addition, air and water temperatures were measured with mercury-in-glass thermometers to the nearest 0.1 °C. Soil moisture content was estimated gravimetrically. For all these methods see Klika *et al.* (1954). The weather on 4th and 5th July 1964 is characterized by the data of the meteorological station at Vodňany: the daily average temperatures, sunshine duration and rainfall were 17.4 and 15.3 °C, 7.1 and 12.5 h, and 6.7 and 0.0 mm, respectively. At the Rožboud fishpond, 4th July 1964 was the second warm day following a cool period, sunny and nearly windless during the morning and with clouds piling up during the afternoon. The sky became overcast at about 16 h, and a light shower with strong wind came between 18 and 19 h. The evening was warm and overcast, followed by heavy rain during the night between 23 h and 2 h. The next day was sunny and bright with a cool north-westerly breeze (up to 3.5 m s^{-1}) and with only few clouds. The two days were thus typical of the situations occurring in Central Europe prior to and after the passage of a cold front in summer.

Table 1

1a: Temperatures in the habitats of the species investigated. Minimum and maximum temperatures [°C] in selected habitats of the shore on the Rožboud fishpond on the two days of transpiration measurement

Habitat:	4 July 1964		5 July 1964	
	min.	max.	min.	max.
Water at shoreline in (1.)	14.5	20.8	15.1	21.2
Water at —5 cm in (2.)	15.4	23.6	15.6	23.2
Air at soil surface in (5.)	9.9	28.7	6.8	23.5
Air above the canopy in (5.)	9.5	28.6	7.5	24.2

1b: Lowest and highest temperatures [°C] recorded with the dry-bulb thermometer of the psychrometer in the air surrounding the transpiring plant organs of the seven species during the two days of transpiration measurement. For the periods of psychrometer measurements each day see Fig. 1.

Species:	4 July 1964		5 July 1964	
	lowest	highest	lowest	highest
1. *Eleocharis palustris*	19.1	28.1	16.5	25.0
2. *Juncus bufonius*	21.0	25.2	17.0	24.5
3. *Gypsophila muralis*	20.2	27.3	18.2	24.6
4. *Trifolium repens*	20.6	24.8	17.0	25.2
5. *Agrostis stolonifera*	21.2	24.8	17.5	25.4
6. *Potentilla anserina*	20.2	26.2	18.2	24.8
7. *Achillea millefolium*	18.7	29.9	20.8	25.2

Results and Discussion

Weather Conditions

Table 1 and Fig. 1 illustrate the microclimatic conditions on the two days of transpiration measurement. 4th July was evidently the warmer day

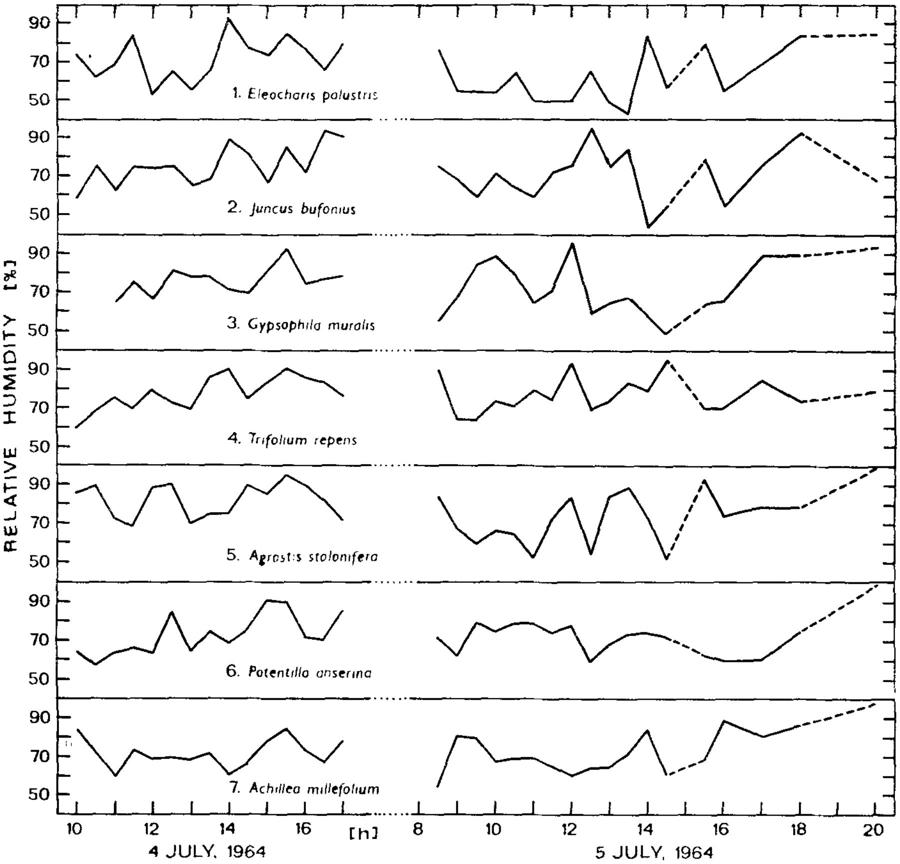


Fig. 1. Relative air humidity in the habitats of the seven species, recorded at the level of their transpiring parts during the hours of intense evaporation.

but the water was still cool. The differences between the maximum temperatures recorded in the habitats of the seven species stood out more clearly on the windless first day than on the somewhat windy next day. In the daytime, the relative air humidity appears to fluctuate least in dense communities of broad-leaved plants (4. and 6.). Here and in (7.), the minimum air humidities are somewhat higher than in the looser communities of (3.) and (5.). The widely fluctuating air humidity in (1.) and (2.) may appear surprising, close to the shoreline, but in (1.) the plants were growing wide apart, and in (2.) the sward was short. On the whole, the weather conditions appeared to favour rapid transpiration on 5th July more than on 4th July although the air temperatures were higher on the latter day. This is also illustrated by the differences in evaporation from Petri dishes, 17 to 18 cm in diameter, filled with water and exposed in habitats of some of the species on both days. On 4th July, from 7.30 to 13 h, the water loss ranged from 15 g in the habitat of (1.) to 40 g in that of (3.) and (4.); on the next day, during the

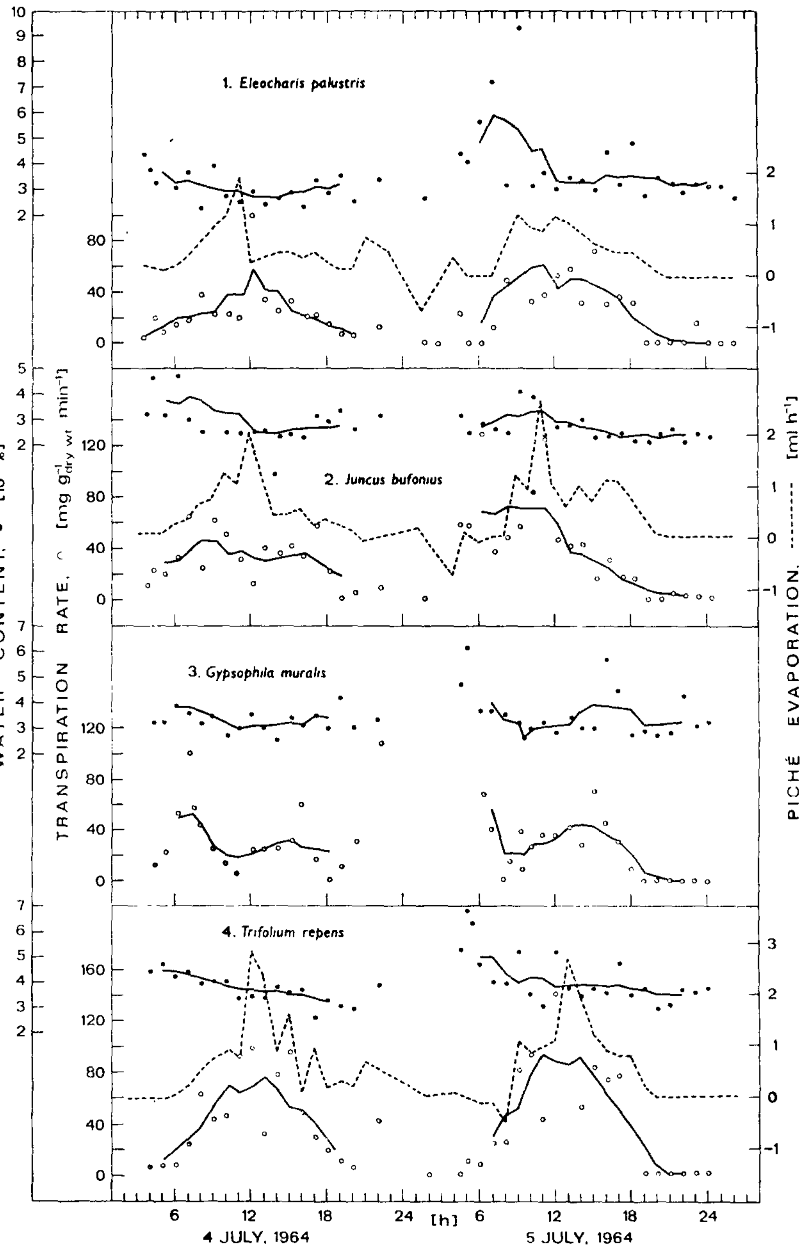
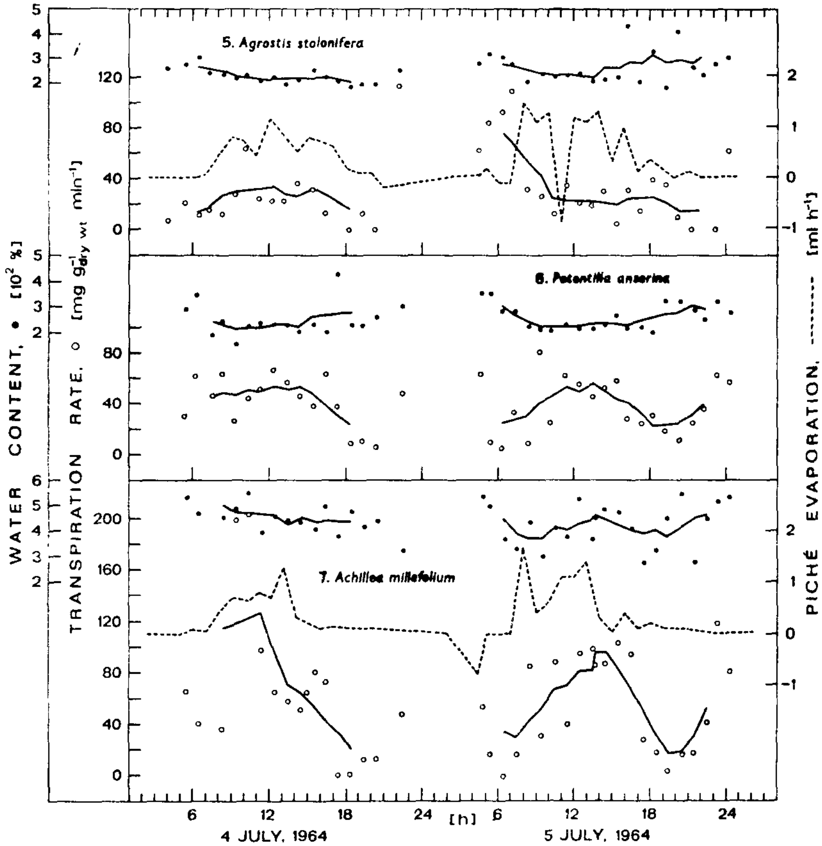


Fig. 2. Daily courses of water content (% of dry weight — gliding averages and original data) and transpiration rate (gliding averages and original data) in the seven plant species, and Piché evaporation (original data) in their respective habitats. Values of Piché evaporation recorded in 4 and 5 are applicable to 3 and 6, respectively.



same period, the corresponding losses ranged from 20 to 65 g. While the afternoon evaporation was poor on 4th July it was appreciable on 5th July.

Soil Moisture Content

Table 2 illustrates the soil moisture conditions in rhizospheres of the species investigated. The decrease of soil moisture content with both vertical and horizontal distance from the water table and shoreline, respectively, is evident; so is the soil moisture content in the sandy soil of the habitats of (2.) to (6.), decreased following a several days' dry period. The habitat of (7.) is exceptional: here the retention of water from the heavy rainfall in the night of 4th—5th July had been apparently noticeable due to the more favourable physical soil properties. The rather low soil moisture content in the habitats of (3.) to (6.) on 9th July suggests that drought may occur and affect plant life even on the shore of a fishpond.

Transpiration and Water Content in the Plants

Figure 2 shows the course of water content and transpiration rate in the seven species during the two days of measurement; comparison with Piché

TABLE 2

SOIL MOISTURE CONTENT EXPRESSED IN TERMS OF PERCENTAGES OF BOTH FRESH WEIGHT [% F. W.] AND DRY WEIGHT [% D. W.] RECORDED IN THE HABITATS OF THE SEVEN SPECIES AT THE BEGINNING OF THE TRANSPIRATION MEASUREMENT ON 4TH JULY AND AFTER A PERIOD OF RAINLESS WEATHER FROM 5TH TO 9TH JULY 1964. ON 4TH JULY, LARGE MIXED SOIL SAMPLES OF 150 TO 200 g WERE TAKEN; ON 9TH JULY, THREE+ OR TWO* SMALLER PARALLEL SAMPLES OF 50 TO 75 g EACH WERE EVALUATED FROM EACH HABITAT.

Species:	4 July 1964 [% f. w.]	4 July 1964 [% d. w.]	9 July 1964 [% f. w.]	9 July 1964 [% d. w.]
1. *Eleocharis palustris*	28.2	39.3	34.8*	54.3*
2. *Juncus bufonius*	25.6	34.5	30.7+	44.4+
3. *Gypsophila muralis* 4. *Trifolium repens*	11.4	12.8	10.0*	11.7*
5. *Agrostis stolonifera*	19.8	24.8	10.7+	12.0+
6. *Potentilla anserina*	19.1	23.6	4.7*	5.0*
7. *Achillea millefolium*	16.2	19.4	22.2+	28.7+

evaporation is also provided. The transpiration rate was apparently largely controlled by the microclimatic conditions: in (1.), (4.) and (6.) on both days, in (5.) only on the warm but windless 4th July, and in (3.) and (7.) on the cooler and somewhat windy 5th July. In the other instances, transpiration becomes depressed at some time during the day following a decrease in water content in the transpiring plant parts. The mesophytic *Achillea* (7.) and shallow-rooted *Gypsophila* (3.) seem to have been unable to adapt their water output to the hot and dry morning conditions of 4th July otherwise than by reducing it. *Gypsophila*, however, was able to restore it partly during the cloudy afternoon while *Achillea* was not. The high night "transpiration" of these two species and of *Agrostis* (5.) was probably due to dew or rainwater evaporation. *Agrostis*, a grass, transpired at a relatively slow rate but its transpiration increased markedly with the improved water supply after the rain, in the cool morning of 5th July. The reaction of the relatively slow

TABLE 3

DAILY TOTAL TRANSPIRATION (Σ TRANSP.) AND WATER TURNOVER RATE (WTR) DURING THE PERIOD OF ACTIVE TRANSPIRATION ON 5th JULY AND THE HIGHEST WATER-SATURATION DEFICIT (WSD), EXPRESSED AS PERCENTAGE OF THE DAILY MAXIMUM "SATURATING" WATER CONTENT RECORDED AT "SAT. TIME" IN THE MORNING OF 5th JULY.

Species:	Σ transp. [$g\ g^{-1}$ (d. w.) d^{-1}]	WTR [$g\ g^{-1}$ (H_2O) d^{-1}]	Period [h]	max. WSD [%]	sat. time [h]
1. *Eleocharis palustris*	32.13	10.90	6 to 20	45.7	7
2. *Juncus bufonius*	43.90	16.13	4 to 20	16.0	6
3. *Gypsophila muralis*	38.79	10.69	5 to 19	22.9	7
4. *Trifolium repens*	46.73	10.88	5 to 19	30.5	6
5. *Agrostis stolonifera*	32.40	12.10	5 to 21	17.6	6
6. *Potentilla anserina*	33.56	13.17	5 to 20	26.5	6
7. *Achillea millefolium*	50.92	12.11	5 to 20	15.0	6

transpiration in *Juncus bufonius* (2.) was similar; here, however, the drastic reduction of transpiration in the afternoon of 5th July might have been explained only if the reactions of the stomata had been followed. The highest instantaneous transpiration rates per unit dry weight, about 100 mg g^{-1} min^{-1}, have been, naturally, recorded in *Achillea* (7.) and *Trifolium* (4.), both mesophytes containing little mechanical tissue in their leaves, but the intense transpiration of *Agrostis* (5.) in the morning of 5th July approaches these values. This species seems to behave in an opportunist way, readily taking advantage of a temporarily improved water supply.

The overall characteristics of water output presented in Table 3 are instructive. All the species appear to transpire intensely, above all again *Achillea* (7.) and *Trifolium* (4.): this priority is, however, largely due to the already mentioned small amount of mechanical tissue in their transpiring organs. The water turnover is also rapid in all the seven species. *Juncus bufonius* (2.), while controlling its water output and maintaining a small water saturation deficit, changed its water content 16 times during the day. The water relations in *Achillea* (7.) and *Agrostis* (5.) were comparably balanced, but less so in *Trifolium* (4.) and *Potentilla* (6.), which is not surprising in view of the low soil moisture content in their habitats. The substantially reduced water content found in *Eleocharis* (1.) is surprising. However merely illustrative all these data are, they may be compared with those reported and discussed by RYCHNOVSKÁ *et al.* (1972), on water relations in grassland plants and vegetation.

PAZOUREK and PRÁT (1954), CETL (1957), and later KVĚT and RYCHNOVSKÁ (1965) demonstrated the usefulness of evaluating the desiccation of plant organs from either the physiological or ecological viewpoint. The daily courses of transpiration and other characteristics of plant water relations presented here require further analysis as well as confirmation. That would be, however, beyond the scope of this brief communication, which is among the first to provide information on water relations in vegetation of the type given. Under constant conditions, water output was measured in another set of 7 species (also including *Juncus bufonius*) colonizing a fishpond shore of the same kind as ours (RYCHNOVSKÁ in HEJNÝ 1969, pp. 370—372). Our estimates of WTR derived from the original data on both stomatal and cuticular transpiration range from some 2.5 g g^{-1} H_2O d^{-1} in *Coleanthus subtilis* (TRATT.) SEIDL to about 12 in *Eleocharis acicularis* (L.) R. *et* SCH., with only 3.7 in *Juncus bufonius* (our value 16.1), all fully turgescent plants. Our results are consistent with the data on grassland plants given by RYCHNOVSKÁ *et al.* (1972) and RYCHNOVSKÁ (1972), and with those on bigger freshwater littoral plants forming compact stands such as *Phragmites* and *Glyceria maxima* (HARTM.) HOLMB., by RYCHNOVSKÁ (1973), KVĚT (1973), RYCHNOVSKÁ and ŠMÍD (1973), KRÓLIKOWSKA (1973) and by other authors. These authors mostly worked with larger shoot portions having presumably a small transpiring surface per unit weight. This probably is why higher WTR values and transpiration rates were found by us in the relatively small detached plant parts. The presence or absence of the so-called "Ivanov effect", *i.e.*, a short-time transient increase in transpiration rate in freshly cut-off plant parts, see SLAVÍK (1974), was not checked in our plant material: this may have led to some over-estimate of water output. The low soil moisture content and intense irradiation associated with a relatively dry microclimate in some of the habitats on sandy fishpond shores also suggest a comparison with the water relations in plants growing in rather dry habitats. Indeed, the rapid water turnover and transpiration, possibly also connected with a great versatility in internal characteristics of water relations, found in at least some of the species colonizing emerged fishpond shores, seem comparable with these features found in plants of dry habitats in Central Europe (see, *e.g.*, RYCHNOVSKÁ and KVĚT 1963, RYCHNOVSKÁ-SOUDKOVÁ 1966, RYCHNOVSKÁ *et al.* 1972).

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