J. Aquat. Plant Manage. 47: 116-121

Seasonal and Vertical Changes in the Surface Area/Biomass Ratio of *Potamogeton lucens* L. in a Clear and a Turbid Shallow Lake

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ABSTRACT

To determine the influence of different growth conditions on the architecture of *Potamogeton lucens* L., we measured several morphological parameters of the plants from May to September 2001 in a clear macrophyte-dominated lake and a turbid phytoplankton-dominated lake in Central Estonia. The main difference between the lakes was the higher summer water transparency in the macrophyte-dominated lake. All size related parameters of *P. lucens* tended to be larger in the macrophyte-dominated lake, but only the total above-ground plant surface area and the surface area of leaves differed significantly ($p < 0.05$) between lakes. The relationship between surface area (A, in cm^2) and dry weight (DW, in g) for the measured 25-cm sections of above-ground parts of the plants could be described as:

$$A = 312.9 \pm 9.4\ DW + 26.5 \pm 6.8\ (\pm \text{ standard error})$$
$$(R^2 = 0.649;\ n = 607;\ p < 0.001)$$

Better light conditions in summer and shorter wind fetch in the macrophyte-dominated lake were likely factors stimulating further ramification on the plants in August and a more uniform vertical distribution of plant surfaces in this lake compared to the plankton-dominated lake.

Key words: macrophytes, macrophyte-dominated lake, plankton-dominated lake, shallow lake, surface area/dry weight ratio.

INTRODUCTION

Rich stands of submerged aquatic macrophytes carpeting the bottom of shallow lakes contribute to water clarity by suppressing sediment resuspension (Barko and James 1998), competing with phytoplankton for light and nutrients, and providing a refuge for zooplankton against planktivorous fish (Jeppesen et al. 1999). However, dense stands of aquatic vegetation can create a nuisance for boating and swimming and obstruct water flow (Nes et al. 2002). Not only the abundance but also the growth form of macrophytes is important in this respect. Studies on the architecture of terrestrial plants show that plant species have different growth strategies (Halle et al. 1978, Barthelemy et al. 1989). Further, plants of the same species living under different light and trophic conditions in terrestrial (Kull 1995, Möller and Cronka 2001) and aquatic systems (Gerber et al. 1994) can exhibit important morphological differences. Knowledge about the distribution of surface area and biomass of macrophytes is important for understanding the ecophysiological role of aquatic plants in lake processes (Gerber et al. 1994). The vertical distribution of leaf surfaces in the water column and the surface area to biomass ratio characterize light adaptation and can be used to assess the growth conditions of plants. The surface area of plants is also often used to describe the quantitative relations between submerged macrophytes and epiphytic organisms (Cattaneo and Carigan 1983, Galanti and Romo 1997, Kelly and Hawes 2005). In shallow lakes rich in submerged macrophytes, epiphyton becomes an important component of the primary productivity and a major regulator of nutrient fluxes (Jorgensen and Loffler 1990, Wetzel 1990). Detailed surface area/DW relationships have been published only for a small number of aquatic plants (Sher-Kaul et al. 1995, Armstrong et al. 2003).

Seasonal variation of biomass and growth rates of submerged plants in shallow waters are often related to light conditions (Sand-Jensen and Madsen 1991, Hawes et al. 1999, Gevaert et al. 2002). Depending on the nutrient status, eutrophic shallow lakes can reach two alternative stable states: a vegetated state with clear water and a turbid state dominated by phytoplankton (Scheffer et al. 1993, Scheffer 1998). Although caused by differences in nutrient availability, the switching of aquatic systems between macrophyte- and phytoplankton-dominated states is triggered by light availability (Sheffer et al. 1993, Schwartz and Hawes 1997).

We hypothesized that the differences in light conditions experienced by plants in clear and turbid lakes create substantial differences in their growth form. For the present study we selected the shining pondweed (*Potamogeton lucens* L.), one of the few species we found in two lakes of different types. Our study had two aims:

(1) to describe the differences in plant architecture in lakes of different light conditions (clear macrophyte-dominated vs. turbid plankton-dominated); and (2) to monitor the changes occurring during seasonal growth.

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Received for publication March 21, 2006 and in revised form April 17, 2009.

TABLE 1. MORPHOLOGICAL, HYDROLOGICAL, AND CHEMICAL CHARACTERISTICS OF STUDIED LAKES FROM APRIL TO OCTOBER 2001 (ACCORDING NÕGES ET AL. 2003).

Characteristic	L. Prossa	L. Kaiavere
Area, km^2	0.33	2.51
Mean (max.) depth, m	2.2 (4.2)	2.8 (5.0)
Water retention time, y	0.56	0.33
PVI of submerged plants, %	40	6
Secchi depth, m	2.5	1.2
pH	8.4	8.6
HCO_3, mmol/l	3.6	3.6
Total P, mg L^{-1}	0.02	0.05
Total N, mg L^{-1}	1.0	1.6

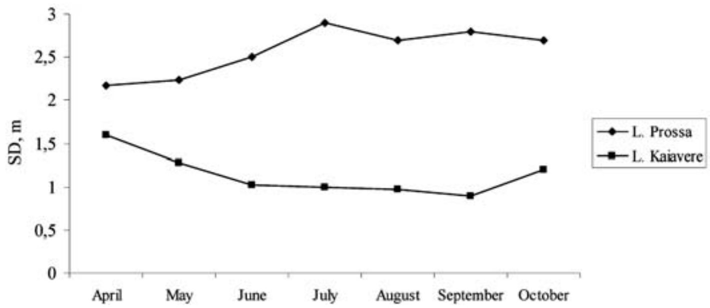

Figure 1. Seasonal dynamics of the Secchi depth in studied a clear (L. Prossa) and a turbid (L. Kaiavere) lake (according Nõges et al. 2003).

SITE DESCRIPTION

The two eutrophic lakes, Prossa and Kaiavere, situated in Central Estonia (Table 1), were selected for our study because of the contrasting light conditions (Figure 1). Smaller Lake Prossa is dominated by submerged macrophytes; the percent volume infested with plants (PVI; Canfield et al. 1984) is 40%. Throughout the year the bottom of the lake is covered with a thick mat of charophytes: *Chara tomentosa* in shallow parts and *Nitellopsis obtusa* in deeper parts. In 2001, after the vernal phytoplankton peak, the water remained clear in L. Prossa during the summer. Much larger Lake Kaiavere, located about 10 km from L. Prossa, is a plankton-dominated lake with a PVI of only 6%, composed mainly of *Potamogeton* spp. In L. Kaiavere the water remained turbid during the whole ice-free period (Nõges et al. 2003). Shining pondweed (*Potamogeton lucens* L.), one of the most frequent plants in L. Kaiavere was present also in L. Prossa.

The relief in this area was formed by the continental ice sheet in the last glaciation and is dominated by elongated moraine drumlins and calcareous eutrophic shallow lakes located between them. The lakes are ice-covered usually from mid-November until the end of April. Most of the catchment area of the lakes is cultivated.

MATERIAL AND METHODS

Samples of *P. lucens* were collected from May to September 2001. At each sampling occasion we collected five sample plants from areas of visually similar plant density (individual shoots cut at the sediment surface), mostly within a depth range of 1.5 to 2.5 m. The plant stands were rather sparse to exclude the effect of density-dependent growth. In the period of fast plant growth in May, samples were collected once a week (only in L. Prossa; no plants were in L. Kaiavere), in June fortnightly, and once a month in July through September. To describe seasonal changes in plant architecture, the shoots were split into 25-cm sections starting from the top. Each plant section was laid out wet on a glass sheet to avoid leaf folding and overlap of plant parts and scanned (O'Neal et al. 2002) in color mode with a resolution of 300 dpi (Epson Perfection 2480 Flatbed Scanner). For area measurements the images were converted to monochrome black-and-white bitmaps and analysed using the program Pindala v.1.0, Indrek Kalamees© 1994. The total area of leaves and stipules was calculated by doubling the measured projection area. The area of stems was calculated as area of cylinder from its projection (Sher-Kaul et al. 1995). After scanning, all plant sections were dried (105 C for 24 h) and weighed for DW using a mechanical torsion prescription balance. To character-

TABLE 2. MEASURED CHARACTERISTICS IN *POTAMOGETON LUCENS* L. IN STUDIED LAKES FROM JUNE TO AUGUST 2001. A = ABOVE-GROUND SURFACE AREA; DW = DRY WEIGHT; CV = COEFFICIENT OF VARIATION (STANDARD DEVIATION/AVERAGE).

	Macrophyte-lake (L. Prossa)			Plankton-lake (L. Kaiavere)		
Characteristic	Median (Average)	Quartiles (Abs. range)	CV	Median (Average)	Quartiles (Abs. range)	CV
Number of plants	30			30		
Height, cm	190 (206)	143-268 (71-343)	0.38	171 (166)	130-194 (76-270)	0.28
DW, g	3.9 (4.4)	1.9-4.6 (1.4-11.3)	0.57	2.5 (3.6)	2-4.8 (0.8-11.9)	0.76
A, cm^2	1464 (1582)	927-1995 (639-3450)	0.47	974 (1227)	628-1902 (311-3375)	0.69
Leaves/stems Area ratio	4.35 (3.57)	2.85-5.26 (1.41-8.33)	0.52	3.13 (2.78)	2.5-5.0 (0.93 6.67)	0.62
Stems % of A	18 (20)	15-25 (11-40)	0.36	23 (24)	16-27 (12 49)	0.40
Leaves % of A	78 (75)	72-81 (43-87)	0.12	72 (72)	67-80 (46 84)	0.14
Stipules % of A	4 (5)	2-5 (1-33)	1.15	4 (5)	3-6 (1 9)	0.47
A/DW of whole plants, cm^2 g^{1}	371 (385)	333-428 (258-602)	0.22	337 (352)	286-416 (204-540)	0.25

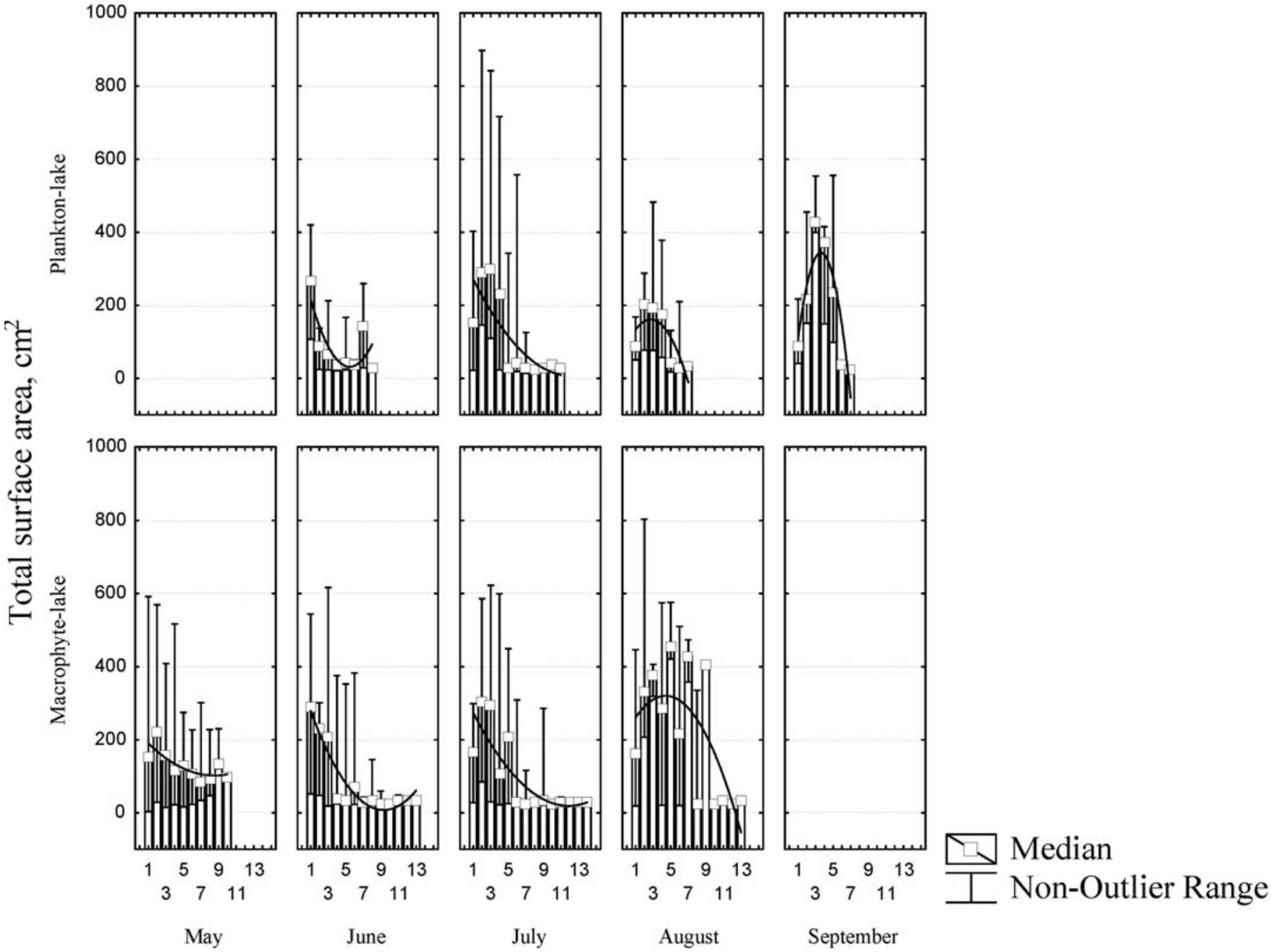

Figure 2. The seasonal dynamics of the vertical distribution of plant surface area in the studied lakes. In each subfigure, column 1 corresponds to the top-most 25-cm section of plants, and the sections are numbered in ascending order downward on the plants. The polynomial fit was added to median values to better visualize the distribution type.

ize plant growth conditions, water temperature, transparency, pH, conductivity, alkalinity, concentration of total phosphorus, total nitrogen, and oxygen were measured in both lakes. Mann-Whitney U-test (Statistica for Windows 7.0) was used to study the differences between sample groups. For comparability purposes we used the variation coefficient (standard deviation/average) to describe the variability of different plant parameters.

RESULTS

At the beginning of sampling in May the average height of *P. lucens* in L. Prossa was already about 1 m. The plants reached their full height (about 2 m) by July. The average total area partitioning among leaves, stems, and stipules was close to 75:20:5%, respectively. Only two plant parameters, the total surface area of shoots and the surface area of leaves, differed significantly ($p < 0.05$) between lakes, with the area of shoots and surface area of leaves being larger in the clear macrophyte-dominated lake (Table 2). In addition, all other size-related parameters of the plants (total height, DW, area/DW ratio, stem and stipule area, leaf percentage of the total area, and leaf/stem area ratio) tended to be larger in the macrophyte-dominated lake; however, these differences remained insignificant because of large variability of the individual plants. The variation coefficient for most absolute size parameters ranged from 0.3 to 0.8 in both lakes but was smaller for relative parameters like the ash content (0.09), the percentage of leaf area (0.12-0.14), and the surface area/DW ratio (0.22-0.25). The latter did not differ between the lakes, and thus the average relationship calculated on the basis of all measured 25-cm sections of plants could be described as:

$$A = 312.9 \pm 9.4\ DW + 26.5 \pm 6.8\ (\pm \text{ standard error})$$
$$(R^2 = 0.649;\ n = 607;\ p < 0.001)$$

In the beginning of the growing season, in May and June, the maximum surface area of plants was located in the topmost

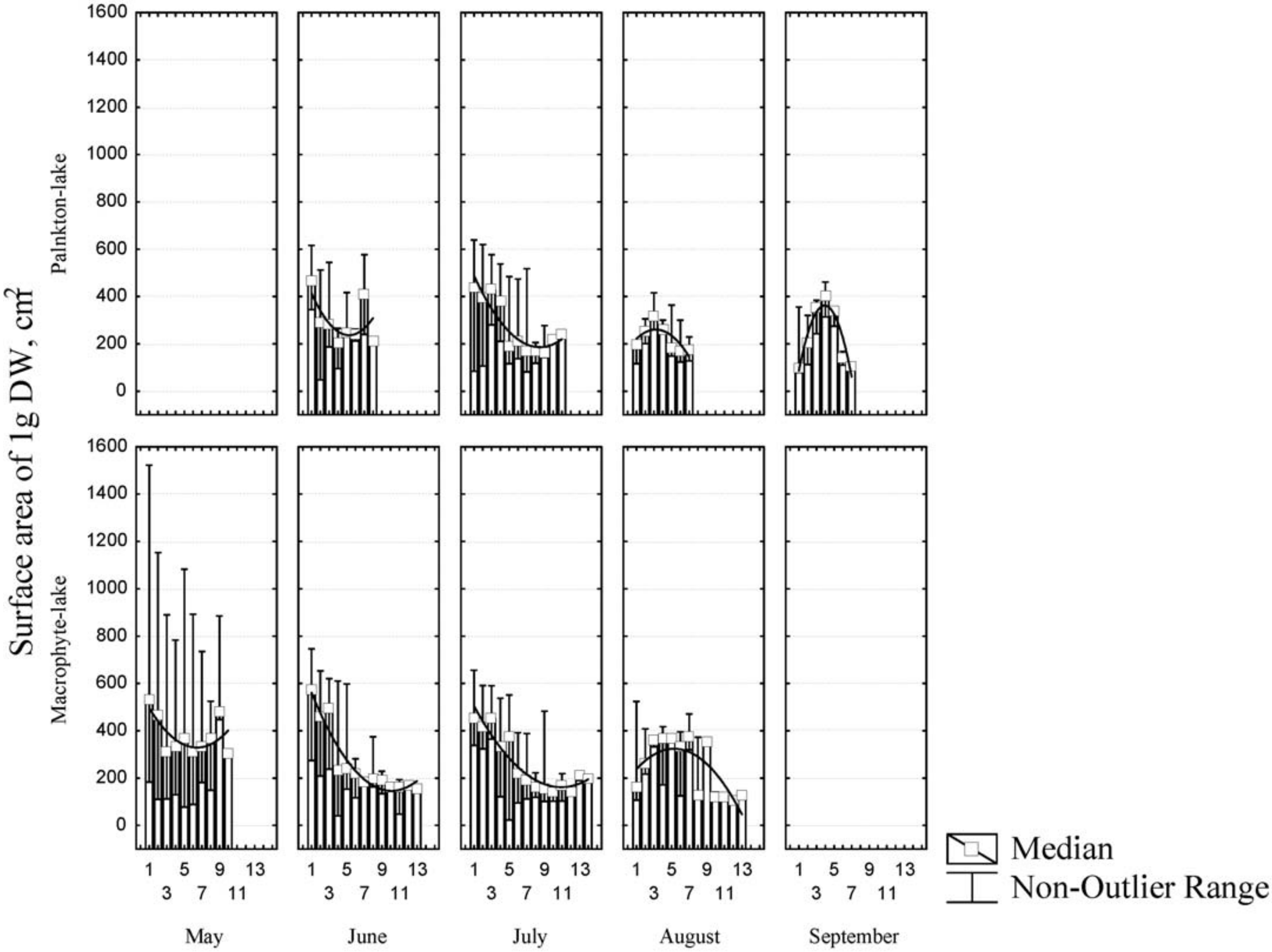

Figure 3. The seasonal dynamics of the vertical distribution of plant surface area/dry weight ratio in the studied lakes. Other explanations as in Figure 1.

sections but shifted in the course of plant growth to lower sections located 0.25 to 0.75 m from the top (Figure 2). In August, a new branching of the plants in the macrophyte-dominated lake created an even more uniform profile of the plant surfaces within the depth range of 0.25 to 2 m. The same pattern also characterized the seasonal changes of the area/DW ratio in both lakes (Figure 3).

DISCUSSION

The published values describing the surface area/DW relationships in aquatic macrophytes (Table 3) vary within one order of magnitude, from around 100 $cm^2 g DW^{-1}$ for simple and thick stems of the emergent *Schoenoplectus lacustris* (L.) Palla (Tessier et al. 2004), *Potamogeton zosteriformis* Fern., and *P. pusillus* L. (Armstrong et al. 2003) to more than 1200 $cm^2 g DW^{-1}$ for *Elodea canadensis* Michx., *Myriophyllum spicatum* L., *Nitellopsis obtusa* (Desv.) J.Gr. (Sher-Kaul et al. 1995), and *Utricularia vulgaris* L. (Armstrong et al. 2003). This variability has been attributed mainly to differences in morphology and thickness of plant stems (Sher-Kaul et al. 1995, Armstrong et al. 2003, Tessier et al. 2004). Armstrong et al. (2003), who made multiple comparisons of the relationship between surface area and biomass of six aquatic plants, found species-specific differences in 14 of 15 cases. Plants with dissected morphology do not necessarily offer the largest surface area per unit biomass (Sher-Kaul et al. 1995), although it has been argued in some studies (Cheruvelil et al. 2001, Gosselain et al. 2005). Armstrong et al. (2003) did not find general groupings of the surface-to-weight relationships based on leaf morphology.

Contrary to our expectations, we did not find substantial differences in the area to biomass ratio of *P. lucens* between the clear and the turbid lake. One possible reason is that light conditions in spring during the fast growth phase of the plants did not differ much (Figure 1), and the plants had already reached nearly their full length by the time one of the lakes cleared. Based on research that measured sur-

TABLE 3. PUBLISHED VALUES DESCRIBING THE ABOVE-GROUND SURFACE AREA TO DRY WEIGHT RELATIONSHIPS IN SOME AQUATIC MACROPHYTES. SD = SECCHI DEPTH; E_{PAR} = EXTINCTION OF THE PHOTOSYNTHETICALLY ACTIVE RADIATION.

Species	A/DW ratio, cm^2 g^{-1} or slope of linear regression (*)	Light conditions	Remarks	Reference
Ceratophyllum demersum L.	230*-427*	E_{PAR} 0.7-1.6 m^{-1}	Averages for different lakes	Armstrong et al. 2003
Elodea canadensis Michx.	1255	Not given	L. Geneva	Sher-Kaul et al. 1995
Myriophyllum exalbescens Fern.	522*	E_{PAR} 0.7-1.6 m^{-1}	Boreal Plain lakes, Canada	Armstrong et al. 2003
M. spicatum L.	1205	Not given	L. Geneva	Sher-Kaul et al. 1995
Nitellopsis obtusa (Desv.) J.Gr.	1205	Not given	L. Geneva	Sher-Kaul et al. 1995
Potamogeton lucens L.	348 (204-602) 313*	SD 1.2-2.5 m	Eutrophic lakes, Estonia	Present study
P. lucens L.	371 (258-602) 313*	SD 2.5 m	L. Prossa	Present study
P. lucens L.	337 (204-540) 313*	SD 1.2 m	L. Kaiavere	Present study
P. lucens L.	653	Not given	L. Geneva	Sher-Kaul et al. 1995
P. pectinatus L.	500	Not given	L. Geneva	Sher-Kaul et al. 1995
P. perfoliatus L.	762	Not given	L. Geneva	Sher-Kaul et al. 1995
P. pusillus L.	124*	E_{PAR} 0.7-1.6 m^{-1}	Boreal Plain lakes, Canada	Armstrong et al. 2003
P. richardsonii (Benn.) Rydb.	766*	E_{PAR} 0.7-1.6 m^{-1}	Boreal Plain lakes, Canada	Armstrong et al. 2003
P. zosteriformis Fern.	108*	E_{PAR} 0.7-1.6 m^{-1}	Boreal Plain lakes, Canada	Armstrong et al. 2003
Schoenoplectus lacustris (L.) Palla	~70	E_{PAR} 0.050-0.064 m^{-1**}	Lago di Candia, Italy.	Tessier et al. 2004
Trapa natans L.	145 (83-238)	Not given	Leaf rosettes (fruits excluded)	Galanti and Romo, 1997
Utricularia vulgaris L.	1779*	E_{PAR} 0.7-1.6 m^{-1}	Boreal Plain lakes, Canada	Armstrong et al. 2003

**—light extinction measured within *S. lacustris* stand.

face area/DW ratio of one species in several lakes, however, the lake specific differences have been small. A study carried out in Boreal Plain lakes in Canada found the relationship between surface area and biomass for three of the four species found in more than one lake was not detectably different among lakes, despite the wide range in nutrient concentration and light extinction coefficient (Armstrong et al. 2003). We also did not find any significant differences in weight specific surface areas between our lakes, despite rather different light conditions in the water column in summer. Considerable variability occurred in both lakes between individual plants, however, as well as in the seasonal scale. In addition to methodical differences in plant surface area measurement, the nearly two times smaller area/DW ratio we found for *P. lucens* in Estonian lakes compared to that measured in L. Geneva (Sher-Kaul et al. 1995) can possibly be attributed to major latitudinal differences in light climate and differences in trophic state and size-related hydrodynamics of the lakes.

The localization of the plant surface area maximum in the top segment of plants during their length growth is related to photomorphogenesis and enables the best light harvesting given the strong attenuation by phytoplankton in spring. After the top of a plant reaches saturating light levels near the water surface, the surface area is maximized in optimum light conditions for photosynthesis. A similar depth distribution of plant biomass as observed by us was also described for *Potamogeton pectinatus* in canals in the Amsterdam Waterworks where the maximum biomass of plants of all length classes was concentrated in the upper 0.2 to 0.5 m of the water column (Best and Boyd 2003). In macrophyte-dominated L. Prossa, the improvement of light conditions in summer possibly stimulated further ramification on plants and the formation of a more uniform vertical distribution of plant surfaces. Another possible explanation for the lower ramification on plants in the plankton-dominated L. Kaiavere, where all size parameters of *P. lucens* tended to be smaller, is the stronger hydrodynamic pressure in this lake because of a longer wind fetch. Numerous studies have shown the importance of fetch on the distribution of aquatic macrophytes (Rea et al. 1998). Idestam-Almquist and Kautsky (1995) show in their study that plants growing in strong wave action area have a different morphology compared to plants growing in a sheltered area.

In our study, the above-ground surface area/biomass ratio of *Potamogeton lucens* L. did not differ significantly between the plankton-dominated and macrophyte-dominated lakes. In contrast, the total surface area and leaf surface area were significantly higher in the macrophyte-dominated compared to the plankton-dominated lake. In the beginning of the growing season the maximum above-ground surface area of plants was located in the topmost sections but shifted in the course of plant growth to lower sections located at 0.25 to 0.75 m from the top.

ACKNOWLEDGMENTS

Funding for this research was provided by Estonian target funding project 0362480s03, by Estonian Science Foundation grant 5738, and by the European Union project CLIME (contract EVK1-CT-2002-00121).

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