Phytoplankton and Macrophyte Response to Increased Phosphorus Availability Enhanced by Rainfall Quantity

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Abstract - Rainfall patterns are becoming more extreme in the northeastern US and are expected to intensify with an increase in extreme precipitation events and a greater frequency of short-term drought. In Northwest Bay, an undeveloped, primarily forested sub-watershed of Lake George, NY, stream discharge and phosphorus loading in 2006 exceeded that of 2007 by more than 3-fold due to unusually heavy rainfall in 2006 and below average rainfall in 2007. The additional phosphorus loading to the open water positively influenced chlorophyll concentrations in 2006, while porewater soluble phosphorus significantly correlated to precipitation in both 2006 and 2007. The elevated porewater concentrations in early summer of 2006 provided a nutrient advantage that resulted in tissue phosphorus in 3 macrophyte species to more than double while no change in nitrogen or carbon was detected. It is believed that the heavy late spring/early summer rainfall in 2006 saturated soils creating additional stormwater run-off and increasing groundwater seepage that supplied ample phosphorus resulting in enhanced phytoplankton biomass and macrophyte uptake of phosphorus.

Introduction

The average annual precipitation in the northeastern US increased ≈10% during the 20th century, with an additional 10–15% expected by the end of the 21st century (Frumhoff et al. 2007, Hayhoe et al. 2007, Mauget 2006). In addition, extreme precipitation events (>5.08 cm in 48 hours) have increased throughout much of the Northeast and are expected to increase an additional 12–13% by 2099 (Frumhoff et al. 2007, Hayhoe et al. 2007, Tebaldi et al. 2006). While precipitation and storm intensity are expected to increase, so are short-term droughts. Historically, short-term droughts occurred about every three years, but are expected to become an annual occurrence by the end of the century (Frumhoff et al. 2007). Increased annual precipitation, storm intensity, and short-term drought will undoubtedly alter hydrology; the extent of change will be influenced by soil type, soil moisture, slope, and vegetation (Kleinman et al. 2006).

Extreme precipitation events may disproportionally increase stormwater runoff by exceeding the soil-infiltration capacity early in an event. Ramos and Martinez-Casasnovas (2009) found that extreme precipitation events did little to increase deep soil moisture during the most intense rain events. Stormwater runoff was influenced more by storm intensity and soil moisture than the overall amount of rain received. The five-year study concluded that when antecedent soil moisture was >20%, soil and nutrient loss were elevated due to increased stormwater runoff

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generated by exceeding the soil-infiltration capacity, agreeing with observations by MacDowell and Sharpley (2002) and Torrent et al. (2007).

Anticipated increases in rainfall and frequency of drought have the potential to benefit xeric and hydric soils while negatively impacting mesic soils. Increased rainfall in xeric systems and short-term drought in hydric systems may result in shorter periods exceeding soil water-stress threshold limits. However, in mesic systems, which are normally within soil water-stress threshold limits, increased precipitation coupled with short-term drought may result in soils exceeding water-stress thresholds more often (Knapp et al. 2008).

Nutrient availability and uptake has been a central research theme on Lake George, NY, since the 1960s with the establishment of the Fresh Water Institute. Focus on Northwest Bay began in the mid-1980s with the introduction of *Myriophyllum spicatum* L. (Eurasian Watermilfoil), a non-native aquatic plant. Northwest Bay was one of the first documented Eurasian Watermilfoil sites and provided an ideal research location due to minimal development and relative isolation. Madsen et al. (1991) and Madsen (1994) examined the displacement of native macrophytes with the establishment of Eurasian Watermilfoil, while Swinton and Boylen (2009) investigated nutrient availability in porewater within the Eurasian Watermilfoil bed and the surrounding native-plant–dominated area.

The anticipated change in rainfall patterns will alter discharge and erosion resulting in varied phosphorus loading to Lake George. Nutrients are supplied to surface water through streams via stormwater runoff and shallow lateral subsurface flow, while porewater nutrients are derived through groundwater seepage (Musy and Higy 2011). The oligotrophic nature of Lake George should respond to changes in phosphorus loading through phytoplankton biomass and macrophyte nutrient content if phosphorus acts as a limiting nutrient during dry years. Comparing these biotic factors in years exhibiting substantially different rainfall patterns will help assess the extent of change primary producers may encounter in the future rainfall regime.

Field-Site Description

Lake George is a large oligotrophic lake, located on the southeast margin of the Adirondack Mountains of New York State. The steep watershed encompasses 618 km^2 with a land-to-lake surface ratio of 4.6:1 and a lake-water residence time of 6.8 years (Shuster 1994). The largest and most pristine sub-watershed of the lake, Northwest Bay, encompasses 76 km^2, accounting for 15% of the land catchment (Shuster et al. 1994). Northwest Bay is predominantly forested with multiple stream reaches draining the sub-watershed into an extensive wetland (≈1.75 km^2) located at Northwest Bay Brook's terminus (Fig. 1). The original establishment of Eurasian Watermilfoil in the bay had never been managed, resulting in approximately a 60-m x 45-m bed area at the time of this study.

Shuster (1994) documented groundwater as being the primary source of stream discharge around the lake during late spring and summer. In Northwest Bay Brook, 86% of the summer discharge originated as groundwater, with deep and shallow groundwater accounting for 49% and 37%, respectively. Direct discharge accounted for only 14% of the summer discharge, typically lasting for one to two days following rain events. The large groundwater influence is likely due to the dominantly forested watershed, well-draining soils, low basin slope, and the presence of a natural fault that continues into the bay.

Methods

Rainfall measurements

Rainfall quantity was recorded at the southern end of Lake George at a continuously monitored weather station, approximately 24 km from Northwest Bay, using

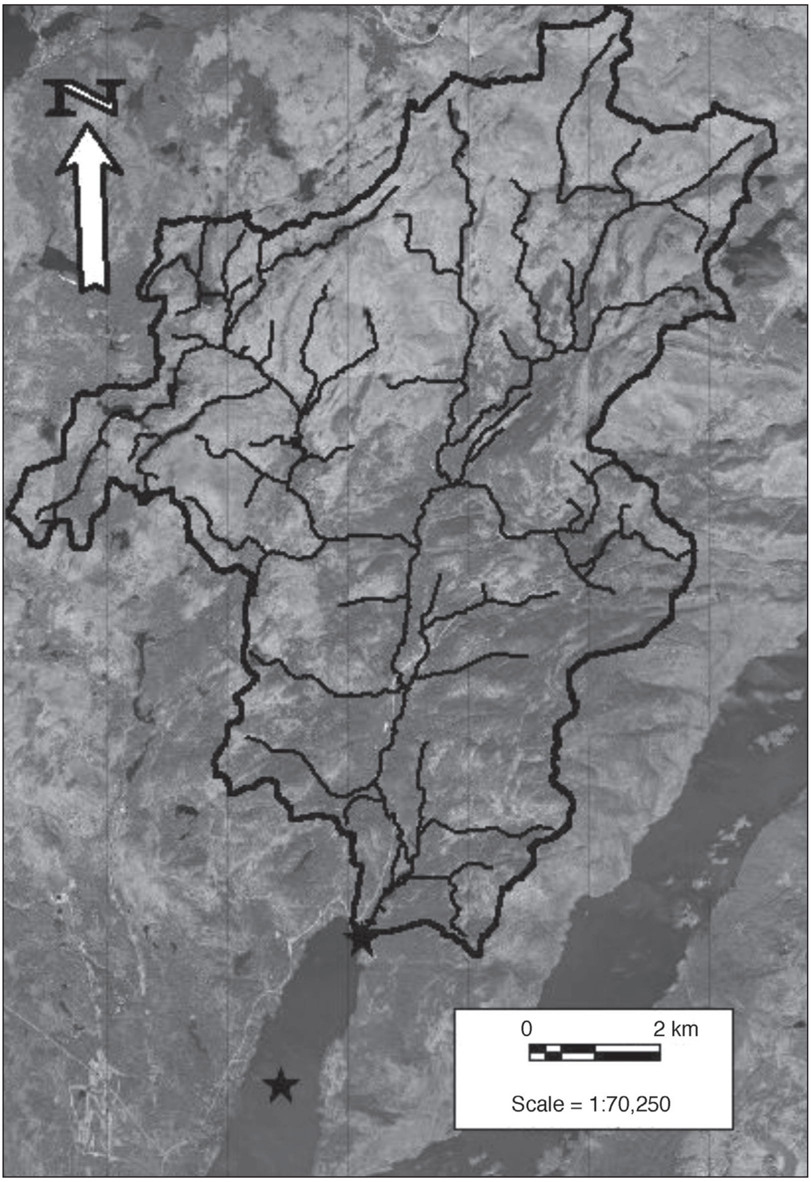

Figure 1. Northwest Bay watershed boundary showing the stream reaches along with the location of the Eurasian Watermilfoil bed at the mouth of the stream and the offshore sampling location to the south (indicated by the stars).

a Qualimetrics tipping bucket (Model 6021A), which recorded hourly rainfall in 0.0254-cm (0.01-inch) increments (Eichler et al. 2008). We confirmed rainfall volume using the capture volume from the wet-fall bucket that was collected for chemical analyses.

Northwest Bay Brook discharge

Northwest Bay Brook was equipped with an ISCO 720 level recorder and pressure transducer approximately 1.5 km upstream of the bay. The ISCO 720 recorded water height (stage) at 5-min intervals, which was verified with staff-gauge height readings during site visits. We conducted stream-flow gaging throughout the study period to verify and enhance the rating curve established for the site. This location was originally established in 1967 by the United States Geological Survey (USGS); the Darrin Fresh Water Institute assumed control of the site in 1994.

Porewater

The porewater-collection location was selected using the original survey in 1987 when Eurasian Watermilfoil was first identified in Northwest Bay (Madsen 1994). We placed a marker at the center of the bed and situated "a channeled Lucite frame" to collect porewater within 1 m of the original bed center; chambers were located at 2-cm intervals to a depth of 30 cm. Particular attention was taken to not repeat insertion at the same location (Fig. 1). We left samplers for a minimum of 2 weeks to allow complete equilibration. Deployment was conducted monthly. Complete methodology for sampler construction, porewater sampling, and analyses can be found in Swinton and Boylen (2009).

Epilimnetic sampling

Monthly sampling of chlorophyll and soluble phosphorus were conducted in Northwest Bay during the summer of 2006 and 2007 as part of the Darrin Fresh Water Institute's Offshore Chemical Monitoring Program (Eichler et al. 2008). Epilimnetic samples consisted of a composite sample of the top 10 m using the hose-integrate sampling method. Samples were analyzed for chlorophyll and soluble phosphorus using Standard Method 10200 and Standard Method 4500-P, respectively (Clesceri et al. 1989). We chose soluble phosphorus for analysis because it includes both soluble reactive phosphorus (SRP) and soluble unreactive phosphorus (SUP). SRP is predominantly orthophosphate, the most bioavailable form of phosphorus, while SUP is composed of compounds that release orthophosphate when converted by enzymes or UV light (Rigler 1973). The detection limit for both phosphorus and chlorophyll was 1 µg/l.

Plant tissue

Upon arrival to the research site, we located the approximate bed center and tossed weighted floats randomly throughout the bed to identify sampling locations. We collected all plant material within a 0.1-m^2 grid placed around each weighted float—a minimum of 20 plants at each site. Samples of Eurasian Watermilfoil, *Potamogeton praelongus* Wulfen (Whitestem Pondweed), and *Vallisneria* *americana* Michx. (American Eelgrass) were collected during peak biomass in 2006 and 2007, within one week of September 1st. Specimens consisted of all above-sediment tissue. We combined specimens by species and washed them a minimum of three times to rid plants of epiphytes, ensuring only plant tissue was analyzed during nutrient analysis. Samples were dried at 100 °C for a minimum of 24 hrs and then homogenized. We measured tissue phosphorus on dried samples (35–50 mg) that were oxidized with 16 ml of 5% potassium persulfate solution and autoclaved for 35 min at 250 °C and 15 psi. We added color reagent and analyzed samples spectrophotometrically (Modified Standard Methods 4500-P; Clesceri et al. 1989). All tissue samples were analyzed twice to ensure measurement reproducibility was within 10%. Nitrogen and carbon analyses were conducted via Infrared Spectroscopy following incineration on the CE Instruments EA1110 CHN analyzer (CE Elantech, Inc., Lakewood, NJ). Approximately 7–8 mg of tissue were analyzed with duplicate samples run to ensure measurement reproducibility was within 10%.

Statistical analysis and comparisons

Throughout the study, we used the Pearson Product Moment Correlation and data based on monthly averages to make all correlations. We conducted the epilimnetic sampling monthly, and the use of our porewater samplers required deployment for a minimum of two weeks for complete equilibration; therefore, sampling multiple sites allowed only monthly sampling to be conducted at the Northwest Bay location. Phosphorus concentrations were compared using a *t*-test. All statements of significance indicate the a priori *P*-value of 0.05 was exceeded.

Results

Rainfall

Rainfall during the summer of 2006 (June–September) exceeded that of 2007 by 15.5 cm (45%), with respective totals of 50.2 cm and 34.7 cm (Fig. 2). The additional May rainfall of 15.0 cm in 2006 and 4.1 cm in 2007 resulted in 68% more rain from May to September in 2006. Average rainfall from June to September for the previous 15 years (1991–2005) was 37.9 ± 10.3 cm. Maximum rainfall recorded was 51.0 cm in 2005, only exceeding 2006 by 0.8 cm.

Northwest Bay Brook discharge

Northwest Bay discharge during the summer (June–September) of 2006 exceeded 2007 by 4.3-fold, with total discharges of $9.05*10^6$ m^3 and $2.12*10^6$ m^3, respectively. Monthly discharge remained relatively constant in 2007, varying less than 40% with a range of $6.01*10^5$ m^3 to $8.33*10^5$ m^3, while discharge in 2006 varied by more than 15-fold from $3.90*10^5$ m^3 to $5.95*10^6$ m^3. Discharge was significantly correlated (Pearson Product, $n = 4$) with rainfall during 2006, but not during 2007 (Fig. 2).

Phosphorus

Soluble phosphorus concentrations in the open water were significantly greater (*t*-test, $n = 4$) during 2006 than 2007 (Fig. 3). Between June and September of 2006, open-water soluble-phosphorus concentrations averaged 2.1 μg/l with a range between 1.6 and 3.0 μg/l, while concentrations in 2007 averaged 1.1 μg/l with a peak concentration of 1.5 μg/l and a minimum concentration below the limit of detection (1 μg/l) in August; a value of 0.5 μg/l represents half the limit of detection and was

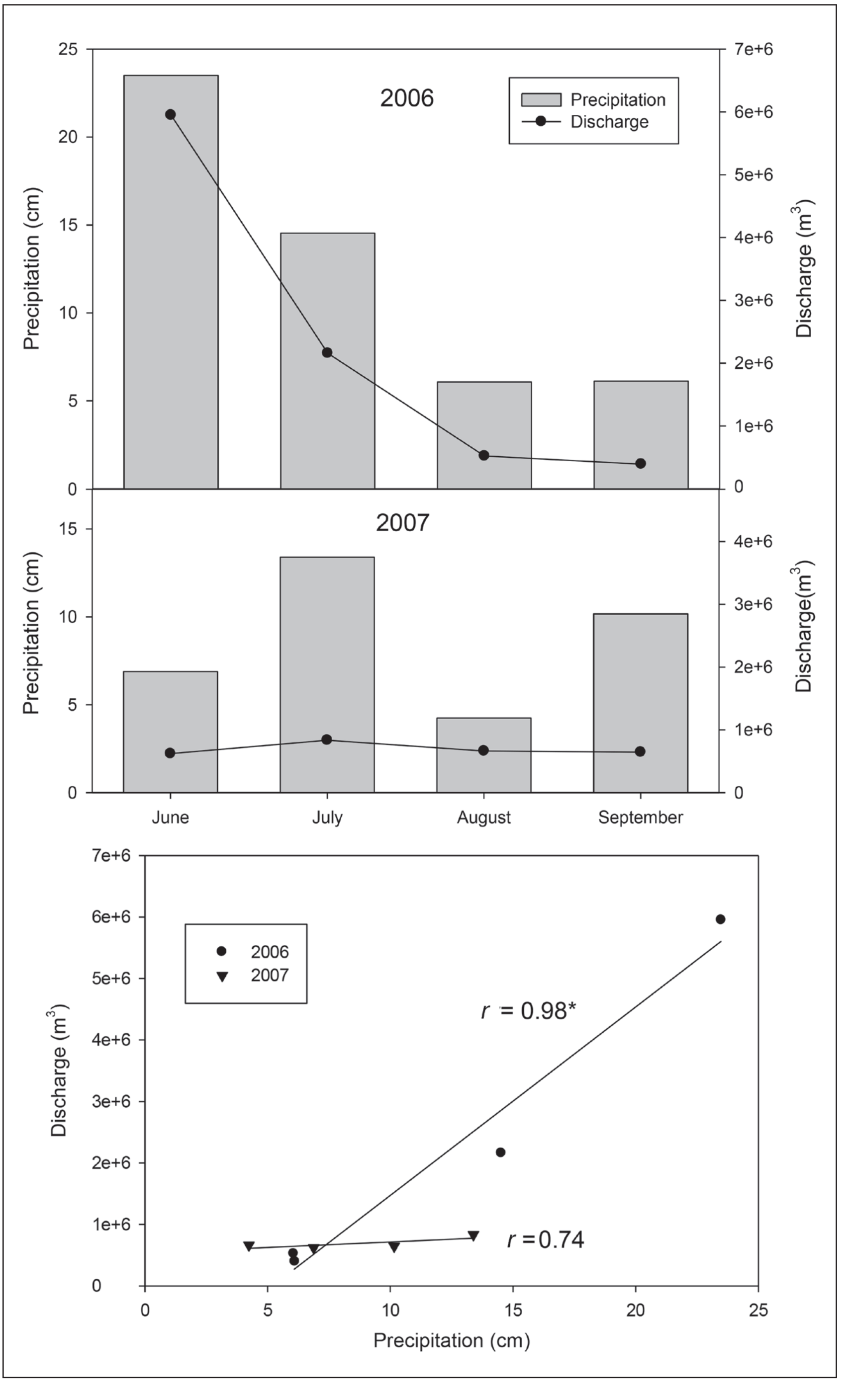

Figure 2. Monthly rainfall and discharge from Northwest Bay Brook during the summers of 2006 and 2007, showing a significant correlation with elevated rainfall in 2006.

used to indicate the August sample was collected and analyzed. Open-water soluble phosphorus was significantly correlated to rainfall in 2006 (Pearson Product, $n = 4$) but not in 2007 (Fig. 3).

Soluble porewater phosphorus at 30 cm below the sediment surface, which was below the deepest observed plant roots in Northwest Bay, represents groundwater entering the macrophyte root zone and was significantly correlated (Pearson Product, $n = 4$) to rainfall in 2006 and 2007 (Fig. 4). The August 2007 measurement was

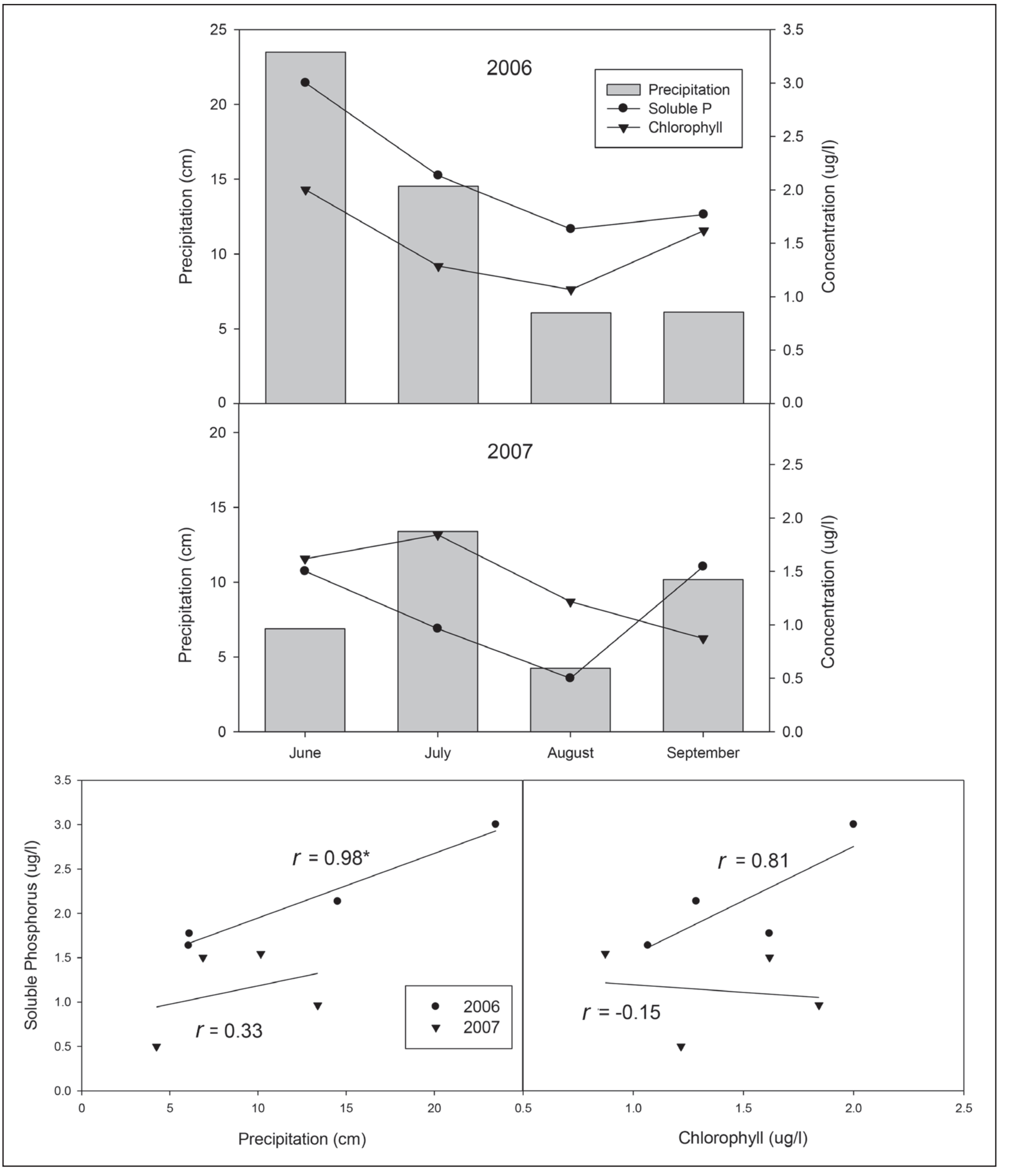

Figure 3. Rainfall, open-water soluble phosphorus, and chlorophyll; stronger relationships between the three variables occur with increased rainfall in 2006. A significant correlation was observed between soluble phosphorus and rainfall in 2006.

below the limit of detection (1 µg/l); the value of 0.5 µg/l was inserted to indicate the sample was collected and analyzed that month.

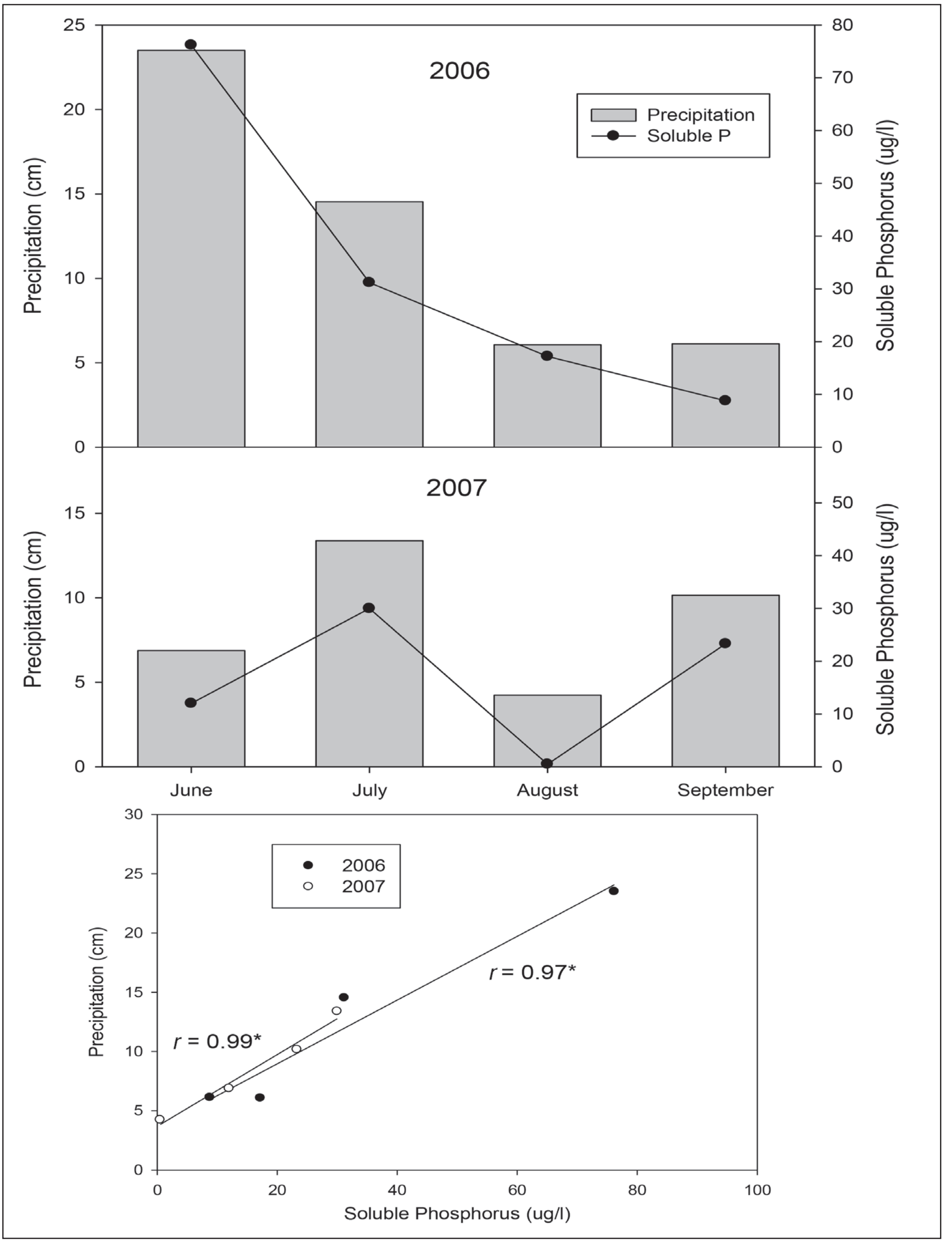

Figure 4. Rainfall and soluble phosphorus entering the root zone of the Eurasian Watermilfoil bed at 30 cm below sediment surface during the summers of 2006 and 2007. Significant correlations between precipitation and porewater soluble phosphorus exists for both 2006 and 2007.

Epilimnetic sampling and plant tissue

Chlorophyll concentrations, a measure of phytoplankton biomass, did not vary significantly between years, but the mean concentration was greater in 2006, and the correlation between rainfall and chlorophyll in 2006 (r = 0.70, n = 4) was more robust than 2007 (r = 0.34, n = 4). The open-water soluble phosphorus and chlorophyll relationship was stronger than with rainfall in 2006 (r = 0.81, n = 4), but in 2007 there was a weak negative correlation (r = -0.15, n = 4; Fig. 3). Phosphorus in the tissues of Eurasian Watermilfoil, *Vallisneria Americana* Michx. (American Eelgrass), and *Potamogeton praelongus* Wulfen (Whitestem Pondweed) at peak biomass was greater in 2006 compared to 2007, but there was no significant difference in nitrogen or carbon between the years (Fig. 5). All three species more than doubled the concentration of tissue phosphorus in 2006 compared to 2007, with Eurasian Watermilfoil, American Eelgrass, and Whitestem Pondweed increasing by 2.06, 2.45, and 2.48-fold, respectively.

Discussion

The summers of 2006 and 2007 received near-record maximum and below-average rainfall in the basin, respectively. The excessive late spring/early summer rainfall in 2006 created a very wet watershed that resulted in elevated stream discharge during the first half of the summer. From research conducted over a 3-year period (2007–2009), we estimate that between June and September, Northwest Bay Brook loaded 22.8 kg of soluble phosphorus to the lake in 2006 and only 5.9 kg in 2007, a 3.9-fold difference. Summer mean soluble-phosphorus concentrations varied little between baseflow (2.0 µg/l) and storm events (2.3 µg/l) (M.W. Swinton, unpubl. data). The abundant rainfall during the summer of 2006 provided a constant supply of soluble phosphorus to the bay, which provided a nutrient advantage to the phytoplankton and resulted in increased biomass. The chlorophyll concentration peaked in June corresponding to the greatest rainfall accumulation and followed the same summertime pattern as soluble phosphorus: a gradual decrease until August and a September rebound. Below-average rainfall in 2007 resulted in a peak soluble-phosphorus concentration that approached the 2006 summer minimum, 1.5 µg/l and 1.6 µg/l, respectively.

Groundwater discharge into Lake George as a whole will similarly be affected by rainfall as it resembles the discharge pattern of the streams. Streams are predominantly fed by groundwater during summer months, and therefore discharge is commensurate to the height of water in the aquifer. Rainfall raises the height of the aquifer to create head pressure; this pressure supplies water to the streams while creating a piston effect that pushes groundwater into the lake (Gordon et al. 1992). Downing and Peterka (1978) demonstrated that seepage rates were positively and significantly related to rainfall; phosphorus and ammonia input rates were positively correlated to groundwater-inflow rates. Schneider et al. (2005) documented that rainfall does not necessarily have to fall directly in the vicinity of a lake to affect seepage rates. Rainfall 18 km away from Oneida Lake resulted in increased seepage rates, and local rainfall greater than 5 mm per day was linked to seepage rate

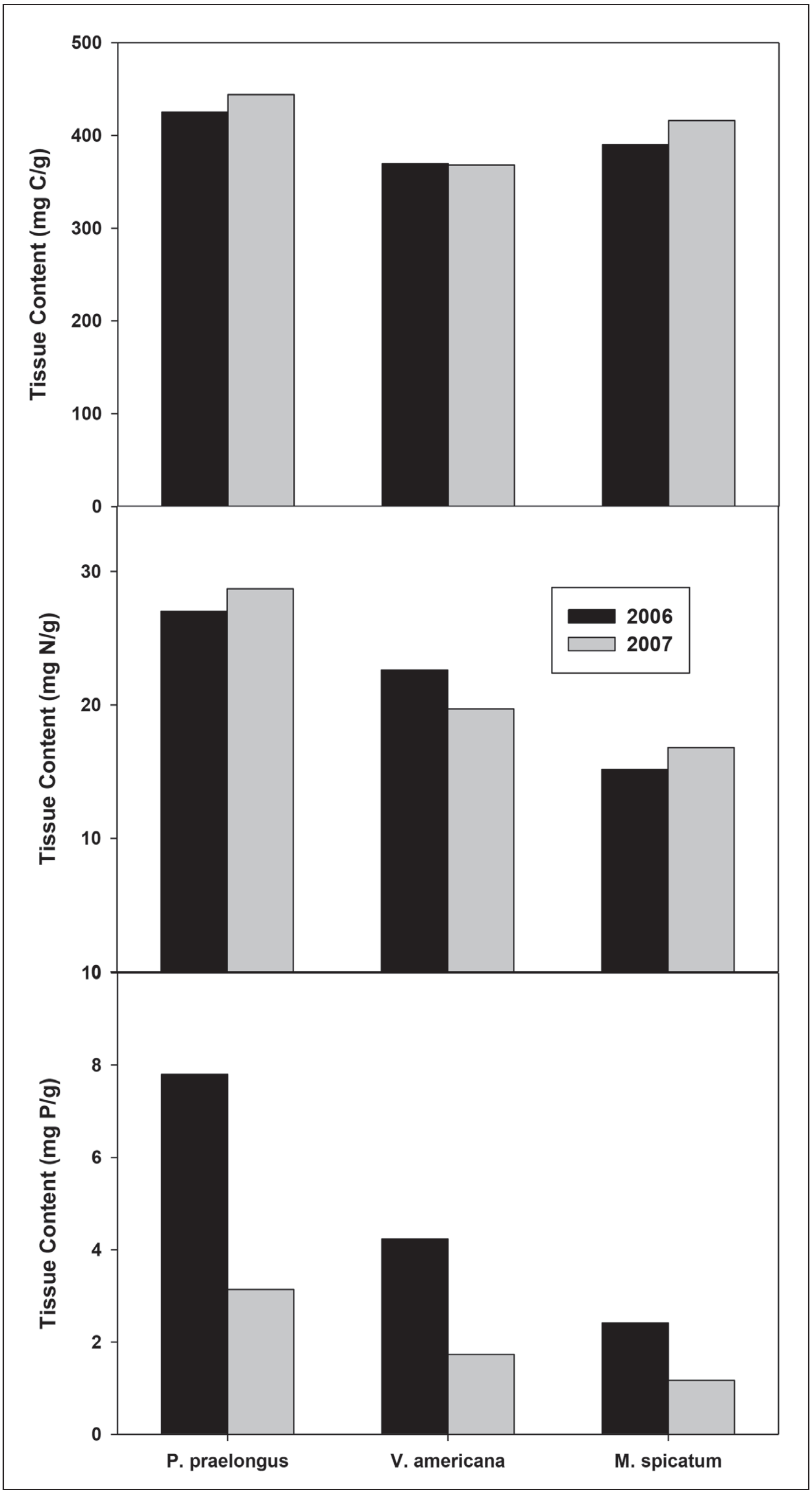

Figure 5. Tissue nutrient concentration for three commonly found species within the Eurasian Watermilfoil bed during peak biomass in 2006 and 2007.

peaks. From this research, it can be surmised that as stream discharge increases, the flow of groundwater to the lake sediments also increases, but to what extent would require further research measuring groundwater seepage rates. However, greater groundwater seepage during early summer of 2006 compared to 2007 is certainly based on stream discharge.

Soluble phosphorus entering the root zone of the Eurasian Watermilfoil bed was significantly correlated to rainfall in both 2006 and 2007, supporting the work of Downing and Peterka (1978). In both years, soluble phosphorus was positively and significantly correlated to rainfall accumulation. The excessive rainfall in June of 2006, which was compounded by the heavy May rainfall, resulted in soluble-phosphorus concentrations approaching 80 μg/l entering the root zone of the macrophyte bed. In contrast, concentrations in 2007 only reached 30 μg/l in the wettest month. The elevated concentrations along with a greater groundwater flux in 2006 provided a nutrient benefit to the rooted plants in Northwest Bay compared to 2007. This interannual variation created a type of natural nutrient enrichment experiment. The oligotrophic nature of Lake George suggests that primary production is phosphorus-limited, and soluble phosphorus concentration differences between years provided two very different scenarios that resulted in all 3 macrophyte species more than doubling tissue phosphorus while no change in carbon or nitrogen content was measured. We believe the increase in macrophyte tissue phosphorus was a "luxuriant uptake" because the N:P ratio ranged from 3.5 and 6.3 in 2006 and from 8.1 to 14.4 in 2007. Nitrogen and phosphorus in macrophyte tissue that is not nutrient-limited normally approximates a ratio of 10:1 (Gerloff 1975, Gerloff and Krombholz 1966). The low N:P ratios in 2006 suggest the macrophytes were nitrogen-limited.

The strong correlation between rainfall, soluble phosphorus, chlorophyll concentration, and macrophyte tissue content in 2006 implies that nutrient loading to both open water and porewater was a primary factor influencing phytoplankton biomass and macrophyte uptake of phosphorus and is a function of rainfall quantity. To verify, multiple porewater profiles are required during months with substantially different rainfall accumulation to confirm spatially that rainfall does increase soluble phosphorus entering the root zone of macrophytes. Additionally, determining the primary production of phytoplankton with increased soluble phosphorus and an assessment of the zooplankton present would be needed to verify whether the increase in phytoplankton biomass was controlled in a top-down or bottom-up manner.

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