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Vegetation structure and primary production in acidified lakes in southwestern Sweden

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Summary. Research during the last two decades has clearly pointed out that dramatic ecosystem changes have occured in lakes due to deposition of acid substances and decreased pH. Today a large number of lakes and running waters in Scandinavia are suffering biological damage with disappearing fish populations, overgrowth of the bottom by mosses and filamentous algae, reduced invertebrate fauna, increased transparency etc. – Of all documented biological changes the effect on macrophyte succession, in particular that of *Sphagnum*, is the most striking effect. Along with the growth of filamentous algae, these changes have brought about major shifts in the composition of the primary producers. The biomass in one lake was estimated to be 6.5 t (dry wt) corresponding to about 24 g m^{-2}, the relevant proportions being 52% for *Sphagnum*, 34% for *Lobelia* and 15% for *Isoetes*. Percentage production in the whole lake is 54% for *Sphagnum*, 29% for *Lobelia* and 17% for *Isoetes*, which gives an estimated production of 2.9 t yr^{-1} or 9 g m^{-2} yr^{-1}. *Sphagnum* is a recent flora element and its occurrence is related to the acidification of the lakes. The investigations also show that the growth of *Lobelia* is reduced in acid lakes compared to other oligotrophic lakes due to shading by the benthic mat of filamentous algae, detritus and *Sphagnum* debris. – One can conclude that there are several quantitative and qualitative changes in the macrophyte community which are related to acidification. One can also conclude that liming of lakes cause elimination of *Sphagnum* and some increase in the production of *Isoetids*.
Key words. Acidification; macrophytes; aquatic mosses; primary production.

Introduction

Research during the last two decades has clearly pointed out that dramatic ecosystem changes have occurred in lakes, due to deposition of acid substances and decreased pH. Today a large number of lakes and running waters in Scandinavia are suffering biological damage with disappearing fish populations, overgrowth of the bottom by mosses and filamentous algae, reduced invertebrate fauna, increased transparency etc.

Over the last decades the pH has decreased by 1–2 pH units in many lakes in Sweden. Besides the low pH, the lake waters contain elevated concentrations of sulfate, aluminum and other metals.

Of all the documented biological changes the effect on macrophyte succession, in particular that of Sphagnum, is the most striking. Along with the growth of filamentous algae, these changes have brought about major shifts in the composition of the primary producers.

Vegetation in oligotrophic lakes in Scandinavia – some characteristics

In small oligotrophic pristine lakes in Scandinavia the most abundant macrophyte species are *Lobelia dortmanna* and *Isoetes lacustris*. Helophyte- and nymphaeid vegetation occurs in small stands and is generally of minor quantitative importance.

Lobelia dortmanna is an evergreen plant widely distributed in oligotrophic lakes of low alkalinity in Europe and North America[12, 14]. The plant usually grows in pure stands at 0–2 m depth. *Lobelia* is a phanerogam with both vegetative reproduction by runners and sexual reproduction by flowering above the water surface. Sometimes the spreading from runners is very rapid and therefore *Lobelia*, like *Littorella*, is important as a pioneer colonist, e.g., on eroded littoral areas. *Lobelia* therefore occurs at a rather early stage of succession in shallow waters.

In Scandinavia the perennial genus *Isoetes* is represented by the two species *I. lacustris* and *I. echinospora*. In Europe *I. lacustris* displays a northern range centered in Scandinavia and northern Russia. Its extension southward into warmer regions is restricted to areas at high latitudes[8]. *Isoetes* belongs to the Pteridophytes. The plants consist of a rosette with awl-shaped leaves and a bulbous stem, from which the roots arise. The plants reproduce exclusively sexually, by spores, and vegetative reproduction is nonexistent. They generally grow in oligotropic lakes on organic muddy bottoms and are therefore distributed over a zone deeper than the *Lobelia* zone. Generally, *I. lactustris* is most abundant at 3–5 m.

In oligotropic lakes inorganic carbon is sometimes a limiting factor for photosynthesis. Therefore the Isoetids have what can be interpreted as special adaptations: gas exchange in *Lobelia dortmanna* occurs through the roots and carbon dioxide can be taken up from the sedi-

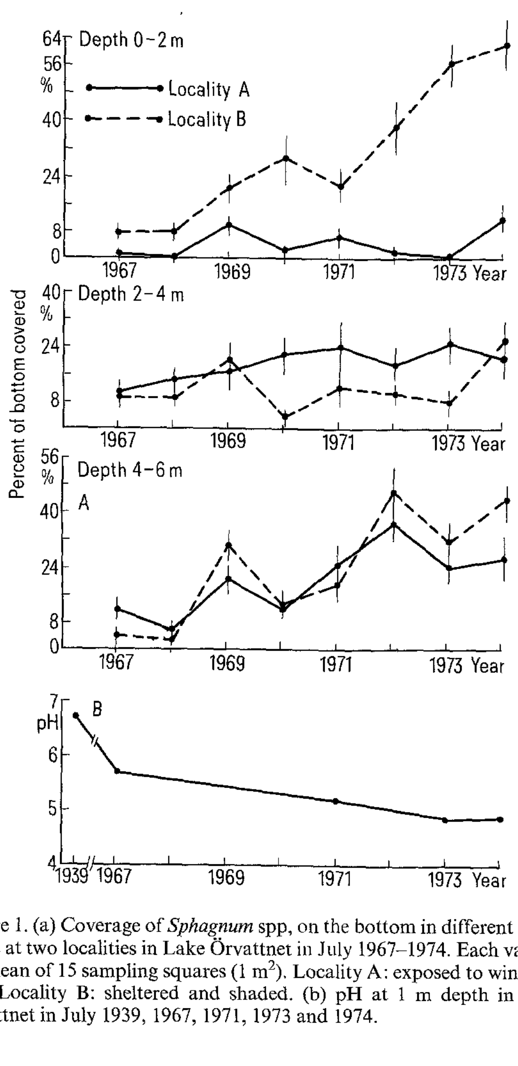

Figure 1. (a) Coverage of *Sphagnum* spp, on the bottom in different depth zones at two localities in Lake Örvattnet in July 1967–1974. Each value is the mean of 15 sampling squares (1 m^2). Locality A: exposed to wind and sun. Locality B: sheltered and shaded. (b) pH at 1 m depth in Lake Örvattnet in July 1939, 1967, 1971, 1973 and 1974.

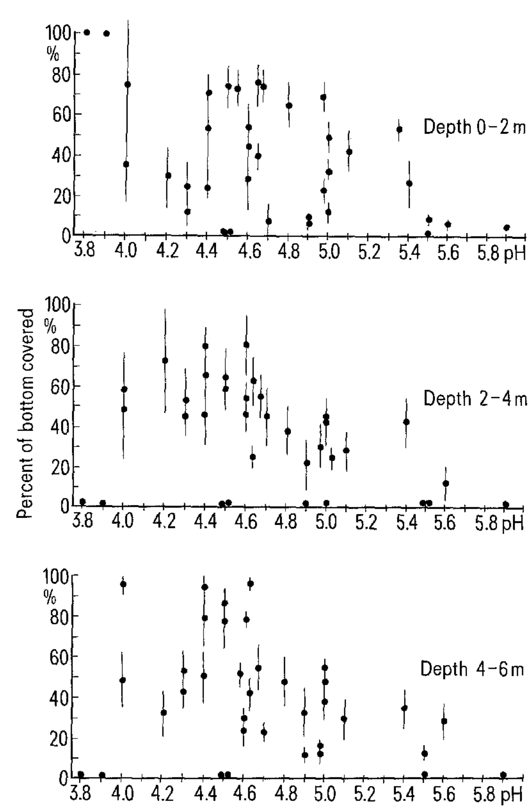

Figure 2. Coverage of *Sphagnum* spp in different depth zones in 36 lakes in western Sweden as a function of pH of the waters.

ment[16,21]. *Isoetes lacustris* is able to fix carbon dioxide into malic acid in darkness; this can then be mobilized and used in carbon assimilation[1,9]. This is called CAM-metabolism (Crassulacean Acid Metabolism). Carbon dioxide from respiration and photorespiration can also be stored in intercellular spaces and aeranchyme[18].

Sphagnum is usually a terrestrial moss occurring near the shoreline of most oligotrophic lakes. Sometimes *Sphagnum,* for largely unknown reasons, can overgrow entire bottom zones of lakes during the acidification process. Probably the concentration of free CO_2 which depends on pH plays an important role in this phenomenon.

Acidification of lakes – direct and indirect changes in the macrophyte community

In Lake Örvattnet, situated in western Sweden, it has been shown that *Sphagnum* has colonized the bottoms during the acidification process[3]. Over the same period the pH has decreased by 0.8 pH units, i.e. acidity has increased nearly 10-fold.

The two investigated localities A and B in Lake Örvattnet differ with respect to exposure both to light and to wave effects (fig. 1). Locality A is situated on the NE side of the lake, with no tall trees near the shoreline, and is therefore exposed to the sun from the early morning hours. South-westerly winds predominate in the area, which lead to relatively strong wave exposure. At locality B, coniferous woods grow all the way to the shoreline. This is situated on the SW side of a bay, which reduces the hours of sunlight, as well as wave exposure. At both localities, the depth zone of 4–6 m is at a distance of 100 m from land and is therefore exposed to the sun for the same number of hours. This has resulted in a similar level of growth by *Sphagnum* at the two sites.

Figure 1 shows the degree of coverage of *Sphagnum* in different depth zones at the two localities in the lake from 1967 to 1974. Dominant among the *Spagnum* species is *Sphagnum subsecundum* coll. Each annual values is a mean of 15 sampling squares (1 m^2). As can be seen from this figure, the growth was maximal at 0–2 m in the sheltered and shaded locality of the lake. Here, the degree of coverage increased from 8 to 63% between 1967 and 1974. At the 2–4 m level, a significant increase from 10 to 26% occurred, whereas at 4–6 m *Sphagnum* increased from 4 to 30%. At the locality exposed to wind and sun, no significant increase in coverage occurred at 0–2 m, but at 4-6 m it increased from 12 to 26%.

In order to study whether the occurrence of *Sphagnum* is representative in lakes in a wider geographic area, and in lakes with different surface areas and different water color, an inventory was performed in 36 lakes along the west coast of Sweden in 1981. The results show that the correlation is general, i.e. the degree of coverage of *Spagnum* is negatively correlated with pH (fig. 2). The occurrence of *Sphagnum* in acid waters varies with water color and on a secondary basis with certain water chemistry parameters. The coverage of *Sphagnum* is quite homogeneous between 0–6 m in shaded and sheltered areas (fig. 3).

As previously stated, *Lobelia dortmanna* and sometimes *Litorella uniflora* usually dominate in the depth zone 0–2 m. In the investigated lakes, *Lobelia* has been driven out of large littoral areas which have been overgrown by thick mats of *Sphagnum.* A large number of dead plants can be found under the moss growth in the lakes. Also, other changes induced by acidification negatively affect the Isoetid flora.

In acid clear-water lakes the upper sediment layer often consists of a thick mat of filamentous algae and detritus together with Sphagnum. The Isoetides are overgrown by or incorporated in the mat. Both the *Sphagnum* and the mat contribute to the considerable reduction of Isoetide flora in the littoral zone of the lakes (fig. 4). In order to get a deeper insight into the macrophyte community on a quantitative basis the total biomass and production was estimated in lake Gårdsjön on the Swedish west coast.

The relationship between abundance, relative coverage and biomasss is plotted in figure 5 for the three common macrophytes. Remaining species of macrophytes made only a minor contribution to the total biomass and net production[4]. For each degree of abundance the mean of the relative coverage and its 95% confidence interval is

Figure 3. *Sphagnum* on the bottom of an acid lake.

Figure 4. *Lobelia dortmanna* in an acid lake incorporated in a mat of bluegreen algae and detritic matter.

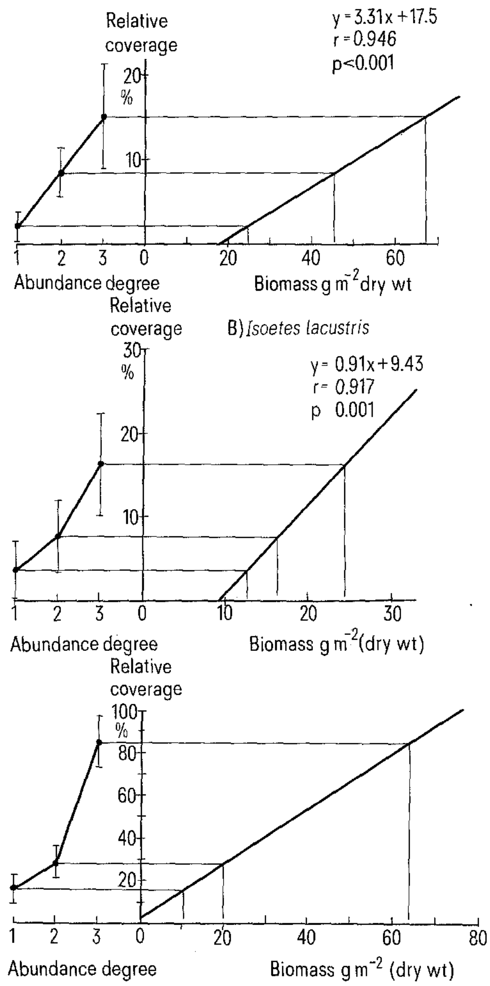

Figure 5. The three-step method for estimating biomass of *Lobelia dortmanna* (a), *Isoetes lacustris* (b) and *Sphagnum* (c) is based on the relationship between abundance degree, relative coverage and biomass. 95% confidence interval is given for the relative coverage.

given. The biomass was in turn estimated from the relative coverage. The arithmetical mean for abundance was then transferred to relative coverage and biomass. There is a good correlation between estimated biomass and relative coverage; r = 0.92, 0.95 and 0.77 for *L. dortmanna, I. lacustris* and *Sphagnum* respectively, all with $p < 0.001$. In table 1 the biomass per m^2 is presented for different abundance degrees, for the total colonization area and for the total lake area. The 95% confidence limit varies between 14% and 31% of the arithmetic mean. The carbon content in *L. dortmanna* and *I. lacustris* is assumed to be 46% of the dry weight[20]. The carbon content in *Sphagnum* was determined as a mean value to be 35% (N = 21 of the dry weight).

The total biomass of macrophytes in the lake was estimated to be 6.5 t (dry wt) corresponding to about 20 g m^{-2}, with 51% *Sphagnum,* 34% *Lobelia* and 15% *Isoetes.* The leaf turnover for *L. dortmanna* during the period May–October 1981 was estimated to be $0.38 \pm 0.05\ y^{-1}$ (90% confidence interval, n = 60). In the nearby Lake Hästevatten the turnover rate during the same period was $0.40 \pm 0.05\ y^{-1}$. Studies on production of new leaves during an annual cycle have shown that the production of new biomass is insignificant during the period November–April[11]. Leaf turnover studies were also performed on *I. lacustris.* For the period May–October leaf turnover was estimated to be 0.53 ± 0.06.

Figure 6 shows the growth in length of *Sphagnum* along two profiles. The profile on the east side of the lake (fig. 6a) which is more exposed to wind and sun, exhibits reduced growth in the shallow waters (0.5–2.0 and 0.5–1.0 m). On the other hand, growth increases in shallow water at the shaded and sheltered locality (fig. 6b).

From 4 to 6 meters, growth declined by about 20% along the investigated profiles. Growth declined more steeply at

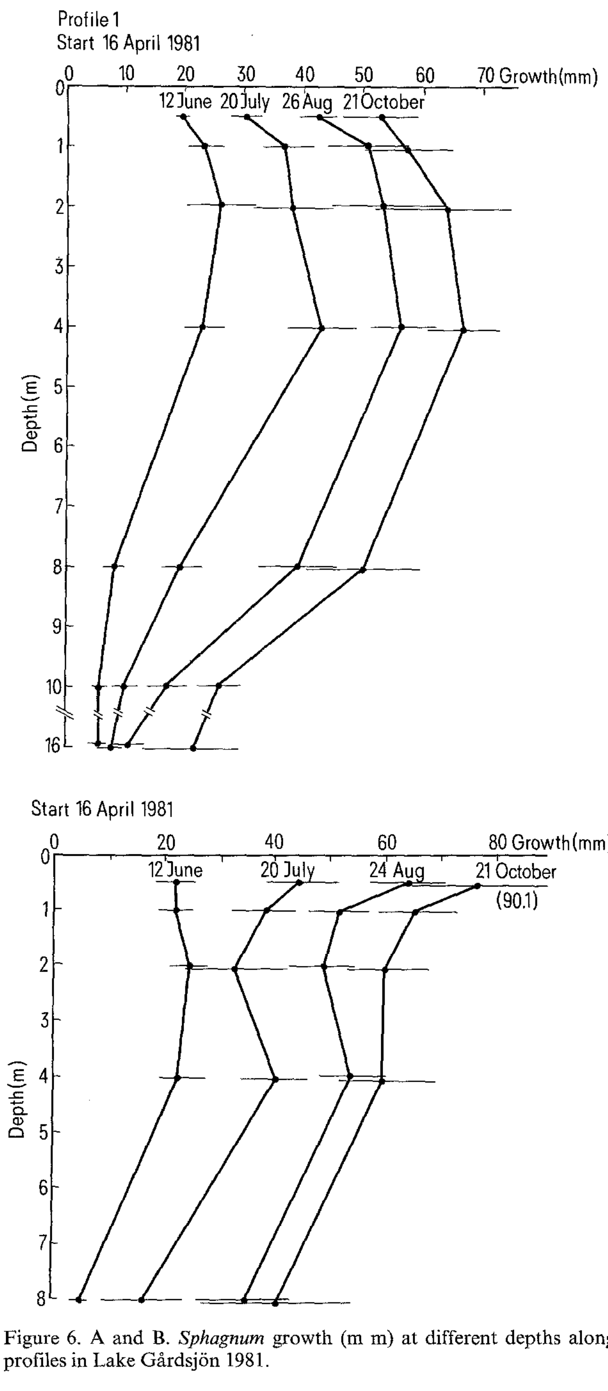

Figure 6. A and B. *Sphagnum* growth (m m) at different depths along profiles in Lake Gårdsjön 1981.

greater depths so that from 10 to 16 m the growth was about 40–50% of that at 4 m. Rapid growth was observed for the profiles at 4 m depth, during the period mid-June to mid-July. The seasonal maximum illumination at this time of year probably caused light inhibition in shallow exposed areas. In shaded and sheltered areas there was no inhibition at depths of about 0–1.5 m and instead the growth was higher.

In table 2 the production for *L. dortmanna, I. lacustris* and *Sphagnum* is presented for the colonization area and the total lake area. Percentage production in the whole lake was 29% for *Lobelia,* 17% for *Isoetes* and 54% for *Sphagnum.* The total net production in the whole lake was estimated at 2900 kg y^{-1} (dry wt) or 1300 kg C y^{-1}.

In another study[15] also on Lake Gårdsjön, photos were taken at fixed sampling stations and used for non-destructive estimation of the biomass and production during the period 1980–1983. In spring 1982 the lake was limed and the pH rose from about 4.5 to about 8.0. From figure 7 it can be seen that the coverage of *Sphagnum* in the investigated sampling areas is about 30–50 g/m^2 (dry wt). In 1982, the first season after liming, there was a successive decrease in biomass and in 1983 *Sphagnum* had completely disappeared. On the other hand there were increases in the biomass of *Lobelia dortmanna* and *Isoetes lacustris* following liming.

Discussion

Among the macrophytes, in acid lakes in Scandinavia *Sphagnum* is a recent element of the flora which, as a single species, often dominates the total macrophyte biomass as well as the total production. Several studies from 1920–1950 have shown that most *Sphagnum* species prefer acid conditions[5,7]. Lake investigations in the 1970s have verified this preference and documented that an invasion of *Sphagnum* takes place during the acidification process[3,6].

Sphagnum populations occur in mire complexes along the shoreline and in the watersheds of most oligotrophic lakes. They are nearly always present. When the physical and chemical conditions in the water change, it is possible for them to spread.

Several factors influence the invasion of *Sphagnum.* One is the availability of CO_2. Many bryophytes utilize free CO_2 in the water for their carbon assimilation[13,19]. This is probably also valid for *Sphagnum.* The concentration of free CO_2 often increases with decreasing pH. In, for example, Lake Gårdsjön the CO_2 content varies between 2 and 8 mg CO_2^{-1}, which means that over-saturation of CO_2 occurs nearly throughout the year.

As *Sphagnum* also prefers shaded conditions, monospecific meadows grow especially in shallow shaded areas, at depths of 0–1 m, and on deeper bottoms at 4–10 m. One possible explanation for this distribution is that light-inhibition affects *Sphagnum* in the same way as it does phytoplankton. Another possible explanation might be differences in carbon dioxide content between shaded and exposed localities.

Sphagnum can invade to greater depths because bryophytes are not limited by hydrostatic pressure as is the case with vascular plants, which normally occur at depths down to 6–7 m.

Acidification induces changes in water quality, such as increased concentrations of mineral micronutrients and heavy metals. Some of these elements may probably also contribute to the spreading of *Sphagnum.* However, little

Table 1. The biomass of abundant macrophytes in Lake Gardsjön, pH of the lake water about 4.5

Species	Biomass in different abundance degress g · m^{-2} (dry wt) 1	2	3	Biomass in the colonization area g m^{-2} (dry wt)	g C · m^{-2}	Biomass in the total lake area g m^{-2} (dry wt)	g C · m^{-2}	Total biomass in the lake kg (dry wt)	kg C
Lobelia dortmanna	24,8 ± 5.6	45.7 ± 9.5	67.2 ± 20.6	36.0 ± 8.4	16.6 ± 3.9	6.8 ± 1.6	3.1 ± 0.7	2201 ± 514	1013 ± 236^a
Isoetes lacustris	12.7 ± 3.0	16.4 ± 3.8	24.2 ± 5.5	16.0 ± 3.7	7.4 ± 1.7^a	3.0 ± 0.7	1.4 ± 0.3^a	984 ± 229	453 ± 105^a
Sphagnum subsecundum var. *innundatum*	10.4 ± 4.9	20.2 ± 4.8	63.9 ± 9.1	14.2 ± 5.0	5.0 ± 1.8^b	10.2 ± 3.6	3.6 ± 1.3^b	3312 ± 1169	1159 ± 538^b
					Total	20.0	9.2	6497	2625

^{a}The carbon content is calculated using a factor of 46% (Westlake[20]). ^{b}The carbon content was measured to 35% of the dry weight.

Table 2. Yearly net production 1981 of abundant macrophytes in Lake Gårdsjön. Ph of the lake water about 4.5

Species	Net production in the colonization area g · m^{-2} (dry wt)	g C · m^{-2}	Net production in the total lake area g · m^{-2} (dry wt)	g C · m^{-2}	Total net production in the whole lake kg · y^{-1} (dry wt)	kg C · y^{-1}
Lobelia dortmanna	13.7 ± 3.2	6.3 ± 1.5	2.6 ± 0.6	1.2 ± 0.3	836 ± 195	384 ± 90
Isoetes lacustris	8.0 ± 1.9	3.7 ± 0.9	1.5 ± 0.4	0.7 ± 0.2	492 ± 115	226 ± 41
Sphagnum subsecundum var. *innundatum*	6.8	2.4	4.8	1.7	1570	550
		Total	8.9	4.1	2898	1160

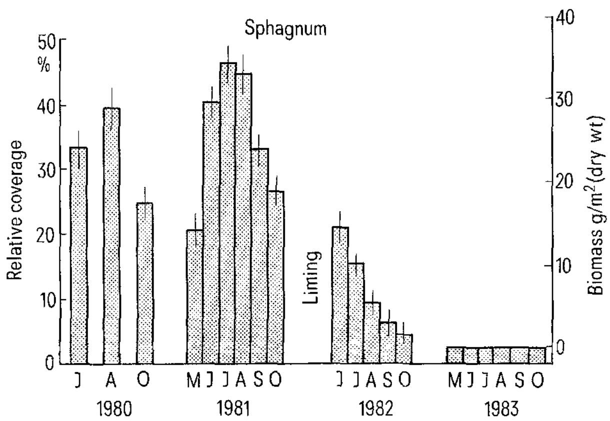

Figure 7. The biomass of *Sphagnum* estimated from the point intercept method on photos from permanent photostations on the bottom of Lake Gårdsjön.

is known about the influence of these elements and how they can interact in the *Sphagnum* expansion.

In the investigations referred to here, there are indications that the growth of *L. dortmanna* is reduced under acid conditions. The reduced leaf turnover rate can probably be explained by shading from the benthic mat, especially in shallow areas. This mat has been found in many acid lakes and consists mainly of blue-green algae, *Sphagnum* debris and detritus[10]. Over large areas only the tops of the leaves can be identified (fig. 4) and in some areas the whole plant can be incorporated in the mat and wiped out[3]. One may therefore expect that further acidification will contribute to a reduced *Lobelia* population. At greater depths, where *I. lacustris* grows (3–6 m), the benthic mat is thinner. The plants of *I. lacustris* are also longer, so the photosynthesizing parts are not incorporated in the mat. The turnover time for *Isoetes* in acid lakes is about the same (0.5 y^{-1}) as reported from a moderately acid humic lake in central Sweden[2].

The total biomass in the vegetated area of Lake Gårdsjön was in the range of 60–80 g m^{-2} in terms of all three species. In Lakes Stugsjön, Hymenjaure (northern Sweden) and Vitalampa (central Sweden), the magnitude of the biomass was about 20 g m^{-2} [2,17].

Literature data indicate that the total macrophyte biomass in acid lakes is higher than that in other oligotrophic lakes in Sweden and North America. This is mainly due to the dominant occurrence of *Sphagnum*. However, there are numerous differences in sampling methods, climate, water color and lake trophic status which affect these comparisons.

Owing to the lack of background data on the macrophyte community from lakes prior to their acidification, and to great individual differences between lakes of the same type, it is today impossible to reach definite conclusions regarding quantitative changes in biomass and production caused by acidification. However, one can finally conclude that there are several quantitative and qualitative changes in the macrophyte community which are related to acidification and that these changes in turn induce shifts in the other trophic levels. One can also conclude that liming of lakes causes elimination of *Sphagnum* and some increase in the production of *Isoetids*.

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