High Inorganic Carbon Extraction Capacity of Submerged Macrophytes from Soft-water Faroese Lakes

Vatnplantur í føroyskum vøtnum við bleytum vatni taka lættliga ólívrunnið kolevni upp

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Úrtak

Vatnplantur (macrophytes) úr tíggju føroyskum vøtnum við millum 0.16 og 0.8 meqv. L^{-1} av alkali í sær vóru tiknar, og kannað varð, hvussu væl tær vóru førar fyri at taka ólívrunnið kolevni upp. Av 26 sløgum, ið vórðu kannað, tók um leið helmingurin væl av kolevni upp samsvarandi við, at tær vóru førar fyri at miðsavna kolevni. Hin helmingurin sýndi eyðkenni samsvarandi við spjadda CO_2 veiting og C-3 fotosamanrenning. Hóast lítið alkali var í føroyskum vøtnum og sostatt lítið hydrokarbonati, megnaðu tey sløg, sum eru før fyri at taka kolevni upp, at troyta tað hydrokarbonat, sum var. Einki samband var funnið millum alkali í vøtnunum og førleikan hjá plantunum at taka upp kolevni.

Abstract

Submerged aquatic macrophytes from ten Faroese lakes with an alkalinity between 0.16 and 0.8 meqv L^{-1} were collected and their inorganic carbon extraction capacity determined. Among the 26 species tested, about one-half had a high carbon extraction capacity consistent with possession of a carbon concentrating mechanism. The other one-half showed characteristics consistent with diffusive CO_2 supply and C-3 photosynthesis. Despite the low alkalinity of the Faroese lakes and, thus, low bicarbonate concentration, the species employing a carbon concentrating mechanism were able to exploit the bicarbonate pool of the water. No relationship between lake alkalinity and carbon extraction capacity of the plants was observed.

Introduction

Submerged plants in lakes and streams are often exposed to environmental conditions significantly different from conditions existing in terrestrial habitats from which vascular plants are believed to have colonised freshwater habitats (Raven, 1995). In particular, the supply rate of CO_2 and O_2 are substantially lower in water than in air due to the 10^4 times lower diffusion rate of gases. The low diffusion rate impedes the gas flux across the stagnant layer of water surrounding the plants and, thereby, restricts the exchange rate between plants and bulk water. As a result, CO_2 saturation for submerged macrophyte photosynthesis is reached only at relatively high concentra-

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tions, often above 500 µM (Steeman-Nielsen, 1947; Maberly and Spence, 1989; Nielsen and Sand-Jensen, 1993; Larcher, 1995). This is more than 30 times the equilibrium concentration in water, which is about 16 µM (at 15°C). However, due to metabolic activity and a slow exchange rate between water and air, disequilibrium is often encountered. Thus, in a survey comprising 1835 lakes and 4665 samples (Cole *et al.* (1994) found that nearly all had CO_2 concentrations different from air equilibrium, with 87% having higher concentrations.

The high CO_2 requirement for saturation of photosynthesis by submerged macrophytes in relation to the low concentrations found in most waters suggests that CO_2 limitation of photosynthesis may be a common phenomenon, an hypothesis that has been confirmed in several investigations (Maberly, 1985; Madsen and Maberly, 1991; Madsen, 1991; Nielsen and Sand-Jensen, 1993; Frost-Christensen and Sand-Jensen, 1995). The CO_2 limitation of photosynthesis might be circumvented or ameliorated by the plants through various structural and physiological adaptations. These mechanisms and strategies can be grouped into two main categories: spatial escape and biochemical/physiological adaptations. Plants that rely on spatial escape grow in habitats rich in CO_2, have the ability to develop aerial leaves or can use sediment CO_2. Biochemical and physiological adaptations include bicarbonate use and different types of C-4 photosynthesis. The biochemical/physiological adaptations are often referred to as Carbon Concentrating Mechanisms (CCM), due to their capacity to enhance the internal concentration above what can be obtained by passive CO_2 uptake and C-3 photosynthesis.

Escape Strategies

In the bulk water of lakes, the concentration of CO_2 might be higher than atmospheric equilibrium concentrations, though concentrations sufficient to saturate photosynthesis of submerged macrophytes are rare (Cole *et al.*, 1994). Higher CO_2 concentrations can also be encountered immediately adjacent to the surface of organic sediment with high bacterial activity (Pedersen *et al.*, 1995). An inorganic carbon source that might be exploited by low stature plants growing close to the sediment.

A quantitatively significant use of sediment-CO_2 among freshwater macrophytes is a widespread trait among the isoetids of which *Littorella uniflora*, *Lobelia dortmanna* and *Isoetes lacustris* are prominent members (Wium-Andersen, 1971; Boston *et al.*, 1987). The isoetids are small plants with short, stiff rosette leaves, a high root: shoot ratio and a well-developed lacunal system. The lacunal system forms a more or less continuous airspace along the entire length of the plants through which CO_2 diffuses from the sediment via the roots to the leaves and oxygen diffuses in the opposite direction (Sculthorpe, 1967). The ecological advantage of sediment-CO_2 use lies in the high CO_2 concentration in the interstitial water, which may be 50 to 100 times higher than in the bulk water (Wium-Andersen and Andersen, 1972; Roelofs *et al.*, 1984; Boston *et al.*, 1987). Despite the high

CO_2 concentration in the interstitial water, the dependence on diffusive transport sets a limit on the maximum leaf-length that can be obtained by the isoetid as diffusion is slow over longer distances even in air. Consequently, the isoetids often dominate the flora of oligotrophic, soft-water lakes, but cannot compete with the taller elodeid vegetation in more alkaline systems.

Use of the more readily accessible atmospheric CO_2 is a characteristic of amphibious plants that have the ability to grow submerged as well as emergent. The exploitation of atmospheric CO_2 requires that the plants develop aerial leaves, either floating on or raised above the water surface. The aerial leaves have functional stomata and resemble leaves of terrestrial plants by being thicker and having a higher photosynthetic capacity and CO_2 affinity than their submerged counterparts when measured in air (Sculthorpe, 1967; Sand-Jensen and Frost-Christensen, 1999).

Biochemical and Physiological Adaptations

A number of aquatic macrophyte species have CO_2 uptake characteristics that deviate from those expected for plants relying on diffusive entry of CO_2 with subsequent fixation by the C-3 carbon fixation pathway. In particular, the rate of photorespiration and the CO_2 compensation point are lower than predicted. This indicates that these plants possess a carbon acquisition or concentrating system that can overcome the limitation imposed by CO_2 diffusion and C-3 photosynthesis. Among these systems, bicarbonate use is the most widespread (Madsen and Sand-Jensen, 1991), whereas C-4 photosynthesis and Crassulacean Acid Metabolism (CAM) is employed by only a few species.

In addition to CO_2, inorganic carbon in water exists as bicarbonate (HCO_3^-) and carbonate (CO_3^{2-}) and the three carbon species form a buffering system, where the relative distribution among species is determined by pH and, to a lesser extent, by temperature and salinity (Stumm and Morgan, 1996). With increasing pH, the equilibrium shifts from CO_2 to bicarbonate and carbonate with pK_a values of 6.38 and 10.38 (20°C) (Prins and Elzenga, 1989). Thus, in waters with pH above 6.4, the concentration of HCO_3^- is higher than the CO_2 concentration. In alkaline waters, plant species with the ability to use bicarbonate, therefore, have an advantage compared to plants that use CO_2 only, an advantage that is greater at higher alkalinity and pH. Based on characteristic electro-chemical potentials of plant cells, it can be calculated that passive entry of HCO_3^- only takes place if the external HCO_3^- concentrations is 10^2 -10^4 times higher than internal concentrations, an observation that has led to the conclusion that HCO_3^- uptake is active (Raven, 1970).

Among freshwater species possessing the ability to use bicarbonate, the affinity for HCO_3^- in general is much lower than the affinity for CO_2, when expressed as the concentration needed to half-saturate photosynthesis and as the initial slope of the dose-response curve (Madsen and Sand-Jensen, 1991; Madsen, 1993; Maberly and Madsen, 1998). The lower affinity for bicarbonate compared to CO_2 potentially reduces the ecological significance of HCO_3^- use, in particular in soft-water and acid lakes and streams.

C-4 photosynthesis has so far been found in *Hydrilla verticillata* only (Reiskind *et al.,* 1997). *Hydrilla* lacks Krantz anatomy to separate the two carboxylation systems of C-4, as known from terrestrial C-4 plants. Instead, the two systems appear to be separated at the cell level, as revealed by immunocytochemical gold-labelling and fluorescence techniques (Reiskind *et al.,* 1989). C-4 carboxylation and phosphoenolpyruvate carboxylase (PEPcase) is found in the cytosol and C-3 carboxylation and ribulose biphosphate carboxylase-oxygenase is confined to the chloroplasts. The ecophysiological benefit of C-4 is the suppression of photorespiration, through which 50% of the fixed carbon may be lost as respiratory CO_2 in C-3 plants.

A number of submerged macrophytes, most belonging to the isoetids (Keeley, 1996), have developed an inorganic carbon uptake system that resembles the terrestrial CAM plant system and allows the plants to take up inorganic carbon throughout most of the light/dark cycle ((Madsen, 1987a). The main benefit of CAM for isoetids in soft-water lakes with low inorganic carbon concentrations is by far the extended period available for carbon uptake. However, it appears that CAM may also have a stimulating effect on net photosynthesis, due to an inhibitory effect on photorespiration caused by the high internal CO_2 concentrations encountered during decarboxylation (Madsen, 1987a).

The physiological and biochemical adaptations in submerged macrophytes as described above are believed to be directed towards maximising inorganic carbon uptake efficiency. The trade-off is enhanced running costs for inorganic carbon uptake and the need for investments in uptake systems. The ability to use CCM is not a constant feature, however, but appears to be regulated in response to growth conditions and only shows high activity when needed, *i.e.* when the availability of inorganic carbon is low relative to the demand. Thus, bicarbonate-users often down-regulate their affinity and capacity for HCO_3-uptake when grown at high CO_2 concentration (Sand-Jensen and Gordon, 1993). Similarly, CAM activity has been found to be suppressed for plants growing at high CO_2 or in low light, where the inorganic carbon requirement is low (Madsen, 1987b).

In the present study, we measured the carbon extraction capacity for a range of submerged macrophyte species from lakes of the Faroe Islands. The lakes are all softwater and low in inorganic carbon (H.-H. Schierup, pers. comm.) and support a submerged macrophyte flora that includes numerous species known from the literature to have the potential for using bicarbonate in photosynthesis (Hansen, 1966; Maberly and Spence, 1983). The specific objectives of the study were 1) to examine if species known to be bicarbonate users in alkaline lakes maintain the ability in the more softwater, Faroese lakes, where the low affinity for HCO_3^- may restrict the ecological advantage of HCO_3^- use, and 2) to test whether the extraction capacity of the plants was related to lake water alkalinity.

Table 1. *Alkalinity (mean ± s.d, n = 2-3) and UTM co-ordinates (zone 29V) for lakes included in this investigation.*

Talva 1. *Alkani (Miðal ± s.d., n=2-3) og UTM samskiparar (øki 29 V) yvir vøtn, sum henda kanning fevnir um.*

Lake	UTM co-ordinates	Alkalinity (meqv L^{-1})
Eysturoy		
Toftavatn	6897580 m.N, 619070 m.E	0.16±0.016
Múlavík	6909700 m.N, 599250 m.E	0.17±0.019
***Streymoy*:**		
Saksunarvatn	6902600 m.N, 595940 m.E	0.19±0.013
Mjáuvøtn	6889940 m.N, 604700 m.E	0.13±0.016
Áarstíggjafossur	6861550 m.N, 605760 m.E	0.29±0.005
Pond at Tórshavn	6878290 m.N, 616490 m.E	0.81±0.058
***Sandoy*:**		
Norðara Hálsavatn	6863700 m.N, 612100 m.E	0.18±0.025
Sandsvatn	6859600 m.N, 614900 m.E	0.37±0.044
Gróthúsvatn	6858620 m.N, 614220 m.E	0.37±0.021
Stóravatn	6858400 m.N, 609140 m.E	0.31±0.016

Material and methods

Specimens of 26 aquatic macrophyte species and water were collected in ten lakes on Eysturoy, Streymoy and Sandoy (Table 1). Several of the species were collected in more than one lake.

Alkalinity of the lake water was measured by Gran titration (Mackereth *et al.*, 1989) of 20 ml samples with 0.1 M HCl using a Radiometer PHM 84 pH-meter with a glass combination electrode (Radiometer GK2401C).

The carbon extraction capacity of the plants was measured employing pH drift experiments. Small apical shoots, young, but with fully developed leaves or thallus segments, were incubated in closed, 25 ml glass bottles and allowed to photosynthesise for 18 hours. The incubation medium was modified from Smart and Barko (1985) by adjusting the amount of $KHCO_3$ and $NaHCO_3$ to give alkalinities of 0.125 meqv L^{-1} and 1.0 meqv L^{-1}. The medium was bubbled with atmospheric air prior to incubation. The bottles were placed on a rotating wheel in a water-bath at 10°C ± 0.1°C and light was provided at 250 μmol photons m^{-2} s^{-1} by a high-pressure metal halide lamp. After 16 hours of incubation, pH was measured and alkalinity determined for 10 ml samples by Gran titration. The carbon extraction capacity is expressed as final-pH.

The concentration of the different inorganic carbon species was calculated from alkalinity, pH and temperature, as described in Maberly (1996).

Results and discussion

The selection of species included in this study is listed in Table 2.

The final-pH reached in the pH drift experiments at an alkalinity of 1.0 meqv L^{-1} varied among the different plant species from 8.55 for *Isoetes lacustris* to 10.87 for the filamentous algae *Vaucheria* sp. (Table

3). Calculated and expressed as the percentage of the inorganic carbon pool extracted from the water, *Isoetes* had removed less than 1%, whereas *Vaucheria* had removed more than 57%.

The differences in extraction capacity among plants are believed to reflect differences in their inorganic carbon uptake mechanisms. For species with low extraction capacity, the data are consistent with diffusive entry of CO_2 and C-3 physiology. In contrast, species with high extraction capacity are expected to employ some kind of carbon concentrating mechanism. Of these mechanisms, active uptake of bicarbonate constitutes the most efficient system in terms of inorganic carbon extraction capacity among submerged macrophytes (Madsen and Sand-Jensen, 1991). Whether plants rely on diffusive entry of CO_2 and C-3 photosynthesis or use a carbon concentrating system cannot be determined from final-pH alone. However, from final-pH and alkalinity of the incubation medium, the CO_2 compensation point of the plants can be calculated and compared to CO_2 compensation points reported in the literature, which vary from about 1.5 μM to more than 100 μM (Maberly and Spence, 1983). For plants incubated in a medium with an alkalinity of 1.0 meqv L^{-1} at 10 °C, as in this study, a compensation point of 1.5 μM will allow the plants to raise pH to about 9.2. Using this value to separate species with and without the ability to operate a CCM, the data in Table 3 show that 14 of the 26 species tested had this ability. Table 3 also shows, however, that the pH drift data do not offer a marked distinction be-

Table 2.
List of species included in this study. Alternative inorganic carbon sources that can be exploited by the different vascular plants and macroalgae are listed. Ability to use sediment-CO_2 was extracted from Spence and Maberly (1985) and Richardson et al. *(1984) and the ability to exploit the atmospheric CO_2 pool was diagnosed from the ability to develop floating or aerial leaves.*

Talva 2
Yvirlit yvir sløgini, sum henda kanning fevnir um. Listi yvir aðrar ólívrunnar kolevniskeldur, sum tær ymisku leggstreingjaplanturnar og makroalgurnar fáa nýtt. Spence og Maberly (1985) og Richardson *et al.* (1984) komu fram á, hvussu væl planturnar vóru førar fyri at nýta CO_2 úr botnsetingini, og alt eftir, hvussu tær megnaðu at menna flóti-ella luftbløð, varð mett um, hvussu væl tær vóru førar fyri at nýta CO_2-puljuna í luftini.

Species	**Alternative Carbon Source**
Callitriche stagnalis	Atmosphere
C. hamulata	Atmosphere
Eleocharis acicularis	Atmosphere
Fontinalis antipyretica	
Isoetes lacustris	Sediment
Juncus bulbosus	
Littorella uniflora	Sediment
Lobelia dortmanna	Sediment
Myriophyllum alterniflorum	
Nymphaea alba	Atmosphere
Polygonum amphibium	Atmosphere
Potamogeton alpinus	Atmosphere
P. filiformis	
P. gramineus	Atmosphere
P. natans	Atmosphere
P. obtusifolius	
P. perfoliatus	
P. polygonifolius	Atmosphere
P. praelongus	
Sparganium angustifolium	Atmosphere
Utricularia vulgaris	
Chara sp.	
Cladophora sp.	
Nitella sp.	
Spirogyra sp.	
Vaucheria sp.	

tween non-CCM and CCM species. Rather, the species show a continuous gradient in carbon extraction capacity, which reflects genotypical differences in carbon uptake efficiency and the great plasticity in inorganic carbon uptake physiology generally observed for aquatic macrophytes. For species restricted to CO_2 use and for species running a CCM, the affinity for inorganic carbon is greatly dependent on environmental conditions. Under conditions where the restriction on inorganic carbon uptake is high, the plants respond by enhancing the resource allocation towards carbon uptake, resulting in an improved affinity and extraction capacity for inorganic carbon (Sand-Jensen and Gordon, 1993; Madsen, 1993; Madsen *et al.*, 1996). The restriction of inorganic carbon uptake rates is not governed by the supply rate of CO_2 and other inorganic carbon species alone; of more importance is the balance between the supply rate and the demand for inorganic carbon by the plants. Environmental parameters other than inorganic carbon will, therefore, affect the extent of inorganic carbon limitation and the extent of limitation will be inversely coupled to the extent to which other factors limit plant growth and, thereby, affect inorganic carbon demand. Thus, it cannot be excluded that among species in the border-zone between non-CCM and CCM species some species categorised as non-CCM might actually have a concentrating system with a very low efficiency and vice versa.

A number of the species tested and found to rely on diffusive entry of CO_2 and C-3 photosynthesis have developed mecha-

Table 3.
Inorganic carbon extraction capacity for submerged macrophyte species in Faroese lakes. Inorganic carbon extraction capacity was measured by pH-drift experiments at an alkalinity of 1.0 and 0.125 meqv L^{-1} and is expressed as final-pH after 16 hours incubation at 10 flC and 250 (mol m^{-2} s^{-1} PAR. Mean (s.d., n = 3-6; n.a. = not analysed.

Talva 3.
Førleiki hjá vatnplantusløgum í føroyskum vøtnum at taka ólívrunnið kolevni upp. pH-rekroyndir mátaðu førleikan at taka ólívrunnið kolevni upp, tá ið alkaliið er 1.0 og 0.125 meqv. L-1 og verður nevnt endaligt pH, tá ið tilgerðartíðin er 16 tímar við 10 °C og 250 (mol m-2 s-1 PAR. Miðal (s.d.) n=3-6; n.a.=ikki sundurgreinað.)

Species	**Final-pH**	
	1.0 meqv L^{-1}	0.125 meqv L^{-1}
Nymphaea alba	8.44±0.16	n.a.
Isoetes lacustris	8.55±0.04	n.a.
Sparganium angustifolium	8.58±0.04	n.a.
Lobelia dortmanna	8.62±0.25	n.a.
Callitriche stagnalis	8.72±0.03	n.a.
Littorella uniflora	8.75±0.24	n.a.
Eleocharis acicularis	8.93±0.15	n.a.
Fontinalis antipyretica	9.02±0.01	n.a.
Juncus bulbosus	9.07±0.02	n.a.
Nitella sp.	9.07±0.05	n.a.
Potamogeton polygonifolius	9.19±0.06	n.a.
Callitriche hamulata	9.27±0.09	n.a.
Potamogeton natans	9.52±0.47	8.52±0.56
Utricularia vulgaris	9.70±0.18	9.43±0.52
Potamogeton alpinus	10.00±0.10	9.92±0.08
P. praelongus	10.03±0.08	9.96±0.07
P. gramineus	10.12±0.16	9.85±0.10
Myriophyllum alterniflorum	10.13±0.02	9.82±0.08
Potamogeton obtusifolius	10.21±0.07	9.51±0.23
P. filiformis	10.26±0.09	9.64±0.03
Spirogyra sp.	10.39±0.41	9.80±0.42
Potamogeton perfoliatus	10.44±0.04	10.22±0.24
Chara sp.	10.52±0.02	9.62±0.07
Cladophora sp.	10.74±0.10	10.26±0.07
Vaucheria sp.	10.87±0.16	9.01±0.59

nisms that allow exploitation of inorganic carbon sources other than those in the bulk water (Table 2). The isoetids (*Littorella uniflora, Isoetes lacustris and Lobelia dortmanna*) use sediment-CO_2. In addition, *Littorella* and *Lobelia*, including the Faroese specimen, are CAM plants (Keeley, 1996; Madsen and Bagger, unpubl. results 1999) and, thereby, have the potential to improve the carbon balance by allowing inorganic carbon uptake in both light and dark. However, the effects of CAM on the carbon extraction capacity appear to be low (Table 3). Of the remaining non-CCM species, *Sparganium angustifolium*, *Potamogeton polygonifolius* and the two *Callitriche* species have the ability to develop aerial or floating leaves allowing acquisition of CO_2 from the more readily available atmospheric pool. *Eleocharis acicularis*, *Juncus bulbosus, Nitella sp.* and *Fontinalis antipyretica* are not known to have developed traits or features improving inorganic carbon uptake (Steeman-Nielsen, 1947; Bain and Proctor, 1980; Allen and Spence, 1981; Morton and Keeley, 1990), except for one report showing that *Fontinalis antipyretica* collected in a Spanish river could use bicarbonate ((Penuelas, 1985). These species, however, often grow close to the sediment and might benefit from the higher CO_2 concentration found there (Maberly, 1985).

The list of species with CCM (final-pH > 9.5, Table 3) agrees with reports in the literature (Spence and Maberly, 1985), except for submerged leaves of *Potamogeton natans* that have been reported to be unable to operate a CCM (Maberly and Spence, 1983). The CO_2 compensation point calculated for *P. natans* varied among sites, but was very low (0.2 µM to 0.6 µM) and unlikely to be achievable without a carbon concentrating system. Interference from epiphytes cannot be ruled out, however, although no visible biofilm was found. The CO_2 compensation point reported for *P. natans* by Maberly and Spence (1983) for submerged leaves was 2.1 µM, which is comparable to the range reported by Frost-Christensen and Sand-Jensen (1995) for floating leaves measured in water. For *Utricularia vulgaris* no report on CCM has been found. Another *Utricularia* species, *U. purpurea*, has been reported to be unable to use bicarbonate, though tested at low alkalinity (<0.07 meqv L^{-1}) only (Moeller, 1978). In contrast, *Utricularia australis* has a high carbon extraction capacity (L. Kristiansen, pers. comm.).

For most of the species categorised as having CCM, only three, *P. natans, P. alpinus* and *P. gramineus*, have the ability to explore alternative inorganic carbon sources, all by the ability to develop floating leaves.

Though not verified directly, it is assumed that the CCM operating in the species tested was based on HCO_3^- use, which is the most widespread among freshwater macrophytes (Prins and Elzenga, 1989; Madsen and Sand-Jensen, 1991). For these species, the HCO_3^- compensation point, calculated from alkalinity and final-pH, varied from 0.1 to 0.77 mM. This range is comparable to the range reported for other macrophytes measured at similar alkalinity (0.5 – 2.0 mM), but substantially higher than the compensation point found for the more efficient microalgae (Allen and Spence, 1981).

The alkalinity of the Faroese lakes from which the plants were collected varied between 0.16 and 0.37 meqv L^{-1} (Table 1) and the concentration of bicarbonate between 0.16 and 0.37 mM (except for one lake with an alkalinity of 0.8 meqv L^{-1}). These bicarbonate concentrations are lower than the compensation point of most of the tested species (0.37 mM HCO_3^- is equivalent to a final-pH of about 10.3). To test whether the compensation point was affected by alkalinity, pH drift experiments were performed at 0.125 meqv L^{-1} for species found to have a CCM.

The final-pH at 0.125 meqv L^{-1} was lower than at 1 meqv L^{-1} (Table 3), which is a result of the lower, total inorganic carbon concentration at low, compared to high, alkalinity at a given pH. The calculated HCO_3^- compensation points, which ranged from 0.12 to 0.03 mM, were also lower at 0.125 meqv L^{-1} than at 1.0 meqv L^{-1}. The lower compensation points show that the CCM species will be able to use HCO_3^- even at the low concentrations found in the Faroese lakes. The relative contribution of HCO_3^- to total inorganic carbon uptake cannot, however, be estimated from pH-drift experiments alone.

The inorganic carbon uptake characteristics of aquatic macrophytes are very plastic within a particular species and change in response to the availability of inorganic carbon and other resources. For *Elodea canadensis* collected in a range of Danish lakes and streams the affinity for bicarbonate has been found to vary from high to no measurable affinity in response to differences in bicarbonate and CO_2 concentrations in the water (Sand-Jensen and Gordon, 1993). Also, for plants grown in the laboratory, substantial acclimation in affinity for both HCO_3^- and CO_2 and in carbon extraction capacity was observed, not only in response to CO_2 and HCO_3^- availability (Madsen *et al.,* 1996), but also in response to other environmental parameters (Madsen, unpubl. results, 1998). For the species collected in this study, however, no correlation was observed between carbon extraction capacity among species and alkalinity of water from the collection site, nor was the distribution of species related to lake alkalinity. These results likely reflect the narrow range in alkalinity found in the Faroese lakes sampled rather than the lack of physiological plasticity and responsiveness among the species.

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