GROWTH RATE OF DUCKWEEDS (LEMNACEAE) IN RELATION TO THE INTERNAL AND AMBIENT NUTRIENT CONCENTRATIONS – TESTING THE DROOP AND MONOD MODELS

ABSTRACT: The Monod model describes the relationship between growth rate and ambient nutrient concentration, the Droop model focuses on internal nutrient resources as the driving factor. Both were applied mainly to explain phytoplankton dynamics in lakes or in experimental cultures. Our test plants were two species of duckweeds – *Lemna minor* L. and *Spirodela polyrhiza* (L.) Schleiden sampled from 18 natural stands situated in 6 different water bodies. Plants were grown outdoor in original lake water or in mineral media of varying N and P concentrations (0–21 mg N-NO₃ L⁻¹ and 0–1853 μg P-PO₄ L⁻¹ for *L.minor* and 0–4.2 mg N-NO₃ L⁻¹ and 0–371 μg P-PO₄ L⁻¹ for *S. polyrhiza*). Moreover, we analysed concentrations of mineral forms of N and P in lake water and tissue nutrient concentrations in plants. Tissue N of both plants was significantly correlated with ambient inorganic nitrogen sources, no such relationship was observed for tissue P. The growth rate of both plants measured under experimental outdoor conditions was better explained by tissue N and P variability (the Droop model) than by the external nutrient availability (the Monod model). We confront obtained results with literature data on N uptake kinetics and postulate that the luxury consumption of nutrients and plant growth dependent mainly on internal N and P resources might be an adaptation of duckweeds to varying habitat conditions typical of astatic water bodies.

KEY WORDS: *Lemna minor*, *Spirodela polyrhiza*, nutrient resources, growth rate, luxury consumption

1. INTRODUCTION

Duckweeds are small free-floating vascular plants known to prefer nutrient-rich waters (Hillman 1961, Lüönd 1980). They have a great capability to take up and store many dissolved substances and therefore they are used in wastewater treatment, also in temperate climates (Ozimek 1996). The growth of duckweeds depends on a variety of factors, mainly nutrient concentration, pH, temperature, light and biotic relationships including inter- and intra-specific competition (Landolt and Kandeler 1987, Szabó et al. 2005, Kufel et al. 2010).

The effect of ambient nutrient concentrations on the growth rate of macrophytes is well
known. In addition, several authors (Gerloff and Krombolz 1966, Denny 1987, Landolt and Kandeler 1987, Oscarson et al. 1989, Rattray et al. 1991, Ozimek et al. 1993, Cedergreen and Madsen 2002) have shown that dissolved inorganic nitrogen (DIN) and dissolved phosphate (DP) may also determine tissue nutrient concentrations. When nutrients are abundant in the environment, autotrophs can sometimes take them up well above their physiological needs. If this excess is not metabolized by organisms into functional or structural compounds, such an uptake is called ‘luxury consumption’. The phenomenon is well known to occur in planktonic algae (Le Rouzic and Bertrun 1997, Powell et al. 2009). Duarte (1992) based on extensive data found N content in phytoplankton to vary from 1.0 to 14.0% dry wt. and P content – from 0.10 to 8.32% dry wt. Respective figures for freshwater angiosperms were lower and ranged between 1.0 and 4.3% for N and between 0.04 and 1.38% for P (Duarte 1992). Nutrient content in duckweed biomass is typically closer to the upper end of these ranges.

Duckweeds are exceptional among macrophytes in that they store relatively large amounts of phosphorus. Lemnaceae store P as orthophosphates within the vacuole, as condensed inorganic phosphates (oligo-, cyclic and high-molecular phosphates) and in phytic acid (Landolt and Kandeler 1987). The latter serves as a long-term P-storage compound while the others are cycled more rapidly. If available nutrients in the water are exhausted, duckweeds may be able to continue their growth by mobilising accumulated internal resources (Bieleski 1968). The main nitrogen source for duckweeds is nitrate and ammonium but *L. minor* L. grows faster when ammonium is available (Lüönd 1980) or when it can be supplied with a mixture of amino acids (Joy 1969). High concentrations of ammonium ions may, however, limit growth of *S. polyrhiza* (L.) Schleiden, especially at relatively high pH of the growth medium due to the appearance of un-dissociated NH$_3$ (Caicedo et al. 2000). Oscarson et al. (1989) showed that *L. gibba* L. can accumulate nitrogen in soluble form (‘non-growth N’) instead of converting it into organic compounds and thereby being capable of luxury consumption. Nitrogen availability can also affect ageing of common duckweed and thus influencing its population growth rate. Ashby et al. (1949) and Lemon et al. (2001) reported that the fronds live for up to 4–6 weeks but they age slower in nitrogen-poor media.

Accumulation of nutrients and biomass production in duckweeds was a matter of many studies due to the application of these plants in wastewater treatment (Vermaat and Hanif 1998, Körner et al. 2003, Chaiprapat et al. 2005). These studies dealt, however, with nutrient concentrations in wastewater, thus far exceeding those normally found in natural conditions. Much less is known about a possible nutrient limitation in duckweeds growing in lakes and ponds and the effect of nutrient deficiency on population dynamics.

The growth rate – nutrient availability relationships are usually analysed with the use of the Monod (1942) or the Droop (1968) models. The first based on Michaelis-Menten kinetics relates the growth rate of plants to external nutrient concentration and allows for calculating the maximum growth rate of a plant and a half-saturation constant (nutrient concentration at which actual growth rate equals ½ of the maximum). The Droop model combines the growth rate with cellular nutrient concentration and gives a minimum nutrient concentration at which the growth rate = 0. The first model often failed to explain experimental data especially when the plant studied exhibited excessive nutrient storage which secured plant growth irrespective of external supply. Both models were usually applied to describe growth rate of phytoplankton in cultures (e.g. Sommer 1991, Legović and Cruzado 1997).

Duckweeds, due to their plasticity in response to nutrient supply, the ability to store nutrients above their metabolic needs and relatively fast growth, are suitable for testing both mentioned models. Therefore, in this paper we aimed at: 1) testing the relationships between the growth rate and nutrient sources in the two duckweed species *L. minor* and *S. polyrhiza*, and 2) exploring potential implications of the adopted model to duckweeds performance in their natural habitats.
2. MATERIAL AND METHODS

We used two experimental protocols in our study. In the first, plants were grown in lake water taken from under plant patches. Plants of \textit{L. minor} and \textit{S. polyrhiza} were sampled from six water bodies: three midfield ponds (Dąbrowa, Miednik, Mościbrody), two oxbow lakes (Trojan, Bużysko) connected with a river (the Bug River) and one lake (Lake Beldany, Masurian Lakeland, Poland). The ponds and oxbow lakes have areas from 1 to maximum 25 ha and are surrounded mainly by grasslands. Lake Beldany has a larger area (874 ha) and its direct watershed is forested. Plants and water were sampled from a sheltered bay in this lake. Three stands of both duckweeds, where plants covered an area not less than 20 m² were selected in each water body and plants from these stands were dealt with as a separate sample (N = 18 for each of the plants). From the same stands water was taken from a depth of ca 0.5 m for chemical analysis and for outdoor cultures.

In the second experimental set, plants were grown in an artificial mineral APHA medium (ISO 20079 2006) modified to obtain a gradient of decreasing N and P concentrations (Table 1) with other components being unchanged. Maximum nutrient concentrations in \textit{Spirodela} cultures were smaller than in \textit{Lemna} cultures since preliminary tests showed that the former plant produced turions when grown in more concentrated medium. \textit{Lemna} plants used for this culture originated from an oxbow lake. \textit{S. polyrhiza} was taken from a midfield pond (ca 1 ha of area) surrounded by abandoned grasslands. As above, both plants were sampled from three sites in each water body and dealt with as separate samples.

In the lab lake water intended for growing plants was filtered through 20 μm plankton net to remove zooplankton and larger algae. Plants from natural sites were separated from accompanying species and rinsed with distilled water before planting. Subsamples of plants from each stand were preserved for further analyses of tissue N and P content.

Culture experiments were performed in plastic pots of a diameter of 13 cm and 4.5 cm deep filled with 250 cm³ of original lake water or artificial medium. Each pot was planted with 25 to 30 \textit{Lemna} fronds or with 15 fronds of \textit{S. polyrhiza}. Pots with both plants were randomly placed in larger trays filled with tap water to mitigate daily temperature variability. The experiment was kept outdoor under poly-carbonate roof at the light:dark ratio of ca 16:8 (mid-June to the end of July). Maximum intensity of solar radiation measured at noon with the LI-250A light meter at the level of water in experimental pots was ca 1200 μM m⁻² s⁻¹ on sunny days and ca 300 μM m⁻² s⁻¹ on cloudy days. Water temperature in pots varied between 25°C and 30°C in midday. All experimental conditions were designed to resemble those in natural plant stands. Every 3 days the number of fronds was counted until the day 9, on which the experiments were ended. The relative growth rates (RGR) of plants were calculated from the formula: \[ RGR = \frac{\log N_t - \log N_0}{t}, \] where \( N_t \) was the number of fronds on day

<table>
<thead>
<tr>
<th>\textit{L. minor}</th>
<th>\textit{S. polyrhiza}</th>
</tr>
</thead>
<tbody>
<tr>
<td>N-NO₃</td>
<td>P-PO₄</td>
</tr>
<tr>
<td>21</td>
<td>1853</td>
</tr>
<tr>
<td>21</td>
<td>185</td>
</tr>
<tr>
<td>21</td>
<td>19</td>
</tr>
<tr>
<td>21</td>
<td>2</td>
</tr>
<tr>
<td>21</td>
<td>0</td>
</tr>
<tr>
<td>2.10</td>
<td>1853</td>
</tr>
<tr>
<td>0.21</td>
<td>1853</td>
</tr>
<tr>
<td>0.02</td>
<td>1853</td>
</tr>
<tr>
<td>0</td>
<td>1853</td>
</tr>
</tbody>
</table>
$t$, $N_0$ – the number of fronds at the start of the experiment and $t$ – the number of days. Statistical significance of RGR was tested with linear regression of log N on t. All RGRs obtained within this study passed this test. After cessation of the experiment plants from each pot were collected for analyses of tissue N and P.

Lake water for chemical analyses was filtered through Whatman GF/C filter. In the filtrate the concentration of ammonium ions was determined with the method of Solórzano (1969), nitrate-nitrogen with phenyl-disulphonic acid and soluble reactive phosphorus (SRP) with the molybdenum blue method (Standard methods 1960). We used dissolved inorganic nitrogen (DIN) i.e. the sum of N-NH$_4$ and N-NO$_3$ as a measure of nitrogen sources for plants in lake water.

Plant material (both before and after the experiment) was rinsed before analyses with distilled water and dried at a temperature of 105°C to constant weight. Samples of a weight of ca 0.1 g were mineralized according to the Kjeldahl procedure. In resulting solution plant tissue N was determined as ammonium ions and phosphorus as soluble reactive phosphorus after appropriate dilution with the methods cited above.

The Monod model has a form:

$$\mu = \mu_{\text{max}} \times \frac{S}{S+k}$$

where: $\mu$ – RGR of $L. minor$ or $S. polyrhiza$, $\mu_{\text{max}}$ – maximum RGR calculated from the model, $S$ – concentration of DIN (in mg N L$^{-1}$) or SRP (in μg P L$^{-1}$) in lake water, and $k$ – half-saturation constant i.e. the concentration of N or P at which $\mu = 0.5 \mu_{\text{max}}$.

The model was calculated for N and P separately. Such an approach assumed that the growth of duckweeds under natural conditions was limited by both nutrients. To differentiate clearly between N and P limitation, we performed culture experiments using a gradient of available nutrient concentrations. In that case the Monod equation for N was calculated using growth rates attained at maximum P concentrations in the medium (1853 μg L$^{-1}$ in *Lemna* cultures and 371 μg L$^{-1}$ in *Spirodea* cultures) and, accordingly, the equation for P was calculated with the growth rates attained at maximum N concentrations in the medium (21 mg L$^{-1}$ for *Lemna* and 4.2 mg L$^{-1}$ for *Spirodea* cultures). Thus, the number of cases was N = 15 for *L. minor* and N = 12 for *S. polyrhiza* (see Table 1).

The Droop model has a form:

$$\mu = \mu_{\text{max}} \times \left(1-q_0/q\right)$$

where: $\mu$ – RGR of $L. minor$ or $S. polyrhiza$, $\mu_{\text{max}}$ – maximum growth rate attained at infinite nutrient supply, $q_0$ – minimum tissue nutrient concentration (cell quota in original Droop model) sustaining plant growth and $q$ – actual tissue nutrient concentration. Data from cultures performed in original lake water were only taken for these calculations.

Statistical data processing and graphs were made with the Statistica 9 software. Both models were calculated using the least

| Plant and nutrient | Droop equation | | | |
|--------------------|---------------|------------------|------------------|
| $L. minor$ N       | 0.147±0.011   | <0.001           | 11.19±1.11       | <0.001 |
| $L. minor$ P       | 0.104±0.020   | <0.001           | 0.97±0.07        | 0.211  |
| $S. polyrhiza$ N   | 0.087±0.011   | <0.001           | 6.10±1.85        | <0.001 |
| $S. polyrhiza$ P   | 0.090±0.013   | <0.001           | 1.25±0.37        | <0.01  |

| Monod equation |
|-----------------|---------------|------------------|------------------|
| $L. minor$ N    | 0.195±0.079   | 0.025            | 0.23±0.18        | 0.209  |
| $L. minor$ P    | 0.094±0.018   | <0.001           | 3.51±3.81        | 0.371  |
| $S. polyrhiza$ N| 0.341±0.235   | 0.167            | 0.72±0.65        | 0.290  |
| $S. polyrhiza$ P| 0.085±0.012   | <0.001           | 7.51±6.06        | 0.234  |

Table 2. Parameters of the Droop (formula 2) and the Monod (formula 1) equations (± SD) calculated for *L. minor* and *S. polyrhiza* grown in original lake water and the significance of parameters ($\mu_{\text{max}}$ in day$^{-1}$, $q_0$ in mg N or P g$^{-1}$ dry wt., $k$ in mg N L$^{-1}$ or μg P L$^{-1}$).
Duckweed growth and nutrient resources

square approximation with the Gauss-Newton iterative method. The significance of differences was tested with the non-parametric U Mann-Whitney test. Correlations between tissue N or P and the concentration of respective nutrients in lake water were checked with the Spearman correlation coefficient.

3. RESULTS

Analysed lake waters overgrown by both duckweed plants largely differed in the concentration of mineral forms of nitrogen and phosphorus. DIN concentrations varied between 0.04 and 0.33 mg N L\(^{-1}\) (with nitrate-N being the dominant N species), those of SRP – between 4 and 282 μg P L\(^{-1}\). Nitrogen concentrations in \(L.\) minor tissue ranged from 13.52 to 42.06 mg N g\(^{-1}\) dry wt., those of P varied between 2.69 and 12.00 mg P g\(^{-1}\) dry wt. The respective ranges in \(S.\) polyrhiza were 9.36–64.75 mg N g\(^{-1}\) dry wt. and 1.87–7.88 mg P g\(^{-1}\) dry wt. Tissue N in \(Lemna\) plants taken from three stands in one of oxbow lake varied between 17.57 and 21.05 mg N g\(^{-1}\) dry wt., tissue P – from 2.69 to 3.16 mg P g\(^{-1}\) dry wt. The ranges of N and P concentrations in the biomass of \(S.\) polyrhiza sampled from pond were 20.92–26.92 mg N g\(^{-1}\) dry wt. and 4.47–5.05 mg P g\(^{-1}\) dry wt. There were no inter-specific differences in the concentration of N or P in the biomass of plants sampled from all water bodies. The two species did not differ also in the tissue N:P ratio which was 6.0 ± 2.1 in \(S.\) polyrhiza and 5.6 ± 2.1 in \(L.\) minor and generally reflected the DIN:SRP ratio in lake water (6.8 ± 6.4).

We expected tissue nutrient content in \(Lemna\) and \(Spirodela\) plants to reflect the abundance of available mineral N and P in lake water. Correlations between tissue N and dissolved inorganic nitrogen in lake water were significant though weak (\(R = 0.57\) and 0.55 at \(P < 0.05\) for \(L.\) minor and \(S.\) polyrhiza, respectively) but those between tissue P and SRP were not significant for any of the plants.

The Droop equation (eq. 2) seemed to better approximate the obtained results. With only one exception, both calculated parameters were highly significant (Table 2). Calculated minimum cell quota differed significantly between plants and nutrients. \(Q_0\) for N was higher (\(P < 0.001\)) in \(L.\) minor and \(q_0\) for P was higher (\(P < 0.01\)) in \(S.\) polyrhiza.

Maximum growth rates in \(S.\) polyrhiza were consistent, irrespective of whether they were calculated upon tissue N or P concentrations. In \(L.\) minor, however, maximum growth rate based on N content was significantly higher (\(P < 0.001\)) than the growth rate based on P content, both being at the same time higher than the respective figures calculated for \(S.\) polyrhiza (Table 2).

On the contrary, parameters in the Monod model (eq. 1) were mostly insignificant – this was particularly true for half-saturation constants, none of which was statistically significant (Table 2). The Monod model also poorly fitted the results obtained from plant cultures in artificial media. While maximum growth rates were calculated with sufficient precision, half-saturation constants were all insignificant (Table 3) and the coefficient of determination did not exceed 13% for any of the regressions calculated with this model.

A substantial decrease of tissue nutrient concentrations was noted in both \(L.\) minor (Fig. 1) and in \(S.\) polyrhiza (Fig. 2) grown for 9 days in original lake water. More severe nutrient depletion was observed in \(L.\) minor where tissue N concentrations decreased close to the minimum determined from the Droop model and tissue P dropped below this threshold value in \(Lemna\) plants from

---

**Table 3. Parameters of the Monod (formula 1) equations (±SD) calculated for \(L.\) minor and \(S.\) polyrhiza grown in artificial mineral media and the significance of parameters (\(\mu_{\text{max}}\) in day\(^{-1}\), k in mg N dm\(^{-3}\) or μg P dm\(^{-3}\)).**

<table>
<thead>
<tr>
<th>Plant and nutrient</th>
<th>(P_{\text{max}})</th>
<th>(P)</th>
<th>(k)</th>
<th>(P)</th>
</tr>
</thead>
<tbody>
<tr>
<td>(L.) minor N*</td>
<td>0.165±0.016</td>
<td>&lt;0.001</td>
<td>0.02±0.01</td>
<td>0.143</td>
</tr>
<tr>
<td>(L.) minor P**</td>
<td>0.142±0.019</td>
<td>&lt;0.001</td>
<td>1.89±1.66</td>
<td>0.274</td>
</tr>
<tr>
<td>(S.) polyrhiza N*</td>
<td>0.128±0.023</td>
<td>&lt;0.001</td>
<td>0.02±0.02</td>
<td>0.440</td>
</tr>
<tr>
<td>(S.) polyrhiza P**</td>
<td>0.156±0.037</td>
<td>&lt;0.01</td>
<td>0.87±2.24</td>
<td>0.703</td>
</tr>
</tbody>
</table>

* – calculated for maximum concentrations of P in the medium
** – calculated for maximum concentrations of N in the medium
two water bodies (Fig. 1). Nitrogen content in the biomass of *S. polyrhiza* remained above the minimum concentration but phosphorus content after the experiment was below the minimum value in plants from two out of six sampled water bodies (Fig. 2).

4. DISCUSSION

Better fit of the Droop model to measured growth rates and the observed decrease of tissue nutrient concentrations after the experiment show that plants grew at the expense of internal nutrient resources. Szabó *et al.* (2005) observed decreased growth rate of *L. gibba* to 28% of the control when plants were grown in N depleted medium and to 49% of the control when the plant was grown in P depleted medium. As in our experiments, they recorded the reduction of internal pool of nutrients after 10 days of culture in nutrient depleted media (from 40.69 to 9.12 mg N g⁻¹ dry wt. and from 13.95 to 4.96 mg P g⁻¹ dry wt.). All these results seem to evidence the mobilization of internal nutrient sources as a common pattern in duckweeds when external N and/or P are in short supply.

Literature data provide different data on minimum tissue N and P concentrations sustaining the growth of aquatic macrophytes. Gerloff and Krombholz (1966) estimated these concentrations at 13 mg N g⁻¹ and 1.3 mg P g⁻¹ dry wt. of macrophytes, Chaiprapat *et al.* (2005) gave 16.5 mg N g⁻¹ and 6.3 mg P g⁻¹ dry wt. as a minimum tissue nutrient content still sustaining the growth of *S. punctata* (G. Mey.) C.H. Thomps. Similar data are given in Landolt and Kandeler...
Duckweed growth and nutrient resources

(1987). However, from experiments made by Oscarson et al. (1989) it appears that the minimum N content in L. gibba is only 1 mg N g⁻¹ dry wt. Our results also showed significant differences between the two studied plant species in the minimum concentrations of both N and P in their biomass. Such differences may have important implications for the in situ growth of duckweeds. Markedly lower minimum cell N quota in S. polyrhiza than in L. minor (Table 2) means that at limiting supply of external nitrogen sources the latter species is the first to stop growing. Lower minimum cell quota may thus be a competitive advantage for S. polyrhiza apart from more developed root system, which was postulated by Wołek (1974) as a reason for faster growth of S. polyrhiza when competing with L. minor for nutrients. However, the minimum tissue P content was significantly lower for L. minor (Table 2) which means that the advantage of any of the two duckweed species depends on whether P or N is the limiting factor.

The growth rate of duckweed plants is an outcome of biomass increments and nutrient uptake necessary to replenish internal resources ‘diluted’ by increasing biomass. Nutrient uptake is a first order process usually described by Michaelis-Menten kinetics. Cedergreen and Madsen (2002) estimated the concentrations in the medium at which the net nitrogen uptake by L. minor plants was zero. These threshold concentrations were different for root and frond N uptake (0.19–0.32 mg N-NO₃ L⁻¹, respectively, in N depleted plants) and depended on N species (0.19 mg N-NO₃ L⁻¹ versus 0 mg N-NH₄ L⁻¹ for the uptake by roots of N depleted plants and 0.93 mg N-NO₃ L⁻¹ versus 0.14 mg N-NH₄ L⁻¹ for the uptake by roots of N-rich plants). Calculated minimum N concentrations of the medium (supplied as both nitrates and ammonium ions) increased and the maximum uptake rate by fronds decreased with increasing N content in plant tissue. Tissue N concentrations in L. minor from our experiments were close to or higher than those in N-rich plants from Cedergeen and Madsen’s (2002) study. At the same time actual N-NO₃ concentrations in lake waters never exceeded the critical values given above and the concentration of N-NH₄ exceeded it in only 2 out of 18 sampled lake stands. Under such circumstances any uptake of N by Lemma plants from our experiments was unlikely which is an additional evidence for internal N as the sole source for plant growth.

Relatively high tissue N and P concentrations were probably the reason why the Monod model did not fit to experimental data from plant cultures in artificial media (Table 3). The amount of nutrients accumulated in plant biomass was large enough to secure plant growth even under N and P deficiency in the artificial medium. Possible N-NO₃ uptake at higher external concentration had probably a smaller effect on plant growth.

Weak correlation between the tissue N and the concentration of mineral N in lake water and no correlation between respective phosphorus pools noted in our study is not surprising. Nutrient accumulation in plant tissue takes time and the present content of N and P in plant tissue is an outcome of both plant growth, nutrient uptake rate and the past variability of available nutrients in lake water. The latter factor is especially important in small astatic water bodies – most common habitats for duckweeds. During our 9-day long experiments the tissue nutrient concentrations dropped to or even below (Figs 1 and 2) the limit sustaining further growth. Under natural conditions internal nutrient pool should be replenished, otherwise the plants would stop growing. The replenishment is possible only under the condition of rapid nutrient cycling in lake water and/or terrestrial nutrient inputs, to which the small astatic water bodies are particularly susceptible.

Our results suggest that, with the exception of a few examples, both plant species experienced nutrient limitation in their natural sites. Plants’ responses to nutrient limitation may range from morphological or biochemical alterations to the reduced reproduction rates. Aerts (1999) based on his earlier studies on terrestrial plants proposed two different strategies to explain plants’ response to nutrient limitation. The first strategy typical of plants from nutrient-poor habitats would be a combination of slow growth rate and low nutrient losses which means more economic nutrient cycling. The second strategy, which should
characterise plants from nutrient-rich habitats, consists in rapid growth and selection on traits that would promote an ability for competitive nutrient acquisition (e.g. root elongation). The effect of this strategy is a high rate of nutrient cycling in the ecosystem. Both strategies imply, however, long-term ecosystem stability. It seems that none of these strategies applies to \textit{L. minor}, \textit{S. polyrhiza} or more generally, to all duckweeds. Duckweed plants may experience nutrient abundance alternated with nutrient deficiency over a short period of time due to fluctuating chemical conditions typical in small water bodies. The capability for accumulating large amounts of nutrients in plant tissue (Lüönd 1980) may be thus considered an adaptation that evolved in duckweeds as a response to unstable aquatic habitat and allows the plants to continue growth under fluctuating nutrient delivery. That is probably the reason why duckweeds are rare in large lakes where nutrients depleted by dominant planktonic algae are not supplemented fast enough to facilitate further growth of duckweed populations.

ACKNOWLEDGMENTS: Final version of this paper benefitted from valuable remarks and comments given by Prof. dr hab. Anna Hillbricht-Illkowska and an anonymous reviewer. This study was financed with funds of the Polish Ministry of Science and Higher Education, grant number N304 072235.

5. REFERENCES

Le Rouzic B., Bertru G. 1997 – Phytoplankton community growth in enrichment bioas-
Duckweed growth and nutrient resources

says: possible role of the nutrient intracellular pools – Acta Oecol. 18: 121–133.


Received after revision October 2011