THE EFFECT OF WATER CONDITIONS ON THE PHENOLOGY AND AGE STRUCTURE OF *LURONIUM NATANS* (L.) RAF. POPULATIONS

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ABSTRACT

The study presents the results of the analysis of development stages of *Luronium natans* (L.) Raf. depending on water conditions (pH, light, total nitrogen, total phosphorus, organic carbon) in 21 populations in north-western Poland. The fractions of seedlings, juvenile, mature and generative stems, as well as the course of phenological phenomena were determined.

Seedlings are sparse and can be found from May to July. Most of them occur in waters ranging from slightly acid to neutral (pH 6.0-7.0) with TP concentrations of 10-20 µg dm^{-3}, TN concentrations < 1.0 mg dm^{-3} and DOC concentrations of 3.5-5.0 mg dm^{-3}, on a mineral (5-10% OC) and fairly well lit (31-40% PAR) substrate. The generative phase lasts from May to October. The flowering period is between August and mid-September. Only 35.2±9.4% of flowering stems produce fruits. The plant flowers abundantly in waters with total nitrogen concentrations > 1.2 mg dm^{-3}, that is above the level of TN concentrations most favourable to seedlings and both juvenile and mature individuals. TP and DOC concentrations, and light intensity (PAR) do not influence the size of the generative stems fraction in populations. However, sediment structure is of importance in this respect: about 62.9% of stems flower and fruit on a mineral substrate (< 1% OC), whereas only 17.4% do so on an organic one. The results of this study may be useful in the conservation of this endangered European endemic species.

KEY WORDS: *Luronium natans*, aquatic plant, development stages, phenology, European endemic plant.

INTRODUCTION

Luronium natans (L.) Raf. (syn.: *Alisma natans* L., *Elisma natans* (L.) Buchenau) is an aquatic or semi-aquatic plant which, according to Tutin et al. (1980), is represented by only one karyotype (*2n = 42*). This clonal perennial plant reproduces both by vegetative and generative means. An individual consists of ramets of a different age connected by means of stolons. The rosette composed of flexible leaves and a filamentous inflorescence stem form on the rhizome. The root system is of fibrous type. Individuals growing in shallow water can also form floating leaves with long stalks. The plant occurs on mineral and organic substrata, in soft and poor to quite fertile waters, and not only in transparent and well lit ones, but also turbid, very shady ones (Greulich 1999; Szmeja, Bazydło 2004a).

Luronium is a European endemic plant occurring in the sub-Atlantic climate of central Europe and Atlantic climate of the north-western and western parts of the continent (Greulich 1999). This plant can also be found in lakeland areas in north-west Poland, where it has 63 stands nowadays (Szmeja 2001). It is worth mentioning that population resources of this species are small and gradually diminishing. Only 13% of stands known in Poland in the 19th century survived the 20th century. After 1950 almost half of the stands (47.5%) recorded in the 20th century became extinct (extinction rate was one stand per year at that time). In Poland, the populations of this species are not numerous and their abundance is gradually decreasing, many of them being in the state of regression. Eutrophication, humication and acidification of lakes, faulty water-control works in catchments as well as degradation caused by scattered waterside housing and the development of commercialised tourism contribute, among others, to the decline of the stands (Bazydło, Szmeja 2004).

Luronium is an European endemic plant threatened with extinction. It is protected by the resolutions of the Bern Convention and the "Habitats – Fauna – Flora" Directive in the Programme "Natura 2000". In Poland it has the status of an endangered species and is fully protected (Szmeja

2001, 2004a). It is worth mentioning, however, that still very little is known about its biology and ecology, which makes its effective protection more difficult. The literature published so far contains little information about the course of the development cycle and seasonal phenomena of *Luronium*. Therefore the aim of this work is to present the results of studies conducted for many years which cover seasonal phenomena in the life of this plant as well as the survival rate of individuals depending on water conditions.

METHODS

The analysis of development stages in *Luronium* populations was conducted between 1999 and 2004 in north-west Poland (Pomeranian Lakeland) in 21 lakes differing in terms of water pH, concentrations of total nitrogen (TN), total phosphorus (TP), dissolved organic carbon (DOC), light intensity PAR and organic carbon (OC) content in the substrate. The proportion of development stages (seedlings, juvenile, mature and generative) in populations was calculated on the basis of 358 samples, 0.1 m^2 each, collected in line with the recommendations given by Szmeja (1987) and Madsen (1993).

In addition, in one of the lakes (Lake Kaliska), phenological observations were made on five permanent plots, each covering 0.25 m^2, every 14 days between April and December from 2000 to 2003. The start and closing date of the study depended on the time when the ice cover melted in spring and formed again on the lake in winter. Each experimental plot was marked indelibly and divided into 25 squares measuring 0.1 m on each side. As a result, it was possible to locate stems, which were later plotted on map projections with a scale of 1:10. Each time the stems were counted and classified into development stages.

The study of water conditions was carried out in home ranges of *Luronium* populations taking interstitial water and sediment into consideration. Six water samples, each 0.5 dm^3 in volume, from each lake were collected by means of diving. Six sediment samples, each 0.25 dm^3 in volume, were collected in the same way from within the root system. In sediments organic matter content [OC;%] was determined by means of incineration of 1 g of sediment dry weight at 550°C. In interstitial water samples the following were determined: (1) pH; (2) DOC concentration [mg C dm^{-3}]: spectrophotometrically (Moore 1985, 1987; Collier 1987, Górniak 1995) from the calibration curve as the relationship between DOC concentration and absorbancy (A_{330}); (3) TP concentration [µg dm^{-3}]: after mineralisation with nitric acid by the molybdate colorimetric method with ascorbic acid as a reducing agent (Golterman 1975; Greenberg et al. 1992; Hermanowicz et al. 1999); (4) phosphate ion concentrations [mg PO_4^- dm^{-3}]: by the molybdate colorimetric method with ascorbic acid as a reducing agent (Hermanowicz et al. 1999); (5) TN concentration [mg dm^{-3}]: by the method of oxidation with potassium persulphate in an alkaline environment (Golterman 1975); (6) light intensity (PAR) with a Li-250 Light Meter.

The statistical analysis consisted in the calculation of: minimal and maximum value (min.-max.), arithmetic mean with standard deviation ($\overline{X} \pm s$), and coefficient of variation ($CV = s/\overline{X}$; Łomnicki 1999). The significance of differences among means was tested by ANOVA, using Tukey's test. The statistical inference was conducted at a 5% error risk.

RESULTS

Development stages

Luronium natans is an evergreen hydrophyte. It reproduces generatively and vegetatively. In the development of this plant the following stages can be distinguished (1-5; Fig. 1):

Seedling: the youngest stage, developing from the seed, with a seed leaf and primary root. Seedlings occur between May and July and constitute a small fraction in a population (ca. 5%).

Juvenile**:** It develops from the seedling or is the youngest stage of the stem established by means of vegetative reproduction. In general, it possesses two (rarely four) small submerged leaves and visible signs of a developing fibrous root system. Juvenile stages occur in populations during the whole vegetative season: from spring (just after ice break-up in March or April) until the beginning of winter (December). At first, roots are formed; then rhizome; next leaves. The juvenile stage lasts from 6 to 8 weeks.

Mature: a fully developed rosette of submerged leaves and root system. A mature stem forms 12.5±4.0 leaves, which are 93.8±21 mm long and 2.5±0.6 mm wide. The rosette area is 30.6±17.1 cm^2. The juvenile stage transforms into the mature stage within a few weeks (5-7) and, after that, lasts at least one year, also in winter under ice cover.

Generative: a fully developed rosette and root system; a flowering and fruiting individual. The generative stem produces inflorescence stems (1-3). There are from 1 to 10 flowers and fruits in the inflorescence (Me = 6). The generative stage lasts from 6 to 10 weeks. During this time, flowers mature, fruits ripen, and rosettes disintegrate (70--100% of leaves die). The development of generative stems can be divided into the following phases (a-c):

(a) development of the inflorescence stem (G_1): the inflorescence stem grows at the centre of the rosette of the mature stem and, after 2-6 weeks (depending on the depth at which it grows), reaches the water surface. Stems develop over several days at water temperature of 10±2°C. With the elongation of the inflorescence stem, the plant produces the first flower buds, which are formed above and under the water.

(b) flowering (G_2): lasts from 2 to 4 weeks. Underwater flowers are closed, whereas the ones formed above the water are open. The temperature of the water and sediment is 19-21°C.

(c) fruiting (G_3): lasts 2-6 weeks and covers the period of time from the development of the first ovules until the formation of ripe seeds. Ripening fruits change colour from greenish to olive-brown. 10±2 seeds, each 6.2±2.0 mg in weight, develop from one flower. Fruits form from flowers both above and under the water. At the time, water and sediment temperature ranges from 20 to 22°C.

Postgenerative: after seed dispersal inflorescence stems die back. Water temperature is ca. 8°C. Postgenerative stems are similar to juvenile ones at this time. A fraction of these stems (ca. 19.9±7.3%) produce new inflorescence stems towards the end of summer and in autumn, but their development is brought to a halt in the initial phase. In ear-

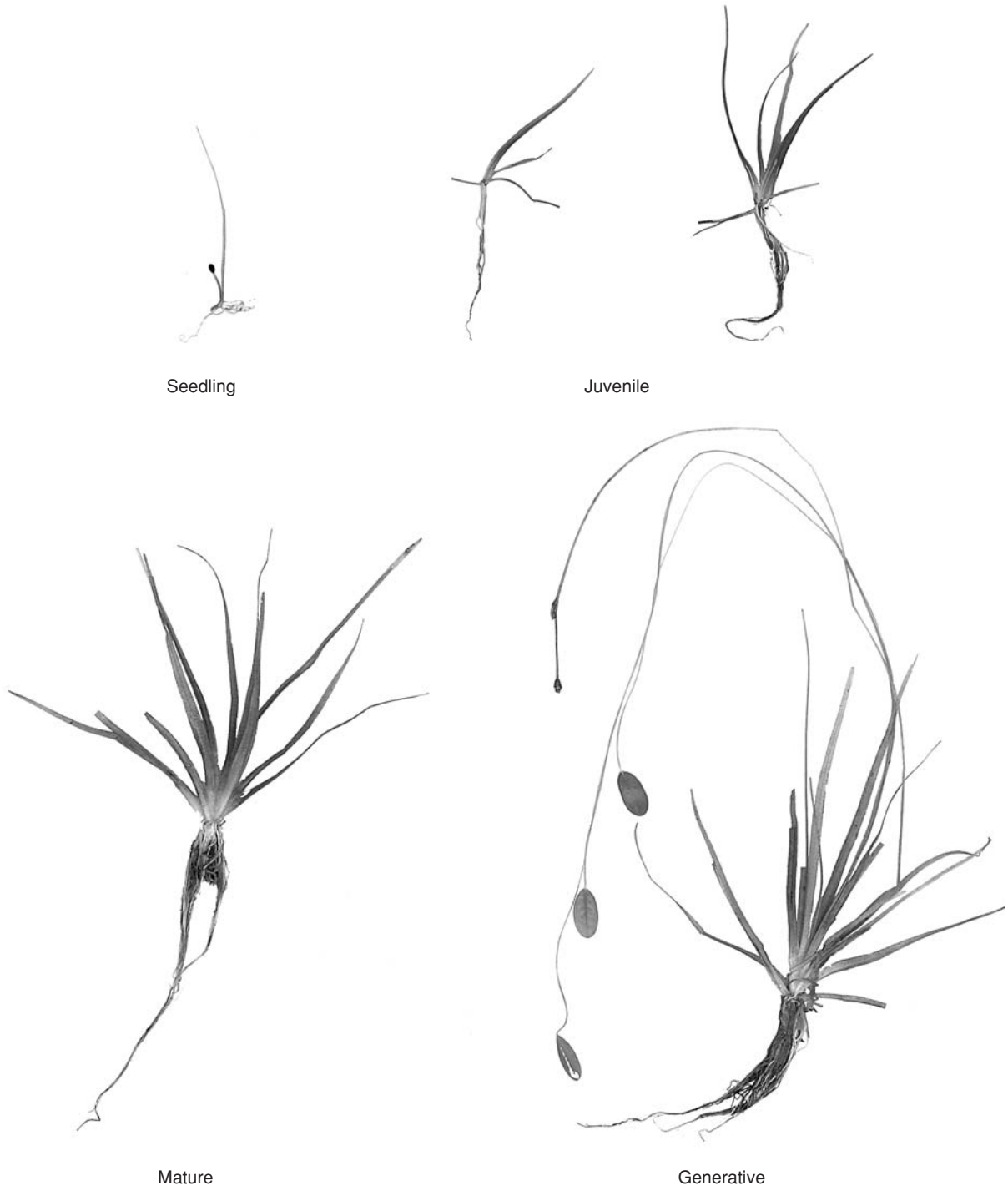

Fig. 1. Development stages.

ly spring in the following year stolons in such stems break and are divided into smaller parts.

In *Luronium* populations, the development rate of individual stages, i.e. the time in which one stage transforms to another, can be represented in the following way:

$$T_0\,(J) \rightarrow T_2\,(M) \rightarrow T_{14}\,(G) \rightarrow T_{26}\,(G)$$

where: J – juvenile, M – mature, G – generative, T – time (in months). Vegetative offspring which develop from vegetative propagules last at least 4 years, flower for the first time in the second year and still flower in the following years. The lifespan of generative offspring (which form from seeds, i.e. genets) was not determined.

Seasonal phenomena in populations

The development of *Luronium* populations can be divided into the following phenological phases (1-7; Fig. 2):

(1) Early-spring vegetation**:** This begins just after ice break-up at the end of March and at the beginning of April, when water and sediment temperatures range from 4 to 10°C. The phase lasts 4-6 weeks. The population is composed of mature (75±11.3%) and juvenile (24±10.6%) stems.

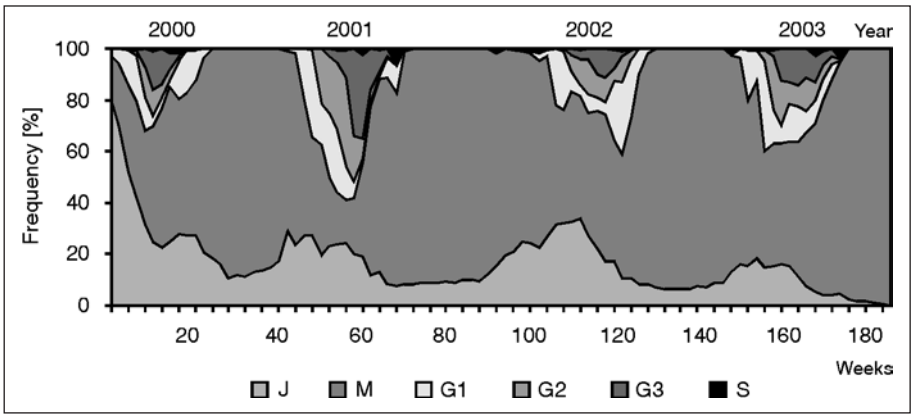

Fig. 2. Phenological spectrum. Development stages and phenological phases: *J* – juvenile, *M* – mature, G_1 – inflorescence stem development, G_2 – flowering, G_3 – fruiting, *S* – senile stage.

(2) Intensive growth of individuals: from April until the end of the first 10 days of May at a temperature of 8-12˚C. Individuals (clones) grow all year round, also in winter. This growth consists in the development of new stems (1--5; Me = 3) which form on stolons.

(3) Development of inflorescence stem buds**:** in water temperatures of 6-14˚C; the phase lasts 4-6 weeks and can be observed in populations twice a year: in May or June as well as in October or November. Inflorescence stems appear on 31.2±0.01%-42.4±4.7% of the number of mature stems in a population (data come from two-year studies). In autumn inflorescence stems are much less numerous (20.4±9.6%). Only 48±25.3% of the total number of stems with inflorescence stem buds begin the flowering phase.

(4) Development of flower buds**:** This begins at the same time as the formation of inflorescence stem buds and lasts 4-6 weeks at a temperature of 6-14˚C.

(5) Flowering: This begins 8-10 weeks after buds have been established and lasts 6-8 weeks in temperatures of 20--22˚C. Optimum flowering can be observed in June/July or August, depending on the date of the formation of inflorescence stem buds and the establishment of flower buds. In a year 21.7±7.7% of stems flower.

(6) Fruiting and seed dispersal: Fruiting begins 4 weeks after the development of flowers; seeds are dispersed 2 weeks after fruit setting. This phase generally lasts from August until mid-September. A small fraction of such stems fruits also in October. Only 35.2±9.4% of generative stems (G_1) which appear within one year produce fruits.

(7) Autumn and winter vegetation: die-back of inflorescence stems. At the time a certain fraction of "delayed" generative stems, i.e. the ones in the phase of inflorescence stem bud (18±8% of population composition) and flower bud (ca. 4%) formation, still exists. None of these stems can finish its reproduction cycle. The winter phase lasts until the following spring and is characterised by slowed down growth and development of stems. 93.3±3.4% of stems survive from autumn until the next spring.

The abundance of development stages in varying water conditions

Seedling and juvenile fractions in populations

Seedlings represent a small fraction in populations. In very acid waters (pH < 5.0) they represent about 7.0% of the population, in slightly acid (pH ≥ 5.0) and neutral (pH 7.0) waters 11.2-21.2%. However, in alkaline waters (pH > 7.0) they occur much more seldom (Table 1). An increase in water pH over 7.0 inhibits seed germination or makes the development of seedlings impossible. Phosphor-poor waters (< 10.0 µg dm^{-3}), like the ones very rich in phosphor (> 30.1 µg dm^{-3}), are also not conducive to seed germination (seedlings represent 9% of the population). What is more, with an increase in total nitrogen concentrations from trace values to 1.0 mg TN dm^{-3}, the proportion of seedlings rose from 8.6 to 15.8%. In concentrations over 1.2 mg TN dm^{-3} seedlings do not occur (Fig. 3). DOC concentration in the water may also influence seedling abundance. The greatest number of seedlings (16%) was recorded in conditions of 3.5-5.0 mg C dm^{-3}, and a much smaller number (up to 10%) under 3.5 mg C dm^{-3} and over 6.0 mg C dm^{-3}. It is also possible that organic matter content in sediments has an effect on seedling abundance. On substrates with OC < 1% seedlings represent 2.5% of population composition, whereas with OC ranging from 5 to 10% as much as 14%. It is also worth mentioning that in very transparent and well lit (PAR > 50%) as well as turbid and very shady waters (PAR < 20%) the fraction of seedlings in populations is similar and remains at the level of a few percent. Most seedlings (16.3%) occur in slightly shady waters (PAR 31-40%). To sum up, conditions favourable to the development of seedlings exist in waters ranging from slightly acid to neutral pH, with low content of total phosphor (10.1-20.0 µg TP dm^{-3}), total nitrogen (< 1.0 mg TN dm^{-3}) and DOC (3.5 do 5.0 mg C dm^{-3}), on a mineral (5.0 to 10.0% OC) and relatively well lit (31-40% PAR) substrate.

The juvenile stage is most numerous in conditions of pH 6.0-6.5 (48.5%). However, their proportion in a population is much smaller when pH < 5.0 or pH > 7.0. Moreover, phosphor concentration in the water probably does not influence the abundance of this age group, but TN content may be significant in this respect. Juvenile stems tolerate waters < 1.2 mg TN dm^{-3}. Below this limit juvenile stems represent from 30.3 to 37.8% of population composition, whereas above the limit only 18.9%. The TN concentration of 1.2 mg dm^{-3} is the upper limit not only for juvenile stages but also for seedlings. Light intensity PAR and DOC concentration in the water and organic carbon concentration in the substrate probably do not significantly influence the abundance of this age group in populations.

The proportion of mature and generative stages in populations

Mature stems, like juvenile ones and seedlings, are the most numerous in slightly acid waters (see Table 1). With pH < 5-6.5 mature stems represent 24.3-41.5% of popula-

TABLE 1. The proportion of development stages in populations (%) in water conditions.
Explanatory notes: N – number of samples; $\overline{X} \pm s$ – arithmetic mean with standard error; TP – total phosphorus; TN – total nitrogen; PAR – photosynthetic active radiation; DOC – dissolved organic carbon; OC – organic carbon.

Stages:	N	Generative	Mature	Juvenile	Seedlings
Feature range of water conditions					
water pH					
< 5.0	9	30.3±24.8	41.5±17.6	26.7±13.8	7.0±3.8
5.0-6.0	12	24.9±21.2	28.5±8.5	43.6±12.0	21.2±7.4
6.0-6.5	12	27.4±29.9	24.3±4.3	48.6±26.6	11.6±6.8
6.5-7.0	18	25.7±26.9	48.9±26.1	24.2±19.2	11.2±4.8
> 7.0	9	78.9±10.4	15.6±22.6	16.5±8.7	1.9±2.9
TP [µg dm^{-3}] in the water					
< 10	12	38.5±29.4	32.4±17.8	30.1±13.5	9.8±4.1
10-15	9	14.6±18.1	63.7±23.0	20.0±11.2	13.3±6.3
15-20	15	28.5±24.0	37.0±13.6	31.0±18.6	13.7±7.9
20-30	15	35.9±34.3	22.6±17.4	41.0±29.9	9.7±6.6
> 30	9	55.7±33.6	22.8±21.5	30.8±20.2	9.2±13.8
TN [mg dm^{-3}] in the water					
< 0.4	6	17.9±18.8	41.7±21.6	36.2±3.6	8.6±4.0
0.4-0.8	21	27.1±29.9	45.1±23.6	30.3±24.7	12.2±6.5
0.8-1.0	12	34.4±25.8	29.2±18.7	32.0±20.7	15.8±7.5
1.0-1.2	15	35.4±29.9	23.6±10.6	37.8±22.6	11.6±9.3
> 1.2	6	77.0±12.7	20.7±26.8	18.9±9.9	0.0±0.0
PAR [%]					
< 20	9	23.5±33.1	52.1±16.2	34.0±8.7	7.6±7.1
20-30	12	52.0±32.3	40.2±29.0	12.9±9.7	8.6±5.1
31-40	12	15.3±20.1	40.6±26.2	43.8±27.4	16.3±8.5
41-50	15	43.9±31.9	18.9±9.8	36.4±22.2	10.4±10.1
> 50	12	33.7±19.7	28.9±7.2	33.0±18.6	12.0±5.9
DOC [mg C dm^{-3}] in the water					
< 3.5	9	36.7±32.2	34.7±20.0	26.5±13.9	8.3±3.4
3.5-5.0	23	37.3±28.7	27.0±11.9	35.2±25.0	16.0±9.1
5.0-6.0	9	11.7±10.8	53.6±25.9	33.4±18.3	11.3±4.0
> 6.0	18	41.9±34.4	32.4±26.2	30.1±21.2	5.9±5.9
OC [%] in sediment					
< 1	9	62.9±23.6	21.4±21.9	22.8±11.3	2.8±5.6
1-5	15	30.3±27.9	33.3±19.2	36.9±28.3	14.5±4.9
5-10	18	33.3±33.6	29.3±21.0	33.1±21.3	14.7±10.3
10-30	12	28.4±25.3	44.8±23.6	29.9±20.8	7.8±4.1
> 30	5	17.4±23.8	48.2±17.4	33.7±6.1	11.9±7.1

tion composition; with pH 6.5-7.0 their proportion increases to ca. 50%. When pH is > 7.0, they constitute a fraction of only 15.6%. Taking phosphor and nitrogen concentrations into account, it can be observed that mature stems represent the most numerous fraction in the water which is not very rich in these elements. In TP concentration conditions of 10-15 µg dm^{-3} mature stems constitute ca. 63.7% of population composition, while when the concentrations are over 30 µg dm^{-3}, only 22.8%. It should be emphasised that in the case of mature stems, as in the remaining development stages, the upper concentration limit tolerated by the stems is 1.2 mg TN dm^{-3} (see Fig. 3). Except for OC, the effect of other environmental factors on the size of the fraction of mature stems is questionable. The analyses of consecutive development stages conducted so far shows that the older a stage is, the greater its tolerance of environmental conditions tends to be.

Luronium is a clonal perennial plant. This may indicate that a clone grows and becomes bigger with time. The analysis of samples taken in the population every 15 days for 14 months indicates that the assumption that the clone and its individual ramets constantly grow is completely wrong. Firstly, clones disintegrate; secondly, the size of stems in the population does not increase in a constant way but undergoes seasonal fluctuations. Over a year, there is a phase of fast growth of stems in spring which is followed by partial and slow disintegration in summer. After that, they grow again in autumn only to fall apart in winter. These changes are correlated with water temperature and seasonal development of the plant under study as well as with a lot of processes which take place in lake ecosystems (Fig. 4).

In acid waters generative stems represent from 24.9 to 30.3% of population composition in the conditions of pH < 5.0-7.0, whereas when pH > 7 they constitute a much more numerous group representing 78.9% (see Table 1, Fig. 3). We find it impossible to explain why in alkaline waters, which are not favourable to the remaining development stages, there is such a numerous fraction of flowering and

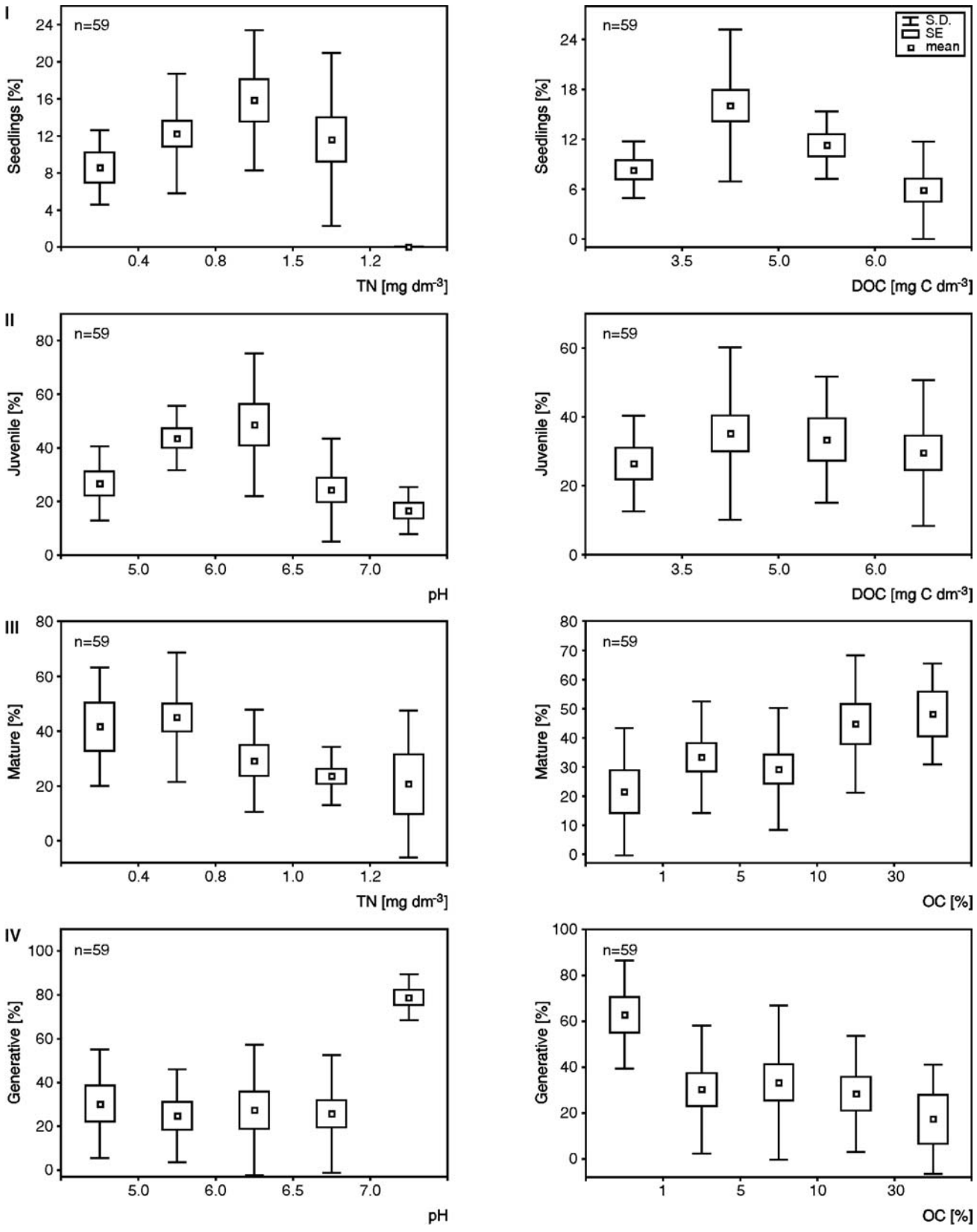

Fig. 3. The proportion of seedlings (I), juvenile (II), mature (III) and generative (IV) stages in water conditions.

fruiting stems, all the more so because neither seeds nor seedlings tolerate such waters. That is why we still work on the assumption that the most favourable conditions for the development of this plant can be found in the water ranging from slightly acid to alkaline.

In Poland, out of 63 *Luronium* stands, more than half (55.5%) occur in acid waters (pH 6.0-6.5) and every tenth stand (11.1%) is situated in very acid water (pH < 5.5). Acidification of lakes is one of the threats facing the population of this species in Poland. Phosphor concentration in

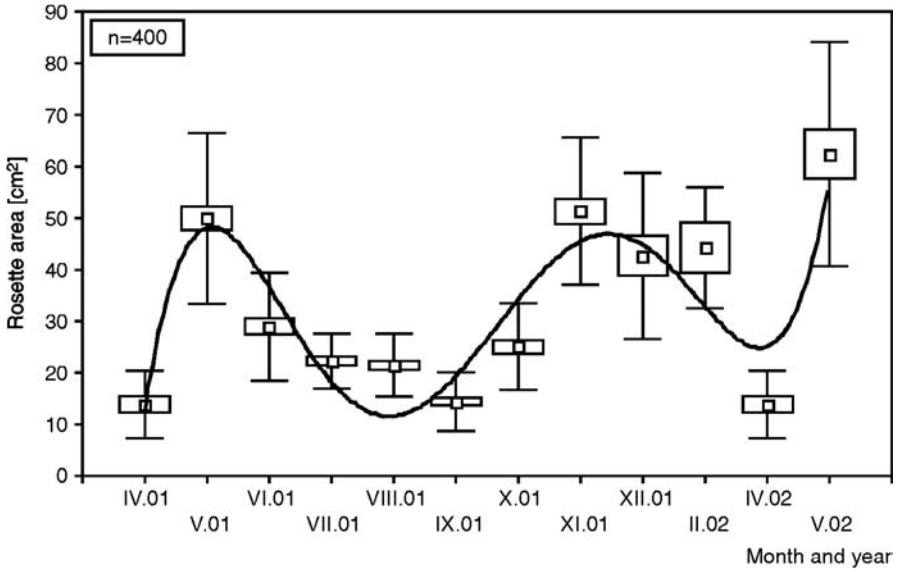

Fig. 4. Seasonal rhythm of the size of mature rosettes. Explanations: 01, 0.2 – year 2001, 2002.

the water of 21 lakes (*Luronium* stands) probably does not affect the size of the fraction of generative stems. Paradoxically, nitrogen may exert an effect on the size of this group, especially at concentrations which are over the safe limit for all the remaining development stages, i.e. seedlings, and juvenile and mature groups. In TN concentrations < 0.4 mg dm^{-3} flowering and fruiting stems constitute only 17.9% of population composition, while over 1.2 mg dm^{-3} their proportion in populations is much bigger and comes to 77%. In the future it should be checked which forms of nitrogen influence the flowering and/or fruiting of *Luronium*. DOC concentrations in the water as well as light intensity (PAR) do not influence the size of the fraction composed of generative stems in populations, but sediment structure may be of importance. On mineral sediments (< 1% OC), on average, 62.9% of stems flower and fruit, whereas on organic sediments (> 30%) only 17.4% ($p < 0.05$; see Fig. 3). However, this does not indicate that a low CO content in the substrate is the necessary condition for abundant flowering. It is rather a consequence of the fact that *Luronium* occurs in places strongly disturbed by wave action and water erosion, which generally contain little organic carbon.

DISCUSSION

Luronium natans is a clonal perennial plant whose ramets occur in the same form in winter as in summer, even though they lose part of their chlorophyll and yellow. The oldest leaves die back. Individuals growing in shallow water or in semiaquatic habitats shed most of their leaves and last until spring with a part of stolon and some of the roots. The inbred features as regards the size and habit of the plant are modified by water conditions (Bazydło 2004a). If the plant grows at an optimal depth, it forms a rosette of submerged leaves. However, if the water is rich in total nitrogen and not deep enough, the plant produces additional floating leaves.

In Poland the stands of *Luronium* occur close to the north-eastern boundary of its geographical range. Winters in this area are slightly harder than in the western part of the continent. That is why it would be interesting to check how numerous a fraction of the population survives the winter. The studies indicate that in north-west Poland almost all individuals in populations survive the winter (93.3%). It follows that in Poland low temperatures do not limit growth or development in the plant under study.

The growth and development of *Luronium* begins after ice melts at the end of April and at the beginning of May in water temperatures of 9-10°C, i.e. in similar conditions to *Lobelia* (Szmeja 1985). At this time vegetative propagules and inflorescence stems are established. Although early-spring vegetation of *Lobelia* begins later than of the plant under study, both plants form the first flowers at a water temperature of 19°C. Such a reaction of the species seems to refute the thesis advanced by Zimmerman, Gross (1984) and Rathcke (1988) that the flowering time is genetically conditioned.

Genetic factors can cause differences in flowering time of individuals from the same population. The phenomenon was observed in *Luronium*, *Lobelia* (Szmeja 1992, 1994a) and other species (Ollerton, Lack 1998; Buide et al. 2002). Flowering time shifts in individuals coming from neighbouring populations may result from the time at which pollen carriers appear, which differs slightly in individual lakes. *Luronium* is a self-pollinating plant, but some flowers are most probably pollinated by insects. Open flowers and their ornamentation in the form of colourful bands visible to pollen carriers create favourable conditions for pollination. In aquatic plants, a similar phenomenon was observed in *Nymphaea alba* for example (Langanger et al. 2000). It should also be mentioned that in *Luronium* populations a fraction of flower buds is formed in autumn, but most often they do not develop into flowers. Such flower buds, which stop developing, were also found in *Lobelia* populations (Szmeja 1987).

Luronium is an isoetid with habitat requirements similar to *Lobelia dortmanna*, *Littorella uniflora* and *Isoëtes lacustris* (Rørslett 1987; Szmeja 1987, 1994a-c; Szmeja et al. 1997), which co-occur with this species in the same lakes. Individuals of this plant live at least 4 years and their growth and development rate is faster than in the case of *Lobelia* and *Isoëtes*, but the same as in *Littorella*. Juvenile

stems transform into mature ones after 4-6 weeks, whereas after 2 years in *Lobelia* and as late as after 3 years in *Isoëtes* (Szmeja 1994a). On the one hand, fast growth, especially in spring, as well as early maturation and flowering, facilitate the occupation of new habitats (lakes). On the other hand, however, as the analysis of historical data indicates, such a phenomenon has not been recorded in Poland. According to Willby and Eaton (1993), this plant, under certain conditions, has the properties typical of invasive species. In Poland, however, taking all the contemporary 63 stands into consideration, no population shows such properties. On the contrary, a substantial number of them have the features of regressive populations.

Just like most clonal aquatic and land species, *Luronium* reproduces by generative and vegetative means (Eriksson 1997; Price, Marshall 1999). The efficiency of vegetative reproduction measured on the basis of the number of juvenile individuals living to the generative stage is high (63.4%), even though it is slightly lower than in *Lobelia* and particularly *Littorella* populations (Szmeja 1992). This may result from the fact that *Luronium* stolons, especially in comparison with *Littorella*, are more susceptible to breaking. A stem which breaks off from the clone does not absorb assimilates (Price, Marshall 1999), and, as it drifts on the water surface, unlike *Littorella*, it cannot get rooted in the substrate (Barrat-Segretain et al. 1999), which undeniably makes it less likely to survive (Bazydło 2004b).

It is worth mentioning that the efficiency of generative reproduction is as low as in other aquatic plants. A small number of flowering and fruiting stems (ca. 31.0%) as well as the fragile structure of inflorescence stems, which are susceptible to damage by waves or herbivores, are factors contributing to the low efficiency. In addition, owing to a small number of seeds in fruits and low frequency of generative stems in populations, the seed bank in the substrate is usually scarce. In places which are not disturbed by waves, on average 200 seeds can be found in 1 m^2 of the substrate. However, according to Combroux et al. (2001), in disturbed places, by and large, seeds do not occur at all. Together with the low frequency of seedlings (only 5%), the above-mentioned issues show how low the efficiency of generative reproduction of *Luronium* is. According to Harper (1977), Cook (1985), Falińska (1998), Erikson (1997) and Szmeja (2004b), such a situation is present in the populations of most clonal plants and is not necessarily the outcome of human pressure on lakes.

Luronium seeds are fairly heavy (0.62±0.56 mg) and sink easily, thanks to which they remain near the parent plant. Seedlings appear from spring to summer, do not form seasonal cohorts and grow almost exclusively within the existing aggregations. In the depositional sections of the littoral seeds do not germinate well. This is probably due to the fact that they are covered by sediments and lie in the dark. Such conditions are not favourable to their germination (Szmeja, Bazydło 2004b), a point in case being also the seeds of *Lobelia* (Farmer, Spence 1987) and *Nuphar lutea* (Smith et al. 1990). Seed coats are hard and decompose slowly, especially in acid water, which may be another cause of the low efficiency of generative reproduction. Smolders et al. (1995) observed a similar regularity in *Alisma plantago aquatica* and *Sagittaria sagittifolia*.

Luronium is rather resistant to the results of eutrophication. On the one hand, with the increase of trophism, individuals become smaller and smaller, population density decreases and the population home range shifts closer to the shore. On the other hand, however, the proportion of generative stems is still high under such conditions. This indicates that increased trophism does not limit the reproductive potential of a population in any significant way. It is also worth mentioning that excessive growth of plankton algae and the development of filamentous algae, which causes water turbidity, decrease of lighting levels and significant changes in the structure of biocenoses are two of the symptoms of advanced eutrophication (Arts et al. 1990, Rørslett 1991, Vestergaard, Sand-Jensen 2000). In such conditions slowly growing isoetids are supplanted by faster growing elodeids (Chambers 1987; Szmeja 1994b). It can be assumed that the plant under study is not as effectively eliminated by elodeids as other isoetids, as its growth rate is quite fast.

The decrease of the size of individuals and their frequency in the littoral of lakes, fertilised as a result of human pressure, is above all caused by light limitation. Excessive development of epiphyte algae and/or phytophages, mainly fungi, is (or can be) one of the factors contributing to light limitation. Under such conditions rosettes are usually covered by a layer of epiphyte algae, which, as Sand-Jensen, Sřndergaard (1981) have shown, reduce light to a level of 20%. The competition from algae for biogenic substances also intensifies (Ozimek 1990, 1992). In addition, according to Chapin (1980), in conditions of increased trophism a lot of nitrogen compounds accumulate in plant tissue. In the case of fast growing plants, the plant under study being undeniably one of them, this can lead to etiolation and the development of epidermis and/or parenchyma tissue which are too delicate and make the plant susceptible to fungal infection (Smolders et al. 2002). These are undeniably only some of many possible consequences of increased trophism which can influence the life and persistence of a population in a lake.

To sum up, it should be mentioned that the conservation of the species in situ consists in a number of activities aimed at creating the conditions for its populations which would enable it to survive in the present time. It goes without saying that this concerns not only the relevant directives limiting the threats and damage (both now and in the future), but also the practical activities undertaken to control the processes which influence population abundance. In order to achieve this, the knowledge of the biology and ecology of endangered species should be spread on a larger scale than it has been done so far, especially as regards their habitat requirements and basic processes taking place in populations.

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LITERATURE CITED

ARTS G.H.P., ROELOFS J.G.M., DE LYON M.J.H. 1990. Differential tolerances among soft-water macrophyte species to acidification. Can. J. Bot. 68: 2127-2134.

BARRAT-SEGRETAIN M.H., HENRY C.P., BORNETTE G. 1999. Regeneration and colonization of aquatic plant fragments in relation to the disturbance frequency of their habitats. Arch. Hydrobiol. 145: 111-127.

BAZYDŁO E. 2004a. Effect of environmental conditions on the populations of *Luronium natans* (L.) Raf. Pol. J. Ecol. 52 (2): 181-189.

BAZYDŁO E. 2004b. Biology and ecology of *Luronium natans* (L.) Raf. populations. University of Gdańsk, Department of Plant Ecology (diss. dr., mscr), Gdańsk.

BAZYDŁO E., SZMEJA J. 2004. The effect of pH, dissolved organic carbon and total phosphorus concentration on selected life history traits of *Luronium natans* (L.) Raf. Pol. J. Ecol. 52 (2): 191-200.

BUIDE M.L., DÍAZ-PEROMINGO J.A., GUTITIÁN J. 2002. Flowering phenology and female reproductive success in *Silene acutifolia* Link ex Rohrb. Plant Ecology 163: 93-103.

CHAMBERS P.A. 1987. Light and nutrients in the control of aquatic plant community structure II. In situ observations. J. Ecol. 75: 621-628.

CHAPIN F.S. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics 11: 233-260.

COLLIER K.J. 1987. Spectral properties of some West Coast waters and their relationship with dissolved organic carbon. Mauri Ora 14.

COMBROUX I., BORNETTE G., WILLBY N.J., AMOROS C. 2001. Regenerative strategies of aquatic plants in disturbed habitats: the role of propagule bank. Arch. Hydrobiol. 152: 215-235.

COOK R.E. 1985. Growth and development in clonal plant populations. In: Jackson J.B.C., Buss L.W., Cook R.E. (eds). Population biology and evolution of clonal organisms. Yale University Press, Newhaven, pp. 259-296.

ERIKSON O. 1997. Clonal life histories and the evolution of seed recruitment. In: de Kroon H., van Groenendael J. (eds). The ecology and evolution of clonal plants. Backhuys Publishers, Leiden, pp. 211-226.

FALIŃSKA K. (ed.) 1998. Plant population biology an vegetation processes. Szafer Institute of Botany, PAN, Kraków.

FARMER A.M., SPENCE D.H.N. 1987. Environmental control of the seasonal growth of the submersed aquatic macrophyte *Lobelia dortmanna* L. New Phytol. 106: 289-299.

GOLTERMAN H.J. 1975. Physiological limnology. Elsevier, Amsterdam.

GÓRNIAK A. 1995. The spectrophotometric method for determination of the concentration and quality of dissolved organic carbon in the water. Gosp. Wodna 2: 31-33.

GREENBERG A.E., CLESCERI L.S., EATON A.D. 1992. Standard methods for the examination of the water and wastewater. American Pub. Health Ass., 18th edition, Washington.

GREULICH S. 1999. Competition, perturbations et productivite potentielle dans la definition de l'habitat d'especes rares: Etudes experimentale du macrophyte aquatique *Luronium natans* (L.) Rafin. Univ. Claude Bernard, Lyon 1, France.

HARPER J.L. 1977. Population biology of plants. Academic Press, London.

HERMANOWICZ W., DOZANSKA W., DOJLIDO J., KOZIOROWSKI B. 1999. Physico-chemical analysis of water and sewage. Arkady, Warszawa.

LANGANGER M., JOKL S., MUSSO M. 2000. UV-reflectance in flowers of *Nymphaea alba* L. and *Nuphar lutea* (L.) Sm. (Nymphaeaceae). Aquat. Bot. 67: 13-21.

ŁOMNICKI A. 1999. Introduction to statistics for naturalists. Wyd. Nauk. PWN, Warszawa.

MADSEN J.D. 1993. Biomass techniques for monitoring and assessing control of aquatic vegetation. Lake and Reserv. Manage. 7: 141-154.

MOORE T.R. 1985. The spectrophotometric determination of dissolved organic carbon in peat waters. Soil Sci. Soc. Ann. J. 49: 1590-1592.

MOORE T.R. 1987. An assessment of a simple spectrophotometric method for the determination of dissolved organic carbon in freshwaters. New Zeal. J. Mar. Fresh. Res. 21: 585-589.

OLLERTON J., LACK A. 1998. Relationships between flowering phenology, plant size and reproductive success in *Lotus corniculatus* (Fabaceae). Plant Ecology 139: 35-47.

OZIMEK T. 1990. Aspects of ecology of filamentous alga in a eutrophicated lake. Hydrobiologia 191: 23-27.

OZIMEK T. 1992. Submerged macrophytes and their relationships with algae in lakes with high trophism. Wiad. ekol. 38: 13-34.

PRICE E.A.C., MARSHALL C. 1999. Clonal plants and environmental heterogeneity. Plant Ecol. 141: 3-7.

RATHCKE B. 1988. Flowering phenologies in a shrub community: competition and constraints. J. Ecol. 76: 975-994.

RØRSLETT B. 1991. Principal determinants of aquatic macrophyte richness in Northern European lakes. Aquat. Bot. 39: 173-193.

SAND-JENSEN K., SØNDERGAARD M. 1981. Phytoplankton and epiphyte development and their shading effect on submerged macrophytes in lakes of different nutrient status. Int. Revue Ges. Hydrobiol. 66: 529-552.

SMITH A.J.M., VAN AVESAATH P.H., VAN DER VELDE G. 1990. Germination requirements and seed banks of some nymphaeid macrophytes: *Nymphaea alba* L., *Nuphar lutea* (L.) Sm. and *Nymphoides peltata* (Gmel.) O. Kuntze. Freshwater Biol. 24: 315-326.

SMOLDERS A.J.P., DEN HARTOG C., ROELOFS J.G.M. 1995. Germination and seedling development in *Stratiotes aloides* L. Aquat. Bot. 51: 269-279.

SMOLDERS A.J.P., LUCASSEN E.C.H.E.T., ROELOFS J.G.M. 2002. The isoetid environment: biogeochemistry and threats. Aquat. Bot. 73: 325-350.

SZMEJA J. 1987. The ecology of *Lobelia dortmanna* L. I. The plasticity of individuals within a constant depth interval in oligotrophic lakes. Ekol. Pol. 35: 497-522.

SZMEJA J. 1992. The structure, spatial organisation and demography of isoetids. An ecological study on submerged plants. Gdańsk University, Rozprawy i Monografie 175: 1-137.

SZMEJA J. 1994a. An individual's status in populations of isoetid species. Aquat. Bot. 48: 203-224.

SZMEJA J. 1994b. Effect of disturbances and interspecific competition in isoetid populations. Aquatic Bot. 48: 225-238.

SZMEJA J. 1994c. Dynamics of the abundance and spatial organisation of isoetid populations in an oligotrophic lake. Aquatic Bot. 49: 19-32.

SZMEJA J. 2001. *Luronium natans* L. (Raf.) In: Zarzycki K., Kaźmierczakowa R. (ed.) The Polish Red Book of Plants., PAN, Kraków, p. 395-396.

SZMEJA J. 2004a. *Luronium natans* (L.) Raf. In: B. Sudnik-Wójcikowska (ed.) A guide to species conservation. (*in press*).

SZMEJA J. 2004b. A guide to the study of aquatic vegetation. In: J.B. Faliński (ed.) Vademecum Geobotanicum, Wyd. Sorus (*in press*).

SZMEJA J., BANAŚ K., BOCIĄG K. 1997. Ecological conditions and tolerance limits of isoetids along the southern Baltic coast. Ekol. Pol. 45: 343-359.

SZMEJA J., BAZYDŁO E. 2004a. Causes of decline in the stands of *Luronium natans* (L.) Raf. within the context of reaction of individuals to varying water conditions. Pol. Bot. Stud. (*in press*).

SZMEJA J., BAZYDŁO E. 2004b. The programme of protection and control of *Luronium natans* (L.) Raf. in the Tuchola Forest (Bory Tucholskie). In: J. Banaszak, K. Tobolski, (eds) "Bory Tucholskie" National Park. Wyd. Nauk. Akad. Bydgoskiej, Bydgoszcz.

TUTIN T.G., HEYWOOD V.H., BURGES N.A., MOORE D.M., VALENTINE D.H., WALTERS S.M., WEBB D.A. (eds)

1980. Flora Europaea, 5, Alismataceae to Orchidaceae. Cambridge University Press, Cambridge.

VESTERGAARD O., SAND-JENSEN K. 2000. Alkalinity and trophic state regulate aquatic plant distribution in Danish lakes. Aquat. Bot. 67: 85-107.

WILLBY N.J., EATON J.W. 1993. The distribution, ecology and conservation of *Luronium natans* (L.) Rafin. in Britain. J. Aquat. Plant Manage. 31: 70-76.

ZIMMERMAN M., GROSS R.S. 1984. The relationship between flowering phenology and seed set in an herbaceous perennial plant, *Polemonium foliosissium* Gray. Am. Midland Nat. 111: 185-192.