Competition between three submerged macrophytes, *Elodea canadensis*, *Elodea nuttallii* and *Lagarosiphon major*

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Summary

Species displacements within aquatic plant communities can be driven by external environmental changes or by competitive processes between species. In some lentic British waters *Elodea nuttallii* has displaced *Elodea canadensis* and is itself now being displaced by *Lagarosiphon major*. During photosynthesis, aquatic plant clumps create "envelopes" of raised pH and O_2 levels and low CO_2 levels. These may extend beyond the plant clump, suppressing photosynthetic performance and increasing photorespiratory stress on neighbouring species. It is suggested that a competitive advantage will be achieved by those species which have the best stress generation/toleration mechanisms.

Introduction

In the last 100 years increasing world-wide travel and trade has resulted in the introduction of many aquatic plant species to countries beyond their native range, where their subsequent spread has sometimes been extremely rapid. For example, *Elodea canadensis*, introduced into the British Isles in the early nineteenth century, soon became a widely distributed and troublesome alien species in many situations (Simpson 1984). The introduction of *Elodea nuttallii* in 1966 and its subsequent spread has resulted in the displacement of *E. canadensis* from many waters where the latter had been well established (Simpson 1990). It was observed that displacement occurred over a relatively short time period of one to two years (Lund 1979; Simpson 1984). More recently a species native to South Africa, *Lagarosiphon major* (Ridley) Moss has been reported to be actively displacing *E. nuttallii* and appears to be competitively superior to *Elodea* spp. (Sculthorpe 1985).

The three species are morphological similar, having long flexuous leafy stems initially rooted in the substrate, but becoming detached later in the life cycle. Reproduction of each species in the British Isles is vegetative, as populations are wholly female (Simpson 1986). In view of the similarities in morphology and reproduction, what is driving these species displacements?

Displacement occurs as a result of a competitive interaction between individuals. In the aquatic environment, availability of dissolved inorganic carbon, light and macronutrients is critical for the photosynthesis and growth of submerged macrophytes. Despite the high concentrations of organic and inorganic substances often found in lowland water bodies, supply may nevertheless limit plant performance, due to the slow diffusion rates of substances through the laminar-flow boundary layers which surround submerged surfaces (Losee and Wetzel 1988). Supply of inorganic nutrients and dissolved inorganic carbon may be restricted by the slow replenishment of depleted resources from the bulk surrounding water body. Conversely, substances released by plants (e.g. oxygen) may accumulate within the boundary layer. Dissolved inorganic carbon (DIC) utilisation and the production of oxygen result in a shift towards high pH and oxygen supersaturation in waters adjacent to the active plant surfaces. Studies suggest that these envelopes of raised pH and oxygen, and lowered DIC may, especially under conditions of low bulk water flow, expand beyond the plant stand itself and hence could potentially interfere with the growth of neighbouring plants.

It is hypothesised that a competitive advantage will be achieved by those species that have the best stress generation/ toleration mechanisms. The aim of this work was to investigate the generation of the pH stress under laboratory conditions and to compare this with the physiological tolerance of species to increasing pH. An initial field study was conduced on *E. nuttallii* to provide evidence of boundary layer formation and for comparison with laboratory data.

Methods

Field example- Stands of *E. nuttallii* in the Rufford Branch of the Leeds and Liverpool Canal (SD 460 171) were studied on 18th August 1997. Vertical profiles of pH (pH Boy-P2, Camlab, Cambridge, UK), oxygen and temperature (OXI 126, WTW, Wielheim, Germany) were made at depths of 0, 10, 20, 30, 40 and 50 cm at 0600 h, 0900 h, 1200 h, 1500 h and 1800 h British summer time. In addition a profile was taken from an adjacent area of open water at 1530 h, when it was assumed that gradients would be close to their diurnal maximum.

Stress generation under laboratory conditions- For measurements of stress generation under laboratory conditions, measurements were made in monocultures of each species grown at two densities for 10 weeks. For each species 10 cm apical lengths of shoot were selected and planted in 250 ml plastic cups filled with canal sediment. These were placed in 10 litre buckets filled with tap water previously aerated for 24 hours, 2 plants and 4 plants per bucket for low and high densities respectively. These were maintained at 15 °C with a light intensity of 100 mmol m^{-2} s^{-1} PAR with weekly additions of nutrients (100 mg l^{-1} P and 1 mg l^{-1} N). pH measurements were made 2 cm below the water surface every 2 to 3 days initially, and thereafter approximately every 10 days. Carbon fractions (free CO_2, bicarbonate and carbonate) were calculated from weekly measurements of alkalinity, pH, temperature and conductivity following the methods of Mackereth *et al.* (1989).

The photosynthetic response to increasing pH - Measurements of photosynthetic response to increasing pH were made on samples of leaves removed from the monocultures. For consistency leaves were taken 3 cm below the apical tip. Oxygen evolution or uptake was measured using a Clarke-type oxygen electrode (Hansatech, King's Lynn, UK) at 15 °C, with an incident light intensity of 290 µmol m^{-2} s^{-1} PAR. Determinations were made in Forsberg solution (Forsberg 1965) with the omission of buffering agents, as these were found to inhibit uptake of bicarbonate at high pH. The pH was measured at the beginning and end of each recording to provide the pH range over which readings were taken.

Results

Results from field studies confirm that extremely stressful conditions develop within a plant stand. These are typified by high pH (and therefore low available CO_2) and high O_2 (Fig. 1). Highest values were recorded in the top 10 cm of the water column. Comparative measurements of pH and oxygen concentration made in open water at 1530 h revealed only a 0.1 pH unit and 1 mg l^{-1} O_2 concentration difference over the whole water column. When cultured within the laboratory, all three species created similar conditions of high pH within the surrounding medium, with values in excess of pH 9 (Fig. 2). Although there were short-lived small differences in the rate of pH increase, all species had attained a similar pH of almost pH 10 after 30 days. Total CO_2, Free CO_2 and bicarbonate decreased similarly over the experimental period for all treatments.

Species exhibited tolerance to a wide range of pH levels. Smoothed lines were fitted to the data using locally weighted regression analysis (Fig. 3a). Net photosynthetic compensation points for all three species were approximately pH 9.7. A visual comparison of 99% confidence limits for *Elodea* spp. and *L. major* revealed little overlap within the range pH 6.0 to 8.5 (Fig. 3b). Above pH 8.5, photosynthetic rates of *L. major* were higher than those of *Elodea* spp., although overlap of confidence intervals indicates that photosynthetic rates were not significantly different. A comparison of confidence intervals for the two *Elodea* spp. (not shown here) revealed considerable overlap over the entire pH range measured.

Increases in pH were not found to have any effect upon respiratory rates.

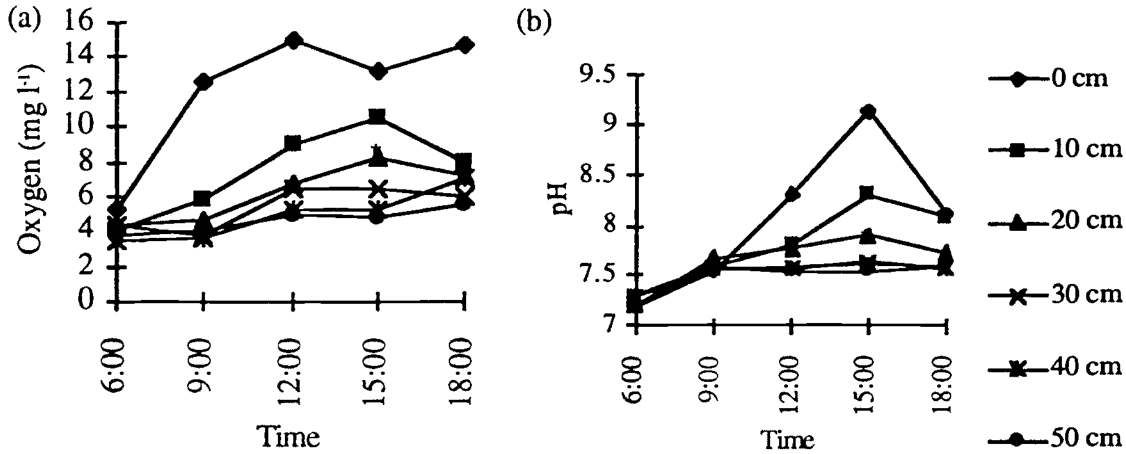

Fig. 1. Profiles of a) dissolved oxygen concentration and b) pH in a stand of *E. nuttallii* over a 12 hour period. * Indicates levels measured in open water at water surface.

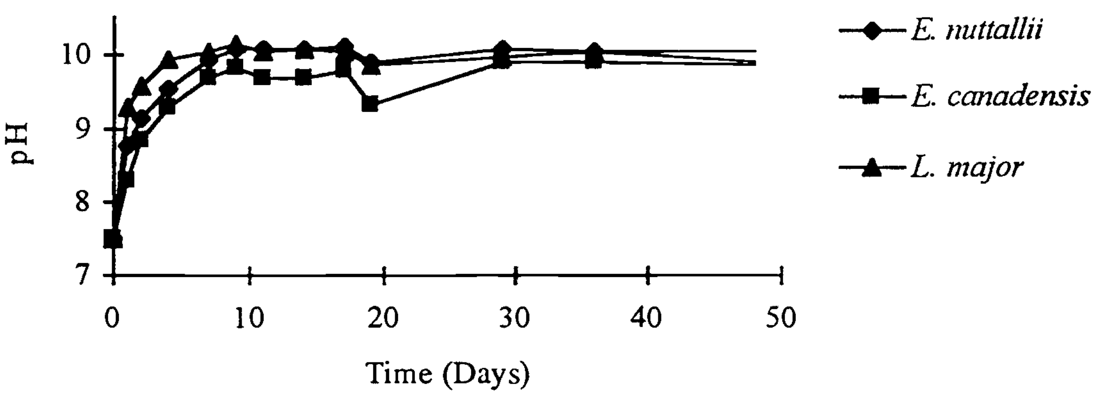

Fig. 2. Changes in pH of media under laboratory conditions over a 49 day period.

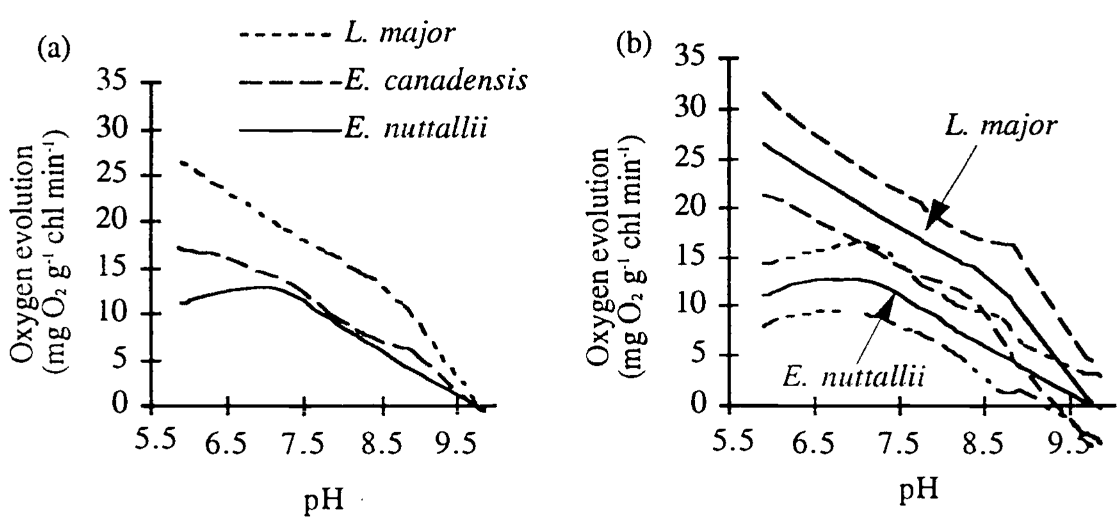

Fig. 3. a) Photosynthetic oxygen evolution of *E. nuttallii* (n = 20), *E. canadensis* (n = 19) and *L. major* (n = 22) in response to increasing pH of medium. b) 99 % confidence intervals displayed (dotted lines) with best fit lines for *E. nuttallii* and *L. major*.

Discussion

Results show that all three species created similarly stressful water conditions of high pH and low CO_2 to extents which agree with previous findings (e.g. Frodge *et al.* 1990; Jones *et al.* 1996). Results suggest that the competitive success of *L. major* may be a consequence of greater toleration to pH stress than either *E. nuttallii* or *E. canadensis*. Thus *L. major* will be successful in outcompeting *Elodea* spp. as a result of some continuing photosynthesis and consequently growth even under very stressful conditions.

These studies do not explain, however, the apparent competitive success of *E. nuttallii* in displacing *E. canadensis*. The conditions created and tolerated by the two species were largely similar. It is likely that competitive ability will depend upon a combination of factors, including canopy architecture, in particular the ability to form dense canopies thus restricting light availability to species growing beneath the canopy (Simpson 1990), and early season growth, allowing the species to gain a head start over competing species (Kunii 1984). These factors are likely to contribute to the overall competitive success of *E. nuttallii* over *E. canadensis*.

Further comparative studies between the three species to investigate the effects of high O_2 and low CO_2 on photosynthesis and respiration are intended.

Acknowledgements

This work was funded by a Natural Environmental Research Council postgraduate studentship to C. James, for which we are grateful. The authors would also like to thank Zoe James for assistance with field work.

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