Cryptogamie, Algol., 2006, 27 (4): 419-434

Experimental studies on the impact of turbulence, turbidity and sedimentation on *Chara tomentosa* L.

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(Received 31 January 2006, accepted 31 May 2006)

Abstract — Shoots of the macroalga *Chara tomentosa* L. were exposed to different levels of turbidity, sedimentation or turbulence in aquarium experiments. Plants in turbid water or with a sediment cover became green, tall and weak. Some of them collapsed towards the end of the treatment period and were partially decomposed at the bases. The plants in turbulent water became orange, short and robust and some of them broke during the treatment. The shading by sediment in the water or on the plants presumably induced growth towards the light. As the plants in all treatments had about the same weight, the length was obtained at the expense of strength. A combination of the treatments could be disastrous. Plants weakened by shading would break even more easily if exposed to turbulence. It seems very plausible that these factors would be the causes for the drastic decrease in the occurrence of *C. tomentosa* at many localities in Southwestern Finland. Shallow bays are often subject to dredgings and motorboat traffic, factors that both increase the water movement and set sediment afloat.

***Chara tomentosa* / charophyte / turbulence / turbidity / sedimentation / experiment**

Résumé — Etudes expérimentales sur l'impact de la turbulence, de la turbidité et de la sédimentation sur *Chara tomentosa* L. Des pousses de l'algue macrophyte *Chara tomentosa* L. ont été exposées, en aquarium, à différents niveaux de turbidité, de sédimentation ou de turbulence. Les plants en eau trouble ou couverts de sédiments sont devenus verts, longs et faibles. Certains d'entre eux se sont effondrés vers la fin de l'expérience ; ils étaient en partie décomposés à leur base. Les plants placés en eau agitée sont devenus oranges, courts et robustes, et certains se sont cassés durant l'expérience. L'obscurité générée par les poussières déposées sur les plantes ou en suspension dans l'eau semblent avoir induit une croissance vers la lumière. Comme toutes les plantes pesaient approximativement le même poids dans tous les traitements, l'élongation fut obtenue aux dépends de leur consolidation. L'association des différents traitements aurait sans nul doute été désastreuse : les plantes affaiblies par l'obscurité se seraient rompues encore plus facilement dans des eaux agitées. Il est très vraisemblable que ces différents facteurs soient responsables de la baisse

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drastique du nombre de *C. tomentosa* dans de nombreuses localités du sud-ouest de la Finlande. Les baies peu profondes sont souvent affectées par des dragages ainsi que par la circulation de bateaux à moteurs, facteurs qui accentuent l'agitation et la turbidité de l'eau.

Chara tomentosa **/ charophyte / turbulence / turbidité / sédimentation / expérimentation**

INTRODUCTION

Chara tomentosa L. (Chlorophyta, Charophyceae) is a freshwater alga that also occurs in brackish water. It is green and orange in colour and stands have a coral-like appearance, which has given the species the English name coral stonewort. Plants may grow to 50 cm high (Langangen *et al.*, 2002) and often occur in very dense stands. The thallus has a main axis consisting of long internodes alternating with short nodes. Each node bears a whorl of branchlets and some of the nodes develop lateral branches. The thallus is anchored to the substratum by rhizoids.

Biotopes

In the Baltic Sea, a brackish water basin, the land uplift processes cause a successional development of shallow water bodies as open bays are gradually cut off from the sea. Munsterhjelm (1997) has described these so called flads and their developmental stages as shallow waterbodies at the coast or in the archipelago, with sills in their openings to the sea. On their soft sediment bottoms luxuriant macrophyte vegetation forms an important ecological unit. Characteristic water plant communities can be distinguished in different development stages (Munsterhjelm, 1997). At the coast of the western part of Southern Finland, the macrophyte vegetation in these flads has been investigated since the 1890's (Häyrén, 1902; Luther, 1951a, b; Munsterhjelm, 1985, 1997; Heinonen, 1986; Wallström *et al.*, 2000). Along the coast of Finland different charophyte species are found in many types of soft bottom biotopes with different degrees of exposition and salinity (Luther, 1951b). The charophytes also play a major role in the succession of the vegetation of flads (Munsterhjelm, 1997).

Chara tomentosa mainly occurs in sheltered shallow localities with mud bottoms. It is particularly typical for flads, where it reaches high coverage at later succession stages. It is considered that *C. tomentosa* is favoured in these biotopes by the relatively high water temperatures, the loose, nutrient-rich bottom, shelter from winds and waves and by the shallowness (usually around 0.5-2.5 m mean depth) giving a good light supply (Luther, 1951a,b; Munsterhjelm, 1997). In the Baltic Sea, *C. tomentosa* occurs in salinities from that of the open sea in the Northern Baltic Proper, about 6‰, down to 0.8‰ (Luther, 1951a). It apparently withstands anaerobic conditions for some time (Munsterhjelm, 1997) and hibernates fully grown with new shoots developing at the nodes (Luther, 1951a; Munsterhjelm, 1997). The environmental conditions of flads, the ability of *C. tomentosa* to withstand anaerobic conditions and its habit of hibernation seem to give the species an advantage in these habitats, compared to other species like *Potamogeton pectinatus* L., *Najas marina* L., *Ceratophyllum demersum* L. and *Myriophyllum spicatum* L. (Munsterhjelm, 1997; nomenclature for angiosperms according to Hämet-Ahti *et al.*, 1998).

Threats

Despite being a strong competitor in flads, *Chara tomentosa* is generally considered to be a weak competitor, sensitive to exposure to air, heavy water movements and freezing (Luther, 1951a, b). As it reproduces mainly vegetatively (Luther, 1951a), it can have difficulties in recovering if the population has diminished and other species have become dominant (Wallström & Persson, 1999).

Large portions of the shallow sheltered bays in the northern Baltic archipelago are influenced by human activity. Mechanical disturbances such as dredging and motorboat traffic increases the water movement and sets bottom sediment afloat, making the water turbid and the vegetation covered by resettling sediment. Nutrients are thereby also released from the sediment into the water, increasing the biomass of epiphytes and filamentous algae. *Chara tomentosa* seems to be sensitive to these kinds of interferences as well (Munsterhjelm, 1997).

Wallström & Persson (1999) also mentioned dredging, motorboat traffic and eutrophication as threats for the charophytes. In the archipelago of Uppland County (Sweden, southern part of the Bothnian Sea), they observed that on shallow bottoms subject to intense motorboat traffic, the vegetation was more or less covered by sediment that had been stirred up from the bottom.

There has been a drastic decrease in the occurrence of *Chara tomentosa*, which has disappeared or decreased notably at many localities in Southwestern Finland where it formed dense stands approximately 20 years ago or earlier (Munsterhjelm, pers. com.). There seems to be a clear connection between human impacts, as mentioned above, and this decline.

During an investigation in 1985-1988, Blindow (1992a) noted a disappearance of charophytes compared to the 1940s (Almestrand & Lundh, 1951; Lundh, 1951) from several lakes in Southern Sweden. She concluded that poor light conditions caused by increased turbidity was the most probable reason for the decline. In the most turbid lakes only small charophytes (*Chara contraria* A. Braun ex Kütz., *C. globularis* Thuill., *C. virgata* Kütz. (in Blindow (1992a) called *C. delicatula* C. Agardh), *C. aspera* Willd., and *C. vulgaris* L.) were found, forming low mats in shallow water, whereas large species (*C. tomentosa, C. hispida* (L.) Hartm., *C. rudis* v. Leonh. and *Nitellopsis obtusa* (Desv. in Loisel.) J. Groves) had disappeared from these lakes (nomenclature for charophytes according to Schubert & Blindow, 2003).

At a nuclear power plant in Forsmark (Sweden, southern part of the Bothnian Sea), the consequences of cooling water discharges on the waterplants in a biotest basin were investigated by Svensson & Wigren-Svensson (1992). Charophytes were favoured by the embankment of the basin but when the cooling water discharge began their occurrence dropped by 50%. The charophytes disappeared completely where the main stream of the cooling water passed from the inlet to the outlet of the basin. After three years of observations no *Chara tomentosa* individuals were found anywhere in the basin. The changes in the vegetation were accompanied with increased water temperature, a reduced wave exposure, a heavy water current and an increased turbidity.

In Finland there are 21 species of charophytes (Langangen *et al.*, 2002; Appelgren *et al.*, 2004). Eleven of them are on the Finnish red list of endangered species (Rassi *et al.*, 2001) and one was found as a new species for Finland in 2004 (Appelgren *et al.*, 2004). *Chara tomentosa* is not on the list but requires special consideration (Blindow, 1994; Wallström & Persson, 1999), as there has been a strong decline of the species in the Baltic Sea (Torn *et al.*, 2003), presumably because of eutrophication and mechanical disturbances in the habitats.

Ecological importance

The *Chara*-vegetation serves as food and shelter for a variety of animal species (Henricson, 2002). Where *Chara tomentosa* thrives, it forms dense meadows with considerable biomass and occurs year-round. According to Hanson (1990) and Hargeby *et al.*, (1994) the biomass of macroinvertebrates seems to be higher among charophytes than in other types of vegetation. These habitats are important also for fish and birds (Milberg *et al.*, 2002), especially for breeding and feeding. The shallow, sheltered flads are rapidly warmed up in spring, the salinity is low after the melting of the ice, and both the charophytes and the associated fauna constitute a good food supply. As the flads have a central role in the maintenance of the fish stock in the archipelago, they are of great importance for the mammalian and avian predators and also for the fishery (Hästbacka, 1991).

Well developed charophyte vegetation is restricted to unpolluted (Ozimek, 1978), clear and nutrient poor water (Ozimek, 1978; Simons & Nat, 1996), and charophyte occurrence indicates good water quality (Krause, 1981). They are the first waterplants to disappear if the water quality becomes poor (Lindholm, 1991) and charophytes have returned to restored localities where the transparency of the water has improved forming extensive meadows (Simons *et al.*, 1994; Coops & Doef, 1996). The luxuriant vegetation also purifies the water by binding nutrients (Blindow, 1992b), stabilizing the sediment (Blindow *et al.*, 1993) and probably also by allelopathic inhibition of phytoplankton (Wium-Andersen *et al.*, 1982). A dense vegetation in general keeps the water clear (Scheffer, 1998) by depleting the water of nutrients and thereby hindering mass-occurrences of phytoplankton and filamentous algae.

The macrophytes and their associated fauna in a water area give a good picture of the general condition of the water. Attached communities and especially perennials are good indicators for analyses of long-term changes in the environment (Hällfors *et al.*, 1987). As *Chara tomentosa* seems to be disturbance sensitive (Munsterhjelm, 1997) its disappearance from a locality can be the first sign of changes in the water quality.

Aims

This study aims to survey factors which may threaten communities dominated by *Chara tomentosa*. Aquarium experiments were set up in order to test whether increased turbidity, sedimentation or turbulence could be the ultimate reason for the diminished occurrence of this charophyte in Southwestern Finland.

MATERIAL AND METHODS

Set-up

Aquarium experiments were carried out from 18^{th} August to 18^{th} October 1999, in a building where the roof and upper parts of the walls consisted of transparent plastic. The light conditions were thus close to natural and no artificial light was used. *Chara tomentosa* plants, water (salinity around 6‰) and sediment were brought from a dense *C. tomentosa* community in the flad Åkernäsfladan. This flad is situated in the archipelago of Ekenäs, on the island Skåldö (coordinates: N59º53'39 E23º28'36). It is a shallow (maximum depth 4 m), sheltered and relatively undisturbed locality with mud bottom. That summer the vegetation was dominated by *C. tomentosa* in depths between about 0.5 and 1.5 m and by *Potamogeton pectinatus* in deeper water. In shallower waters there were only sparse stands of *Najas marina* and *P. pectinatus*. The water was clear and no great amounts of filamentous or planktonic algae were observed.

Small plastic pots (2dl, 8 cm Ø) were filled with sediment. Algal shoots of about 5 cm, consisting of the apex, three internodal cells and three nodes with branchlets were cut and planted with the lowermost node and internode under the sediment surface, one plant per pot. The shoots were robust and had a rather dark orange colour. The sediment was covered by a mesh net with an opening for the alga. Ten potted plants were placed in each of ten 80 litres aquaria filled with water. The plants were acclimatized for ten days before the treatments started. By the time the experiment began, they had already developed rhizoids and had started to grow.

Three experimental set-ups each consisting of three treatments with different degrees of exposure were established. A fourth set-up with no treatment served as a control (Figs 1-4).

In the first set-up (SUS) sediment from the flad was suspended into the water every second day, in three aquaria. The volumes of added sediment were 25, 100 and 400 ml, respectively. Before being poured into the aquaria, the sediment was suspended in a small amount of water taken from the aquaria, in order to get a uniform suspension. The sediment was not only suspended in the water, but also settled down on the plants. The following abbreviations are used for these treatments: SUS25, SUS100 and SUS400 (Fig. 1).

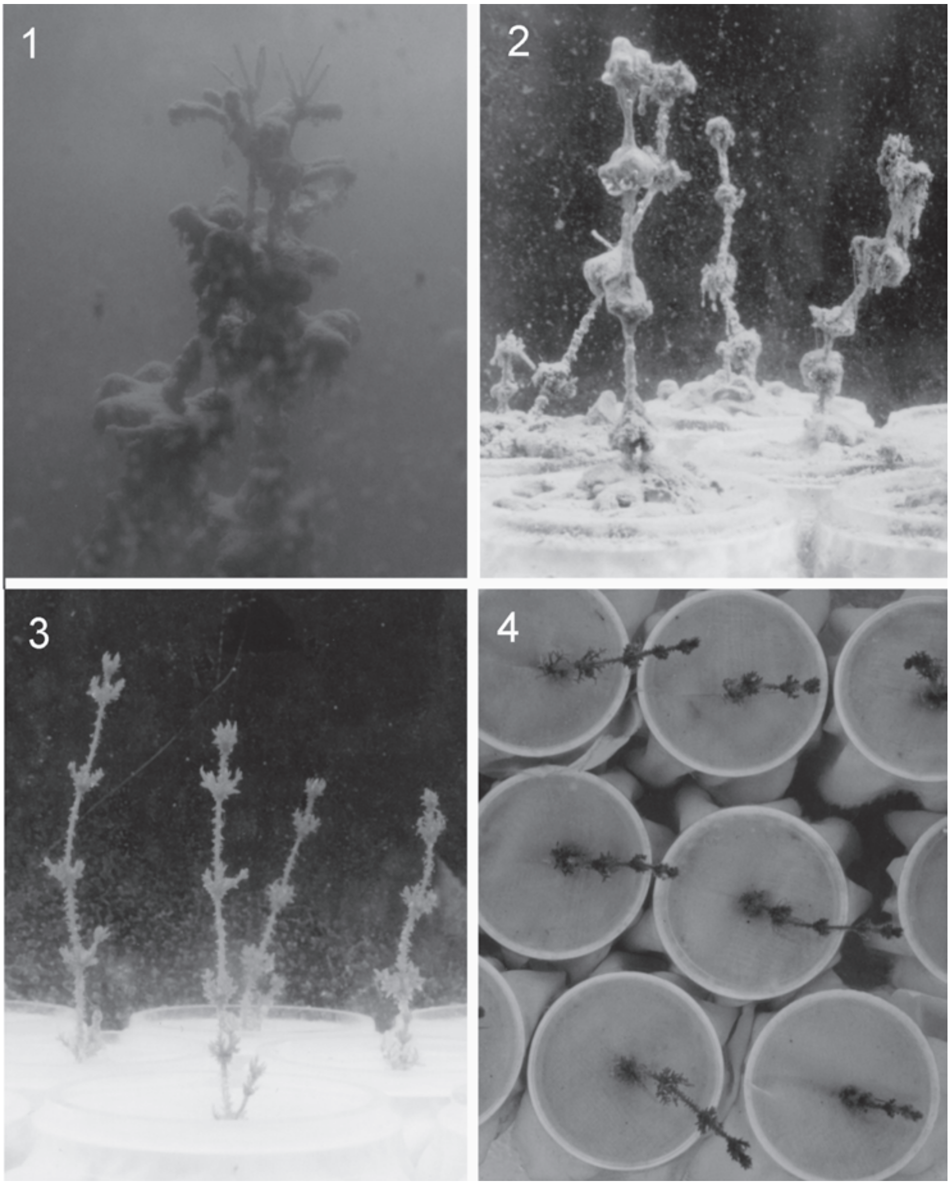
In the second set-up (COV) sediment was strewn over the plants in three aquaria. In the first, plants where covered by a thin "dust"-layer of sediment (COV1), in the second thick clods were laid on the plants (COV2) and in the third aquarium the tops and branchlets were almost entirely covered by the sediment (COV3). During the experiment more sediment was added a couple of times to keep the amount of covering sediment constant (Fig. 2).

In the third set-up (CUR) the plants were exposed to different degrees of water currents. In the first treatment (CUR200) one aquarium pump (NOVA) circulated the water at the speed of 200 L/h, in the second treatment (CUR800) one pump created a circulation of 800 L/h and in the third (CUR1600) there were two pumps with the effect of 800 L/h each (Fig. 3).

The aquaria were placed in a random order. Water from the flad was added during the experimental period to keep the water level at least a couple of centimetres above the highest plants and at the same level in all treatments. The temperature of the water was kept around +20°C with aquarium heaters.

Measurements

To avoid disturbance (mechanical damage of plants and suspension of sediment) during the experiment, no precise measurements of the growth of the plants were made before the termination of the experiment. Only the height of the longest plant in each treatment was measured every 10^{th} day. The measurements were made under water, with a ruler, without touching the plants.



Figs 1-4. Plants in different treatments. **1.** Turbidity (SUS100). **2.** Sediment cover (COV3). **3.** Control. **4.** Turbulence (CUR200).

As such the values are indicative and should only be used as approximations for the growth rate.

Total phosphorus and total nitrogen content of the water was analysed with a spectrophotometer (Hitachi U-1100) (Grasshoff, 1976) after 40 and 60 days. The amount of suspended material (as described in Svensk standard 1996) was analysed after 60 days. Several times during the summer water samples from the Åkernäsfladan were taken for comparison. Values given in the results are means of these samples which did not differ much between sampling occasions.

At the beginning and at the end of the experiment the length of the thallus and of the longest branchlet and branching were measured with a ruler for each plant. The number of colourless cells, branchlet whorls and branchings were also counted. Further, at the end of the experiment, the length of the rhizoids was measured and the wet weight of the plants was weighed after the removal of external water with a paper towel. The plants were photographed and after that they were pressed.

Statistical and numerical approach

A Wilk-Shapiro test showed that the data of the measurements of the plants were normally distributed but the variances were not equal, not either after log-transformation. Therefore the data were analysed by Kruskal-Wallis one-way nonparametric AOV. Comparisons of mean ranks were made by post-hoc tests (Tukey). The program used was Statistix. In pictures, figures and tables the treatments and set-ups are arranged according to the results obtained, this in order to make the patterns more visible.

RESULTS

Hydrography

After 40 days the total phosphorus concentration of the water in the experiment aquaria was lower (8-21 μg/L) than in the Åkernäsfladan water (25 μg/L) in all treatments but the two with the most turbid water (SUS100: 63 μg/L and SUS400: 318 μg/L). After 60 days the total phosphorus concentration had increased in every treatment to levels higher than in the flad (69-423 μg/L) (Tab. 1).

The total nitrogen concentrations after 40 days were somewhat lower (522-590 μg/L) than in the water of the flad (626 μg/L) in all treatments, except for those two with the highest turbidity (SUS100: 1102 μg/L and SUS400: 2054 μg/L) and the one with the strongest turbulence (CUR1600: 698 μg/L). After 60 days the total nitrogen in the treatment with medium strong turbulence (CUR800: 628 μg/L) had also risen to a higher level than in the flad water (Tab. 1).

Compared to the flad water (25.0), the N/P ratio had increased (28.1-65.8) after 40 days in all treatments except the two most turbid (SUS100: 6.5 and 400:17.5). After 60 days the N/P ratio had decreased in all treatments to levels between 2.3 and 7.7 (Tab. 1).

The amounts of suspended material were much higher in the treatments with turbid water than in the flad (the flad: 4.6 mg/L, SUS25: 13.7 mg/L, SUS100: 93.7 mg/L and SUS400: 327.0 mg/L). In the rest of the treatments they were at about the same level (4.4-5.8) as in the flad (Tab. 1).

Table 1. a) Total phosphorus and total nitrogen content of the water from every treatment, measured after 40 and 60 days of treatment and suspended material after 60 days.
b) The same analyses were made of water from Åkernäsfladan (given as mean values of several samplings during the summer).

a)

Treatment	*Tot. P (μg/l)*		*Tot. N (μg/l)*		*N/P ratio*		*Susp. mat. (mg/l)*
	40 d	60 d	40 d	60 d	40 d	60 d	60 d
SUS400	318	322	2054	2147	6.5	6.7	327.0
SUS100	63	423	1102	986	17.5	2.3	93.7
SUS25	21	150	590	554	28.1	3.7	13.7
COV3	10	98	522	556	52.2	5.7	5.8
COV2	9	94	556	571	61.8	6.1	5.6
COV1	10	118	545	568	54.5	4.8	5.8
Control	13	109	583	551	44.8	5.1	5.6
CUR200	8	69	526	534	65.8	7.7	4.4
CUR800	9	90	573	628	63.7	7.0	5.6
CUR1600	11	126	698	855	63.5	6.8	5.7

b)

Åkernäsfladan	*Tot. P (μg/l)*	*Tot. N (μg/l)*	*N/P ratio*	*Susp. mat. (mg/l)*
	25	626	25.0	4.6

Growth and decay

When planted, the shoots in the different aquaria did not differ from each other in any of the measured factors: length of the thallus, number of colourless cells, number of branchlet whorls, number of branchings, length of the longest branching and length of the longest branchlet ($p > 0.05$). After 60 days of treatment all these variables and also the weight of the plants and the length of their rhizoids (measured only at the end of the experiment) differed between different aquaria ($p < 0.05$) (Kruskall-Wallis one-way nonparametric AOV).

The most notable differences were found between the set-ups with turbulence (CUR) and those with turbidity (SUS). In the comparisons between set-ups these two differed in all cases. The set-ups with turbidity (SUS) or sediment cover (COV) did not differ in any case except for the length of the longest branchlet. CUR and control had more colourless cells than COV and SUS. SUS had more whorls of branchlets but less branchings than CUR. SUS also had longer longest branchlets than COV, control and CUR while it had shorter rhizoids than control and CUR (Kruskall-Wallis one-way nonparametric AOV).

In all treatments the *Chara tomentosa* plants grew several centimetres (up to 6 cm) in length during the first ten days. After this the growth rate slowed down somewhat, except for the plants in the most turbid water (SUS400). Plants in the treatments with turbulence (CUR) appeared to have ceased growing after 20 days. Four of these plants broke during the treatment, one in CUR200, one in CUR800 and two in CUR1600. Those four were not taken into account in the figures and mathematical comparisons, as they would have distorted the data. A fast growth after 20 days was sustained only in SUS100 and 400.

At the end of the experiment the plants in the treatments with turbidity (SUS) started to collapse. They were leaning towards each other or lying down on the bottom. Two plants in SUS25 were almost entirely decomposed and all ten in SUS400 where partially decomposed at the base, six of them to such an extent that they were broken. One of these plants in SUS400 had developed new rhizoids from a node, which originally was above the sediment, but had sunk down due to the decomposition of lower parts. The two almost entirely decomposed where not used in the figures and numerical comparisons.

Length and weight

When comparing the total length of the thallus and the weight to length relationship at the termination of the experiment, a significant difference ($p < 0.0001$, Kruskal-Wallis one-way nonparametric AOV between the four set-ups) was found between plants in the control and those in turbid water (SUS), as well as between plants in the set-ups SUS, COV and CUR (Tables 2a and b). The longest plants were those grown in turbid water (mean length for SUS: 21.5 cm ± SD 6.6), followed by those grown with a sediment cover (COV: 14.5 cm ± SD 2.5), and those in the control (13.5 cm ± SD 2.0). The plants exposed to turbulence were the shortest (CUR: 10.8 cm ± SD 2.5). Despite the different lengths the weight was almost equal for all plants ($p = 0.6704$, Kruskal-Wallis one-way nonparametric AOV between the four set-ups) (mean weight: 1.1223 g ± SD 0.3193), giving the mean weight/length quotients: SUS: 0.0578 g/cm ± SD 0.0191,

Tables 2a-d. Comparisons of mean ranks by post-hoc tests (Tukey) of a) length and b) weight/length quotient by set-up and c) length and d) weight/length quotient by treatment (Kruskal-Wallis one-way nonparametric AOV, $p < 0.0001$ for all four).

a) Length

Set-up	*Homogenous groups*		
SUS	I		
COV		I	
Control		I	I
CUR			I

b) Weight/length

Set-up	*Homogenous groups*		
SUS			I
COV		I	
Control	I	I	
CUR	I		

c) Length

Treatment	*Homogenous groups*		
SUS100	I		
SUS400	I	I	
SUS25	I	I	I
COV3	I	I	I
COV2	I	I	I
COV1		I	I
Control		I	I
CUR200			I
CUR800			I
CUR1600			I

d) Weight/length

Treatment	*Homogenous groups*			
SUS400				I
SUS100			I	I
COV2		I	I	I
SUS25	I	I	I	I
COV3	I	I	I	I
COV1	I	I	I	
Control	I	I	I	
CUR1600	I	I	I	
CUR800	I	I		
CUR200	I			

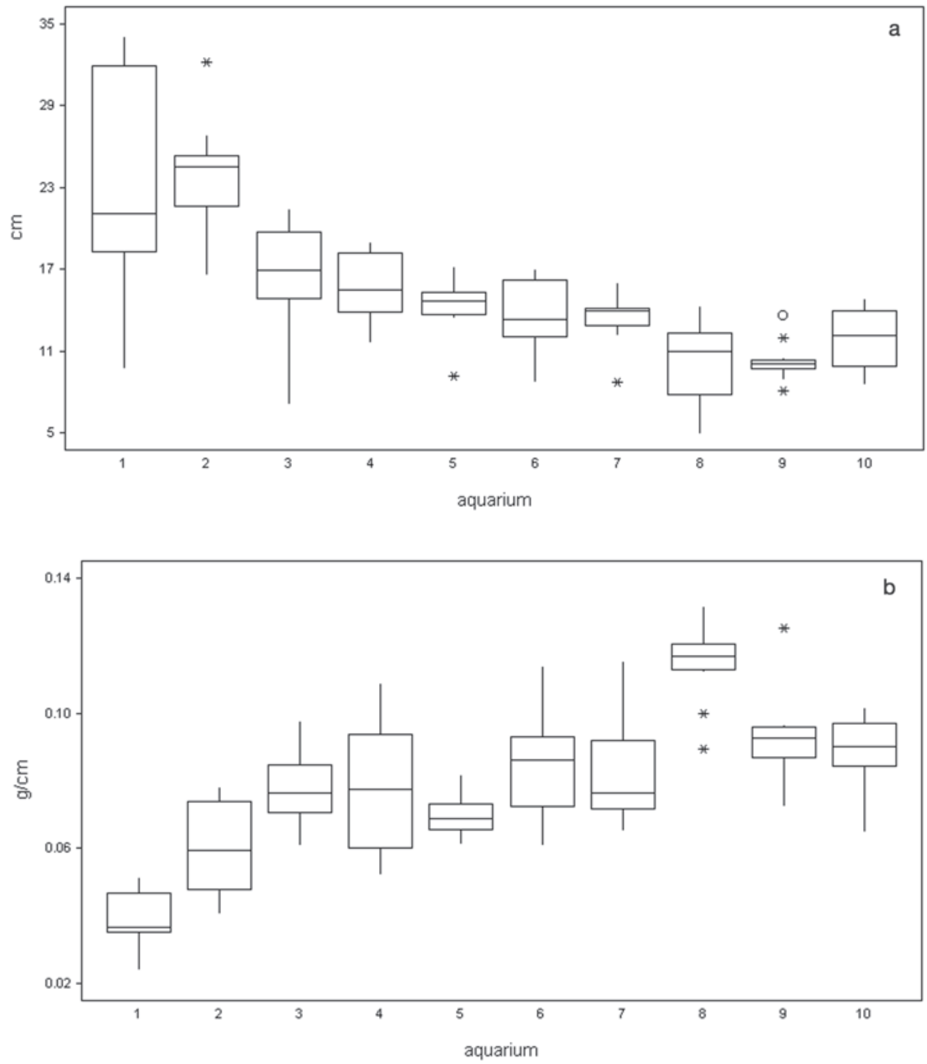


Fig. 5. Box and whisker plot for a) the length (cm) and b) the weight/length (g/cm) relationship of the plants from the different treatments: 1 = SUS400, 2 = SUS100, 3 = SUS25, 4 = COV3, 5 = COV2, 6 = COV1, 7 = Control, 8 = CUR200, 9 = CUR800 and 10 = CUR1600. The boxes show the middle half of the data with the median as a horizontal line. The vertical lines indicate the range of typical data values. Extreme values are displayed as "*" for possible outliers (values outside the box boundaries by more than 1.5 times the size of the box) and "o" for probable outliers (values outside the box boundaries by more than 3 times the size of the box).

COV: 0.0767 g/cm ± SD 0.0151, control: 0.0822 g/cm ± SD 0.0148 and CUR: 0.1001 g/cm ± SD 0.0181. For comparisons of all treatments (control, SUS25, 100 and 400, COV 1, 2 and 3 and CUR200, 800 and 1600) separately see Table 2c and d, Tab. 3 and Fig. 5.

Table 3. Means and standard deviations of length (cm), weight (g) and weight/length (g/cm) of the plants from the different treatments.

Treatment	*Length (cm)*	*Weight (g)*	*Weight / length (g/cm)*
SUS400	22.8 ± 8.0	0.8900 ± 0.3635	0.0393 ± 0.0089
SUS100	24.1 ± 4.0	1.4400 ± 0.3340	0.0603 ± 0.0134
SUS25	16.5 ± 4.7	1.2375 ± 0.2722	0.0776 ± 0.0115
COV3	15.6 ± 2.4	1.2000 ± 0.3367	0.0768 ± 0.0187
COV2	14.3 ± 2.1	1.0000 ± 0.1764	0.0697 ± 0.0059
COV1	13.6 ± 2.7	1.1200 ± 0.2440	0.0837 ± 0.0156
Control	13.5 ± 2.0	1.0900 ± 0.1449	0.0822 ± 0.0148
CUR200	10.3 ± 3.2	1.1778 ± 0.3993	0.1149 ± 0.0130
CUR800	10.3 ± 1.6	1.0000 ± 0.3000	0.0956 ± 0.0184
CUR1600	11.9 ± 2.4	1.0750 ± 0.3151	0.0886 ± 0.0115

Morphology

The plants in the control became light orange in colour and were rather robust with short branchlets. Those in turbid water (SUS) became thin and light green with long branchlets and internodes. Plants treated with a sediment cover (COV) became dark green with long internodes. Although the plants in the sedimentation treatments (SUS and COV) became green, the bases were still orange at the end of the experiment. The plants in the turbulent water (CUR) became robust and bowed with short incurved branchlets. The colour of their internodes was rather dark orange, while most of the branchlets were dark green. If there were very small newly developed cells at the ends of the apices and branchlets, they were always orange-coloured (Figs 6-9).

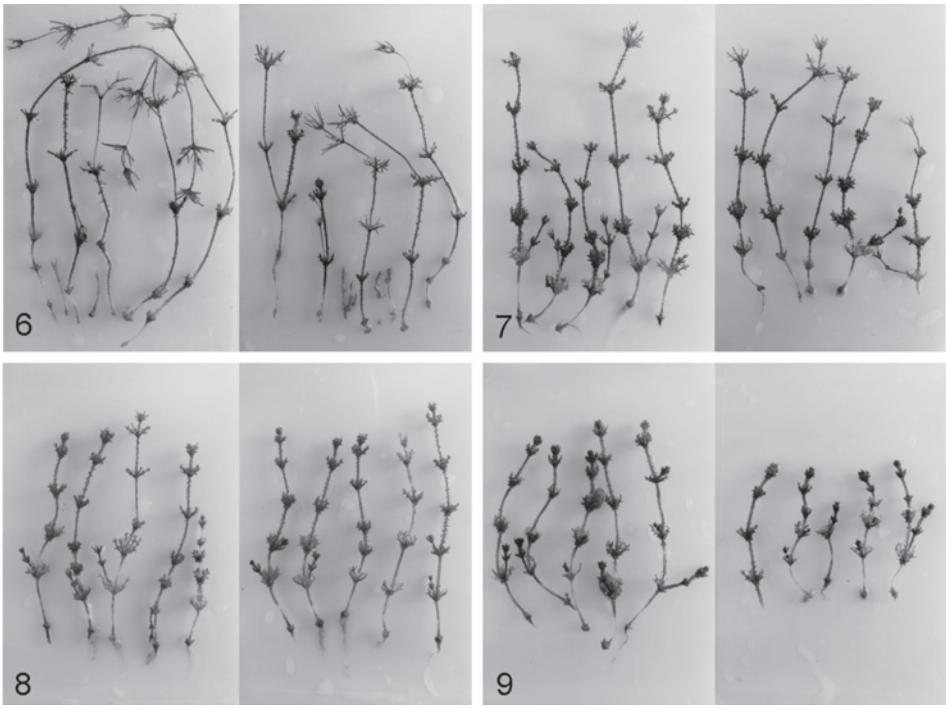
DISCUSSION

Growth

The tallest growth of *Chara tomentosa* was measured in the aquaria with sediment treatments (SUS and COV). Although the plants exposed to turbulence (CUR) became short, those exposed to the strongest turbulence (CUR1600) grew taller than those exposed to lighter turbulence. It was observed that the strongest current suspended some of the sediment into the water even though the sediment was covered by mesh net.

Nutrients in the suspended sediment were apparently dissolved into the water. High total phosphorus and total nitrogen values and suspended material in the water coincided with high length growth of *Chara tomentosa*. The plants grew well in remarkably high total phosphorus levels (> 300 µg/L). This indicates that charophyte growth is not inhibited by high phosphorus concentrations, a finding contrary to Forsberg (1964) but in accordance with Blindow (1988) and Simmons *et al.*, (1994).

Chara tomentosa is known to accumulate nutrients, and thus to make the water clear. In Lake Krankesjön (Sweden), Hargeby *et al.*, (1994) noted that



Figs 6-9. *Chara tomentosa* grown: **6.** In turbid water (SUS400), **7.** with a sediment cover (COV3) **8.** In control. **9.** In turbulent water (CUR1600).

although there was no change in nutrient input, a simultaneous expansion of *C. tomentosa* and a decrease in turbidity and total phosphorus levels occurred, the latter resulting in an increased N/P ratio. Also in the present study, with the exception of the two treatments where a lot of sediment was regularly suspended (SUS100 and 400), the phosphorus levels had decreased and the N/P ratio increased after 40 days of treatment (relatively to the flad water). After 60 days, however, this was not the case, probably because the plants in the sediment treatments (SUS and COV) had started to decay and the others (CUR and the control) had ceased growing at the end of the experiment period.

According to Kufel & Ozimek (1994), *Chara aspera* has a high capacity to rapidly absorb and store soluble reactive phosphorus. They showed that increased phosphorus concentrations enhanced biomass production. In the present study with *C. tomentosa* the high nutrient levels in some aquaria obviously did not cause the differences in length as the biomasses of the plants were not greater the higher the nutrient levels in the aquaria were.

The sediment treatments (SUS and COV) did not only have higher nutrient levels but also decreased light availability. The reason why the plants became notably tall in these treatments was probably that they tried to reach better light conditions near the water surface. Even if they grew tall they did not weigh more than plants in other treatments, presumably because they used most of their energy to growth length-wise and not on strength. They became long but weak. *Chara tomentosa* has long internodes in deep water (Hasslow. 1931).

Forsberg (1965) found, for *Chara globularis,* that the height of plants and also the length of internodes and branchlets increased with increasing depth and diminishing light energy.

The collapse of the plants in turbid water (SUS) in the end of the treatment period indicates that shading and increased sediment weight finally became too much for them. Although the longest plants were found in SUS400, their measured mean length was shorter than for the plants in SUS100. This because the bases of the plants in SUS400 were partially decomposed and thereby not measurable. Increased turbidity in the water increased the growth in length at the expense of strength and finally the plants broke.

Andrews *et al.* (1984a) noted that for *Chara hispida* the growth of the apex was balanced by death at the base. This was suggested to be a "self-pruning" mechanism, also known for other charophytes, to cope with the high light attenuation within a stand. Shading might thus have induced the partial decomposition at the bases of plants in SUS400. The shading in this case was caused by turbidity and covering sediment. The development of rhizoids from a node that had sunk under the sediment when the original base had died (in one plant in SUS400) indicates that the plants may be able to continue growth even if the bases die. Andrews *et al.* (1984a) also stated that new rhizoids can be produced from appropriate nodes.

The plants with a sediment cover (COV) did not grow as tall as those in turbid water (SUS). In both treatments the sediment had a shading effect. The turbidity treatments included sediment settlement while the plants with a sediment cover grew in clear water and probably received more light. Plants in the control had a good light supply. They were shorter than plants in the sediment treatments (SUS and COV) but longer than plants exposed to turbulence (CUR). The plants grown in turbulent water were shorter, bowed and more robust than plants in other set-ups. Still there were no big differences in the results of the water analyses from COV, control and CUR. Thus the different habitus must be due to the mechanical effect of the water current.

Habitus

Hasslow (1931) observed, especially for a species he called *Chara foetida* A. Br. (*C. vulgaris* according to Schubert & Blindow, 2003), that when the plants reached the water surface, the branchlets were short, convex and pressed against the internodes. When the tips of the plants remained a few centimetres under the water surface, the branchlets were somewhat longer, peaking diagonally upwards. When growing in greater depths they were even longer and horizontally extended or bent back. He suggested the reason to be different light intensities and the ability to regulate the assimilation and the development of the oogonia. The streamline form with bowed internodes and branchlets, observed on plants in turbulent water (CUR) in this experiment, seems more to be a phenotypic response to the water current. Also the more robust appearance of these plants is likely to be an adaptation. In spite of these responses, several plants in the treatments with turbulence broke, which shows that turbulence damages the alga.

Colour

Plants with green colour have been observed growing in deep water while brownish-red coloured plants are typical in shallower water (Luther, 1951b, own observations in the field). The pigment responsible for the red colouration, γ-carotene, may have a protective role against strong light or UV-radiation (Schagerl & Pichler, 2000). Carotenoids serve as accessory pigments and photoprotective agents (Taiz & Zeiger, 1998). The orange colour of the plants in the treatments without shading (CUR and the control) seems thus to have been caused by an excessive light supply. It is notable that plants that otherwise had become green still had orange coloured bases at the end of the experiment. It is possible that the pigment composition of the bases did not change during the treatments. More probably, the green chlorophyll broke down at the bases, making a small amount of carotenoids visible. The chlorophyll-a content was lower in old parts than in young parts of *Chara rudis* A. Braun (nomenclature as in the reference) (Pereyra-Ramos, 1981). Andrews *et al.* (1984b) found low pigment concentrations in the lower parts of *C. hispida*, and attributed this to cell breakdown. According to Schagerl & Pichler (2000) younger parts of the plants have red colouration, while older parts are green. In the present study, that was obvious for newly developed cells which were orange in all treatments.

The impact of the treatments

Goldsborough & Kemp (1988) observed stem elongation of *Potamogeton perfoliatus* as a response to shade. They argued this to be a beneficial adaptation in turbid lakes but nonadaptive in turbulent waters because of increased susceptibility of the weakened stems to fragmentation. In the field, turbulence and turbidity go together on soft bottoms. Occasional water movements stir up bottom sediment, which then is resedimented on the vegetation. The combination of increased turbulence, turbidity and sedimentation, caused by human induced disturbances, seems to be the reason for the observed decrease or disappearance of charophytes in many originally suitable localities in Southwestern Finland. Plants weakened by turbidity and sedimentation do probably not stand a strong turbulence as the current tends to easily break them. In a strong current, broken plants are transported away by the flow which unables them to settle down and develop new rhizoids.

CONCLUSIONS

In the aquarium experiments both turbulent and turbid water as well as sediment on the plants were deleterious to *Chara tomentosa*. It can be assumed that a combination of these effects could be disastrous for *C. tomentosa*-communities.

Our experiments support that these disturbances, which often occur in bays subjected to dredging works or intense boat traffic, could be the reason for the decrease of charophytes in many coastal habitats.

An increased turbulence may break the plants. It usually also increases the resuspension of sediment. Increased amounts of sediment in the water and on the plants lead to increased shading. This in turn increases the length growth of the plants. If much energy is used for growth in length, the plants become weak and eventually collapse. In strong water currents, the weak plants break even more easily.

Because of their sensitivity to turbulence, turbidity and sedimentation the *Chara tomentosa*-communities should be protected from mechanical interferences.

Acknowledgements. Tvärminne Zoological Station and the Hydrobiological laboratory (University of Helsinki) offered excellent facilities making the work possible to carry out. This study was made within the framework of the project Miljötillstånd i grunda havsvikar (Wallström *et al.*, 2000). Petri Ojala, Catharina Grundin, Kerstin Wallström and all others in the project are thanked for co-operation and good advice. Hannu Pietiäinen, Hendrik Schubert, Irmgard Blindow, Brad Balukjian, Erik Bonsdorff, Johanna Ikävalko, Olof Rönnberg and two reviewers, gave useful comments on the manuscript. Walter and Andrée de Nottbeck Foundation supported the work financially.

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