EKOLOGIA POLSKA (Ekol. pol.)	26	2	193–212	1978

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THE TRANSPIRATION OF HELOPHYTES*

ABSTRACT: In the years 1974–1975 investigations were carried out into the transpiration dynamics and water content of the helophytes during the growing season. The investigations covered the following 6 helophyte species, dominant in the lake littoral: *Phragmites australis* (Cav.) Trin. ex Steud., *Glyceria aquatica* (L.) Wahlb., *Typha latifolia* L., *T. angustifolia* L., *Acorus calamus* L., *Schoenoplectus lacustris* (L.) Palla. The helophytes were found to use in the transpiration process up to 3 m^3 of water per 1 m^2 surface area of the community during the growing season. Helophytes show maximum transpiration rate at noon, or an impeded transpiration rate at this time of the day, this feature depending on the species. During the growing season, the transpiration rate increases from spring until midsummer, and then towards the autumn it steadily decreases.

KEY WORDS: Lakes, helophytes, transpiration, water content.

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1. INTRODUCTION

The use of water by plants during the transpiration process is an important element in the hydrologic balance of an ecosystem. During transpiration, that is, evaporation of water from the tissues, plants utilise over 80% of the radiant energy absorbed by the leaves (Strebeyko 1966).

In view of the ever-increasing demand for water by the industry, agriculture, communal administration, and other areas of economy, there has been a world-wide interest in the utilisation of water for transpiration and evaporation in bodies of water. It was Otis (1914)

*Praca wykonana w ramach problemu węzłowego nr 09.1.7 („Produktywność ekosystemów słodkowodnych").

who already pointed out that the amounts of water removed by aquatic plants may many times exceed the quantities evaporated from the open water surface. Similar findings have been reported by Uryvaev (1953), Wolny (1956), Brežny, Mehta and Sharma (1973). The predominance of evapotranspiration over evaporation compensates, with an excess, for the limitation of the evaporation from the open water surface between plants by the plants themselves, due to the shading and thereby reducing the radiant energy inflow to the water surface, and making impossible a free outflow of the water vapour (Eisenlohr 1966).

As regards Poland, the relevant literature contains little information on the utilisation of water for the transpiration by helophytes. The available data refer to fish ponds (Kocół 1952, Wolny 1956), or lakes, but the studies concerned were carried out under experimental conditions and the results were adjusted to a per lake basis (Bernatowicz, Leszczyńska and Tyczyńska 1976, Tyczyńska – in press). Under natural conditions, Durska (1972, 1974) conducted studies of the effect of fungal parasites on helophyte transpiration.

In connection with the situation presented above, in the years 1974–1975 studies of helophyte transpiration under natural conditions were carried out. The studies covered the following 6 helophyte species, dominant in the lake littoral: *Phragmites australis* (Cav.) Trin. ex Steud., *Glyceria aquatica* (L.) Wahlb., *Typha latifolia* L., *T. angustifolia* L., *Acorus calamus* L., *Schoenoplectus lacustris* (L.) Palla. The research was carried out at the Wetland Research Laboratory of the Institute of Ecology, Polish Academy of Sciences, Mikołajki.

2. TERRAIN DESCRIPTION, MATERIAL AND METHODS

The study area included 3 eutrophic lakes in the Masurian Lakeland, situated in the largest lake-group in the Region of the Masurian Great Lakes: Lake Bełdany, Lake Tałty and Lake Inulec (Table I). In the littoral of the lakes, 4 sites were set out. They were located in plant communities in which the helophyte species studied were found to occur in monospecific patches, or constituted a typical association Scirpo-Phragmitetum, with 1 or 2 dominant species.

Table I. Characteristics of the lakes (data from the Institute of Inland Fisheries, Olsztyn)

Lake	Area (ha)	Length of shore line (m)	Volume in m^3 (thousands)	Emergent plants		
				area (ha)	per cent of total area	per cent of length of shore line
Bełdany	940.6	33,300	94,847.6	*	*	*
Tałty	1,831.2	57,200	248,407.2	121.8	6.6	74.2
Inulec	178.3	10,600	8,263.9	27.1	15.1	93.7

* No data available.

Site 1 was set out at the north-western shore of Lake Bełdany, in an area where there was a *Glyceria aquatica* belt, several metres broad and extending along the shoreline. At its borders single stalks of *Phragmites australis* occurred, gradually passing over into a unispecific patch with *Phragmites australis*. In the central part of the *Glyceria aquatica* community, on the water side, there was a small patch with *Typha latifolia*.

Site 2 was situated in a shallow, small, sandy bay (50–70 cm deep) at the eastern shore of Lake Tałty. There was a monospecific patch with *Phragmites australis* on the southern side of the bay, and on the water side *Schoenoplectus lacustris* shoots were found in small aggregations. In the northern part of the site a multispecific community was found, in which *Phragmites australis*, *Glyceria aquatica*, *Typha angustifolia* and *Acorus calamus* occupied areas of similar size. In this community small numbers of *Sparganium ramosum* Huds. and *Iris pseudoacorus* L. occurred, in addition to the above-enumerated species.

Site 3 was set out at the north-eastern shore of Lake Tałty. The community, in which it was situated, consisted of: on the shore side – a patch with *Phragmites australis* along which on the water side a belt of *Typha angustifolia* extended, with numerous shoots of *T. latifolia*, and a belt with *Schoenoplectus lacustris*. On the water side *Equisetum limosum* L. shoots occurred in small numbers.

Site 4 was situated in the littoral of Lake Inulec, in a small bay located on the north-eastern shore of the lake. *Typha angustifolia* formed a belt, 5–7 m in breadth, along the shore. At the borders of the belt patches with *Phragmites australis* and with *Schoenoplectus lacustris* were found, but they occupied much smaller areas than those occupied by *Typha angustifolia*. On the shore side, shoots of *Acorus calamus*, *Sparganium ramosum*, *Iris pseudoacorus* and *Carex* spp. occurred in small numbers.

The study sites were set out in plant communities characteristic of the particular lakes, so they were representative of the vegetation present in the lakes on which the investigations were carried out.

All the helophyte species under study belong to the association Scirpo-Phragmitetum, in which they occur in various numeric ratios. This is the most widely occurring association of aquatic plants, most frequently found in eutrophic lakes (P o l a k o w s k i 1963). The individual patches of the association may differ in respect of the dominant species, or the size of the areas occupied by the particular species.

Phragmites australis – it appears to be a plant showing the highest viability in the association Scirpo-Phragmitetum (S z a f e r 1972). It is the most widely spread monocotyledonous hydrophyte species (S c u l t h o r p e 1967), being common also in the littoral of the lakes in the Masurian Lakeland. It represents there about 72% of the hard emergent vegetation (B e r n a t o w i c z and W o l n y 1974). It attains a height of 4 m, its leaves being up to 50 cm long and about 5 cm broad, arranged in two rows along the stalk. The average density of *Phragmites australis* in the lake littoral is 70 shoots per 1 m^2, varying between 18 and 240 shoots/m^2 (B e r n a t o w i c z and W o l n y 1969). F. Szajnowski (unpublished data) has reported that the average density of *Phragmites australis* (as determined on the basis of studies of 44 reed-belts of the lakes of northern Poland) amounted to 52 ± 4 individuals/m^2. This plant flowers from July to August.

Glyceria aquatica – like *Phragmites australis*, it is representative of Gramineae, being a species commonly occurring at the shores of bodies of water, where it often forms a monospecific community Glycerietum aquaticae. It is a distinctive species of the alliance Phragmition (S z a f e r 1972). This plant attains a height of up to 2 m, its leaves being up to 40 cm long and up to 2 cm broad, arranged in two rows along the stalk. Flowering time – June to August.

Typha latifolia – a representative of Typhaceae; a widely distributed species, distinctive of the association Scirpo-Phragmitetum (S z a f e r 1972). It is a perennial attaining a height of up to 5 m, with long leaves up to 2 cm broad, their lower parts being submerged in the water. During the flowering time, June to August, the leaves are usually longer than the stalk and the inflorescence together. Most frequently found in nutrient-rich waters. It occurs even in areas with a poor substrate aeration, its rhizomes sometimes reaching a level much below the water table (D a u b e n m i r e 1973).

Typha angustifolia – a representative of Typhaceae; common in the east and north of Poland, where it forms close, monospecific stands (S z a f e r, K u l c z y ń s k i and P a w ł o w s k i 1953). It often forms mixed communities with *Typha latifolia*, with which species it is known to form hybrids (B e r n a t o w i c z and W o l n y 1969). This is the distinctive species of the alliance Phragmition (S z a f e r 1972). The species attains up to 3 m in height, its leaves being arranged in a way similar to that in *Typha latifolia*, except for the fact that they are only 1 cm, at the most, broad. Flowering time – June to August. As in the case of *Typha latifolia*, during the flowering period the leaves are much longer than the shoot and inflorescence together.

Acorus calamus – a representative of Araceae, was imported to Poland from Asia in the 16th century. At present, it forms natural communities common in sheltered, nutrient-rich waters, and displaces other plant species (B e r n a t o w i c z and W o l n y 1969). It is also a distinctive species of the alliance Phragmition. This plant species attains a height of up to 1.2 m. Its leaves are sword-shaped with undulate edges, due to which their physiologically active surface is larger. Flowering from June to July.

Schoenoplectus lacustris – a representative of Cyperaceae, a plant enduring strong wave-action, growing in clumps and forming monospecific patches in the lake littoral. It is a distinctive species of the Scirpo-Phragmitetum association, occurring commonly in the Lowland of Poland and distributed almost throughout the world (S z a f e r 1972). The plant has a cylindrical, leafless stem, rising to a height of 3 m, with its lower diameter amounting to 1.5 cm. Flowering in June and in July.

Measurements of the transpiration of the helophytes were performed using the leaves, because, as had been found in earlier studies (K r ó l i k o w s k a 1971), they are the main transpiring organ of the plants. Only in *Schoenoplectus lacustris* were shoots taken into account. In this species, the shoots function as leaves. For each of the species under study the transpiration rate was measured in the afternoon hours every 14 days, from May to September in the years 1974–1975, in order to determine its seasonal variations. For the measurements 3 of the youngest, fully developed leaves of each plant were collected; in the case of *Schoenoplectus lacustris*, 3 randomly selected shoots were taken, which constituted 1 sample. For each species 3 samples were collected each time. In 1975, also during the period May to September, the biomass of the helophyte leaves and of *Schoenoplectus lacustris* shoots was determined, every 14 days, and the following quantities were calculated: the leaf weight of one plant, mean weight of a *Schoenoplectus lacustris* shoot. Each of the samples used for this purpose consisted of the leaves of 50 plants (10 from each species) and 10 shoots of *Schoenoplectus lacustris.* Each time 3 samples were taken, and at the same time the density was determined of the individual species at the sites. Every 7 days, from May to October, the water content in the plants was determined using leaves, leaf sheaths (Gramineae), stems, inflorescences and underground parts of the helophytes, as also young underwater shoots. A sample consisted of 3 analogous parts (fragments) from 3 plants of a given species. For each plant organ 3 samples were taken for each of the species studied. *Schoenoplectus lacustris* has not been taken into account.

For each of the species studied the transpiration rate was measured every hour in the day, between 8,00 and 19,00 hours. The samples were taken in the same way as in the studies of the variations in the helophyte transpiration rate during the growing season. The transpiration of the helophyte leaves, depending on their age and position on a plant, was measured by taking the leaves in age order, from the youngest to the oldest. A sample consisted of the leaves of 3 plants of each helophyte species, and each time 3 samples were collected. *Schoenoplectus lacustris* has not been taken into account.

The transpiration rate was determined by the quick weighing method (Ivanov, Silina and Cel'niker 1950), because this method makes possible the field determination of the transpiration of each plant component in a natural community, and it had already been used in earlier studies of the water regime of the helophytes (Królikowska 1971, 1972). Transpiration rate was calculated from the change of the weight of the evaporating leaves, and was expressed in milligrams of water transpired from 1 g of wet leaf weight during 1 hour. The amount of the water used for transpiration (in mm per months) was worked out by using Novikova's (1963) formula:

$$E_T = \frac{n \cdot E'_T \cdot P}{1000}$$

where: n – number of days in the given month, E'_T – transpiration rate during the light time of the day (12 hours) in g/g of wet leaf weight, P – leaf biomass in g/m^2 of community surface area.

The content of water in the plant material was worked out on the basis of the difference between the wet and the dry weights, after the material had been dried to a constant weight at 105°C, and was expressed in mg/g of wet weight.

For each study site, the density of plants in monospecific helophyte patches was worked out from 10 samples, each collected from an area of 0.25 m^2.

3. RESULTS

The growing seasons of the years 1974 and 1975 differed considerably by the weather conditions. In 1974, the weather conditions were less favourable for the process of evaporation than in the next year. For the growing season of the first year lower air temperatures, insolation and evaporation were recorded, and higher precipitation than for the growing season of 1975 (Table II).

Studies of the seasonal variations in the transpiration rate of the helophytes have shown that in each of the growing seasons the plants transpired different amounts of water, depending on the species and weather conditions. In the first year, when the growing season was colder and wetter, the highest transpiration rate was recorded for June and July, and the lowest for August. In the next year, the highest values were recorded for July, and the lowest for September (Figs. 1–3). The greatest differences in the transpiration rates of the helophytes during the two seasons were found for August, this being related to the differences in the weather conditions, because in the August of 1975 the amount of precipitation was higher by 75% than that recorded for the same month in 1974, whereas the insolation and evaporation were higher by about 25% than in the August of 1974. September was the only month of the year 1974 in which the transpiration rate of *Glyceria aquatica* and *Typha angustifolia* was greater than in the same month of the next year (Figs. 1, 2), while the transpiration rate of the remaining species was higher in 1975. The smallest differences in the transpiration rate between the two seasons were found for *Schoenoplectus lacustris* (Fig. 3). On an average, the helophytes

Table II. Climatic conditions during the growing seasons of 1974, 1975 (data from the Regional Observatory, Institute of Meteorology and Water Management, Mikołajki)

Month	Year	Monthly total			Monthly mean			
		rainfall (mm)	evaporation (mm)	sunshine duration (h)	relative air humidity (%)	daily temperature of air (°C)		
						max.	mean	min.
May	1974	75.0	215.3	207.2	74.9	14.8	10.3	6.4
	1975	38.3	216.1	233.2	77.6	19.2	13.7	9.2
June	1974	154.5	156.6	208.8	78.7	18.6	14.2	10.5
	1975	114.9	192.6	221.8	76.2	20.6	15.7	11.7
July	1974	92.1	126.0	143.0	83.5	19.3	15.2	11.7
	1975	136.2	212.8	261.3	76.0	23.7	18.7	14.1
August	1974	56.8	173.5	258.9	77.8	22.0	17.3	13.2
	1975	14.2	215.7	313.8	76.3	23.7	18.5	13.4
September	1974	35.9	128.2	172.9	80.5	17.9	13.6	9.9
	1975	61.6	184.3	212.2	76.7	20.9	15.5	10.7

transpired more water during the growing season of 1975 than during the corresponding period of 1974 by: *Acorus calamus* 72%, *Phragmites australis* 50%, *Glyceria aquatica* and *Typha latifolia* 35%, *Typha angustifolia* and *Schoenoplectus lacustris* 33%.

The weather conditions of the growing season of 1975, which favoured the evaporation, were reflected in the dynamics of the helophyte leaf biomass during the growing season. On the basis of the biomass determinations, performed during the measurements of the transpiration rate, it has been found that in *Glyceria aquatica* the highest leaf biomass values occurred in July, in *Typha angustifolia* in September, and in the remainder of the helophyte species in August (Fig. 4). Among the helophyte species studied the largest leaf biomass values per unit of community area were found for *Typha latifolia*, and the smallest for *Phragmites australis* (Table III). In the communities under study, the average plant density per unit area during the growing season was: *Phragmites australis* 107, *Glyceria aquatica* 156, *Typha latifolia* 50, *T. angustifolia* 98, *Acorus calamus* 78 and *Schoenoplectus lacustris* 220 shoots/m^2. With such high densities, and thereby high values of the helophyte leaf biomass, and high transpiration rates, during the growing season of 1975 the helophytes utilised large amounts of water for transpiration (Table IV), relative to the quantities evaporated (Table II). Each month they used for transpiration, on an average, between 240 and 600 mm of water/m^2 of community area. The largest amounts of water for transpiration were used by *Typha latifolia* and *Acorus calamus* – 3.0, and *Typha angustifolia* – 2.9 m^3/m^2, which are plants characterized by a low transpiration rate, but a high unit biomass of the leaves. *Phragmites australis* and *Glyceria aquatica*, plants with a small unit biomass of the leaves but with a high transpiration rate, were found to use for the process of transpiration, respectively, 1.2 and 1.5 m^3 of water per 1 m^2 of the community area, that is to say, half the amount used by the former species. *Schoenoplectus lacustris* was found to use during the growing season 2.1 m^3 of water from 1 m^2 of the community area, thus taking, with respect to the utilisation of water for transpiration, an

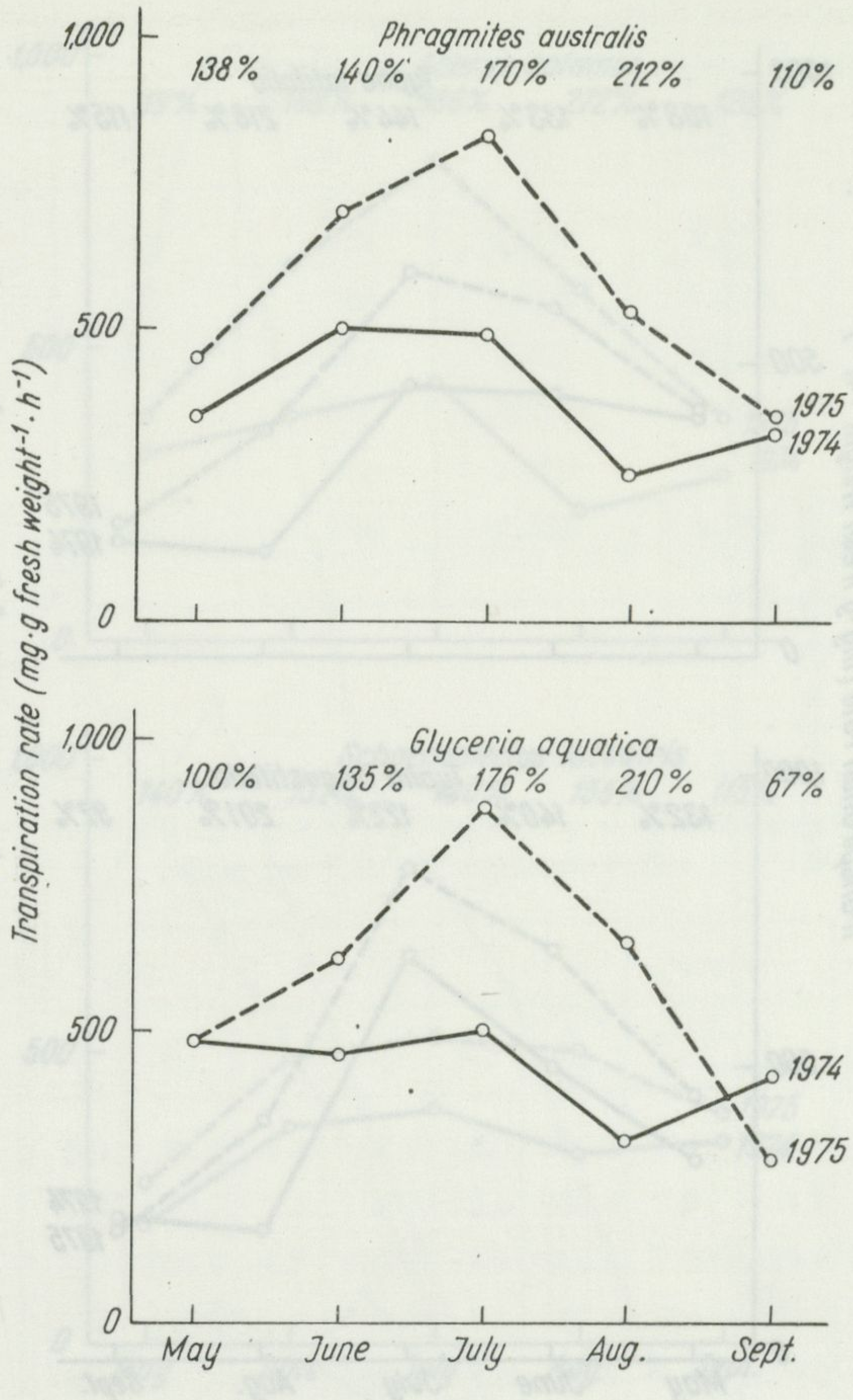

Fig. 1. Changes in the transpiration rate of ***Phragmites australis*** and ***Glyceria aquatica*** during the growing season of 1974, 1975

Per cent – transpiration in the year 1975 in the comparison with 1974

intermediate place among the helophyte species studied. Assuming that the sites selected for the study were representative of the plant communities of the particular lakes, the amount of water used by the helophytes for transpiration was estimated at 1.8 and 7.5% of the volume of Mikołajskie Lake and Lake Inulec, respectively.

Measurements of the water content of the helophytes have shown that during the growing season the amount of water contained in the individual organs of the plants was subject to variations slightly different from those observed for the transpiration rate. The content of water in the plants decreased from spring towards autumn (Figs. 5, 6). Most marked changes could be seen in the representatives of Gramineae, namely in *Glyceria aquatica* and Phragmites australis (Fig. 5). Variations in the content of water in the individual organs of these plants during the growing season were similar, except for the fact that the content of water in the leaves and inflorescences was subject to faster changes than in the stems or leaf sheaths. For *Glyceria aquatica* a higher fall in the water content in the inflorescences was

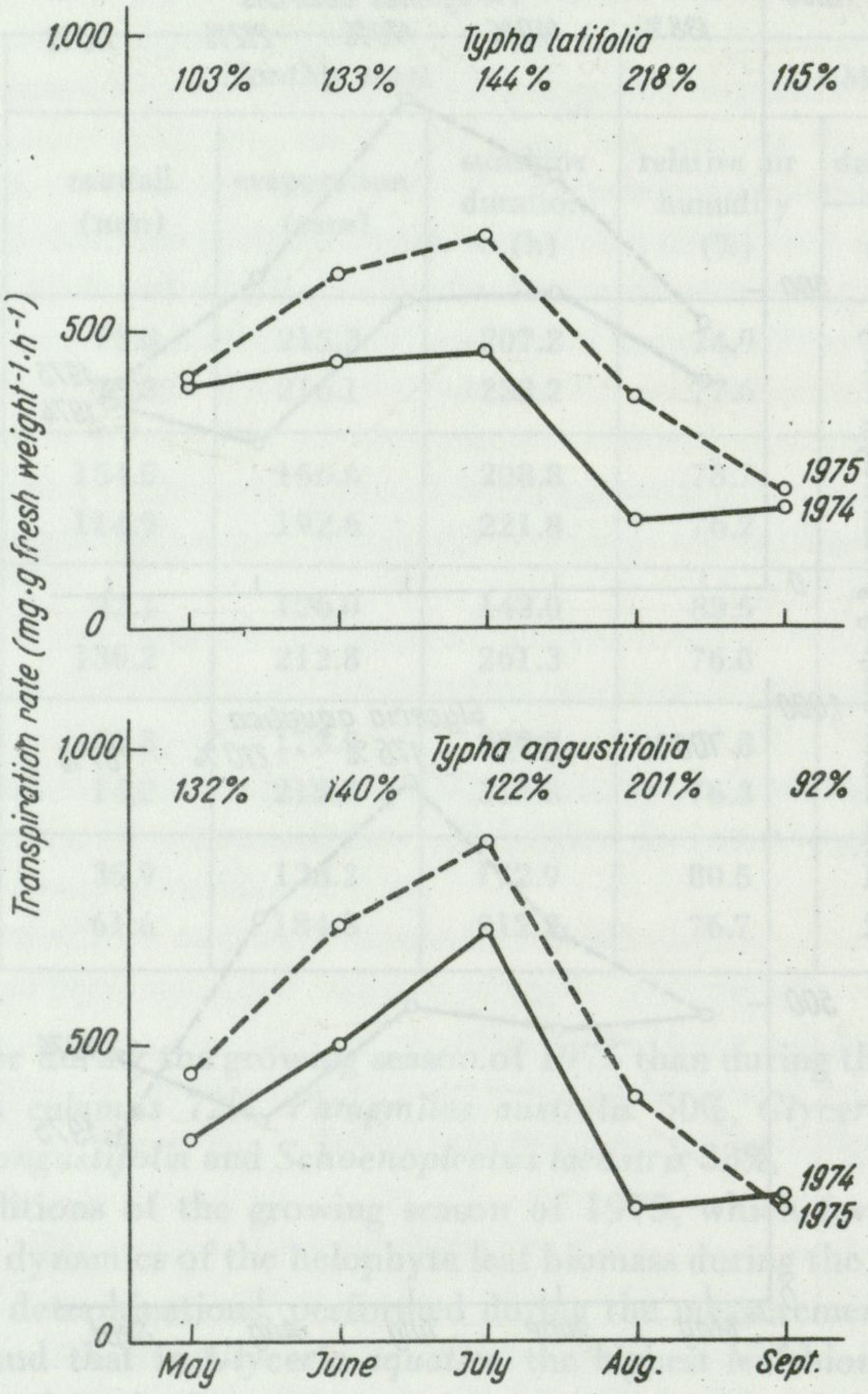

Fig. 2. Changes in the transpiration rate of *Typha latifolia* and *T. angustifolia* during the growing season of 1974, 1975

Per cent — denotations as in Figure 1

recorded than for *Phragmites australis*. Between July and October, the content of water in the inflorescences of *Glyceria aquatica* dropped from 600 to 100 mg/g of wet weight, whereas in *Phragmites australis* the content of water decreased from 680 in June to 240 mg/g in October (Fig. 5). In *Typha latifolia* (Fig. 6), as in the remainder of the helophytes studied, i.e., *Typha angustifolia* and *Acorus calamus*, changes in the content of water in the leaves, shoots and inflorescences were not so great, although the course of the changes was similar to that found in the representatives of Gramineae. There were some differences in the seasonal variations in the water content of the inflorescences. The content of water in the inflorescences of *Acorus calamus* dropped from 760 in July to 520 in October, in *Typha angustifolia* from 760 in August to about 620 in October, and in *Typha latifolia*, in the same period, from 820 to 600 mg water/g wet weight (Fig. 6). For all the helophytes studied the lowest seasonal variations in the content of water were recorded for the underground parts and the young underwater shoots, the water content decreasing by 2.4 up to 10.5% (Table V).

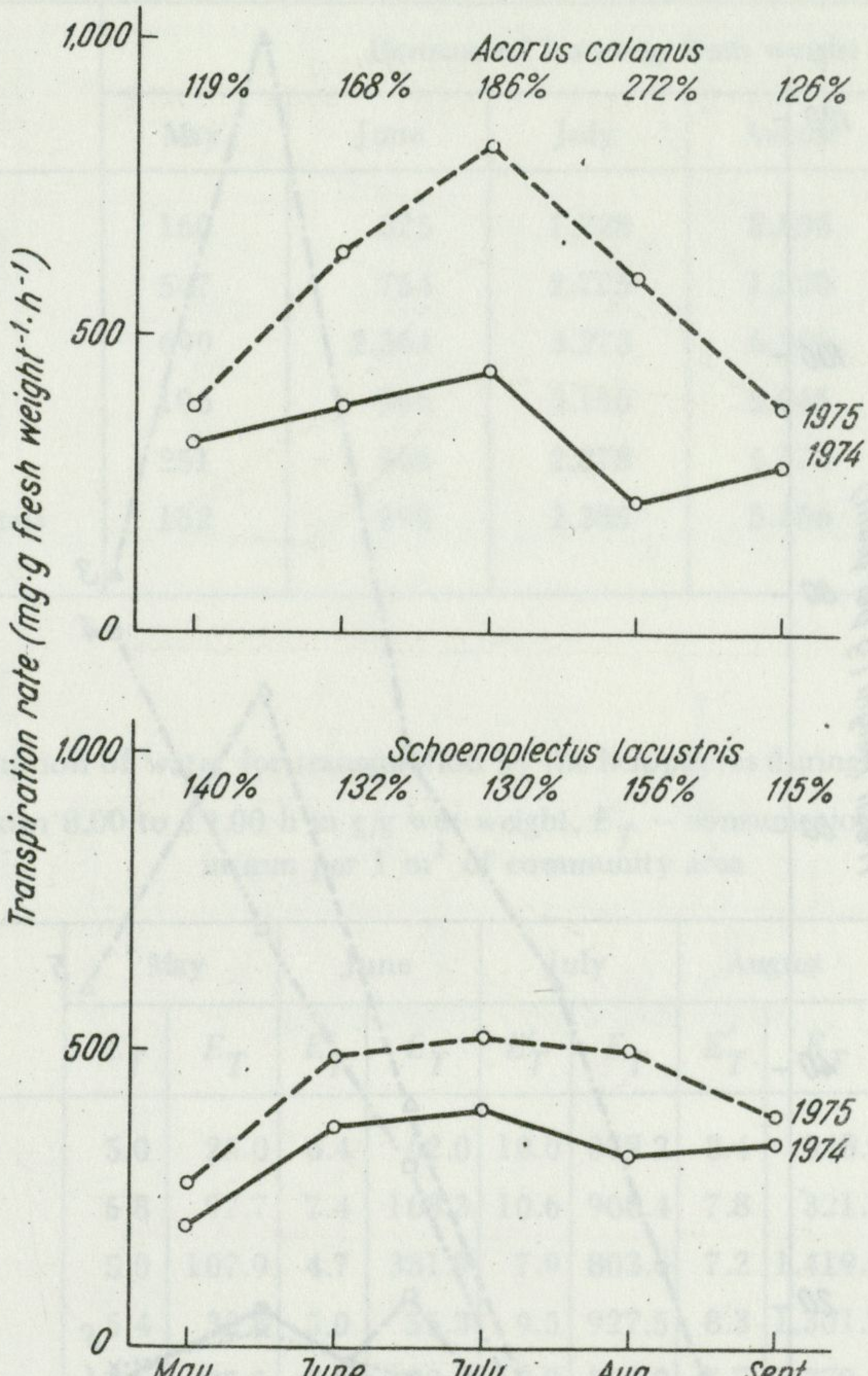

Fig. 3. Changes in the transpiration rate of *Acorus calamus* and *Schoenoplectus lacustris* during the growing season of 1974, 1975

Per cent – denotations as in Figure 1

During the day, fairly high rates of transpiration of the helophytes were recorded. On the basis of the daily variations in the transpiration process two plant groups have been distinguished. One of them included *Phragmites australis, Glyceria aquatica* and *Schoenoplectus lacustris*, the other group including *Typha latifolia, T. angustifolia* and *Acorus calamus*. The helophytes of the first group showed the highest transpiration rate at noon when the temperature was at its highest and the relative air humidity at its lowest (Fig. 7). In the helophytes of the second group at the same time of the day a decrease of transpiration could be seen (Fig. 8). Thus for the first group a single-peak curve of daily transpiration rates was obtained, the peak corresponding to the noon, whereas for the second group a transpiration rate curve was obtained with two peaks: at the first maximum value occurring before noon, and the second immediately following the noon. On the basis of the transpiration measurements made in the hours 8–19 the daily process of transpiration has been divided into 3 periods. For the first period the results from the measurements performed at 8, 9, 10 and 11 hours were adopted; for

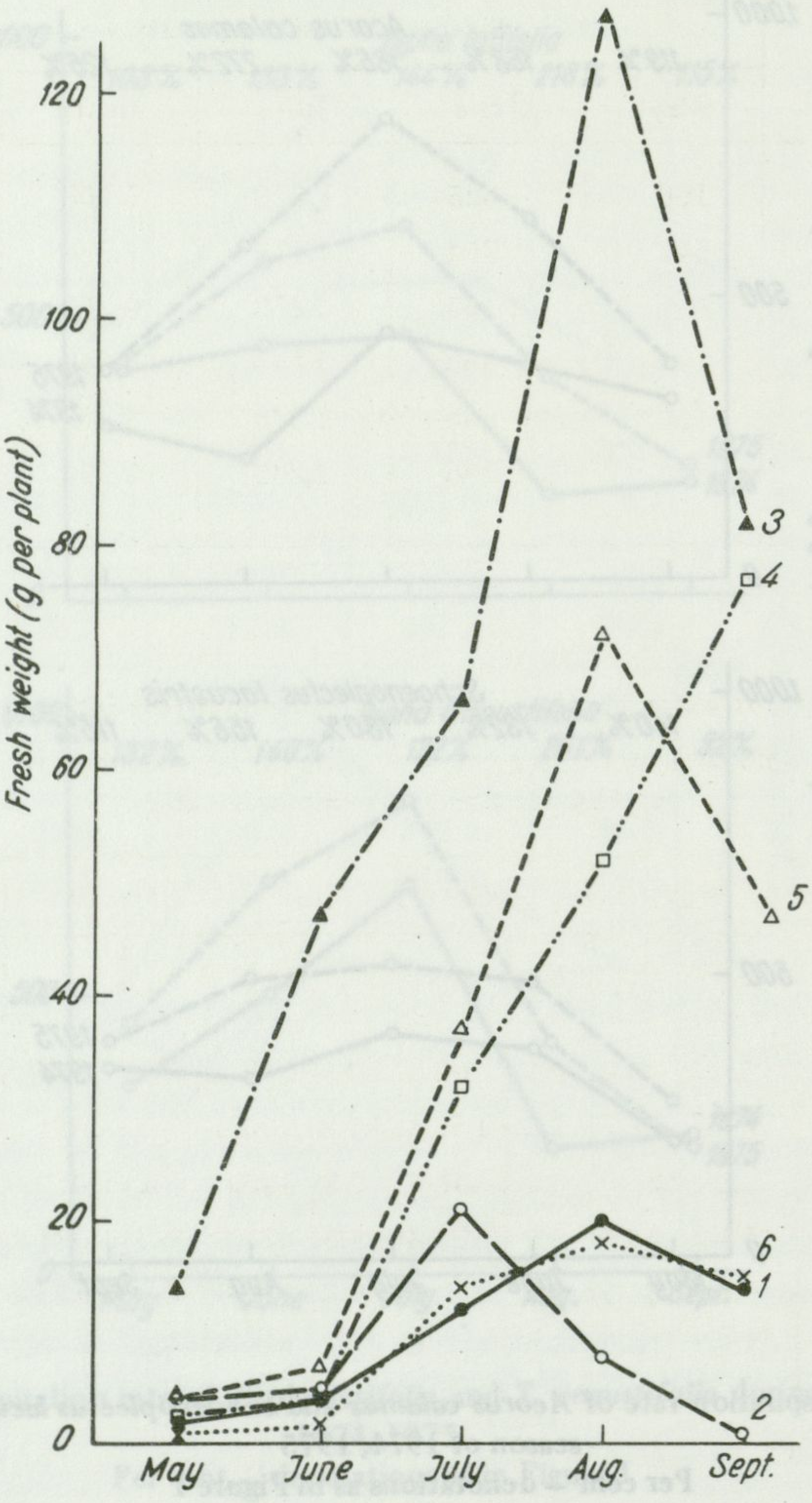

Fig. 4. Seasonal changes in the leaf biomass of the helophytes
1 – *Phragmites australis*, 2 – *Glyceria aquatica*, 3 – *Typha latifolia*, 4 – *T. angustifolia*, 5 – *Acorus calamus*, 6 – *Schoenoplectus lacustris* (shoots)

the second – at 12, 13, 14 and 15 hours; for the third – at 16, 17, 18 and 19 hours. It was found that during the first period, the morning period, *Typha latifolia*, *T. angustifolia* and *Acorus calamus* transpired on an average 40% of the amount of water transpired during the whole day. During the third, the afternoon period almost the same amount was transpired. *Phragmites australis*, *Glyceria aquatica* and *Schoenoplectus lacustris* transpired during the second, the noon period about 52% of the daily amount transpired. All the helophytes under study transpired the least during the third, the afternoon period – from 14.1 (*Schoenoplectus lacustris*) to 26.8% (*Typha latifolia*) of the amount of water transpired during the whole day (Table VI). The largest amounts of water per unit wet weight per day were transpired by

Table III. Changes in the biomass of transpiring leaves of the helophytes during the growing season of 1975

Plant	Biomass of leaves (g fresh weight per 1 m^2)					
	May	June	July	August	September	mean
Phragmites australis	160	325	1,228	2,108	1,498	1,063.8
Glyceria aquatica	547	754	2,775	1,328	97	1,100.2
Typha latifolia	699	2,364	3,273	6,360	4,085	3,356.2
T. angustifolia	196	366	3,156	5,045	7,546	3,241.8
Acorus calamus	251	566	2,878	5,373	3,650	2,543.6
Schoenoplectus lacustris (shoots)	152	298	2,285	5,106	4,444	2,457.0

Table IV. The consumption of water for transpiration by the helophytes during the growing season of 1975 E'_T – transpiration from 8,00 to 19,00 h in g/g wet weight, E_T – consumption of water for transpiration in mm per 1 m^2 of community area

Plant	May		June		July		August		September		Mean	
	E'_T	E_T	E'_T	E_T	E'_T	E_T	E'_T	E_T	E'_T	E_T	E'_T	E_T
Phragmites australis	5.0	25.0	6.4	62.0	10.0	379.2	8.4	548.9	3.8	172.6	6.72	237.5
Glyceria aquatica	5.8	97.7	7.4	168.3	10.6	908.4	7.8	321.1	3.4	9.8	7.00	301.0
Typha latifolia	5.0	107.9	4.7	331.9	7.9	803.6	7.2	1,419.6	2.7	335.8	5.50	599.7
T. angustifolia	5.4	32.8	5.0	55.3	9.5	927.5	8.3	1,301.2	2.6	586.3	6.16	580.6
Acorus calamus	4.6	35.5	7.2	122.3	9.8	877.9	7.7	1,279.2	4.6	636.0	6.78	590.2
Schoenoplectus lacustris	3.2	15.3	5.9	52.6	6.2	442.0	6.0	949.7	4.7	623.9	5.20	416.7

Phragmites australis and *Glyceria aquatica*, the smallest by *Typha latifolia* and *Schoenoplectus lacustris*.

Differences in the transpiration rate were observed not only between the individual helophyte species, but also between the successive leaves of the same plant (Figs. 9, 10), depending on the age of the leaves and their position on the plant. The leaf transpiration rate was found to vary depending on the developmental stage of the plants the successive leaves of which were taken for the measurement. All the helophytes showed a lower average transpiration rate of the leaves of flowering individuals (Figs. 9, 10). For younger leaves higher transpiration rates were recorded than for the older ones, regardless of whether or not they derived from flowering individuals. The leaves of the flowering plants transpired less than did the leaves from plants without inflorescences, on an average by about 30% – *Phragmites australis*, *Typha latifolia* and *Acorus calamus*, and by 10% – *Glyceria aquatica* and *Typha angustifolia*.

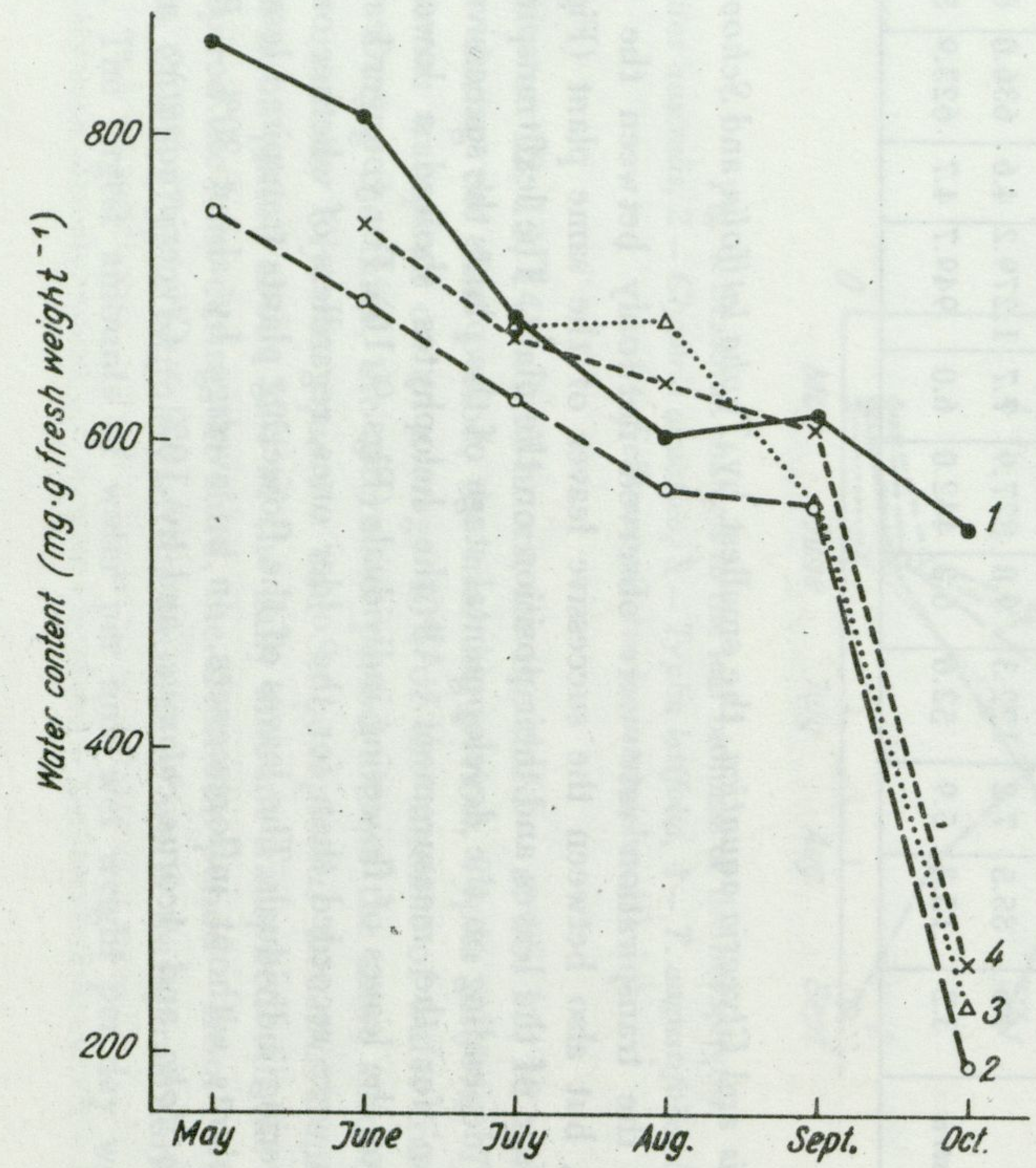

Fig. 5. Changes in the water content of *Phragmites australis* during the growing season 1 – stem, 2 – leaf, 3 – inflorescence, 4 – leaf sheath

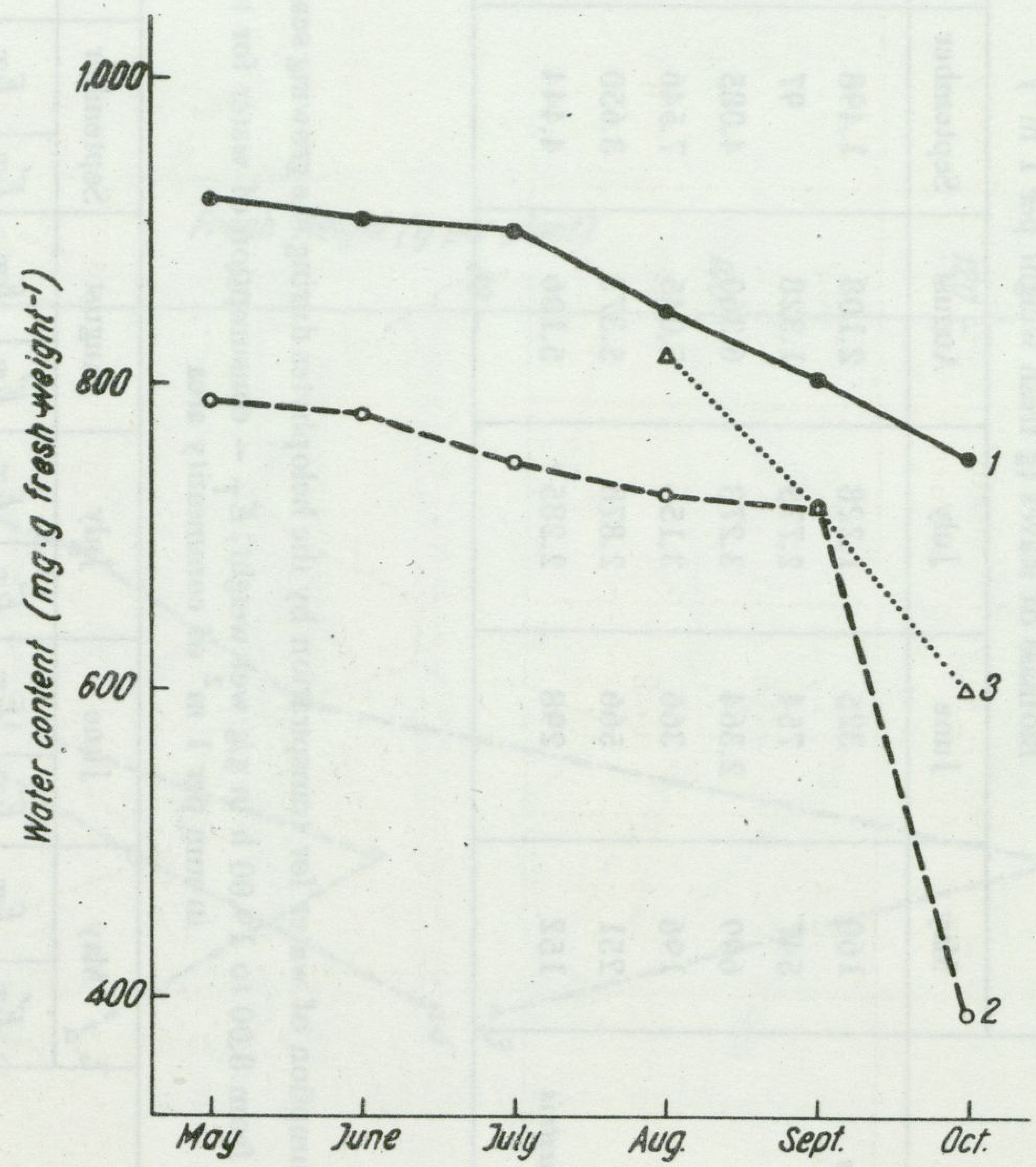

Fig. 6. Changes in the water content of *Typha latifolia* during the growing season 1, 2, 3 – denotations as in Figure 5

Fig. 5. Changes in the water content of *Phragmites australis* during the growing season 1 – stem, 2 – leaf, 3 – inflorescence, 4 – leaf sheath

Fig. 6. Changes in the water content of *Typha latifolia* during the growing season 1, 2, 3 – denotations as in Figure 5

Table V. Differences (per cent) in water content of the helophytes between the beginning (100%) and the end of the growing season (inflorescences of *Typha* spp. in August, the remaining plants in July)

Plant	Stems	Leaves	Sheaths of leaves	Inflore-scences	Underground parts	Young underwater plants
Phragmites australis	37.3	74.5	64.9	66.2	10.5	9.5
Glyceria aquatica	28.7	80.0	78.0	83.3	7.8	3.2
Typha latifolia	18.5	50.6	–	26.8	2.4	4.2
T. angustifolia	15.9	68.8	–	19.7	8.6	8.0
Acorus calamus	22.7	51.2	–	31.6	5.3	8.1

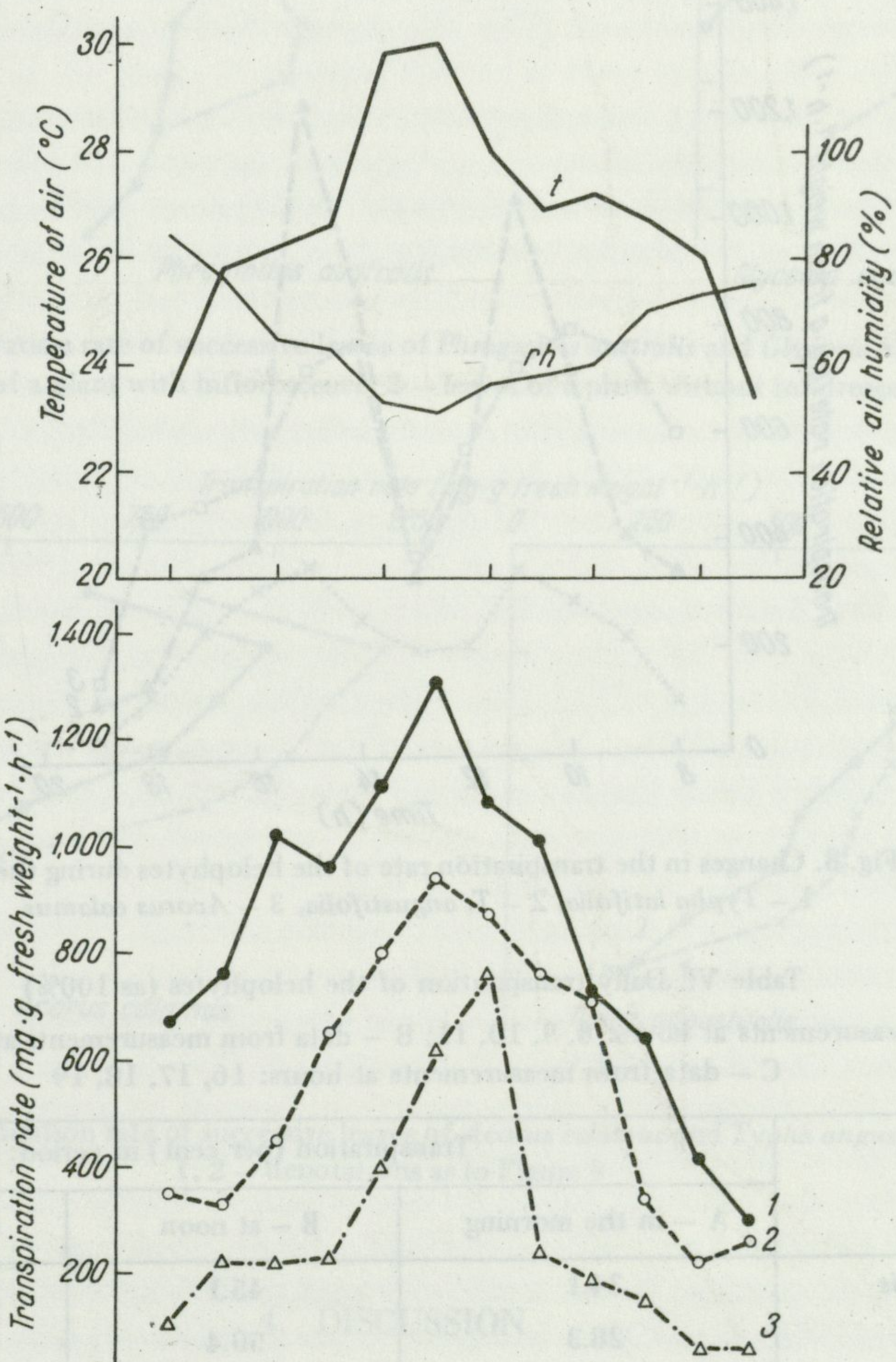

Fig. 7. Changes in the transpiration rate of the helophytes during the day
1 – *Phragmites australis*, 2 – *Glyceria aquatica*, 3 – *Schoenoplectus lacustris*

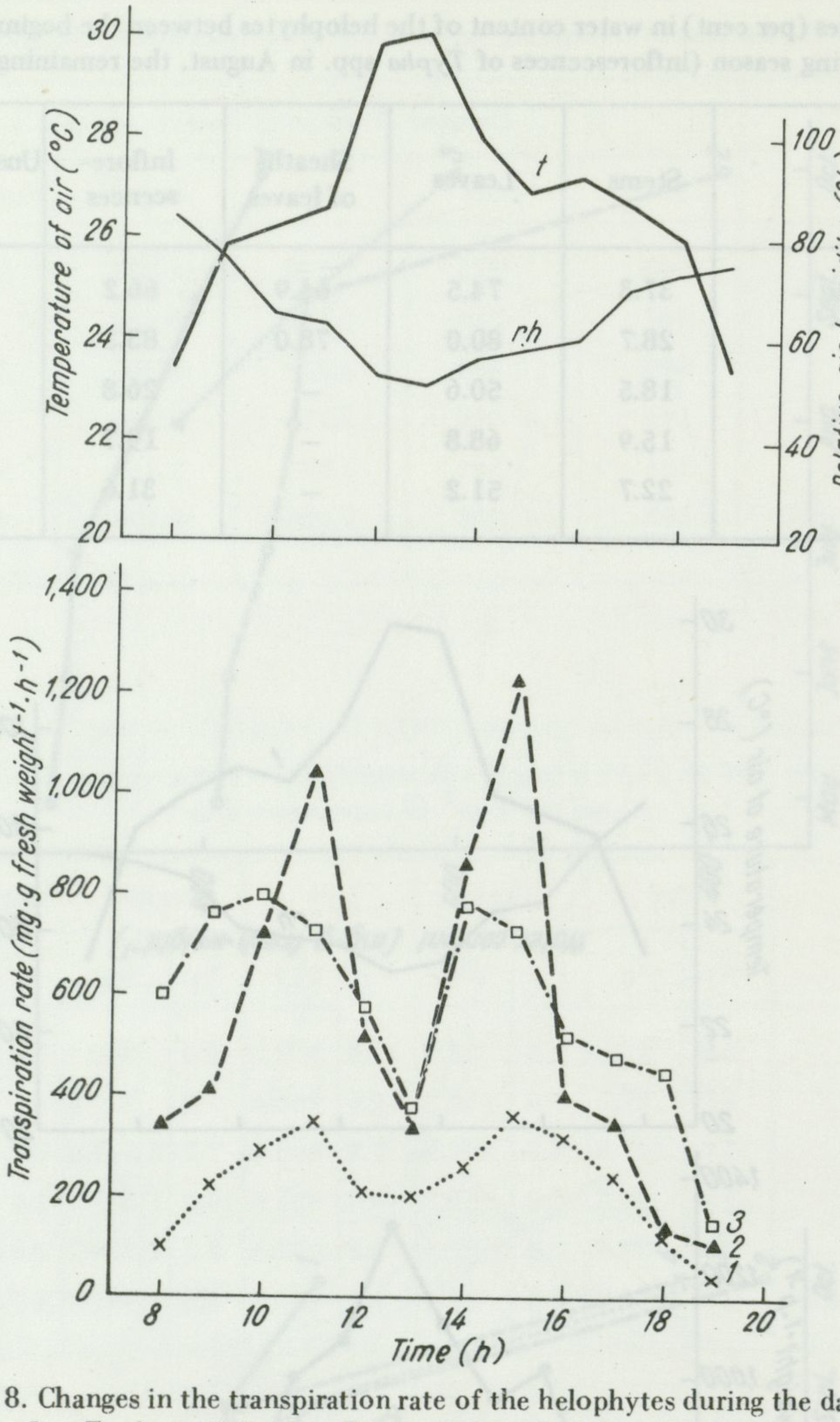

Fig. 8. Changes in the transpiration rate of the helophytes during the day
1 – *Typha latifolia*, 2 – *T. angustifolia*, 3 – *Acorus calamus*

Table VI. Daily transpiration of the helophytes (as 100%)

A – data from measurements at hours: 8, 9, 10, 11; B – data from measurements at hours: 12, 13, 14, 15; C – data from measurements at hours: 16, 17, 18, 19

Plant	Transpiration (per cent) in period:		
	A – in the morning	B – at noon	C – in the evening
Phragmites australis	34.1	45.1	20.8
Glyceria aquatica	28.3	50.4	21.3
Typha latifolia	35.5	37.7	26.8
T. angustifolia	38.9	45.6	15.5
Acorus calamus	41.8	35.8	22.4
Schoenoplectus lacustris	23.7	62.2	14.1

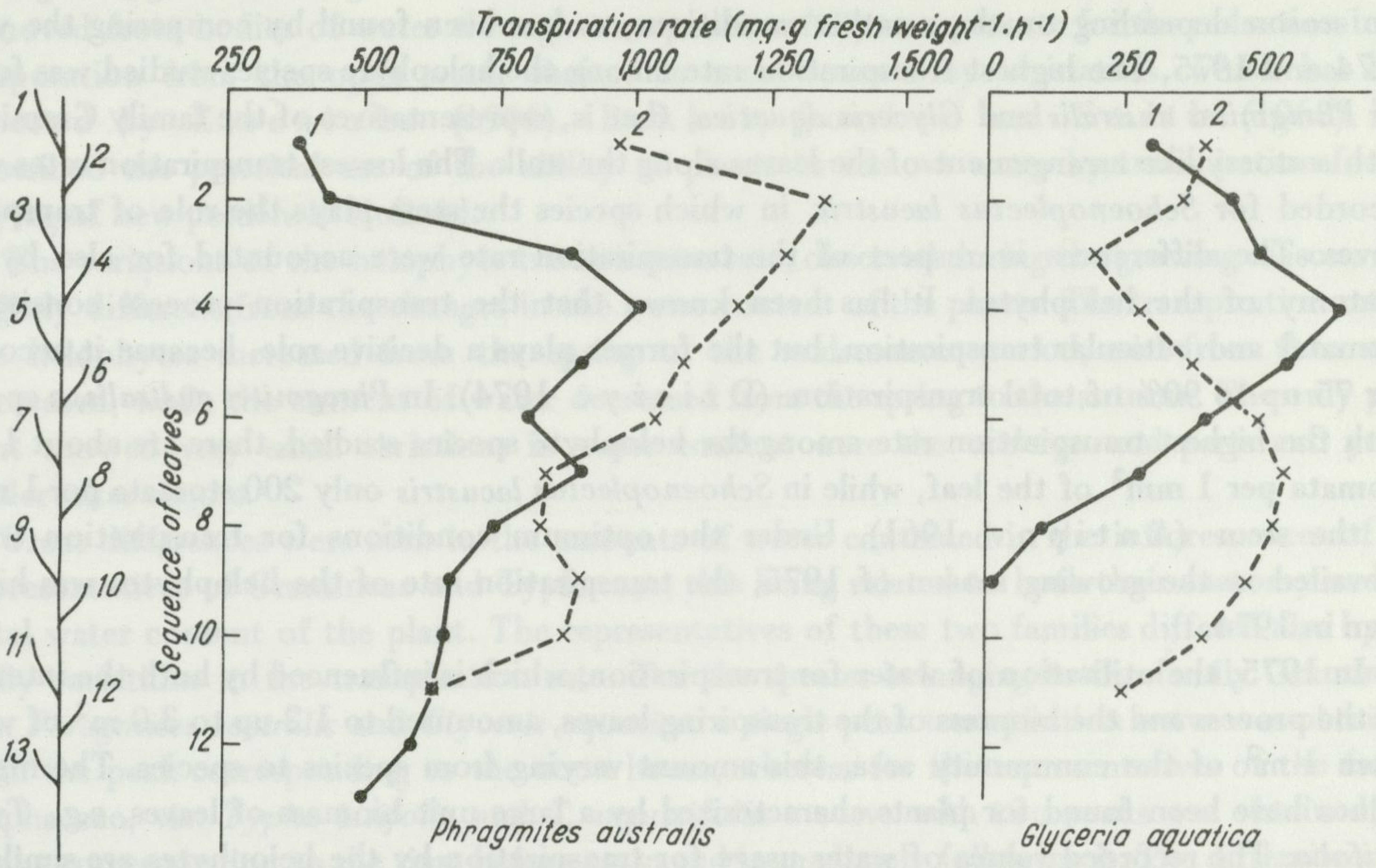

Fig. 9. Transpiration rate of successive leaves of *Phragmites australis* and *Glyceria aquatica*
1 – leaves of a plant with inflorescence, 2 — leaves of a plant without inflorescence

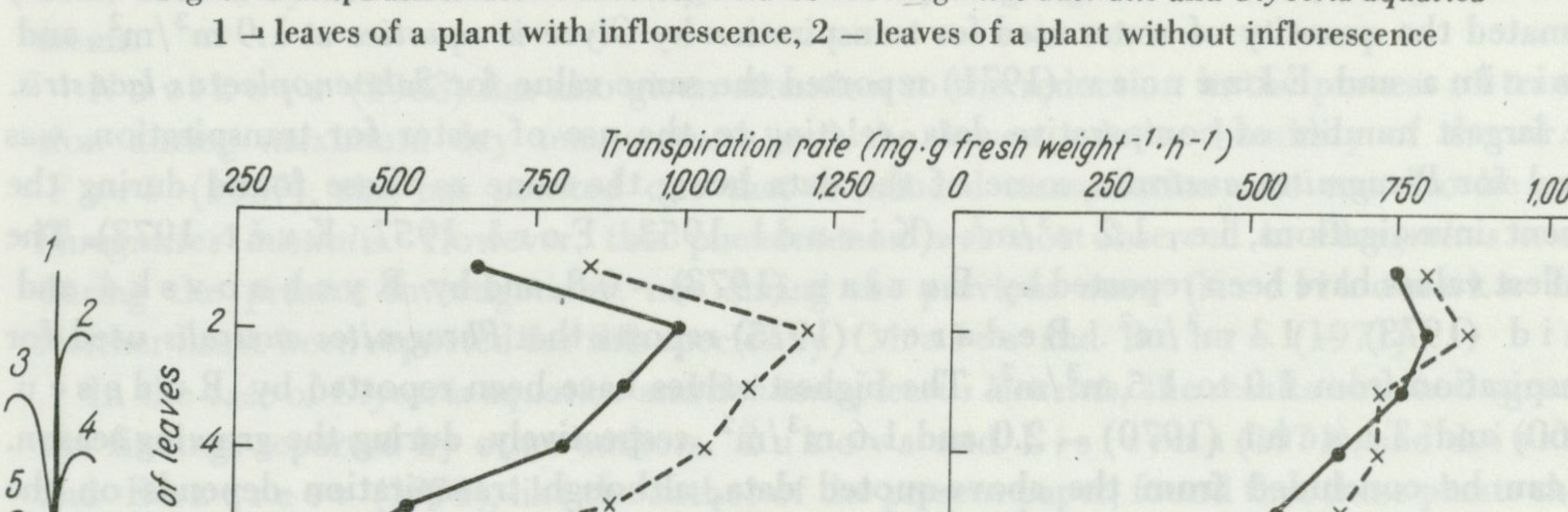

Fig. 10. Transpiration rate of successive leaves of *Acorus calamus* and *Typha angustifolia*
1, 2 — denotations as in Figure 9

4. DISCUSSION

The plants growing in the lake littoral transpire different amounts of water during the growing season and during the day, this depending on the environmental conditions and the species of the plant. During the growing season, the transpiration rate of the helophytes increased from spring to the midsummer, whereafter its decrease followed, the highest rates in the season depending on the weather conditions, as has been found by comparing the years 1974 and 1975. The highest transpiration rate among the helophyte species studied was found for *Phragmites australis* and *Glyceria aquatica*, that is, representatives of the family Gramineae with a storey-like arrangement of the leaves along the stalk. The lowest transpiration rates were recorded for *Schoenoplectus lacustris*, in which species the stem plays the role of transpiring leaves. The differences in respect of the transpiration rate were accounted for also by the anatomy of the helophytes. It has been known that the transpiration process consists of stomatal and cuticular transpiration, but the former plays a decisive role, because it accounts for 75 up to 90% of total transpiration (D z i e ż y c 1974). In *Phragmites australis*, a species with the highest transpiration rate among the helophyte species studied, there are about 1,800 stomata per 1 mm^2 of the leaf, while in *Schoenoplectus lacustris* only 200 stomata per 1 mm^2 of the stem (A n t i p o v 1961). Under the optimum conditions for transpiration which prevailed in the growing season of 1975, the transpiration rate of the helophytes was higher than in 1974.

In 1975, the utilisation of water for transpiration, which is influenced by both the intensity of the process and the biomass of the transpiring leaves, amounted to 1.2 up to 3.0 m^3 of water from 1 m^2 of the community area, this amount varying from species to species. The highest values have been found for plants characterized by a large unit biomass of leaves, e.g., *Typha latifolia.* The recorded values of water usage for transpiration by the helophytes are similar to those reported by other authors from different regions of the world. K i e n d l (1953) estimated the quantity of water used for transpiration by *Glyceria aquatica* at 1.9 m^3/m^2, and L i s i c i n a and E k z e r c e v (1971) reported the same value for *Schoenoplectus lacustris.* The largest number of comparative data, relating to the use of water for transpiration, was found for *Phragmites australis*, some of the data being the same as those found during the present investigations, i.e., 1.2 m^3/m^2 (K i e n d l 1953, F o r š 1957, K v ě t 1973). The smallest values have been reported by B u r i a n (1973) – 0.8, and by R y c h n o v s k á and Š m i d (1973) – 1.1 m^3/m^2. B e d a r e v (1975) reports that *Phragmites australis* used for transpiration from 1.0 to 1.5 m^3/m^2. The highest values have been reported by R u d e s c u (1960) and T u s c h l (1970) – 2.0 and 1.6 m^3/m^2, respectively, during the growing season. As can be concluded from the above-quoted data, although transpiration depends on the environmental conditions, the amounts of water transpired during the growing season by *Phragmites australis* in different regions of the world are similar.

When considering the water balance of ecosystems, the high values of water utilisation for helophyte transpiration found during the present investigations should be taken into account, this being even more important when the fact is considered that evapotranspiration by plants may many times exceed evaporation. As reported by F o r š (1957) and D u n i n - B a r k o v s k i j (1975), *Phragmites australis* transpired amounts of water which were twice and three times, respectively, as large as the amount evaporated from the open water surface. For *Glyceria aquatica* the following values have been found: 1.5–2.8 (U r y v a e v 1953), for *Typha latifolia* 5.0 (W o l n y 1956), 3.1 (O t i s 1914), 3.0 (E v s t i g n e e v and P o p o v 1957) and 1.7 (B r e ż n y, M e h t a and S h a r m a 1973). As regards *Typha angustifolia*, N o v i k o v a (1963) found that transpiration was smaller by 12% than the open water surface evaporation. B e r n a t o w i c z, L e s z c z y ń s k i and T y c z y ń s k a (1976) have found that the value of the evapotranspiration to evaporation ratio for Lake Śniardwy was 0.92, and that for Lake Warniak – 1.27, thus, as indicated by these data, this depends on the body of water. The main cause of this seems to be the ratio of the open water surface to the emergent-vegetation-overgrown surface. It is certain, however, that the amounts of water removed from bodies of water through transpiration fully compensate for the reduction in the evaporation from the open water surface in areas covered by vegetation, which has been reported by Eisenlohr (1966). Bakker, Jonker and Smith (1960) have described the practical use of the ability of plants to remove water by transpiration for the drying of new polders in Holland.

The variations of the helophyte transpiration rate, observed during the growing season, were slightly different from the changes in the water content of the plants. The transpiration rate of the helophytes increased from the spring to the midsummer period, and from then on it decreased, while the content of water decreased from the spring to the autumn. The only parts that showed very small variations in water content were the underground parts and young underwater shoots.

Great differences were seen in the amounts of water contained in the inflorescences of the representatives of Gramineae and Typhaceae, this being related to both their anatomy and the total water content of the plant. The representatives of these two families differed also by the daily variations in the transpiration rate. For the species belonging to the family Gramineae, i.e., *Phragmites australis* and *Glyceria aquatica*, a single-peak transpiration curve was obtained, with the peak corresponding to the noon hours, whereas for the representatives of the family Typhaceae, viz. *Typha latifolia* and *T. angustifolia* a curve with two peaks was obtained, the peaks corresponding to the time before noon and immediately following it. The differences had been caused by the different anatomy of the transpiring organs and their arrangement on the stems.

Novikova (1963) has also given attention to the reduction in the process of transpiration during maximum day temperatures and the lowest relative humidity of the air. Like Forš (1957), she has pointed out that a reduced transpiration rate can also be seen in *Phragmites australis*. However, this phenomenon was not observed in *Phragmites australis* during the present investigations, nor during the previous ones (Królikowska 1971). Neither has it been reported for this species by Chašes and Bobro (1971).

In the case of *Glyceria aquatica* and *Schoenoplectus lacustris*, the results obtained agree with the findings reported by other authors. Žukova and Lisicina (1971), and Lisicina and Ekzercev (1971), like the author of the present paper, found that these plants showed maximum transpiration in the hours 11–14. Gessner (1959) related the highest transpiration rates during the noon hours to the midday intensification of photosynthesis and thereby to an increased osmotic potential of the cell sap. The reduced rate during the late afternoon hours was connected with an increase in the air humidity and a fall of the temperature.

The amount of water vapour contained in the air at the time of humidity deficiency at high temperatures is sufficient for the saturation of air at lower temperatures, which factor in its turn has a reducing effect on the transpiration process (Bernatowicz and Wolny 1974). It should also be noted that the dew that condenses on the leaves in the evening makes it impossible to observe transpiration under natural conditions.

The observed differences in the transpiration rate between the younger leaves and the older ones were caused by both the different anatomy of the leaves and their position on the stem. Younger leaves transpired more than the older ones, which was particularly evident in the representatives of Gramineae, i.e., *Phragmites australis* and *Glyceria aquatica*, in which species the younger leaves are positioned higher above the open water surface, and therefore have better light conditions and are to a larger extent subjected to the action of the wind. Furthermore, younger leaves have a larger number of stomata per unit surface

(Demidovskaja and Kiričenko 1964). Rychnovská (1967) found a higher transpiration rate for the young leaves of *Phragmites australis*, and of *Glyceria aquatica* – Rychnowská et al. (1972). However, in his studies of *Typha latifolia* McNaughton (1973) did not find any clear differences in the transpiration of the leaves, related to their age.

The present investigations of the transpiration process, and of the use of water during this process by the helophytes, have fully confirmed the assumption that when occupying large areas in bodies of water, these plants contribute to the removal of water into the atmosphere. In the case of small bodies of water this may considerably affect the water balance of a water body, which is important from the economical point of view if fish ponds are taken into account. In view of the increasing world-wide deficiency of fresh water, the role of the process of plant transpiration in the hydrological systems of the particular regions should be taken into account.

5. SUMMARY

In the years 1974–1975 investigations were carried out into the transpiration rates of helophytes. The investigations covered the following 6 helophyte species dominant in the lake littoral: *Phragmites australis, Glyceria aquatica, Typha latifolia, T. angustifolia, Acorus calamus* and *Schoenoplectus lacustris.* The study area consisted of sites set out in three eutrophic lakes of the Masurian Lakeland: Lake Bełdany, Lake Tałty and Lake Inulec (Table I).

During the growing season the transpiration rate of the helophytes was found to increase from the spring to the midsummer period, whereafter its decrease followed. Maximum transpiration values were recorded for July, or August, depending on the prevailing weather conditions (Figs. 1–3). For the process of transpiration, the plants under study used different amounts of water, depending on their transpiration rate and on their leaf biomass, so they differed in respect of the amounts of water they removed from the bodies of water. The amounts transpired ranged from 1.2 to 3.0 m^3/m^2 of community area per growing season. Higher water utilisation rates were recorded for helophyte species with a lower transpiration rate but with a higher unit biomass of the evaporating leaves, i.e., *Typha latifolia, Acorus calamus* and *Typha angustifolia* (Fig. 4, Table IV).

On the basis of the daily variations in their transpiration rates the helophytes studied were divided into two groups: a group including *Phragmites australis, Glyceria aquatica* and *Schoenoplectus lacustris,* for which a single-peak transpiration curve was obtained, with the peak corresponding to the midday hours, and another group including *Typha latifolia, T. angustifolia* and *Acorus calamus.* For the latter group a two-peak transpiration curve was obtained, with the peaks corresponding to the hours preceding the noon and those immediately following it. Plants of the first group showed maximum transpiration during the highest daily temperatures and lowest relative air humidities, while plants of the second group showed during the same period lower transpiration rates (Figs. 7, 8).

Differences in the transpiration rate were also found between individual leaves, depending on their age, younger leaves showing a higher transpiration rate than that found for older leaves (Figs. 9, 10).

The amounts of water contained in the helophytes decreased from the spring to the autumn, the amounts of water contained in the leaves, inflorescences and stems being subject to greater variations than the amounts contained in the underground parts and in young underwater shoots (Figs. 5, 6, Table V).

6. POLISH SUMMARY

W latach 1974–1975 prowadzono badania nad intensywnością transpiracji helofitów biorąc pod uwagę 6 dominujących w litoralu jezior gatunków helofitów: *Phragmites australis, Glyceria aquatica, Typha latifolia, T. angustifolia, Acorus calamus* i *Schoenoplectus lacustris.* Miejscem badań były stanowiska wyznaczone w zbiorowiskach roślinnych w litoralu trzech eutroficznych jezior Pojezierza Mazurskiego: Bełdany, Tałty i Inulec (tab. I).

Stwierdzono, że w ciągu sezonu wegetacyjnego intensywność transpiracji helofitów wzrasta od wiosny ku środkowi lata i maleje ku jesieni, osiągając maksymalne wartości w lipcu lub w sierpniu, w zależności od panujących warunków klimatycznych (rys. 1–3). Zużycie wody na proces transpiracji, uzależnione zarówno od intensywności transpiracji jak i biomasy liści, było różne u poszczególnych gatunków. Ilość wody od-

prowadzana ze zbiornika w procesie transpiracji wynosiła od 1,2 do 3,0 m^3/m^2 powierzchni zbiorowiska w ciągu sezonu wegetacyjnego.

Większym zużyciem wody charakteryzowały się te gatunki helofitów, które miały mniejszą intensywność transpiracji, lecz większą biomasę jednostkową parujących liści, tzn. *Typha latifolia, Acorus calamus* i *T. angustifolia* (rys. 4, tab. IV).

Na podstawie przebiegu intensywności transpiracji helofitów, w ciągu dnia, wyróżniono dwie grupy roślin: pierwsza, do której należały *Phragmites australis, Glyceria aquatica* i *Schoenoplectus lacustris,* charakteryzowała się jednowierzchołkową krzywą przebiegu ze szczytem w południe, i druga, do której należały *Typha latifolia, T. angustifolia* i *Acorus calamus,* mająca krzywą dwuwierzchołkową, ze szczytami przed i po południu. Rośliny pierwszej grupy transpirowały maksymalnie w okresie panowania najwyższych w ciągu dnia temperatur powietrza i najniższych wilgotności względnych, podczas gdy rośliny drugiej grupy miały w tym okresie znacznie obniżone natężenie procesu transpiracji (rys. 7, 8).

Zróżnicowanie w intensywności transpiracji stwierdzono także między poszczególnymi liśćmi rośliny w zależności od wieku liści; młodsze miały większą intensywność transpiracji niż starsze (rys. 9, 10).

Zawartość wody w helofitach malała od wiosny ku jesieni, przy czym uwodnienie liści, kwiatostanów i łodyg ulegało większym zmianom niż uwodnienie części podziemnych i młodych pędów podwodnych (rys. 5, 6, tab. V).

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