Growth Response of *Potamogeton crispus* to Lime Application in Experimental Mesocosms

by William F. James

PURPOSE: The objectives of the research were to examine *Potamogeton crispus* shoot, root, and propagule (i.e., turions) growth response to lime application in experimental outdoor mesocosms.

BACKGROUND: *Potamogeton crispus* is a nonnative species that has become widespread in temperate regions of North America (Bolduan et al. 1994). Because densities are often high and senescence occurs in mid-summer, *P. crispus* also represents an important source of internal nutrient loading for algal assimilation (James et al. 2002). Its life cycle is unusual in that it propagates primarily via vegetative structures called turions. *P. crispus* grows rapidly in early spring and develops a thick canopy by early to late May in northern climates. Turion development is believed to be triggered by water temperatures greater than 20 °C and a photoperiod greater than 12 hours (Chambers et al. 1985). Shortly after turion production, the population senesces in late June through early July and turions settle to the sediment for germination and overwintering as small plantlets. Dense plant populations can produce greater than 1000 turions·m^{-2}, thereby ensuring a large turion bank for production of next year's cohort (Woolf and Madsen 2003). Thus, *P. crispus* management plans need to target turion production versus peak biomass in order to achieve long-term population reduction (Poovey et al. 2002; Woolf and Madsen 2003).

One of the management concerns is specifically targeting *P. crispus* propagation with minimal impact to the native macrophyte community. Its rapid growth cycle in early spring while native species are still dormant provides a window for control prior to turion formation. Herbicide application (Diquat and Endothall) during this period can be very effective in reducing both biomass and turion formation (Netherland et al. 2000). Although efficacy declines as water temperatures fall below 25 °C, control via herbicide can still be achieved if exposure time is greater than one day (Poovey et al. 2002). Endothall combined with low doses of 2,4-D can also be effective in targeting turion production with minor impact to many native macrophytes, particularly monocots (Skogerboe and Getsinger 2006).

Lime application may be effective in temporarily stressing *P. crispus* propagation by inducing dissolved inorganic carbon (DIC) limitation of photosynthesis. Although lime has primarily been used for reducing internal phosphorus loading from sediments in eutrophic pelagic systems (Prepas et al. 1990), relatively low lime application rates (100 to 200 mg·L^{-1}) and modest increases in pH (~10 or less) have been shown to be effective in both suppressing submersed macrophyte growth and changing species composition in a variety of water bodies (Babin et al. 1992; Chambers et al. 2001; Prepas et al. 2001a, 2001b). Applied as a slurry to aquatic systems, lime causes an increase in pH and induces water column depletion of calcium (Ca^{+2}), CO_2, and HCO_3^- via precipitation as calcite. Higher pH also drives equilibrium toward CO_3^{-2} dominance, a form which cannot be assimilated by macrophytes (Lucas 1983). It is also well known that carbon (i.e., CO_2, DIC, and HCO_3^-)

compensation points vary for different macrophyte species (Allen and Spence 1981; Maberly and Spence 1983; Bowes and Salvucci 1989), which may be exploited for selectively targeting certain species while having less impact on others. For instance, Maberly and Spence (1983) reported a greater carbon compensation point for *P. crispus* than for many native species in alkaline waters. Thus, use of lime to selectively stress *P. crispus* growth and turion production may be a feasible technique for long-term reduction of populations. The objectives of this research were to examine biomass and turion production response of *P. crispus* to a single lime application using experimental outdoor mesocosms.

METHODS: Sprouted turions (average stem length of 30 cm) collected in mid-April 2006 from Half Moon Lake, Wisconsin, were transplanted into polyethylene containers (10 cm wide × 10 cm deep × 15 cm height) filled with homogenized sediment (obtained from Eau Galle Reservoir, Wisconsin; moisture content = 71 percent; bulk density = 0.29 g mL^{-1}; total sediment N = 4.702 mg g^{-1}; porewater ammonium-N = 5.750 mg L^{-1}; total sediment P = 0.971 mg g^{-1}; porewater P = 0.359 mg L^{-1}) to a depth of 10 cm (~ 1 L of sediment) for growth in outdoor mesocosms. Three sprouts were planted in each container. The sediment surface was sealed with 1 cm of fine-grained sand to minimize disturbance and resuspension during transfer to mesocosms. Clear fiberglass mesocosms (1.2 m dia × 1.2 m height; 1400 L capacity) were filled with locally obtained tap water prior to the start of the experiment (total alkalinity = 130 - 150 mg·L^{-1}; DIC = 50 mg·L^{-1}; total Ca = 57 mg·L^{-1}; Conductivity = 422 µS; Mg = 28 mg·L^{-1}; NO_2NO_3-N = 0.2 mg·L^{-1}; Na = 1.6 mg L^{-1}; K = 0.8 mg· L^{-1}; SO_4 = 21 mg·L^{-1}; initial pH = 7.8). These mesocosms were set up in late spring to house the planted containers under various treatment conditions. Natural lighting was controlled with a 30-percent shade cloth suspended 2 m above mesocosm surfaces. Circulation pumps (Beckett Versa Gold G90AG; 0.34 m^3·min^{-1}) provided gentle water circulation in each tank during the entire study. On 19 April 2006, 35 replicate containers were transferred to the control mesocosm (i.e., no lime addition) and another 35 replicate containers were transferred to the experimental mesocosm. Plants were grown in the mesocosms for 20 days before lime treatment.

The objective of the lime treatment was to increase pH from 8.8 to near 10 in order to lower DIC and HCO_3^- alkalinity during plant growth. A lime concentration (as mg $Ca(OH)_2$·L^{-1}) of 100 mg·L^{-1} was estimated based on a jar test conducted on mesocosm water (James 2007). Commercially obtained lime (as $Ca(OH)_2$) was applied as a slurry to the experimental mesocosm by mixing the appropriate dry powder mass with 8 L of tap water, then dispersing it evenly over the surface of the experimental mesocosm. Plants were allowed to grow for 42 days after treatment.

Shoot, turion, and root biomass were determined at the time of initial planting and lime application and at week 1, 4, and 6 after treatment (10 replicates for each mesocosm and time period). Shoot biomass was briefly soaked in a 1 N hydrochloric acid solution to remove any calcium carbonate deposits on the plant, gently rinsed several times in tap water, and dried at 65 °C for dry mass determination. Turions collected from each plant were dried in the same manner. Roots sieved from the sediment were dried to determine below-ground biomass (root material was not pretreated with 1 N HCl). Relative growth rates (*RGR*; d^{-1}) for shoots, turions, and roots over the entire treatment period (42 days) were calculated as:

$$RGR = \frac{(\overline{lnM_2} - \overline{lnM_1})}{(t_2 - t_1)} \quad (1)$$

where M_1 and M_2 were the mean of natural log-transformed biomass replicates (Hoffmann and Poorter 2002) and t_1 and t_2 represented the day of treatment and the final day of the study, respectively. Relative growth rate ratios (*RGRR*, dimensionless) for shoots and roots were calculated as:

$$RGRR = \frac{RGR_{control}}{RGR_{treated}} \quad (2)$$

where $RGR_{control}$ and $RGR_{treated}$ were the relative growth rates of shoots, turions, or roots for plants grown under control and lime treatment conditions.

In situ temperature, pH, dissolved oxygen, and conductivity were monitored in each mesocosm using a data sonde (Hydrolab Quanta System; Hach Company, Loveland, CO) that was calibrated against known buffers and Winkler titrations. Integrated water column samples were collected for the determination of alkalinity species, DIC, and dissolved calcium (DCa). Total alkalinity (expressed as mg $CaCO_3 \cdot L^{-1}$) was determined via titration with 0.02 N sulfuric acid to an end-point of pH 4.5 (American Public Health Association (APHA) 1998). Free CO_2 and HCO_3^-, CO_3^{-2}, and OH^- alkalinities at 25 °C were calculated based on ionization constants (APHA 1998). Alkalinity titrations were conducted within 1 to 2 hours of sampling. Samples for DIC were immediately filtered through a 0.45-µm syringe filter, carefully preserved in glass scintillation vials (no air headspace) in a refrigerator at 4 °C, and analyzed within 48 hours of collection by infrared spectroscopy (Shimadzu model TOC-5050; Shimadzu Scientific Instruments, Columbia, MD). DCa was determined using flame atomic absorption spectroscopy (Perkin-Elmer AA Analyst 100; Perkin Elmer Life and Analytical Sciences, Inc., Wellesley, MA) after filtration through a 0.45-µm syringe filter (APHA 1998).

RESULTS: pH increased from 8.8 to 9.7 in the experimental mesocosm as a result of lime application (Figure 1a). It remained elevated relative to the control throughout post-treatment, fluctuating between 9.7 and 10.0 pH in the control mesocosm increased linearly over the first 17 days of post-treatment and then was constant at 9.6 over the remainder of the study period. Lime application resulted in an initial 95, 50, 60, and 40 percent decline in free CO_2, DIC, HCO_3- alkalinity, and total alkalinity, respectively, in the experimental mesocosm relative to pre-treatment concentrations (Figures 1b-1e). Concentrations of these variables were relatively constant at 0.02 $mg \cdot L^{-1}$ free CO_2, 17.7 $mg \cdot L^{-1}$ DIC, 60 $mg \cdot L^{-1}$ HCO_3^- alkalinity, and 100 $mg \cdot L^{-1}$ total alkalinity in the experimental mesocosm after treatment. In the control mesocosm, these variables declined in a linear pattern during the post-treatment period, reaching levels similar to those observed in the experimental mesocosm near the end of the study period. In contrast, lime application resulted in an immediate increase in carbonate and hydroxide alkalinity in the experimental mesocosm (Figures 1f and 1g). These variables reached maxima at week 4 of treatment, then declined. They increased linearly in the control mesocosm over the post-treatment

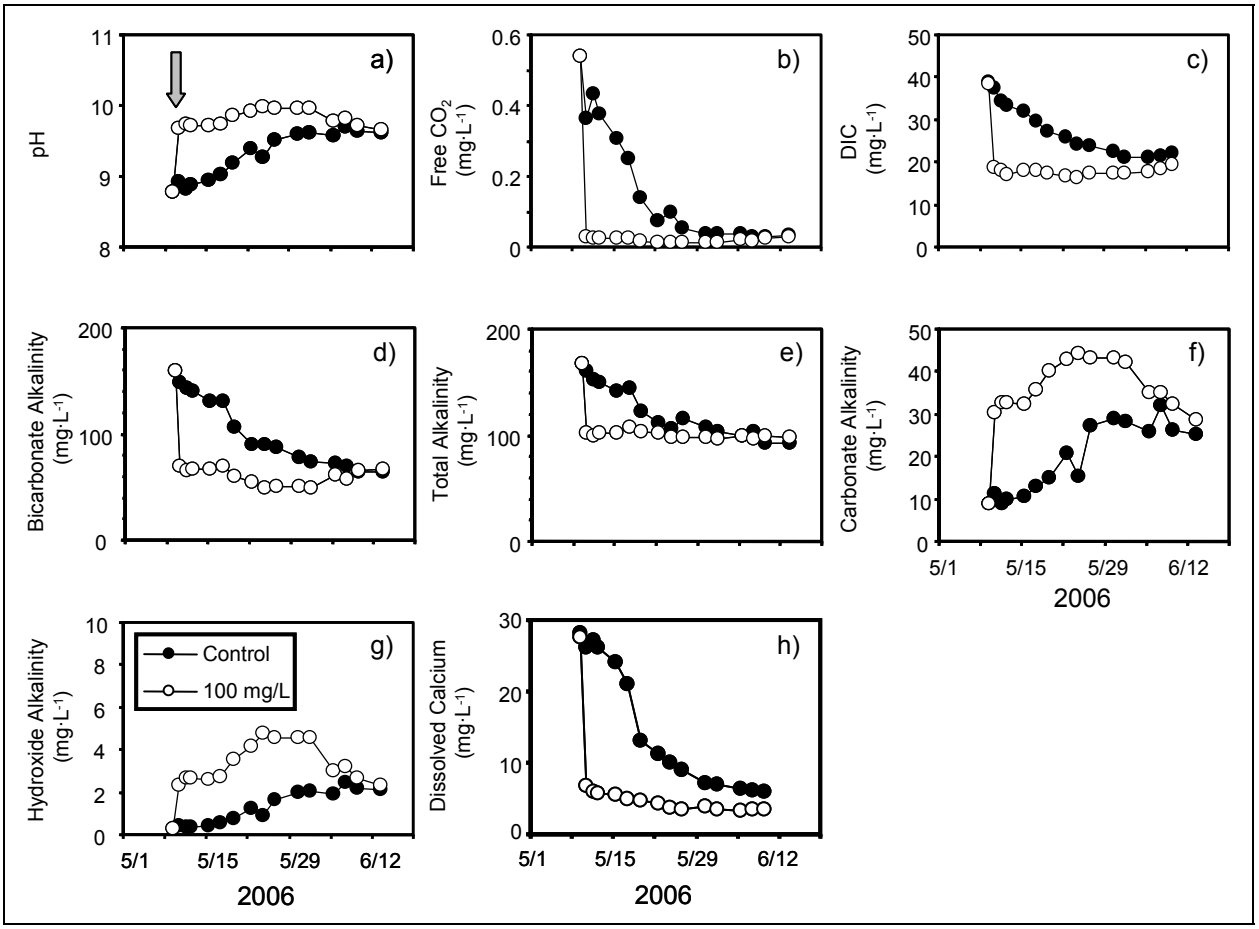

Figure 1. Variations in pH, dissolved inorganic carbon (DIC), and alkalinity species in the control and experimentally treated mesocosm (100 mg·L^{-1} lime). Arrow denotes the time of lime application.

study period and reached experimental levels at the end of the study. DCa declined in the experimental mesocosm immediately after lime application (Figure 1g) as a result of calcite formation and deposition from the water column. Concentrations in the experimental mesocosm were less than 5 mg·L^{-1} throughout the post-treatment period. DCa declined more gradually in the control mesocosm and approached values observed in the experimental mesocosm near the end of the study.

P. crispus shoot growth was slow during the first two weeks of the treatment period (Figure 2a), coinciding with a drop in water temperature due to the passage of a cold front (Figure 3). As water temperature increased, shoot biomass increased in a linear pattern between 9 May and 20 June in the control mesocosm. Net shoot growth occurred in the experimental mesocosm after lime application, reaching a peak in early June; however, it was suppressed relative to shoot growth in the control mesocosm. A net decline in experimental mesocosm shoot biomass was observed between early and late June that contributed to a low shoot RGRR over the entire treatment period (Figure 4).

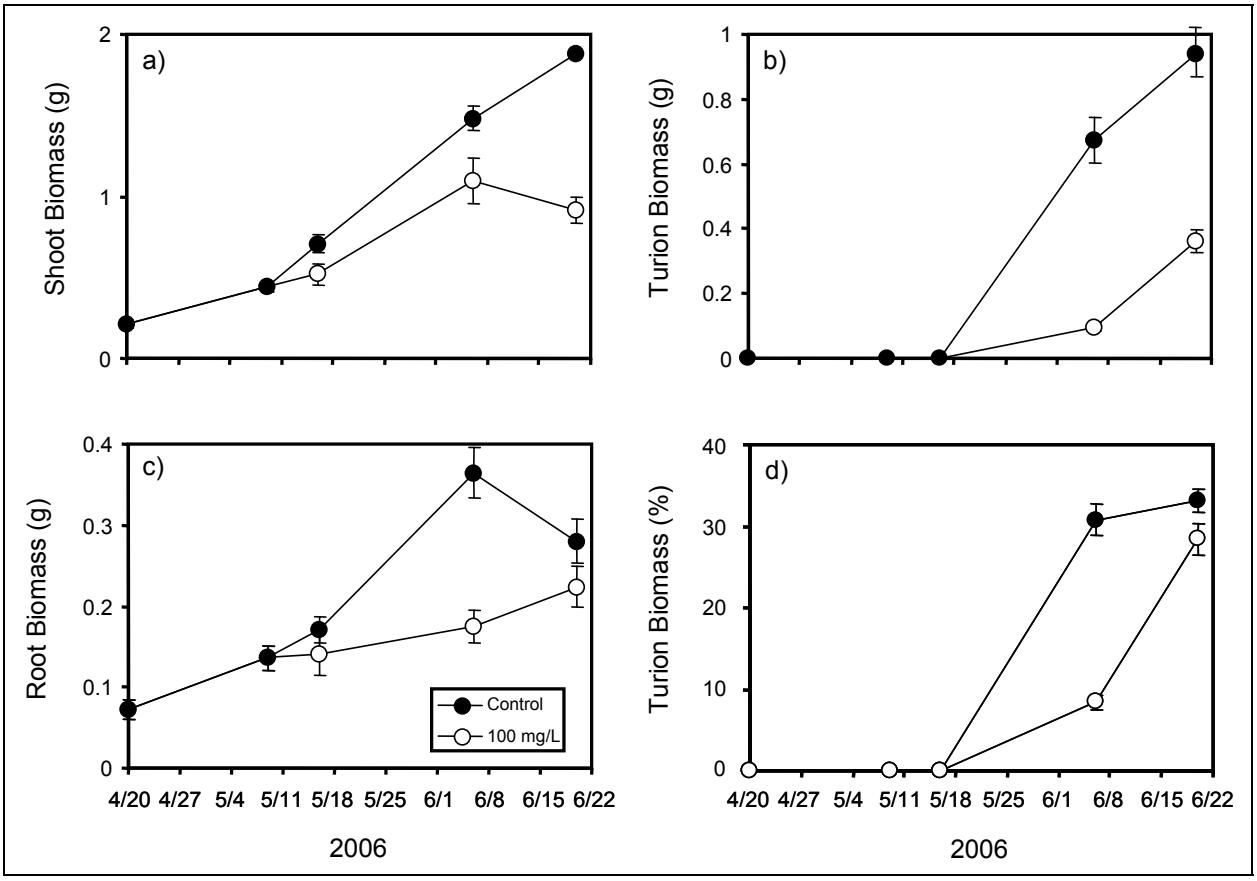

Figure 2. Variations in mean (±1 standard error) P. crispus shoot, root, and turion biomass and the percent turion biomass (i.e., turion biomass⁄shoot + turion biomass) as a function of time of control and experimentally treated (100 mg·L^{-1} lime) mesocosm.

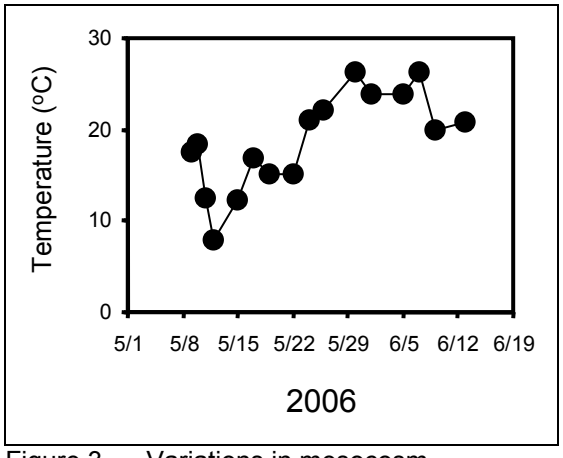

Figure 3. Variations in mesocosm temperature.

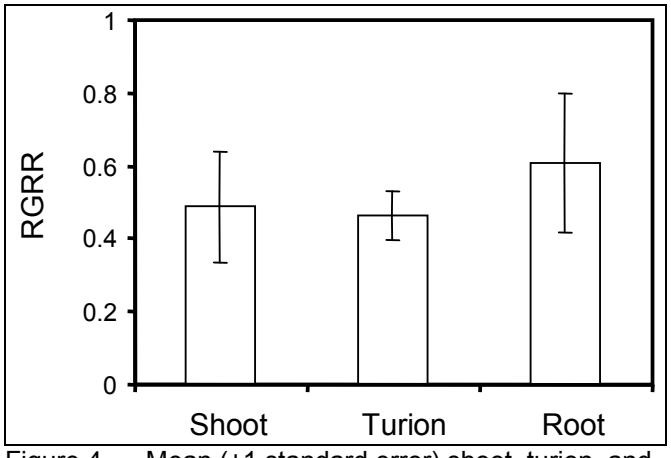

Figure 4. Mean (±1 standard error) shoot, turion, and root relative growth rate ratio (RGRR) for *P. crispus* experimentally treated with 100 mg·L^{-1} lime. An RGRR of less than 1.0 indicates lower growth rate in experimental treatments relative to the control.

Turions were observed on both control and treated plants in early June. By late June, turion biomass was 2.5 times greater in the control versus the experimental mesocosm (Figure 2b). Turion RGRR in the experimental mesocosm was only 0.46 (Figure 4). The percentage of aboveground biomass accounted for by turions was 33 percent in the control mesocosm and 28 percent in the experimental mesocosm in late June (Figure 2d). The high percent turion biomass contribution in the experimental mesocosm reflected the net decline in shoot biomass during June (Figure 4).

Root biomass reached a peak in the control mesocosm in early June and declined at the end of the study. Like shoot and turion biomass patterns, *P. crispus* root growth was suppressed in the experimental mesocosm relative to the control (Figure 2c). The root RGRR calculation was biased by decreased root biomass in the control mesocosm at the end of the study (Figure 2b). Nevertheless, it was much less than 1.0, suggesting impacts of lime application on root growth (Figure 4).

Although the number of turions produced per plant was suppressed in the experimental mesocosm relative to the control in early June there were no significant differences in turion number by late June (Figure 5a). In contrast, individual turion mass for experimental plants was more than 60 percent less than those produced by control plants at the end of the study period (Figure 5b).

DISCUSSION: Although shoot biomass increased linearly in the control mesocosm during the post-treatment phase, increases in pH and declines in free CO_2, HCO_3^- alkalinity, and DIC suggested that inorganic carbon concentration was becoming limiting and plant growth was approaching the compensation point (i.e., the C concentration at which net photosynthesis approaches zero; Hough and Wetzel (1978)) near the end of the study period. In addition to assimilation by *P. crispus*, photosynthetically induced calcite precipitation was probably responsible for some of the DIC depletion in the control mesocosm as indicated by declines in DCa and total alkalinity. Using a pH drift technique, Allen and Spence (1981) reported an HCO_3^- compensation point of 1440 $\mu mol \cdot L^{-1}$ (~ 17 $mg \cdot L^{-1}$ DIC expressed as C) at a final pH of 9.52 for *P. crispus* incubated in water that was 2.0 $mequiv \cdot L^{-1}$ alkalinity (~100 $mg \cdot L^{-1}$ total alkalinity as $CaCO_3$). By 13 June, conditions in the control mesocosm were just above these laboratory-derived values as pH was 9.62 and the DIC concentration was 22.0 $mg \cdot L^{-1}$, suggesting that DIC was limiting growth.

Lime application to the experimental mesocosm resulted in a rapid decline in free CO_2 to near zero due to increased pH, equilibrium shifts to HCO_3^- and CO_3^{-2}, and precipitation as calcite. Although *P. crispus* favors CO_2, it can assimilate HCO_3^- for growth; however, photosynthetic rates are less efficient and decline with increasing pH (Sand-Jensen 1983). pH increased to an average 9.8 while DIC declined to 17.7 $mg \cdot L^{-1}$ as a result of lime application suggesting that *P. crispus* was limited by DIC availability and near the compensation point throughout the post-treatment period versus plants in the control mesocosm, which were probably growth-limited only toward the end of the study. Increased carbonate alkalinity could have additionally stressed growth in the lime-treated mesocosm by directly inhibiting HCO_3^- uptake (Lucas et al. 1978; Lucas 1983; Sand-Jensen 1983) or by buffering the flux of H^+ (i.e., H^+ pump; Lucas 1983; Prins et al. 1982).

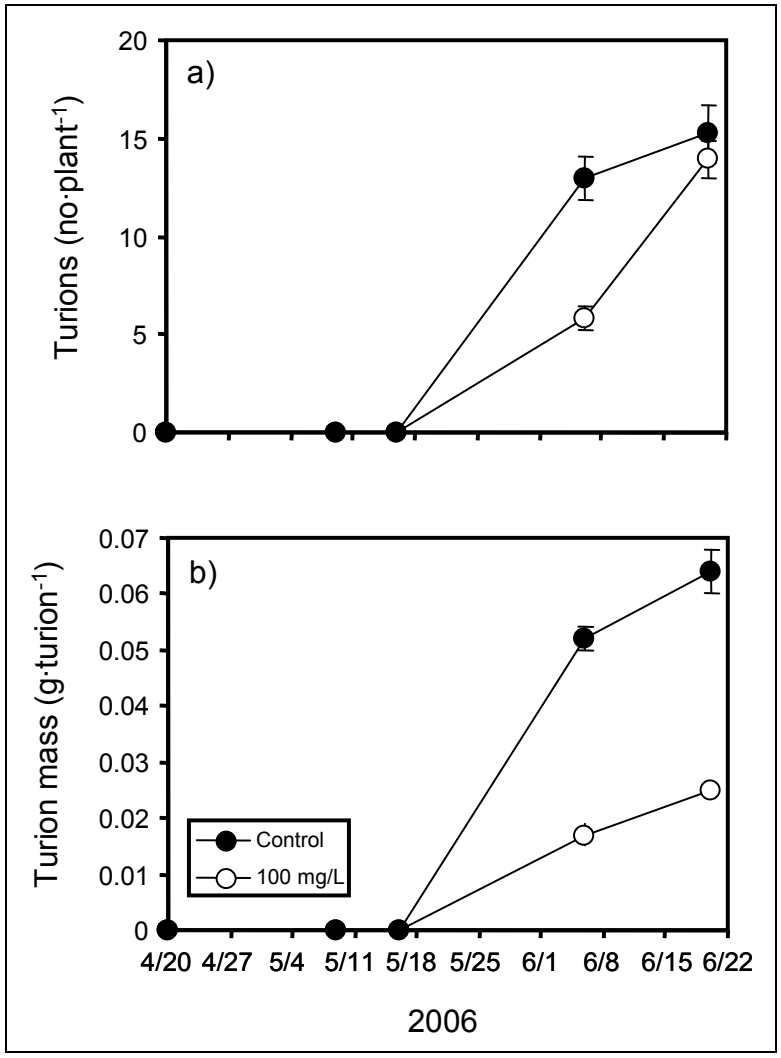

Figure 5. Variations in mean (±1 standard error) turion number per plant and turion mass as a function of time of control and experimentally-treated (100 mg·L^{-1} lime) mesocosm.

Surprisingly, some net growth occurred under very low DIC conditions, although the shoot and root RGRR were less than 60 percent relative to the control plants. Root RGRR might have been lower, but late June net declines in the root biomass of plants grown in the control mesocosm offset the slower root growth observed for experimentally treated plants. This pattern may have been attributed to the onset of plant senescence in the control mesocosm, which occurs between late June and early July in the upper Midwest (USA) after turion formation (Woolf and Madsen 2003). Another possible explanation is carbohydrate reallocation from roots toward turion development (Woolf and Madsen 2003). In contrast, growth suppression in the experimental mesocosm may have delayed or disrupted the timing for completion of the lifecycle and the onset of senescence, resulting in some continued net root growth relative to the plants grown in the control mesocosm.

For plants grown in the control mesocosm, turion production (~ 30 percent of shoot biomass) and individual turion mass (0.06 g·turion^{-1}) at the end of the study were within ranges reported by Woolf and Madsen (2003). Although turion number was similar, mass was 60 percent lower for experimental versus control plants at the end of the study period, indicating that lime-induced DIC limitation had an effect on *P. crispus* propagule production by suppressing turion development. Woolf and Madsen (2003) reported that *P. crispus* total nonstructural carbohydrate (TNC) storage increased in shoots and roots prior to turion development and that these reserves were reallocated toward turion production later in the life cycle. Their findings implied that lime-induced DIC limitation could have interfered with TNC storage for use in turion development. Although turion viability was not determined in this study, lower mass was likely associated with lower TNC reserves and lower viability. This hypothesis needs to be tested experimentally.

Since *P. crispus* propagates primarily via turions, targeting and suppressing turion production is a management goal in reducing its proliferation and density. Although lime treatment did not kill plants in this study, it suppressed growth and turion development at a modest application rate and pH level, suggesting the potential for its use in targeting annual replenishment of the turion bank. However, optimum timing of lime application in the plant's life cycle to target turion development is currently unknown. TNC storage and reallocation need to be considered in relation to turion development in future research on lime-induced DIC limitation. For instance, application of lime to *P. crispus* populations shortly before the onset of turion development may not be as effective as an application that occurs earlier in the plant's life cycle, particularly if shoot and root TNC storage is sufficient to produce turions at the time of application. Since the mode of action appears to be induction of DIC limitation, temperature and exposure time will likely be important factors in efficacy as well. For instance, DIC limitation during periods of lower temperature and dormant metabolic activity may not be as effective as during warmer temperatures and active growth.

The response of *P. crispus* shoot and root growth to lime application supported results reported in James (2007); namely, that the mode of action appeared to be indirect growth limitation versus herbicidal action. Thus, when lime is used to increase pH to near the HCO_3^--CO_3^{-2} equivalence point (10.3), reductions in DIC concentration and shifts in equilibrium to HCO_3^- and CO_3^{-2} are associated with suppression of shoot and root growth, suggesting that lime induces an environmental stressor to plant growth by limiting DIC availability.

One of the objectives of this study was to examine *P. crispus* growth and propagation response to a modest increase in pH to levels that were within ranges observed in natural lakes, as higher pH can have an impact on other biota. The application rate of 100 mg·L^{-1} was within ranges (100-200 mg·L^{-1}) reported by Prepas et al. (2001a, 2001b) and Chambers et al. (2001), resulting in a pH increase to near 10, which was sufficient to suppress *P. crispus* growth and propagule mass. Results also suggested that the DIC compensation point should be considered in lime application. *P. crispus* has a relatively high DIC compensation point in alkaline waters relative to other species (Table 1, Maberly and Spence 1983), suggesting the possibility that its growth might be more impacted at lower lime dosage rates than some native species.

SUMMARY: Response of *Potamogeton crispus* shoot, turion, and root growth to lime-induced reductions in dissolved inorganic carbon (DIC) were determined in outdoor mesocosms containing replicate planted containers. Lime as $Ca(OH)_2$ applied to the experimental mesocosm at a concentration of 100 $mg \cdot L^{-1}$ resulted in a rapid 95, 50, 60, and 40 percent decline in free CO_2, DIC, bicarbonate (HCO_3^-) alkalinity, and total alkalinity, respectively, and an increase in pH from 8.8 to a maximum of 10.0 relative to the control. DIC remained below 20 $mg \cdot L^{-1}$ and near the carbon compensation point in the experimental mesocosm throughout the post-treatment period. Although some net shoot, turion, and root growth occurred in the experimental mesocosm, it was suppressed relative to the control. The post-treatment relative growth rate ratio (RGRR) was only 49, 46, and 61 percent for shoots, turions, and roots, respectively. *P. crispus* produced similar numbers of turions per plant in the control and experimental mesocosm. However, individual mass was 60 percent less in the experimental mesocosm versus the control, suggesting suppressed turion development. These patterns indicated *P. crispus* growth and propagation were susceptible to lime-induced reduction in DIC.

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