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The interaction of water flow and nutrients on aquatic plant growth

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Abstract

A long-term experiment was conducted to compare the effects of flowing and still water on growth, and the relationship between water flow and nutrients, in *Aponogeton elongatus*, a submerged aquatic macrophyte. *A. elongatus* plants were grown for 23 weeks with three levels of nutrition (0, 0.5 and 1g Osmocote Plus® fertiliser pot^{-1}) in aquaria containing stirred or unstirred water. Fertilized plants grew much better than non-fertilized. The highest fertilizer level produced 29% wider leaves and 58% higher total dry weight in stirred water. Stirred water increased leaf area by 40% and tuber size by 81%, but only with the highest level of nutrition. These results suggest that this plant depends on its roots for mineral uptake, rather than from the open water, and the major limitation to growth in still water is the supply of dissolved inorganic carbon. It was the combined effects of nutrient availability and stirring that produced the strongest response in plant growth, morphology and composition. This study provides some explanation for the observations of others that these plants grow best in creeks or river systems with permanently flowing water.

Introduction

The Australian native aquatic macrophyte *Aponogeton elongatus* F. Muell. ex Benth, grows predominantly submerged in still or gently flowing water in streams, creeks and rivers (Aston, 1973) although it also has been commonly observed in fast flowing waters (Sainty & Jacobs, 1994; Hellquist & Jacobs, 1998). It is found only in permanent fresh water, rooted in mud or silt (Aston, 1973; Sainty & Jacobs, 1981, 1994) or in mixed sediment of silt, sand and gravel. *A. elongatus* is often found growing in water heavily shaded by overhanging trees as well as in full sun (Sainty & Jacobs, 1981; Hellquist & Jacobs, 1998). It produces a crown of leaves from a tuber buried in the sediment. Most of the leaves remain submerged but some floating leaves are produced, usually when the plant is flowering (Sainty & Jacobs, 1981, 1994).

Little is known about the physiology of *A. elongatus*, particularly in relation to its growth habit, reproduction and response to the environment but there have been some morphological and taxonomic studies (Van-Bruggen, 1969; Aston, 1973; Hellquist & Jacobs, 1998).

In other submerged aquatic macrophytes (SAM), water flow from 1.5–100 cm s^{-1}, depending on the species, increased net photosynthetic rate (Schwenke, 1971; Carpenter et al., 1991; Chambers et al., 1991; Losse & Wetzel, 1993). However, many of these studies have been based on short-term measures of photosynthetic rate or field measurements and observations. The significance of this study is that it measures long term growth rates of plants under controlled conditions in aquaria. Such long-term growth rates may reveal differences that are difficult to detect with short-term measures of photosynthetic rate (Titus et al., 1990).

It is known that for SAM in general, moderate water flow improves leaf uptake of nutrients as well as dissolved inorganic carbon (DIC), and oxygen (Smith & Walker, 1980; Larkum et al., 1989; Stevens & Hurd, 1997). It is also well recognised that flowing water reduces the thickness of the unstirred (boundary) layer

that surrounds leaves of SAM (Schwenke, 1971; Carpenter et al., 1991; Chambers et al., 1991; Losse & Wetzel 1993; Madsen et al., 1993). The thinner the boundary layer, the lower the diffusion resistance to leaf uptake of nutrients and DIC (Smith & Walker, 1980; Larkum et al., 1989; Stevens & Hurd, 1997). Given its observed habitat, it is likely that growth of *A. elongatus* is also greater in water of moderate flow compared to still water. This greater growth may be due to the improved foliar uptake of nutrients and/or DIC. The aims of this study were, to test the hypothesis that *A. elongatus* growth is increased by water flow (stirring), and to examine the interactions between water flow, nutrients and growth.

Materials and methods

Growth conditions

This experiment was conducted from 13 July to 22 December 1998, in a controlled temperature room at the University of Queensland, Gatton. Air temperatures within the room were maintained at 22.4 ± 1.0 °C (± SD). The mean daily water temperature was 23.7 ± 0.4 °C (± SD). Light was provided by banks of 120 cm long fluorescent tubes (40 watt Grow Lux Wide Spectrum® tubes) to give a mean photosynthetically active radiation (PAR) level of 101 ± 3 (± SE) μmol m^{-2} s^{-1} measured 5 cm above the water surface. Light was provided continuously throughout the experiment.

Twelve identical glass aquaria (tanks) were used, each 587 mm wide × 457 mm deep × 380 mm in height (100 l). Two tanks were placed under each light bank, partially surrounded by black polyethylene sheeting to exclude the extraneous light from other light banks. A 1:1 mixture of tap water and deionised water was used to reduce the concentration of nutrients, particularly phosphate, to minimise algal growth. Tanks were filled with this water to a height of 340 mm (90 l) and were topped up with deionised water weekly to replace evaporated water. The average electrical conductivity of the water was 237 ± 1 μS cm^{-1} over all tanks.

Where required, water was stirred using submersible (4.6 watt) power water filters (Rio-PF400) installed in a back corner of each tank, providing a measured flow rate of 515 ± 5 l h^{-1} (± SE). The maximum water speed at pump outlets was approximately 182 cm s^{-1}. The swirling action created by each pump would have resulted in a wide range of reduced water speeds across a tank.

Experiment design

The experiment was a two-factor, split plot design with two main plot treatments (stirred and unstirred water) and three subplots (slow release fertilizer; 0 g, 0.5 g and 1 g). A pair of tanks under a single light bank were allocated the main plot treatments, one tank stirred, the other unstirred. Within each tank, individually potted plants (the experimental unit) received the sub plot fertilizer treatments; three plants to each subplot treatment, giving nine plants per tank. Each of pairs of tanks under a single light bank represented one complete block and there were six blocks.

In an attempt to reduce experimental error, plants were ranked by total leaf length then allocated sequentially to the six blocks. Treatments were assigned randomly to the plots (tanks) and subplots (plants).

Preparation of potted plant material

One hundred and eight 100 mm diameter plastic pots (420 ml) were lined internally with clear polyethylene bags, then 0.5 g or 1 g of controlled release fertilizer were placed in 72 of the pots before filling with sediment. The fertilizer was 8–9 month Osmocote Plus® (16 N : 3.5 P: 10 K: 1.2 Mg plus trace elements). The approximate plant nutrient composition of the sediment at the start of the experiment is shown in Table 1. Due to the slow release nature of this fertilizer, these nutrients were not available to plant roots in the concentrations outlined in the table. The sediment was equal parts of washed fine white sand and coarse river sand (bulk density 1.43 g ml^{-1}) mixed with 1.7 g of powdered iron (55.85% Fe) per pot.

A. elongatus plants, about 12 months old, were planted into the pots. The majority of plants were originally propagated by tissue culture from parent stock collected from a single site in southeast Queensland. However, 15 seedlings of similar size and maturity to the micropropagated plants, were also used to make up the required numbers.

The sediment was packed into each pot firmly around the plant, to within 15–20 mm of the rim of the pot. After this, granulated zeolite (2 mm Horticulture Grade) was added to the top of the sediment to a depth of 10–15 mm. The plastic liner was raised above the rim of the pot by about 20–30 mm to create a zone of unstirred water (boundary layer) above the potting

Table 1. The mineral composition of the sediment (μg g^{-1}) at the start of the experiment. Based on one gram of the controlled release fertilizer Osmocote Plus® per pot. (Calculated from data supplied by the fertilizer manufacturer)

Major elements	μg g^{-1}	Trace elements	μg g^{-1}
Nitrogen	265.7	Boron	0.3
Phosphorus	58.1	Copper	0.8
Potassium	166.0	Iron	6.6*
Sulphur	39.9	Manganese	1.0
Magnesium	19.9	Molybdenum	0.3
Calcium	0	Zinc	0.3

*Available iron levels may be much higher due to the addition of powered iron.

mix. The placement of the fertilizer and inclusion of powdered iron in the medium, plus the plastic liner and zeolite, were all designed to minimise the diffusion of nutrients, particularly phosphate, from the potting mix into the surrounding water.

Plant measurements

Total leaf number, length (leaf blade base to leaf tip, ignoring the petiole) and blade width (at the widest portion of each leaf blade) of each plant were measured at the beginning of the experiment and in the 14th week. Leaf blades of non-senescent, fully developed leaves were measured.

For dry weight measurements, one plant was randomly selected from each treatment in the 22nd week. After removing the potting mix, each plant was divided into foliage, tuber and roots then fan forced oven dried at 60 °C for 5 days before being weighed.

Nutrient levels in water

A 'Palintest® Photometer 7000'(Palintest Ltd, Tyne & Wear, England) and reagents from Palintest® kits were used to measure nitrate nitrogen, ammonium nitrogen, phosphate, potassium, magnesium and iron in the water of each of the tanks at the end of the experiment following the instructions provided in the Palintest kits.

Dissolved CO_2 levels

Total dissolved inorganic carbon (DIC) and dissolved free CO_2 (dissolved CO_2 and H_2CO_3) were measured after 12 weeks using titration techniques described by Frith et al. (1993). One of the limitations with the dissolved free CO_2 technique is that it could not measure CO_2 levels below 4.5 μM. One sample was tested for each of 12 tanks.

Monitoring

A waterproof, hand-held 'TPS WP-80' (TPS Pty Ltd, Brisbane, Australia) pH meter was used to measure pH weekly and a waterproof, hand-held (TPS WP-84) electrical conductivity meter was used to measure tank water conductivity every 2 weeks throughout the experiment. Water temperature (in 4 tanks) and air temperature (2 locations) were measured hourly using thermocouples connected to a data logger ('Datataker 500', Pacific Data Systems Ltd, Brisbane, Australia).

Statistical analysis

ANOVA were applied to the leaf area, dry weight and chlorophyll fluorescence data (SAS release 6.12) and LSDs computed (MS Excel version 97). Leaf area data were transformed to their square root before ANOVA. Dry weight data were transformed to their log to account for one outlier in each of the data sets of leaf, tuber and root. *F* tests and *t* tests were applied to DIC, pH, conductivity and temperature data using MS Excel. A significance level of $P < 0.05$ was adopted unless otherwise indicated.

Results

General observations

By the end of the experiment, the fertilized plants appeared much larger than the unfertilized plants. Plants fertilized with 1.0 g Osmocote were larger than those with 0.5 g Osmocote, particularly in the stirred tanks. Plants in the unstirred tanks lost more leaves and appeared smaller than those in the stirred tanks. The leaves of plants in stirred tanks were dark red to purple green while those in unstirred tanks were a paler green with little or no red or purple.

Leaf morphometrics

The average leaf length and width, and total leaf area were greater on plants growing in stirred water than in unstirred water (Tables 2 and 3). Plants without fertilizer had fewer and smaller leaves than the fertilized plants ($P < 0.001$). Leaf number and average

leaf length and width were not significantly different between the two levels of fertilizer (0.5 g and 1 g) however leaf area was greater on plants with 1 g of fertilizer. There was no significant interaction between fertilizer level and ± stirring for these parameters (Table 3).

Dry weight

Plants with the largest total dry weight were those growing in stirred water and fertilized with either 0.5 g or 1 g of Osmocote (Fig. 1). The difference between 0.5 g or 1 g of Osmocote was not significant. Stirred water produced greater leaf dry weight than unstirred water at the highest rate of fertilizer (1 g) but there was no difference with 0 or 0.5 g.

Fertilizer application had no significant effect on dry weight of the tuber but plants in stirred water had significantly greater tuber dry weight than those in unstirred water ($P < 0.01$) (Fig. 1, Table 3). In contrast, there were no differences in root dry weight between plants growing in either stirred or unstirred water, or between different fertilizer levels (Fig. 1).

Water nutrient levels

There was considerable variation in nutrient levels between tanks (Table 4) but most nutrients except potassium (in some tanks) and magnesium were very low. The total nitrogen in the water was no more than 1%, phosphorus 3% and potassium 36% of that originally supplied as Osmocote. In contrast, magnesium was 45% higher than in Osmocote because of the high level in the tap water used (Table 4).

A comparison of the means using a paired t test revealed no differences in any nutrients between stirred and unstirred water tanks. However, nutrient levels (nitrogen, phosphorus and potassium) were more variable in unstirred tanks than stirred tanks using a Two-Sample *F*-Test ($P < 0.008$). The exception was magnesium which was more variable in stirred tanks ($P = 0.008$).

Dissolved CO_2 levels

The dissolved inorganic carbon level (DIC) ranged from 941 to 1120 μM between tanks while dissolved free CO_2 ranged from 0 to 41 μM. Total DIC varied little between stirred and unstirred tanks, while dissolved free CO_2 in unstirred tanks was much more variable according to a two-sample *F*-test (Table 4). However, when the means were compared using a

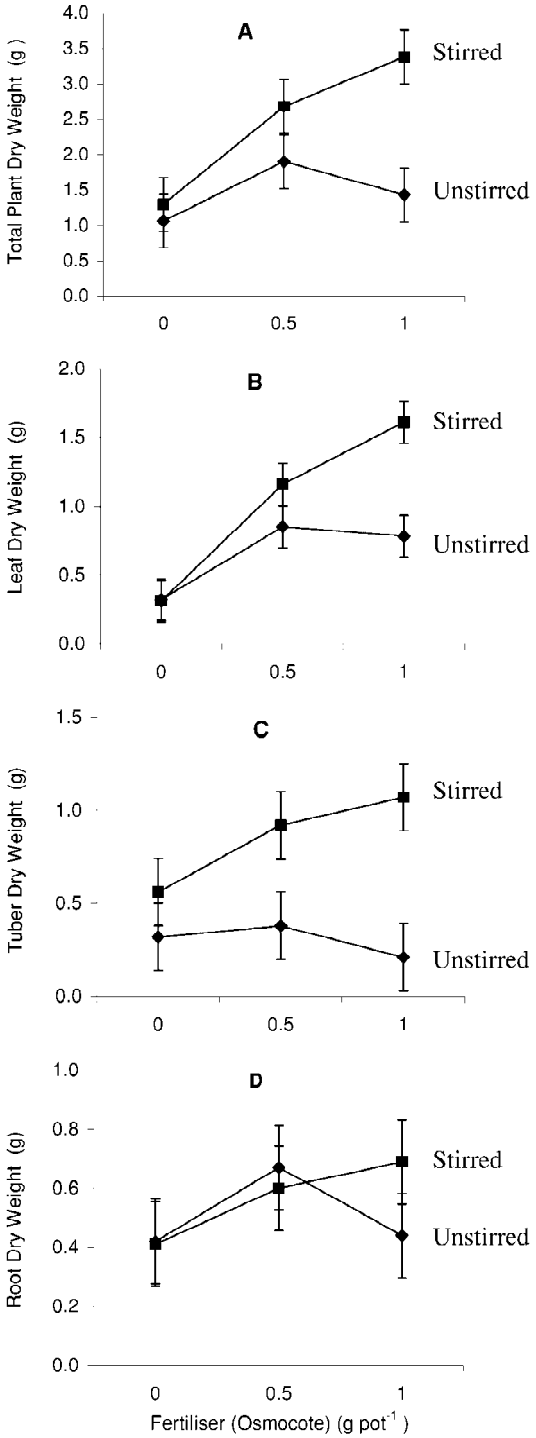

Figure 1. Growth of *A. elongatus* after 22 weeks at a mean temperature of 24 °C and PAR of 102 μmol m^{-2} s^{-1}. The only significant interaction occurred between leaf dry weights. The differences between the treatment means for roots are not significant. (Means ± 1 SE).

Table 2. Effects of stirred or unstirred water and three levels of fertilizer on *A. elongatus* mean leaf number and area per plant and average leaf length and width after a 22-week growth period with a mean temperature of 24 °C and PAR 101.6 μmol m^{-2} s^{-1}. Leaf area data were transformed to the square root before ANOVA and LSD comparisons (All means in table are from original untransformed data). All data are an average of six blocks. Means within a column having a common letter are not significantly different at 5% level. There are no significant two-factor interactions

Treatments	Leaf number per plant	Average leaf length (cm)	Average leaf width (cm)	Leaf area (cm^2) per plant
Osmocote® 0 g	22.6 a	9.8 a	1.56 a	400 a
0.5 g	31.8 b	14.4 b	2.03 b	973 b
1.0 g	33.9 b	15.2 b	2.08 b	1297 c
Stirred	31.5 a	14.5 b	2.06 b	1113 b
Unstirred	25.3	11.8 a	1.72 a	667 a

Table 3. A summary of ANOVA results showing stirring and fertilizer effects on *A. elongatus* leaf morphometrics and plant dry weight after a 22-week growth period. Leaf area data were transformed to the square root and all dry weight data to log 10 before ANOVA and LSD comparisons. Non significant ANOVA results ($P > 0.05$) have been excluded

Effect	d.f.	MS	*F*-ratio	*P*-value
Leaf number				
Fertilizer	2	3572	21.39	<0.001
Average leaf length				
Stirring	1	68.4	25.96	0.004
Fertilizer	2	104	23.65	<0.001
Average leaf width				
Stirring	1	0.99	22.97	0.006
Fertilizer	2	0.13	21.79	<0.001
Leaf area per plant				
Stirring	1	85212	12.86	0.016
Fertilizer	2	121802	30.89	<0.001
Total dry weight per plant				
Stirring	1	0.59	9.90	0.025
Fertilizer	2	0.31	6.25	0.008
Leaf dry weight per plant				
Stirring	1	0.06	7.15	0.044
Fertilizer	2	0.15	21.45	<0.001
Stirring × Fertilizer	2	0.02	3.55	0.048
Tuber dry weight per plant				
Stirring	1	0.19	20.31	0.006

d.f., degrees of freedom; MS, mean square.

paired *t* test, Total DIC appeared higher ($P = 0.054$) in stirred tanks than in unstirred tanks while there was no difference in dissolved free CO_2.

pH, electrical conductivity and temperature

There was a steady rise in mean pH from 8.1 in the first week to pH 8.58 in unstirred tanks and pH 8.49 in stirred tanks after 4 weeks (Fig. 2A). In week 10, the mean pH peaked at 8.74 in unstirred tanks and 8.54 in stirred tanks. The pH remained higher in the unstirred tanks than the stirred tanks through to the last measurement in week 20. The maximum pH recorded was 9.14 in an unstirred tank compared to 8.59 in a stirred tank. As indicated by the larger standard errors, the pH level varied much more between unstirred tanks than between stirred tanks (Fig. 2A).

Electrical conductivity increased slowly from a mean of 238 to 294 μS cm^{-1} at the end of the experiment. The differences between tanks became more pronounced towards the end of the experiment as indicated by the error bars (Fig. 2B). However, there was no difference either in the variances or between the means of stirred and unstirred tanks. Mean daily water temperatures in stirred tanks were 0.4–0.7 °C warmer than in unstirred tanks ($P < 0.01$) (Fig. 2 C).

Discussion

This study indicates that *A. elongatus* grows larger in flowing (stirred) water. Larger leaf area and leaf dry weight per plant were the main responses to increasing nutrient level and stirred water. Tuber weight was also greater in stirred water but was not significantly affected by fertilizer level, which suggests that some

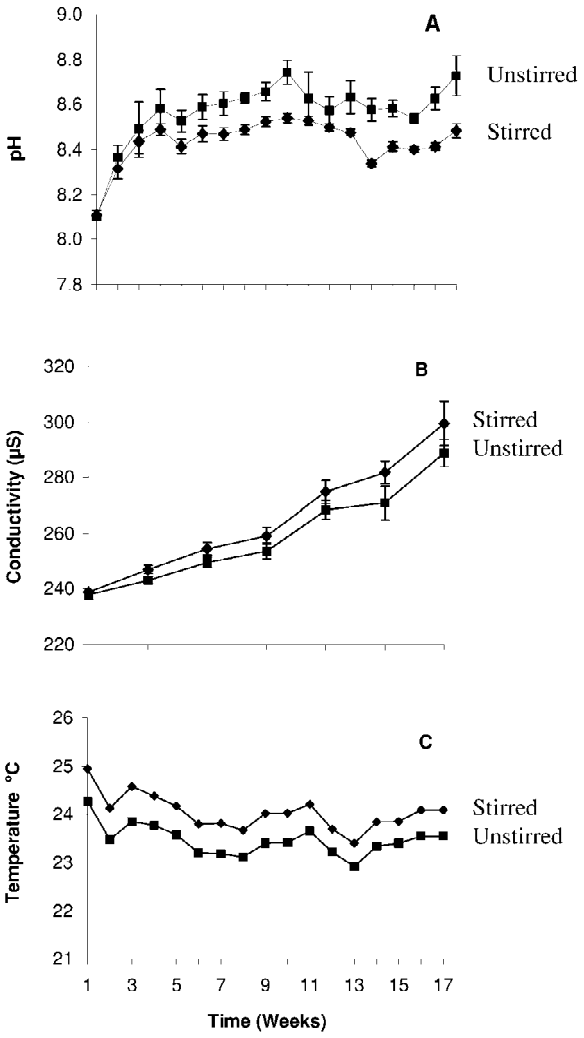

Figure 2. Comparison of stirred and unstirred water over time: (A) pH (based on 18 weekly measurements; mean ± 1 SE, $n = 6$); (B) conductivity (based on seven measurement times; mean ± 1 SE, $n = 6$) and (C) mean weekly water temperatures.

factor other than mineral nutrition limited growth in unstirred water.

A. elongatus and other species of *Aponogeton* in creeks and rivers, have longer leaves in rapidly flowing water (Islam, 1996; Hellquist & Jacobs, 1998). In this study, the leaves were both longer and wider but proportionally narrower in stirred water compared to unstirred water (based on length breadth ratio). For many SAM, light and/or nutrition may have a much greater influence on leaf shape compared to water velocity (Kirk, 1994; Spence, 1976). *A. elongatus* may have much thinner and broader leaves in dense shade caused by overhanging trees (Hellquist & Jacobs, 1998). This is similar to the leaves of land plants that are adapted to dense shade (Salisbury & Ross, 1992). In this study, the leaves are likely to be adapted to shade, as the plants were grown with an irradiance level equal to approximately 5% sunlight. Based on an approximate leaf thickness of 0.1 mm, the plants had a leaf surface area to leaf volume ratio of approximately 20:1. Leaf surface area to leaf volume ratios equal to or greater than this are common in SAM (Madsen et al., 1993). Apart from more efficient light interception, thin leaves may be more efficient in nutrient or DIC uptake (Sculthorpe, 1967).

Roots of many aquatic macrophytes may have a primary role in nutrient uptake, particularly nitrogen and phosphate (Bristow & Whitcombe, 1971; Barko et al., 1988; Rattray et al., 1991; Robach et al., 1995; Best, et al., 1996; Wigand & Stevenson, 1997). However, it has been shown that aquatic plant foliage can also take-up nutrients from the water (Bristow & Whitcombe, 1971; Rattray et al., 1991; Robach et al., 1995; Best et al., 1996). Whether nutrients such as phosphate are taken up by foliage or roots is dependent on the nutrient concentration gradient between interstitial water and the surrounding water (Rattray et al., 1991; Best et al., 1996). The present study indicates that *A. elongatus* obtained most of its nutrients from the substrate via its roots. Those plants without the added fertilizer grew poorly and were significantly smaller in leaf number, length and width, and leaf dry weight, even though the unfertilized plants and fertilized plants were growing in the same tank of water. Water flow (stirred water) is known to assist nutrient uptake via the foliage (Stevens & Hurd, 1997). Adding nutrients to the water may improve nutrient uptake by the plants without fertilizer in the substrate. However, the more eutrophic water would result in an increase in both benthic and pelagic algae likely out competing *A. elongatus* for nutrients, light and DIC.

There was a leaf dry weight interaction between stirred water and 0.5 g, and 1 g of Osmocote® but not unstirred water. This suggests that fertilizer is not the limiting factor in unstirred water. It is more likely that improved DIC uptake is the primary reason for the greater growth in stirred versus unstirred water. Perhaps the strongest indication that DIC is the limiting factor is tuber weight. Tubers produced by these plants are primarily storage organs rich in carbohydrates such as starch (based on starch iodine test), therefore tuber weight must be strongly linked to photosynthetic productivity. It is likely that tubers in stirred water are larger because the reduced boundary layer around

Table 4. Water nutrient concentrations, conductivity and temperature, 5 months from the start of the experiment. Total dissolved inorganic carbon (DIC) (μmole CO_2), dissolved free CO_2 and pH, measured after 3 months. The 'original water' data are estimates of minerals in the tank water at the start of the experiment (tap water plus deionised water 1:1), based on measurements from the tap water. 'Fertilizer per tank' is an estimate of the amount of nutrients supplied in the Osmocote (calculated from data supplied by the manufacturer)

Treatment	$N–NO_3$ μM	$N–NH_4$ μM	Total N μM	P μM	K μM	Mg μM	Fe μM	Dissolved inorganic carbon μM	Dissolved free CO_2 μM	pH	Conductivity μS cm^{-1}	Temperature °C
Mean Stirred	**0.36**	**0.71**	**1.07**	**1.16**	**3.32**	**411**	**0.18**	**1048**	**22.7**	**8.41**	**303**	**23.7**
Std Error	0.36	0.29	0.36	0.23	2.05	24	0.05	20	1.6	0.02	5	0.3
Mean Unstirred	**0.71**	**3.57**	**4.14**	**0.84**	**46.3**	**420**	**0.18**	**986**	**18.2**	**8.58**	**285**	**23.2**
Std Error	0.36	2.14	0.03	0.06	23.5	7	0.05	40	6.5	0.04	7	0.2
Original water	**3.57**	**0**	**3.57**	**1.29**	**46.0**	**267**	**0.18**					
Fertilizer per tank	**194**	**171**	**366**	**36.1**	**128**	**283**	**N. A.**					

leaves in stirred water allowed greater DIC assimilation than in unstirred water (Smith & Walker, 1980; Larkum, et al., 1989; Stevens & Hurd, 1997).

An interesting question is why pH was high overall. One unstirred water tank reached a pH of 9.14. Some tanks, particularly the unstirred tanks, had a small amount of algal growth, both benthic and pelagic. The uptake of dissolved free CO_2 by both the algae and *A. elongatus* could have contributed to the rise in pH (Kirk, 1994). The uptake of bicarbonate could also contribute to the high pH. Other aquatic plants increase the pH by releasing OH^- ions in exchange for bicarbonate ions, for example *Elodea nuttallii* and blue green algae (Miller & Colman, 1980; Allen & Spence, 1981; Jahnke et al., 1991).

The slightly lower pH (difference 0.16) in stirred water could be due to the stirring action of the water increasing the rate of CO_2 replenishment from the surrounding air (Sand-Jensen, 1983). Conversely, in unstirred tanks there may be a rise in pH because of plant removal of CO_2 coupled with slower replenishment from the air.

The dissolved free CO_2 levels represents nearly double the approximate air equilibrium value of 10 μM (Stumm & Morgan,1970; Bowes & Salvucci, 1989). This level of dissolved free CO_2 may still result in a deficit in stirred tanks, as boundary layer resistances although reduced, are still high, (Bowes & Salvucci, 1989). This is likely to be more evident under higher irradiance levels than were used in this study. The ability to use bicarbonate would be an advantage as there was approximately 46 times as much bicarbonate present as dissolved free CO_2.

It is plausible that stirring the water increased DIC uptake irrespective of whether the form used by the plant is bicarbonate or dissolved free carbon. Most fresh water macrophytes have a higher affinity for dissolved free CO_2 than bicarbonate (Allen & Spence, 1981; Sand-Jensen, 1983). *A. elongatus* may be able to use bicarbonate but have a preference for dissolved free CO_2. Clearly, further investigation is required to confirm whether this plant is able to use bicarbonate.

In conclusion, *A. elongatus* growth was limited by nutrient levels equal to or less than 0.5 g of fertilizer per pot. Above this nutrient level, the availability of DIC appears to be the main factor limiting growth for *Aponogeton* normally dependent on submerged leaves. Presumably, stirred water improves DIC uptake due to the decrease in diffusion boundary layer resistance around the leaves (Larkum et al., 1989; Stevens & Hurd, 1997). The resulting increase in photosynthetic productivity enabled greater growth of both the tuber and leaves. This provides some explanation for the observations of others that these plants flourish in creeks or river systems with permanently flowing water (Sainty & Jacobs, 1994; Hellquist & Jacobs, 1998).

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References

Allen, E. D. & D. H. N. Spence, 1981. The differential ability of aquatic plants to utilise the inorganic carbon supply in fresh waters. New Phytol. 87: 269–283.

Aston, H. I., 1973. Aquatic Plants of Australia. University Press, Melbourne.

Barko, J. W., R. M. Smart, D. G. McFarland & R. L. Chen, 1988. Interrelationships between the growth of *Hydrilla verticillata* (L.f.) Royle and sediment nutrient availability. Aquat. Bot. 32: 205–216.

Best, E. P. H., H. Woltman & F. H. Jacobs, 1996. Sediment-related growth limitation of *Elodea nuttallii* as indicated by a fertilisation experiment. Freshwat. Biol. 36: 33–44.

Bowes, G. & M. E. Salvucci, 1989. Plasticity in the photosynthesis carbon metabolism of submersed aquatic macrophytes. Aquat. Bot. 34: 233–266.

Bristow, J. M. & M. Whitcombe, 1971. The role of roots in the nutrition of aquatic vascular plants. Am. J. Bot. 58, 8–13.

Carpenter, R. C., J. M. Hackney & W. H. Adey, 1991. Measurements of primary productivity and nitrogenase activity of coral reef algae in a chamber incorporating oscillatory flow. Limnol. Oceanogr. 36: 40–49.

Chambers, P. A., E. E. Prepas, H. R. Hamilton & M. L. Bothwell, 1991. Current velocity and its effect on aquatic macrophytes in flowing water. Ecol. Appl. 1: 249–257.

Frith, M., N. Forteath & L. Wee, 1993. Appendix II. Chemical determination of selected water quality parameters. In Hart P. & D. O'Sullivan (eds), Aquaculture Source Book: Recirculation Systems, Design and Management. Turtle Press, Launceston, Tasmania: pp 111–127.

Hellquist, C. B. & S. W. L. Jacobs, 1998. Aponogetonaceae of Australia, with descriptions of six new taxa. Telopea 8(1): 7–19.

Islam, Q. R., 1996. Morphology and nutritional value of *Aponogeton undulatus* Roxb. growing in deeply flooded areas in Bangladesh. Hydrobiologia 340: 317–321.

Jahnke, L. S., T. T. Eighmy & W. R. Fagerberg, 1991. Studies of *Elodea nuttallii* grown under photorespiratory conditions: I. Photosynthetic characteristics. Plant Cell Environ. 14: 147–156.

Kirk, J. T. O., 1994. Light and Photosynthesis in aquatic ecosystems, 2nd edn. Cambridge University Press, Cambridge: 509 pp.

Larkum, A. W. D., G. Roberts, J. Kuo & S. Strother, 1989. Gaseous movement in seagrasses. In Larkum A. W. D., A. J. McComb & S. A. Shepherd (eds), Biology of Seagrasses. Aquatic Plant Studies. Elsevier, Amsterdam, N. Y.: 686–722.

Losse, R. F. & R. G. Wetzel, 1993. Littoral flow rates within and around submerged macrophyte communities. Freshwat. Biol. 29: 7–17.

Madsen, T. V., H. O. Enevoldsen & T. B. Jorgensen, 1993. Effects of water velocity on photosynthesis and dark respiration in submerged stream macrophytes. Plant Cell Environ. 16: 317–322.

Miller, A. G. & B. Colman, 1980. Evidence of HCO3 transport by the blue green alga (Cyanobacterium) *Coccochloris peniocystis*. Plant Physiol. 65: 397–402.

Rattray, M. R., C. Howard-Williams & J. M. A. Brown, 1991. Sediment and water as sources of nitrogen and phosphorus for submerged rooted aquatic macrophytes. Aquat. Bot. 40: 225–238.

Robach, F., I. Hajnsek, I. Eglin & M. Tremolieres, 1995. Phosphorus sources for aquatic macrophytes in running waters: water or sediment? Acta Bot. Gallica. 142: 719–731.

Sainty, G. R. & S. W. L. Jacobs, 1981. Water Plants of New South Wales. Water Resources Commission, New South Wales: 550 pp.

Sainty, G. R. & S. W. L. Jacobs, 1994. Water Plants of Australia: A Field Guide. Sainty and Associates, Darlinghurst: 327 pp.

Salisbury, F. B. & C. W. Ross, 1992. Plant physiology. Wadsworth Publishing Co., Belmont, California: 682 pp.

Sand-Jensen, K., 1983. Photosynthetic carbon sources of stream macrophytes *Callitriche stagnatis*, *Potamogeton crispus*, *Potamogeton pedenatus*, *Sparganium simplex*. J. exp. Bot. 34(139): 198–210.

Schwenke, H., 1971. Water Movement. In Kinne, O. (ed.), Marine Ecology, A Comprehensive, Integrated Treatise on Life in Oceans and Coastal Waters, Environmental Factors, Part 2. Wiley-Interscience, a division of John Wiley and Sons Ltd, London, Vol. 1: 1091–1121.

Sculthorpe, D. C., 1967. The Biology of Aquatic Vascular Plants. London, Edward Arnold (Publishers) Ltd. London: 610 pp.

Smith, F. A. & N. A. Walker, 1980. Photosynthesis by aquatic plants: effects of unstirred layers in relation to assimilation of CO_2 and HCO_3^- and to carbon isotopic discrimination. New Phytol. 86: 245–259.

Spence, D. H. N., 1976. Light and plant response in fresh water. In Evans, G.C., R. Bainbridge & O. Rackham (eds), Light as an Ecological Factor: II. Oxford, Blackwell Sci. Publ.: 93–133.

Stevens, C. L. & C. L. Hurd, 1997. Boundary-layers around bladed aquatic macrophytes. Hydrobiologia. 346: 119–128.

Stumm, W. & J. J. Morgan, 1970. Aquatic Chemistry: an Introduction Emphasising Chemical Equilibria in Natural Waters. Wiley-Interscience, N Y.

Titus, J. E., R. S. Feldman & D. Grise, 1990. Submersed macrophyte growth at low pH. I. CO2 enrichment effects with fertile sediment. Oecologia 84: 307–313.

Van-Bruggen, H. W. E., 1969. Revision of the genus Aponogeton (Aponogetonaceae) III. The species of Australia. Blumea 17: 122–133.

Wigand, C. & C. J. Stevenson, 1997. Facilitation of phosphate assimilation by aquatic mycorrhizae of Vallisneria americana Michx. Hydrobiolohis. 342/343: 35–41.