



Chara beds acting as nutrient sinks in shallow lakes—a review

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Abstract

The capability of *Chara* beds to act as nutrient sinks in shallow lakes is reviewed. Under favorable conditions charophytes form dense meadows. Biomass and nutrient content in such beds are comparable or even higher than in beds of vascular aquatic macrophytes. As some *Chara* species are capable of overwintering, the nutrient storage in plant biomass may extend beyond the growing season. Some commonly observed phenomena in vascular plants (nutrient uptake and mobilization of nutrients from the sediment) appear to be unlikely or negligible in Characeae. Charophytes have been reported to decompose slower than their vascular counterparts prolonging nutrient storage in plant biomass.

Charophytes may also indirectly affect nutrient cycling in lakes. Utilization of bicarbonate is accompanied by precipitation of calcite during periods of intensive photosynthesis, favoring immobilization of P by binding in the crystal structure or sorption on sedimenting mineral particles. Charophytes are able to deliver oxygen to the sediment, thus potentially enhancing nitrification/denitrification processes and preventing iron-bound sediment phosphorus from being released to the overlying water. Furthermore, dense *Chara* meadows restrict sediment resuspension, consequently blocking an important internal source of nutrients to planktonic algae. We conclude that *Chara* meadows probably are an efficient nutrient trap in shallow lakes. © 2002 Elsevier Science B. V. All rights reserved.

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1. Introduction

Charophytes are a common component of the littoral zone in oligo- and moderately eutrophic water bodies. Along with increasing eutrophication, charophytes are known to give way to angiosperms, mainly to *Potamogeton* species (Ozimek and Kowalczewski, 1984; Pieczyńska et al., 1988; Blindow, 1992a), to disappear finally from extremely turbid

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lakes. The reverse process—the recovery of characean communities after lake restoration has also been reported (Blindow, 1992b; Simons et al., 1994; Van den Berg et al., 1999).

Characeae may play a role in nutrient cycling in a lake. This aspect might be especially essential in shallow lakes overgrown with dense *Chara* meadows. According to the alternative stable states hypothesis (Scheffer et al., 1993), charophytes, among other macrophytes, are postulated to stabilize the macrophyte-dominated state of shallow lakes both at a naturally low trophic status and after lake restoration measures undertaken to restrict phytoplankton abundance (Scheffer, 1998). This stabilizing action may operate in various ways, e.g. through nutrient trapping and competition for nutrients with planktonic algae. Whether charophyte communities stabilize the macrophyte-dominated state depends on many factors.

This paper is intended to assess the capability of charophytes to efficiently store nutrients in shallow lakes. To do this, we will first briefly review the factors which might influence massive growth of charophytes with special emphasis on chemical composition in ambient water. Then we will discuss possible advantages and disadvantages of charophytes over vascular macrophytes in competing for nutrients and finally we will try to estimate the extent of nutrient storage in *Chara* beds.

2. Factors influencing the growth of charophytes

Light is a crucial factor in lake colonization by charophytes. In clear lakes, charophytes have been found at depths of 65 m (Lake Tahoe, CA), 40 m (Lake Vattern, Sweden) and 38 m (Lake Vrana, Yugoslavia) (Spence, 1982 after various authors). Besides aquatic mosses, charophytes are the deepest macrophytic colonists in lakes. This particular behavior arises from the high shade tolerance typical for most representatives of the Characeae family (Damska, 1964; Blindow, 1992a; Middelboe and Markager, 1997). While this property gives a competitive advantage to charophytes over vascular aquatic plants in deep, clear lakes, caulescent and/or canopy forming angiosperms may outcompete charophytes in shallow and turbid waters (Blindow, 1992a).

For massive occurrence in lakes, most charophytes require hard waters of relatively high alkalinity. According to Stroede (1937) (cited after Damska, 1964), the minimum calcium concentration for *Nitellopsis obtusa* (Desvaux) J. Groves, *Chara delicatula* Ag. and *C. fragilis* Desvaux ranges between 15 and 25 mg Ca l⁻¹. The minimum for *C. aspera* (Deth.) Willd. is 47 mg Ca l⁻¹, for *C. vulgaris* L. 55 mg Ca l⁻¹ and for *Nitella mucronata* A. Br. 60 mg Ca l⁻¹. Generally, species of the genus *Chara* prefer waters of higher Ca content than those of the genus *Nitella* (except *N. mucronata*). In hard water lakes, calcium cations are usually accompanied by bicarbonate anions, which are often the main source of inorganic carbon for macrophytes. Charophytes were reported to have a higher affinity to HCO₃⁻ than vascular macrophytes: under experimental conditions, *C. aspera* had a higher photosynthetic rate and a lower photorespiration than *Potamogeton pectinatus* L. over a wide range of HCO₃⁻ concentrations (Van den Berg et al., in press). Bicarbonate is often depleted in dense *Chara* beds and the commonly found calcite encrustation on *Chara* (up to 60% of CaCO₃ in dry weight of charophytes (Hutchinson, 1975)) is a visualization of bicarbonate uptake during intensive growth. This tendency of decalcification by *Chara* may

be an indirect effect upon phosphorus cycling since P may co-precipitate with calcite (Otsuki and Wetzel, 1972; Murphy et al., 1983) or convert calcite into hydroxyapatite (Stumm and Morgan, 1970).

Earlier findings of phosphorus toxicity to *Chara* (Forsberg, 1964, 1965; Hough and Putt, 1988) have not been confirmed in later papers. Blindow (1992a) found various species of Characeae in Scanian lakes, in which soluble reactive phosphorus ranged up to 370 mg P m⁻³ thus, far exceeding the value of 15 mg P m⁻³ given by Forsberg (1964) as growth inhibiting for *Chara*. Blindow (1988) found no growth limitation of *C. tomentosa* L. and *C. hispida* L. at inorganic P concentrations up to 1000 mg P m⁻³, while Kufel and Ozimek (1994) showed that *C. aspera* can grow successfully at soluble reactive P concentrations up to 770 mg P m⁻³. In the latter experiment, *C. aspera* exhibited an increasing uptake rate of phosphorus as a response to increasing inorganic P concentrations in the ambient water (Kufel and Ozimek, 1994). Such an adaptation might be important for phosphorus trapping in lakes with irregular inputs of external P.

3. Charophytes versus vascular aquatic plants

Data presented in Table 1 demonstrate that nitrogen and phosphorus concentrations in charophytes may vary considerably even within the same species. Such a variability probably reflects differences in nutrient abundance in natural habitats since some *Chara* species are able to increase their nutrient content in response to increased nutrient availability. This was demonstrated, e.g. for *C. aspera* by Kufel and Ozimek (1994) and for *C. rudis* A. Braun by Pereyra-Ramos (1981). Generally, however, charophytes do not seem to differ much from vascular macrophytes (excluding perhaps *Ceratophyllum demersum* L.—Table 1) in nitrogen and phosphorus concentration. Such a rough conclusion may, however, be misleading since charophytes are known to produce abundant incrustation composed mainly of calcium carbonate (Riemer and Toth, 1968; Hutchinson, 1975; Best, 1981). Literature data are often lacking the notice whether the incrustation was present on plants and whether it had been removed before chemical analyses. When data on Ca or ash content are available, one can perform a simple correcting calculation. Królikowska (1997) gave Ca concentration in four species of *Chara* from Lake Łuknajno (Poland) between 234 and 246 mg Ca g⁻¹ and in *N. obrusa* of 216 mg Ca g⁻¹. In contrast, calcium concentration in *C. demersum* from the same lake was only 19 mg Ca g⁻¹ and in *P. pectinatus* L. 50 mg Ca g⁻¹. Assuming all Ca is bound in calcite and neglecting other metal oxides, one can calculate nutrient concentration in plants analyzed by Królikowska on an ash free dry weight basis. Recalculated P concentration would, thus, be 3.88, 3.58, 2.84 and 3.01 mg P g⁻¹ AFDW for *C. aspera*, *C. aculeolata*, *C. tomentosa* and *C. contraria*, respectively. These figures are not much lower than 5.23 mg P g⁻¹ AFDW calculated for *C. demersum* and higher than 1.98 mg P g⁻¹ AFDW in *P. pectinatus*. The same calculations run for nitrogen would give values of 25.8, 26.3, 29.4 and 20.0 mg N g⁻¹ AFDW in *C. aculeolata*, *C. tomentosa*, *C. demersum* and *P. pectinatus*, respectively. Similarly, Blindow (1992 b) stated that *C. tomentosa* and *N. obrusa* contained less nutrients than *Myriophyllum spicatum* L. and *P. pectinatus* from Lake Takern and Lake Krankesjön (see Table 1). The former two species contained, however, 70% ash in dry weight as compared to only 17% ash in *M. spicatum* and 19% ash in *P. pectinatus*. If,

Table 1

Nutrient concentration (mg g^{-1} DW) in charophytes and in some aquatic vascular species according to various authors (range or mean \pm S.D. where available)

Species	N (mg g^{-1})	P (mg g^{-1})	Reference.s
Macroalgae	19 \pm 8	1 \pm 0.7	Duarte(1992)
<i>Chara</i> sp.	24.6	2.50	Boyd(1967)
	17.1	2.90	Riemer and Toth (1968)
<i>C. aculeolata</i>	10.4 \pm 0.9 ^a	1.44 \pm 0.10	Królikowska(1997)
<i>C. aspera</i>		1.40	Kufel and Ozimek (1994)
		1.52 \pm 0.20	Królikowska(1997)
<i>C. contraria</i>		1.16 \pm 0.21	Królikowska(1997)
	10.0	1.70	Pereyra-Ramos(1981)
<i>C. globularis</i>	33.0-22.0 ^b	3.1-4.2 ^b	Best(1981)
<i>C. rudis</i>	8.3	1.10	Pereyra-Ramos(1981)
	15.2	0.30	Bematowicz (1969)
<i>C. tomentosa</i>	10.9 \pm 1.7 ^a	1.18 \pm 0.35	Królikowska(1997)
	9.4	1.20	Pereyra-Ramos(1981)
	14.0 \pm 0.6	0.80 \pm 0.08	Blindow(1992h)
	10.5 \pm 0.5	0.63 \pm 0	Blindow(1992b)
<i>C. vulgaris</i>	9.3	1.00	Pereyra-Ramos (1981)
	14.3	0.20	Bematowicz (1969)
	2.43-3.19	0.36-0.46	Dykyjova and Kvet (1982)
<i>N. obtusa</i>	12.3 \pm 2.0 ^a	0.88 \pm 0.13	Królikowska(1997)
	10.2	1.20	Pereyra-Ramos (1981)
	11.1 \pm 1.5	0.88 \pm 0.06	Blindow(1992b)
	21.0-37.0 ^b	3.3-4.2 ^b	Best(1981)
Freshwater angiosperms	24 \pm 7	2.9 \pm 2.3	Duarte(1992)
<i>C. demersum</i>	34.2	4.90	Riemer and Toth (1968)
	28.0 \pm 1.8 ^a	4.98 \pm 0.52	Królikowska(1997)
	20.7	6.10	Bematowicz (1969)
<i>M. spicatum</i>	41.4	4.20	Boyd(1967)
	28.9	5.0	Riemer and Toth (1968)
	16.7	0.30	Bematowicz (1969)
	24.2 \pm 2.4	2.51 \pm 0.30	Blindow(1992b)
<i>P. pectinatus</i>	17.2	2.60	Riemer and Toth (1968)
	17.5 \pm 1.6 ^a	1.73 \pm 0.31	Królikowska(1997)
	16.1	0.40	Bematowicz (1969)
	24.5	2.11 \pm 0.28	Blindow(1992b)

^a Kufel and Kufel, unpublished data.

^b mg g^{-1} AFDW.

again, nutrient concentrations would be calculated on AFDW basis, it would appear that *C. tomentosa* and *N. obtusa* contained more nitrogen and equal amounts of phosphorus than their vascular counterparts.

These comparisons are valid for nitrogen only. In the case of phosphorus, they encumber the error of an unknown amount of P combined with mineral incrustations and probably reflect an approximate upper limit of P concentrations in the biomass of *Chara*. Analyses of ash and carbonate concentrations in *C. globularis* made by Best (1981) and the comparison of his results with others presented in Table 1 seem to suggest that P is not incorporated into mineral incrustations in stoichiometric proportions as those, e.g. in hydroxylapatite.

4. Efficiency of Charophyta in nutrient trapping

Dense *Chara* beds may act as nutrient sinks in several ways. The first, most obvious way is nutrient incorporation in plant biomass. The amount of nutrients trapped in that way will depend on the productivity of Characeans, their maximum biomass and nutrient availability in their environment. The final net effect of nutrient storage will depend also on whether a given species is able to overwinter, on the rate of plant decomposition and on nutrient withdrawal from decomposing detritus. Charophytes may affect nutrient cycling in other ways as well. Being able to form dense stands, charophytes enhance sedimentation and counteract resuspension of sediment particles, thus restricting the return of nutrients already stored in bottom sediments. Charophytes that grow on highly organic bottom sediments are able to deliver oxygen to the reduced sediment/water interface and thus to create favorable conditions for nitrification/denitrification and nitrogen loss to the atmosphere (Lijkiema, 1994). Finally, since they inhabit rather hard, alkaline waters, *Chara* species tend to increase biological decalcification of ambient waters. Calcite precipitation as a result of *Chara* primary production may in turn result in phosphorus sedimentation either in the form of hydroxylapatites or as non-stoichiometric P compounds sorbed on calcite crystals. This effect may also be of importance in the nutrient budget of *Chara* beds.

4.1. Nutrient incorporation in the biomass of charophytes

Once established, Charophytes may produce dense meadows of plants, the biomass of which often exceeds that of vascular macrophytes. Data presented in Table 2 are mean values of biomass per unit overgrown area, hence maximum biomasses may still be higher. Królikowska (1997), for example found 1200 g dry weight m⁻² of biomass in a dense, monospecific stand of *C. tomentosa*. Taking average values from Tables 1 and 2 one may assess that roughly 3.5 g N m⁻² and 0.3 g P m⁻² can be stored in summer biomass of a *Chara* bed. Actual content of nutrients in various *Chara* sp. may vary considerably. Boyd (1967) estimated N and P content in the standing crop of *Chara* spp. at 27.5 and 2.8 g m⁻², respectively. Pereyra-Ramos (1981) calculated a nitrogen content in a dense *C. rudis* stand between 4.0 and 12.9 g m⁻² and a phosphorus content between 0.5 and 1.7 g m⁻², the lower values representing the spring situation and the higher ones the maximum plant biomass in July. Blindow (1992b) estimated a nitrogen content in *C. tomentosa* of 6.5 g N m⁻² and phosphorus content of 0.4 g P m⁻² within vegetated areas of Lake Takern. Slightly lower storage of nutrients was estimated for *C. tomentosa* in Lake Krankesjön. These values exceeded the amounts of nutrients stored in the biomass of *M. spicatum* or *P. pectinatus* from the same lakes by several times (Blindow, 1992b). Phosphorus accumulation in several *Chara* spp. from Lake Łuknajno (Królikowska, 1997) varied between 0.19 and 0.43 g P m⁻².

Data on in situ primary production of charophytes are scarce, sometimes hardly comparable and quite variable both seasonally and from site-to-site. For *C. rudis*, Pereyra-Ramos (1981) estimated a maximum gross primary production of 41.3 mg O₂ g DW⁻¹ 24 h⁻¹ and a respiration of 15.3 mg O₂ g⁻¹ 24 h⁻¹. This is roughly equal to a daily net primary production of 8.11 mg C g⁻¹ assuming a weight-to-weight conversion ratio of C:O₂ = 0.312 (Vollenweider, 1969). Hough and Putt (1988) measured maximum photosynthesis in *C. vulgaris* between 8 and 13 mg C g⁻¹ h⁻¹ in early summer and a minimum in the range of

Table 2 Biomass of *Chara* sp. and of some vascular macrophytes after various authors

Species	Biomass (g DW m ⁻²)	Lakes	Reference
<i>Chara</i> sp.	58.0-220.0	Mamry complex	Bematowicz and Radziej (1964)
<i>C. aculeolata</i>	231.1	Łuknajno	Królikowska (1997)
<i>C. aspera</i>	220.6	Łuknajno	Królikowska (1997)
	500	Veluwemeer	VandenBergetal.(1998)
<i>C. contraria</i>	81.0	Majcz Wielki	Pereyra-Ramos (1981)
	172.3	Łuknajno	Królikowska (1997)
<i>C. rudis</i>	310.5	Majcz Wielki	Pereyra-Ramos (1981)
<i>C. tomentosa</i>	42.0	Majcz Wielki	Pereyra-Ramos (1981)
	465	Takem	Blindow(1992b)
	478	Krankeşjon	Blindow(1992b)
	383.5	Łuknajno	Królikowska (1997)
<i>C. vulgaris</i>	241.5	Majcz Wielki	Pereyra-Ramos (1981)
<i>N. obtusa</i>	36.0	Majcz Wielki	Pereyra-Ramos (1981)
	335	Takem	Blindow (19920)
	118.5	Łuknajno	Królikowska (1997)
<i>C. demersum</i>	43.4	Łuknajno	Królikowska (1997)
	0.7-5.6	Mamry complex	Bematowicz and Radziej (1964)
<i>M. spicatum</i>	42	Takem	Blindow (1992b)
	6.1	Łuknajno	Królikowska (1997)
	03.-7.0	Mamry complex	Bematowicz and Radziej (1964)
<i>P. pectinatus</i>	73	Krankeşjon	Blindow (1992b)
	8.2	Łuknajno	Królikowska (1997)

1-3 mg C g⁻¹ h⁻¹ in late summer. The extreme values of carbon assimilation would convert to the approximate daily uptake of N between 0.56 and 7.22 mg N g⁻¹ AFDW and between 0.08 and 1.01 mg P (assuming 45% C in AFDW, 10 h day length and the average N and P content in *Chara* as calculated in the previous paragraph). An average *Chara* bed of a biomass equal to 279 g m⁻² (mean of data from Table 2) equivalent to 112 g AFDW m⁻² (i.e. assuming after Hutchinson (1975) a 60% content of mineral incrustation) will, therefore, take up from 0.06 to 0.81 g N m⁻² and from 0.01 to 0.11 g P m⁻² per day. These amounts are comparable with the content of nutrients in a 1 m deep column of moderately eutrophic lake water.

Such figures, however illustrative they might be, do not fully explain the real role of charophytes in nutrient cycling in a lake. In particular, despite many experiments, the dilemma whether sediments or ambient water are the main source of nutrients for macrophytes requires attention. Numerous studies (reviewed extensively in Hutchinson, 1975) demonstrated that bottom sediments are the main source of nutrients for aquatic vascular plants and charophytes. Representatives of several *Chara* species have been reported to grow better when planted with rhizoids than when the rhizoids were removed and specimens planted on mud grew better than in water alone (Vouk, 1929 cited after Hutchinson, 1975). Carignan and Kalff (1979) found that phosphorus taken up by three species of macrophytes originated entirely from the mobile sediment pool of the nutrient. Nitrogen, however, may be acquired by macrophytes from both lake water and bottom sediments as it was shown by Nichols and Keeney (1976) for *M. spicatum*. It seems that two factors might be of special importance

when regarding possible nutrient source, namely the proportion of available nutrients in interstitial and lake water (Carignan, 1982), and the development of underground organs of a given macrophyte (shoot/root biomass ratio). The first factor usually favors bottom sediments as a source of nutrients. In the sediments of Lake Łuknajno (Kufel and Kufel, 1997), otherwise poor in total phosphorus ($0.77 \text{ mg TP g DW}^{-1}$), concentration of soluble reactive P in interstitial water was on average 168 mg P m^{-3} , thus more than 10 times that in the overlying lake water. On the other hand, under experimental conditions *C. aspera* grown without sediment was found to efficiently take up phosphorus from ambient water at a rate proportional to the initial P concentration (Kufel and Ozimek, 1994). Moreover, the biomass of charophyte rhizoids is small in comparison to the above-ground green parts and much smaller than root systems of most aquatic angiosperms. These facts taken together allow for a conclusion that shoot uptake of nutrients is of primary importance in *Chara* sp.

Maximum accumulation of nutrients takes place in early summer, whereas later on the amount of stored N and P declines. This is probably due to the decline in biomass rather than due to changes in the nutrient concentration. Pereyra-Ramos (1981) observed maximum biomass of *C. rudis* equal to $7.5 \text{ kg fresh wt. m}^{-2}$ in July and a sharp decrease afterwards, so that the plant biomass remaining in November was near $4 \text{ kg fresh wt. m}^{-2}$. At the same time, her experiments on decomposition of *C. rudis* showed no changes of P content in decomposing plants and even a slight increase in the N content. As a result, after 90 days of experiment c. 41 % of the initial N content and 35% of the initial P remained in plant material decomposing in a mesotrophic Lake Majcz. Decomposition of *C. rudis* in a eutrophic Lake Mikołajskie proceeded faster, nutrients remaining there after 90 days of decomposition amounted 18% of the initial N and 18% of the initial P content (Pereyra-Ramos, 1981). The differences between the two experiments resulted probably from a different composition of the microorganisms involved. Bastardo (1979) demonstrated that vascular submerged macrophytes decompose faster than *Chara* sp.: the time of 50% loss of dry weight was 82.6 days for *Chara* sp. but only 32.5, 22.0 and 12.9 days for *C. demersum*, *M. spicatum* and *P. perfoliatus*, respectively.

Several species of the genus *Chara* (i.e. *C. tomentosa*, *C. vulgaris*, *C. rudis*, *C. hispida*) and some of *Nitella* (*N. translucens*, *N. mucronata*) are known to grow in temperate shallow lakes in winter under the ice cover, some others may overwinter under favorable conditions of deeper waters and milder winter temperatures (Dambaska, 1964). Pereyra-Ramos (1981) observed young parts of *C. rudis* all the year, even in winter under the 0.5 m thick ice cover and the biomass of a dense stand of the species did not change markedly between November and March the next year. Biomass of the plant in late autumn (and in the winter) was nearly half that of the maximum standing crop in July, which means that half of the accumulated nutrients remained stored in plants to the next growing season. Similarly, Blindow (1992b) reported of another species—*C. tomentosa*, which overwintered in Lake Takem and Lake Krankesjön but no data on winter biomass are available. According to Królikowska (1997), the biomass of *C. aspera* in Lake Łuknajno declined five-fold between its maximum in June and in the autumn but the plant remained green under the ice cover. It may be assumed that the winter amount of nutrients stored in the plant biomass was also one-fifth of its maximum in June. Biomass of the same species, however, was found to disappear entirely by December in Lake Veluwemeer (Van den Berg, 1999), which proves that not only species-specific features and climatic conditions (certainly more severe in northeastern Poland than in The

Netherlands) but other factors might be involved in the ability of charophytes to remain green and retain nutrients in the wintertime.

4.2. Indirect impact of *Chara* beds on nutrient cycling

Apart from nutrient incorporation into standing crop, a dense bed of charophytes may affect nutrient cycling in shallow lakes in several indirect ways. Of these mechanisms, calcite formation, alteration of redox potential at the sediment/water interface and the influence on sedimentation/resuspension equilibria seem to be the most important.

Most species of Characeae inhabit waters of relatively high alkalinity and high calcium content. Being able to utilize bicarbonate as a carbon source (Van den Berg et al., in press), the growing plants increase pH and consequently shift the chemical equilibrium towards the formation of carbonate ions (Stumm and Morgan, 1970), which precipitate with calcium in the form of calcite. This process manifests itself in a significant depletion of bicarbonate ions, which has indeed been observed within a dense *Chara* cover (Van den Berg et al., 1998). McConnaughey et al. (1994) demonstrated that the ratio of net photosynthesis to calcification is 1:1 in *Chara* sp. if only the supply of Ca ions is secured. It means that the amount of photosynthetically accumulated carbon equals that of calcite incrustations or marl sediment deposits. Knowing pH, alkalinity and calcium concentration in ambient water, one can calculate whether calcite would precipitate under given conditions. For example, a pH = 8.5, Ca = 40 mg l⁻¹ and alkalinity = 2 mM (a composition quite common in water within *Chara* meadows) is sufficient to exceed the solubility product of calcite nearly four times at an ambient temperature of 15° C (calculated after Stumm and Morgan, 1970). An open question is to what degree calcite precipitation affects P concentration in lake water. Calcite may transform into hydroxylapatite at relatively high concentrations of phosphates (Stumm and Morgan, 1970). Calculations performed for Lake Łuknajno in Poland (Kufel and Kufel, 1997) failed to demonstrate hydroxylapatite formation in lake water and in the interstitial water of sediments overgrown by charophytes. Calcite may also co-precipitate with phosphorus in probably non-stoichiometric proportions (Otsuki and Wetzel, 1972; Murphy et al., 1983). Phosphorus can, thus, efficiently be stored in a form of the calcium-bound fraction of sediment phosphorus (Andersen and Ring, 1999), whatever its chemical composition. This effect is redox-insensitive and, therefore, may bind phosphorus even under anoxic conditions, under which iron-bound P is released to the overlying water. Consequently, photosynthesizing charophytes may additionally enhance phosphorus storage in sediments.

Bottom sediments overgrown by dense *Chara* beds are less susceptible to resuspension, which is one of the sources of internal nutrient loading to shallow lakes (Søndergaard et al., 1992). Plants mitigate turbulent wave action upon sediments and restrict the access of large bottom-feeding fish to the sediment (Barko and James, 1998). Van den Berg et al. (1998) found the water within a dense field of *Chara* to be more clear than outside the bed. Water within vegetated areas contained significantly less chlorophyll, detritus and inorganic suspended solids. There were, however, no significant differences in phosphates and ammonia between two sites and nitrates were depleted among vegetation only on a single sampling occasion. This indicates that reduction of resuspension (or the enhancement of sedimentation) within *Chara* beds is not necessarily combined with nutrient restriction. Some authors

(Scheffer, 1999, for example) associate the occurrence of clear water within macrophyte stands in otherwise turbid lakes with the enhanced presence and activity of zooplankton grazers rather than with strictly abiotic interactions. Nevertheless, by analogy to other submersed macrophytes (Carpenter, 1981), we can expect charophytes to promote sediment accretion and to prevent resuspension of particles within densely overgrown stands. Charophytes, with their maximum biomass situated close to the bottom, may influence redox potential at the sediment/water interface. Growth of *Chara* plants may deliver oxygen to anaerobic layers of bottom sediments. An oxygen gradient formed in that way may inhibit the release of iron-bound sediment phosphorus and promote nitrification/denitrification nitrogen losses (Lijkiema, 1994; Weisner et al., 1994).

5. Concluding remarks

Before arriving at final conclusions, we must confess that data on nutrient cycling within *Chara* beds are still insufficient to lead to any generalization. The properties of Characeae, even if carefully studied, may result in quite contradictory effects. For example— bicarbonate uptake should promote precipitation and P immobilization in sediments as suggested. However, the very same process increases pH of the ambient water, which in turn might result in mobilization of iron-bound P from sediments under oxic conditions (Barko and James, 1998). Charophytes may sequester nutrients from lake water but, by providing a refuge for zooplankton grazers, the plants mediate the process of nutrient recycling through grazing. In every case, the final effect is difficult to assess a priori.

Much has been said here of calcium-carbonate-phosphate equilibria. In the authors' opinion, this aspect is often underestimated in evaluating the role charophytes may play in phosphorus cycling. Calcium-mediated storage of phosphorus may be recognized as a positive feedback in stabilizing *Chara* dominance in lakes. This "bottom-up perspective" in the growth and colonization abilities of charophytes certainly needs further study.

The contrasting data indicate that the total effect of charophytes on nutrients varies from lake to lake and even between the years. In Lake Okeechobee, *Chara* sp. covered 65% of the overgrown area of the lake in 1990 (Zimba et al., 1995). The amount of nitrogen and phosphorus bound in *Chara* biomass, however, comprised only 15.5% of total N and 12.7% of total P accumulated in the submersed vegetation. On the opposite extreme, in Lake Łuknajno, several species of charophytes produced nearly 90% of the submerged plant biomass and stored the same proportion of nutrients (Kufel and Ozimek, 1994; Kufel and Kufel, 1997; Królikowska, 1997). The amount of nutrients stored in the charophyte summer biomass was comparable to the annual nutrient load into the lake (Kufel and Ozimek, 1994). Water within *Chara* stands in Lake Łuknajno was markedly depleted in nutrients (Królikowska, 1997). The last observation is in contrast to the findings of Van den Berg et al. (1998), who found no statistically significant differences in phosphate and ammonium concentrations in water within and out of the dense *Chara* stands and especially to the situation in Lake Wolderwijd (Meijer and Hosper, 1997), where water above the *Chara* meadows appeared enriched with soluble reactive P.

There is an abundant literature on the role of aquatic vascular plants in mobilizing nutrients from sediments (Carignan and Kalff, 1980; Carpenter, 1981, among many others). Poorly

rooted species, like *Chara*, differ in nutrient acquisition from rooted vascular plants, so the conclusions on the effect of both would hardly be comparable. It can be expected that nutrients stored in the biomass of charophytes originate mainly from the ambient water. After the decomposition of plant, biomass nutrients return in part to water but the contribution of sediment-derived nitrogen and phosphorus is most probably small.

Shoot uptake, which is supposedly more important in charophytes than in vascular plants, relatively slower decomposition rates and the possibly prolonged storage over winter of nutrients in the plant biomass are properties which make charophytes more efficient nutrient sinks compared to vascular macrophytes growing in shallow lakes. Indirect effects of charophytes can additionally contribute to lowered dissolved nutrient levels within dense stands of *Chara*. The impact the plants exert upon nutrient cycling in a lake is probably most effective in moderately eutrophic conditions, under which *Chara* is able to successfully compete with both submersed macrophytes and planktonic algae.

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