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Morphological and anatomical changes in the petioles of *Nymphaea alba* L. and *Nuphar luteum* (L.) Sm. caused by oscillations of the water level in lakes

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Abstract

In this study we present morphological and anatomical changes in the petioles of *Nymphaea alba* and *Nuphar luteum* from two lakes greatly differing from each other in respect to the oscillation of their water level (Lake Salno — a stabilized natural reservoir, used for comparison; Lake Kwiecko — a natural reservoir for the Hydroelectric Plant in Żydowo, where the changes in the water level oscillate up to 3.1 m during a day under conditions of maximum retention). Nonrhytmic and turbulent water flows in Lake Kwiecko cause the elongation of petioles, a decrease in their diameter, and to a significant degree, the reduction of supporting elements — collenchyma, vascular bundles and idioblasts. These changes take place to a lesser extent in *Numphar luteum*. Although this species has a very wide ecological amplitude and does not need to adapt to changing habitat conditions, through anatomical modifications the oscillations in the water level have an unfavorable effect on its population in Lake Kwiecko.

Key words: Nymphaea alba L., Numphar luteum (L.) Sm., anatomy, biometry, water level oscillations

INTRODUCTION

Up until the middle of the 19th century, morphological and anatomical changes in plants caused by an aqueous environment were considered to be degenerations. These essentially false hypotheses have with time been completely abolished. Henslow (1894) found that the changed morphological and anatomical structure of aquatic plants is not a symptom of degeneration, but a phenomenon which is a part of the universal adaptation of organisms to the specific conditions prevailing in an aqueous environment. Schimper (1884) associated the morphological and anatomical changes in aquatic plants with the effect of hydrostatic pressure. Warming (1900) underscored the great influence of the mechanical effect of water on the external and internal form of aquatic plants. In his opinion, strong water currents cause the elongation of stems. He held that the length of aquatic plant petioles is dependent on the depth of the water. The opinions of Henslow, Schimper and Warming are called upon in the works of, among others, Starmach et al. (1976), Mikulski (1974) and Bernatowicz and Wolny (1974). Podbielkowski and Tomaszewicz (1979) attibute an important role in causing morphological and anatomical changes in hydrophytes to water currents and oscillations in the water level of lakes.

Oscillations in the water level of stable lakes are connected with the weather pattern whereas in hydroelectric and retention reservoirs, they are artificially regulated.

Conway (1940) and Laing (1940) worked on the aeration systems of water lillies. On the basis of their results, these authors found that in hydrophytes, the oxygen metabolism is independent of the amount of this gas in the water. Conrad (1905) was the first to distinguish three types of bundles in the cross section of a *Nymphaea alba* petiole: colateral, bicolateral and the so-called "simple" bundles. Strasburger (1972) described the simple bundles as incomplete vascular bundles or isolated sieve strands.

The effect of water retention in hydroelectric plant reservoirs on morphological and anatomical changes in hydrophytes has not been the subject of studies done in Poland until now.

MATERIAL AND METHODS

The material used for the morphological and anatomical studies was collected from two natural, post-glacial lakes — Salno and Kwiecko. These lakes form the experimental grounds of the Chair of Botany and Ecology of the Technical-Agricultural Academy in Bydgoszcz. Lake Salno, which has an area of 13 ha, is located in the Bydgoszcz Voivodship, north-west of Koronowo, at an altitude of 90 m above sea level. It is an eutrophic, flow-through reservoir, part of a series of lakes on the Byszewsko-Skarbiewska gutter (Spanidis 1984). Lake Kwiecko, covering an area of 88 ha, lies in the Koszalin Voivodship, about 1 km west of Żydowo at an altitude of 80 m above sea level. It is a fertile, flow-through reservoir. The Debrzyca River empties into it and the Radew River rises from it (Śpiewakowski 1974). These lakes differ in respect to the oscillation of their water levels.

Lake Salno is a relatively stabilized reservoir in which the oscillation of the water level depends mainly on the meteorological conditions. Lake Kwiecko, on the other hand, functions as the lower reservoir for the hydroelectric complex of the Żydowo Hydroelectric Plant. The oscillations in the water level in this lake reach, at maximum retention, 3.1 m. The oscillations of the water level in Lake Kwiecko during 1982-1983 are illustrated on Fig. 1.

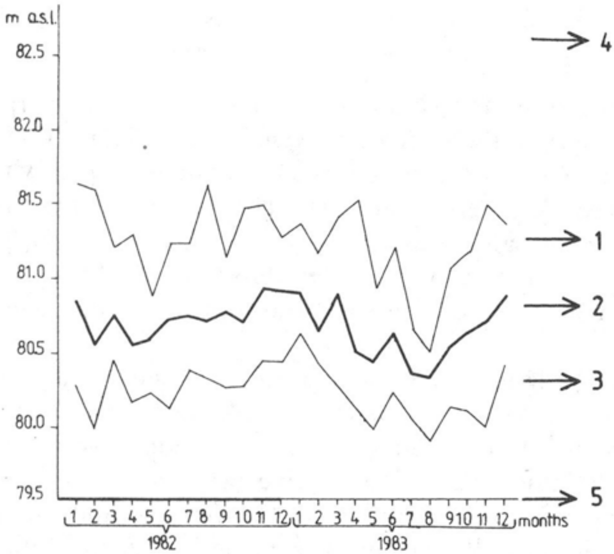

Fig. 1. Oscillations in the water level in Lake Kwiecko in 1982-1983. 1 — average maximum monthly water level; 2 — average daily water level; 3 — average minimum monthly water level; 4 — maximum recorded water level; 5 — minimum recorded water level; m a.s.l. — meters above sea level

In both of the studied lakes, on the inner side of the reed belt, patches of nympheids, mainly *Nymphaea alba*, are found.

The petioles of *Nymphaea alba* L. and *Nuphar luteum* (L.) Sm. from both lakes were studied. The material was collected in August in 1983 and 1984; 60 samples in all (15 of each species from each lake) were taken. The morphological studies of the *Nymphaea alba* and *Nuphar luteum* petioles pertained to their length and diameter. For anatomical studies, 5 cm pieces from the upper, middle and lower parts of the petiole were used, after which they were dehydrated in 70% ethyl alcohol. Sections approximately 90 μm thick were made with a sled microtome, next they were fixed in a mixture of ethyl alcohol and glycerine at a ratio of 1:1. These slides were used in the analysis of the internal structure of the petioles and in the comparison of the changes taking place in various places in them. The results of the measurements and the statistical work-up using variance and Duncan's test are given in Tables 1 and 2. The internal structure of the petioles is illustrated on microphotographs (Figs. 2-4).

RESULTS

NYMPHAEA ALBA L. PETIOLES

The starting point for comparative analysis of the morphological and anatomical changes in the petioles of *Nymphaea alba* and *Nuphar luteum* was the material gathered from the stabilized Lake Salno, with which the results from Lake Kwiecko were compared. The length of the *Nymphaea alba* petioles from Lake Salno was on average 127 cm, their thickness increased from the base of the petiole in the direction of the rhizome, its cross section had an oval shape. The statistical average of the petiole was in the range of 6213 μm.

Under the epidermis there was a rather regular ring of collenchyma which attained an average thickness of 246 μm. Under the collenchyma, bicolateral, colateral and simple vascular bundles were arranged in an alternating fashion in a rather regular ring while in the center of the petiole, they were dispersed. There were few xylem elements and the simple bundles were made exclusively of phloem. The numerical diferentiation of vascular bundles all through the length of the petiole was quite clear and was on average: bicolateral — 10.5, colateral — 11.3 and simple — 11.3. The vascular bundles were surrounded by a ring of oval paranchyma cells filled with starch. The amount of starch around the bundles decreased with increasing distance from the leaf blade. In a few of the segments from the lower part of the petiole, no starch at all was found. The middle part of the petiole was filled with aerenchyma with four large air channels in the middle. The average area of the channels was 0.84 mm^2. In the network of aerenchyma cells, as well as in the collenchyma, dispersed, incrusted with calcium oxalate trichomes — idioblasts, were found. Their number averaged 43.9 (Table 1, Fig. 2).

In Lake Kwiecko, which has an instablized water level, differences in the external and internal structures of the *Nymphaea alba* petioles from this lake in comparison with petioles from Lake Salno, were found (Table 1, Fig. 2). When the petiole lengths were compared, they turned out to be much longer, 80 cm on average. The diameters of the petioles indicated a significant reduction of their thickness of about 1000 μm over each segment. The average diameter of the petioles over all of the segments

Table 1

Some measurements of cross sections of *Nymphaea alba* L. petioles

Studied trait, units	Lake Salno				Lake Kwiecko				LSD $\alpha = 0.05\%$	
	petiole section			average	petiole section			average	for stand	for petiole sections
	upper	middle	lower		upper	middle	lower			
Petiole length, cm				127				207	31.0	
Petiole diameter, µm	6005	6065	6570	6213	5645	4603	5061	5103	514	630
Average thickness of colenchyma, µm	315	210	214	246	308	138	151	199	24.2	29.6
No. of collenchyma layers	8.6	6.7	6.9	7.4	6.9	4.8	5.1	5.6	0.6	0.7
No. of collenchyma bundles	11.5	11.0	11.5	11.3	5.4	5.7	5.0	5.4	0.6	0.8
No. of bicolateral bundles	10.6	10.1	10.8	10.5	7.1	7.3	8.1	7.5	0.4	0.7
No. of simple bundles	13.2	10.3	10.4	11.3	9.6	8.3	8.4	8.8	0.3	0.4
No. of idioblasts	83.6	25.7	22.3	43.9	37.9	3.8	1.7	14.5	3.8	4.7
Area of 4 central air channels, mm^2	0.70	0.80	1.03	0.85	0.92	0.64	0.67	0.74	0.17	0.24

Table 2

Some measurements of cross sections of *Nuphar luteum* (L.) Sm. petioles

Studied trait, units	Lake Salno				Lake Kwiecko				LSD $\alpha = 0.05\%$	
	petiole section			average	petiole section			average	for stand	for petiole section
	upper	middle	lower		upper	middle	lower			
Petiole length, cm				171				198	11.0	
Petiole diameter, µm	3527	3166	3087	3260	3308	2708	2656	2891	161	198
Average thickness of collenchyma, µm	222	173	121	172	183	126	104	138	10.0	11.0
No. of collenchyma layers	7.9	6.7	5.2	6.6	6.5	5.3	5.2	5.7	0.2	0.3
No. of colateral bundles	16.2	16.1	16.2	16.2	17.9	16.8	16.7	17.1	0.4	0.5
No. of idioblasts	44.6	29.8	29.1	34.5	21.8	10.5	8.6	13.6	3.3	4.1

was 5103 μm. In addition, there were very thin petioles growing out of the youngest parts of the rhizomes, 197 cm in length and 1386 μm in diameter.

In the arrangement of the tissues, a regular ring of collenchyma was noticed, but it was much thinner all over, having an average thickness of 199 μm. The thickness of the collenchyma layer in the upper segment of petioles from both lakes was similar. Significant differences could be observed in the middle and lowest segments of the petioles. The number of collenchyma layers of *Nymphaea alba* from both lakes differed in each of the three segments by 1.7-1.9. Differences in the number of vascular bundles between the samples from both lakes were also found. The number of sieve tubes and vascular bundles in the *Nymphaea alba* material from Lake Salno in all three segments was clarly higher, but no significant differences between the individual types were found. The lowest number of colateral bundles was found in the material from Lake Kwiecko, and slight differences had arisen within the segments. The number of bicolateral bundles was smaller in the material being compared. The most numerous group in this material was the simple bundles, which exhibited a tendency for reduction the greater the distance from the water surface. The aerenchyma and air channels were arranged analogically as in the material from Lake Salno. However, the average area of the air channels was lower. The area of the four main air channels in the material from both lakes was an interesting element. The petioles from Lake Salno inicated that the channels in the lower segment had the largest area, and their size lessened as the distance to the water surface decreased. In Lake Kwiecko, the size distribution was the opposite (Table 1). Significant differences were found in the number of idioblasts; there were approximately 30 fewer in plants from Lake Kwiecko. In respect to the position of the starch sheath and its starch content, no differences were found between the studied materials.

The statistical data (LSD) presented for the two stands and three segments of the petiole of *Nymphaea alba* have shown a significantly greater length and smaller diameter of the petioles from Lake Kwiecko. Significantly larger, however, was the thickness and number of collenchyma layers, number of idioblasts and three types of vascular bundles in the material from Lake Salno.

NUPHAR LUTEUM (L.) SM. PETIOLES

The length of *Nuphar luteum* petioles from Lake Salno averaged 171 cm. Their cross sections had a round shape with two horn-like extensions. The diameter of the cross sections of the petioles was about 3260 μm.

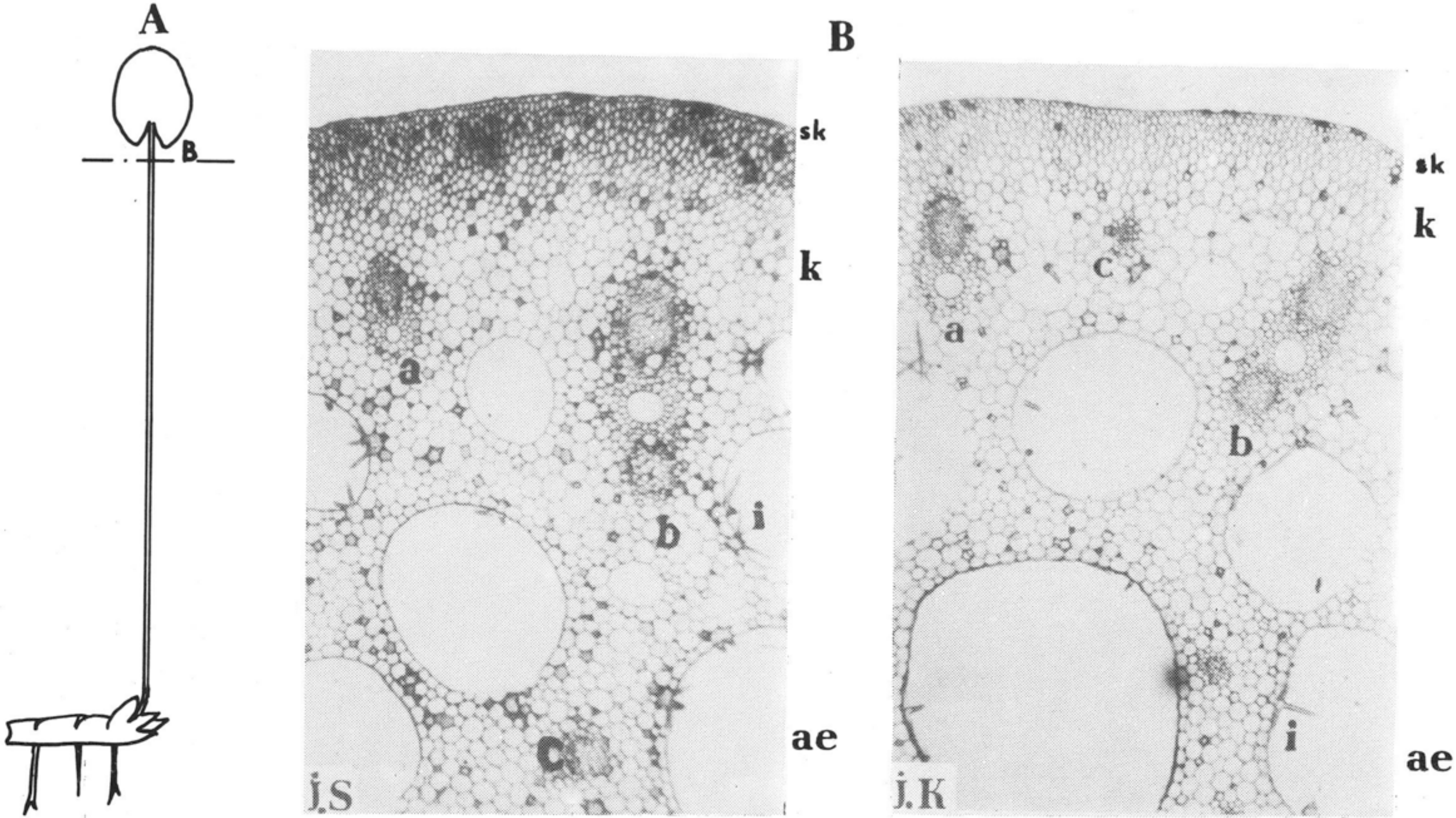

Fig. 2. A — Diagram of a petiole on which sites of cross sections have been marked, B — Cross section of a petiole of *Nymphaea alba* L. from Lake Salno (jS) and Lake Kwiecko (jK), 36 x. sk — epidermis, k — colenchyma, a — colateral vascular bundles, b — bicolateral vascular bundles, c — simple vascular bundles, i — idioblasts, ae — aernchyma

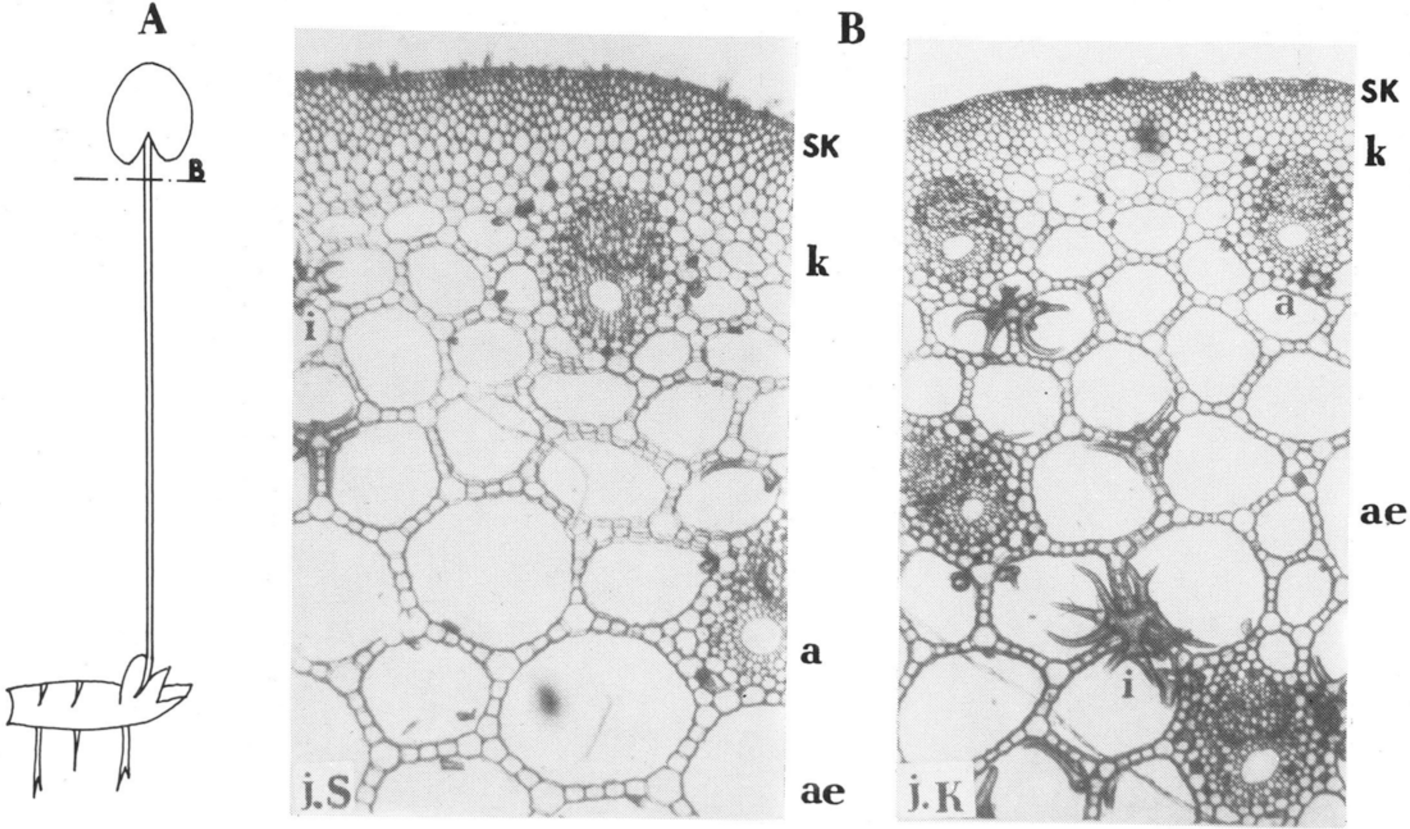

Fig. 3. A — Diagram of a petiole on which sites of cross sections have been marked. B — cross sections of petioles of *Nuphar luteum* (L.) Sm. from Lake Salno (jS) and Lake Kwiecko (jK), 36 x. Remaining symbols as in Fig. 2

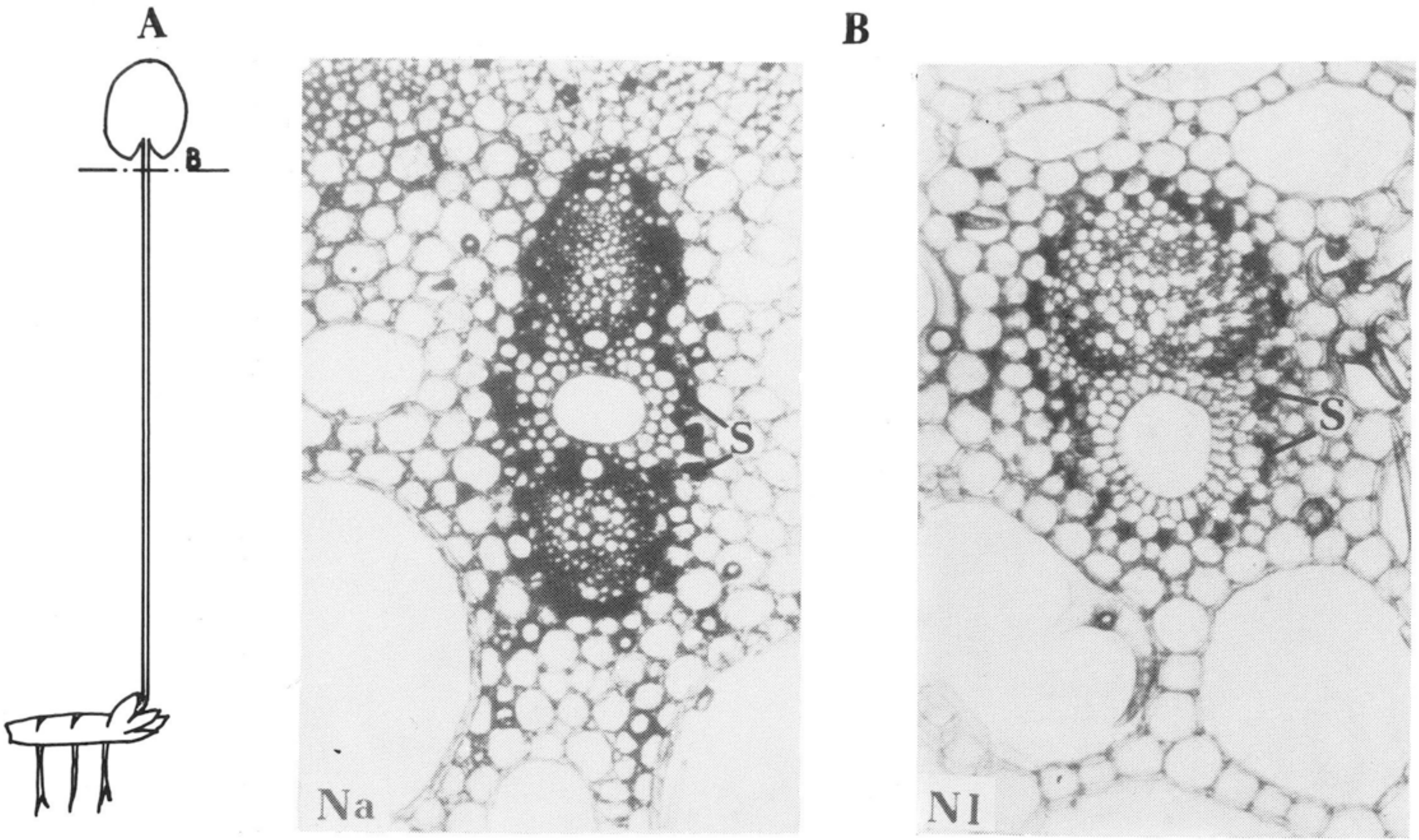

Fig. 4. A — Diagram of a petiole on which sites of cross sections have been marked. B — Cross sections of petioles of *Nymphaea alba* L. (Na) and *Nuphar luteum* (L.) Sm. (Nl), 72 x, S — starch

There was a rather regular ring of collenchyma with an average thickness of 172 μm under the epidermis. In the petioles of *Nuphar luteum*, only colateral bundles were found. They were positioned under the collenchyma in a more or less regular ring and dispersed in the aerenchyma network. There was an average of 16.2 of these bundles per petiole. The vascular bundles were surrounded by a ring of oval parenchyma cells filled with starch. The amount of starch around the bundles decreased as the distance from the leaf blade increased. In a few petioles, no starch at all was found in the lower segment. There was an average of 34.5 idioblasts in the aerenchyma.

Differences were found in the external and internal structures of *Nuphar luteum* petioles from Lake Salno and Lake Kwiecko (Table 2, Fig. 3). When the petiole lengths were compared, they were found to be slightly longer, on average 27 cm. The diameters of the segments taken for analysis were about 369 μm smaller. A regular ring of collenchyma was also found when analysing the tissue structure, but it was thinner, with an average thickness of 138 μm. Vascular bundles were arranged analogically as in the material from Lake Salno. In respect to the position of the starch sheath and its contents, no differences between the materials were found. Significant differences were found in the number of idioblasts, which was smaller and averaged 13.6. The largest significant difference in this respect was 3.3 for stands and 4.1 for petiole segments.

Statistical analysis of all of the studied traits in three *Nuphar luteum* petiole segments confirmed the variability of significant traits.

DISCUSSION

Changes in the ecological conditions as the result of increased water undulation and water level oscillations in lakes evokes as a consequence a series of modifications in the morphological and anatomical structures of *Nymphaea alba* L. and *Nuphar luteum* (L.) Sm. petioles.

The formation of clearly longer and thinner petioles by *Nymphaea alba* is connected with the quick adaptation of this species to periodic water level build up. The process of etiolation of the petioles under conditions of decreased illumination takes place concomitantly. Similar observations have been published by Warming (1900), Starmach et al. (1976). As a result of adaptation processes, *Nymphaea alba* remains in its stands without disruption of its development. *Nuphar luteum* exhibits significantly smaller adaptive capabilities in respect to elongation of its petioles, finds it thus more difficult to adapt to large oscillations in the water level and so its population in Lake Kwiecko is gradually decreasing.

An especially distinct sign of plant adaptation to quick changes in the water level and to strong turbulence is the significant reduction of collenchyma in the petiole structure. This increases the elasticity of the petioles, thus protecting them from damage from the undulation of the surface layers of water. Our observations find confirmation in the studies by Mikulski (1974) and Podbielkowski and Tomaszewicz (1979). Along with the process of reduction of supportive elements, gradual simplification of vascular bundles and a significant decrease in the number of idioblasts takes place. The storing of starch around the vascular bundles in the upper segments of the petioles and the formation of larger air channels in this zone are clearly connected with the intensification of photosynthetic processes in these plant parts, dependent on the intensity of illumination.

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Zmiany morfologiczno-anatomiczne w ogonkach liściowych u Nymphaea alba L. i Nuphar luteum (L.) Sm., wywołane wahaniami poziomu lustra wody w jeziorach

Streszczenie

W pracy przedstawiono zmiany morfologiczne i anatomiczne ogonków liściowych u *Nymphaea alba i Nuphar luteum* pochodzących z dwóch jezior o dużym zróżnicowaniu wahań lustra wody

(jez. Salno — zbiornik naturalny ustabilizowany, porównawczy; jez. Kwiecko — zbiornik naturalny Elektrowni Wodnej Żydowo, w którym wahania lustra wody przy maksymalnym piętrzeniu w ciągu doby wynoszą 3,1 m). Nierytmiczne i turbulencyjne ruchy wody w jez. Kwiecko powodują wydłużenie ogonków liściowych, zmniejszenie ich średnicy oraz w znacznym stopniu elementów wzmacniających — kolenchymy, wiązek przewodzących i idioblastów. Zmiany te w mniejszym stopniu zachodzą u *Nuphar luteum*. Wprawdzie *Nuphar luteum* jest gatunkiem o bardzo szerokiej amplitudzie ekologicznej i nie musi adaptować się do zmieniających warunków siedliskowych przez zmiany anatomiczne, to jednak wahania poziomu lustra wody wpływają niekorzystnie na stan jego populacji w jez. Kwiecko.