

Effects of Water Column Nutrient Enrichment on the Growth of *Potamogeton maackianus* A. Been

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ABSTRACT

Laboratory aquarium experiments were conducted to study the effects of water column nutrient enrichment on the growth of *Potamogeton maackianus* A. Been, a dominant submersed macrophyte in Lake Donghu before the 1970s. The plant was grown in fertile sediment, gradients of water nutrients and different shade intensities for 40 days. At the end of the experiment, redox potential of the sediment was negatively related to the water nutrient concentration, while nitrogen and phosphorus concentration, and peroxidase activity of the plant tissue was positively related to the nutrient gradient. Plant growth reduced at light levels corresponding approximately to the depth range of 0.9-1.5 m given current water transparency within Lake Donghu. Within this stress zone, plant chlorophyll content, total shoot length increased primarily with the increased stress and peaked at 1.2 to 1.3 m depths, showing a narrower adaptive range of the plant than the low light stress range. The present study indicates that growth of *P. maackianus* is strongly inhibited by consequences of nutrient enrichment in water. Thus, eutrophication in Lake Donghu during 1970s may have played an important role in the disappearance of this species from the lake.

Key words: Low light, sediment redox potential, tissue nutrient, peroxidase.

INTRODUCTION

Declines of submersed macrophytes have been reported in many European and American lakes (Broenmark and Weisner 1992, Jupp and Spence 1977, Krolikowska 1997, Moss 1976, Nichols and Lathrop 1994, Orth and Moore 1983, Ozimek and Kowalczewski 1984), and in some Chinese lakes (Ni 1996, Yu et al. 1996, Yu et al. 2000). Decline of submersed vegetation in shallow lakes causes a switch from a macrophyte-dominated clear-water-state to an algae-dominated turbid-water-state, indicating the decrease of water quality (Hosper 1994). This is because submersed macrophytes play a key role in maintaining both the stability and biodiversity of other aquatic organisms, and act as a living interface between the sediment and water phases (Barko et al. 1986, Carpenter and Lodge 1986). Thus, conservative management of submersed vegetation is important for the sustainable uses of shallow lakes.

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Lake Donghu (East Lake, 30°33'N, 114°23'E) is a subtropical shallow lake located near the middle reaches of the Yangtze River. Decline of aquatic vegetation in this lake started in the 1970s, mainly after the disappearance of *P. maackianus*, a submersed macrophyte distributed in East Asia (Sun et al. 1995). This species dominated the aquatic vegetation of the lake before the 1970s and then declined rapidly with eutrophication and increased fish stocking to the lake (Chen 1990). The mechanism for the decline of *P. maackianus* is responsible for the vegetation dynamics in the lake.

Eutrophication and overstocking of herbivorous fish have been the main causes for the decline of submersed macrophytes in shallow lakes, in which the bottom-up effects of eutrophication on macrophytes were considered to be more critical than the top-down effects of fishery (Barko et al. 1986, Broenmark and Weisner 1992, Chen 1990, Jupp and Spence 1977, Moss 1976, Ni 1996, Nichols and Lathrop 1994, Scheffer et al. 1993, Stevenson et al. 1993). In order to seek the reason for the decline and disappearance of *P. maackianus* from Lake Donghu during 1970s, laboratory aquarium experiments were conducted to test the effects of eutrophication, including low sediment redox potential, excessive nutrient supply and low light stresses, on the growth and shoot development of this plant; and to evaluate the tolerance of the plant to the stresses of eutrophication.

MATERIALS AND METHODS

P. maackianus was collected from Lake Niushanhu of Hubei Province in April of 1999, and then was cultivated in tanks of the Donghu Experimental Station for one month before the experiment. The aquarium experiments were conducted from May 10 to June 19, 1999.

The first experiment is designed to test the stress of excess nutrient accumulation on the growth of macrophyte. The fertile sediments were amended with enough slow-release fertilizer to provide sufficient nutrients to supply the growth requirements of the plants. Shoots of the plant (15 cm long) were planted individually to plastic cups containing 50 g gravel in the bottom, 150 g DW sediment of Lake Donghu and about 20 g fertilizer in the middle, and 3 cm washed sand on the top. The fertilizer (TerraMineral, Bioplast GmbH, Erkrath, Germany) contains all vital minerals and plant nutrients. Three plant cups were put into each aquarium (40 cm by 30 cm by 60 cm deep), which was filled with tap water to its capacity. TN, TP, NH₃-N and PO₄-P of the tap water are 1.71, 0.014, 0.0 and 0.011 mg l⁻¹, respectively (Xie L., unpubl.). One week later, three nutrient gradients in the water of aquaria (NH₄-N: 0.0, 0.3 and 0.6 mg l⁻¹, NO₃-N: 0.0, 0.5 and 1.0 mg/l, and PO₄-P: 0.0, 0.1 and 0.2 mg/l) were set in tripli-

cate. In the low light stress experiment, 20 plant shoots were grown in each aquarium containing 4kg DW fertile sediment of Lake Donghu. One week later, a gradient of seven shade levels were set by coating the side walls of the aquaria with 1 to 7 layers of dark paint. Light extinction (K_d) of the aquaria relative to radiation on the water surface of Lake Donghu were 1.44 (no shade on the side wall), 1.92, 2.4, 2.88, 3.12, 3.36, 3.84, and 4.08, corresponding to light extinctions at 0.6 m, 0.8 m, 1.0 m, 1.2 m, 1.3 m, 1.4 m 1.6 m and 1.7 m water depths of the lake. These treatments were duplicated. Initial nutrient contents in the water columns of the aquaria were adjusted to those of the lake water ($\text{NH}_4\text{-N} = 0.6 \text{ mg l}^{-1}$, $\text{NO}_3\text{-N} = 1 \text{ mg l}^{-1}$, $\text{PO}_4\text{-P} = 0.25 \text{ mg l}^{-1}$). Reactive N and P concentrations in the water of the aquaria were measured at two days intervals and the diminishing of N and P from water were then supplied with NH_4Cl , KNO_3 and NaH_2PO_4 in 2-3 days interval. Both experiments lasted for 32 days. During the experiment, average water temperature and light intensity at noon were 26C and $320 \mu\text{E m}^{-2}\text{s}^{-1}$, respectively.

At the end of the experiment, plants were harvested. Their biomass (in fresh weight) and lengths of the main and total shoots were weighed and measured, respectively. Samples were dried in oven at 90C to constant weight (dry weight). Fresh weight to dry weight ratio of the plant for each plant was calculated. Then samples were grounded for carbohydrate, N and P measurements. Redox potential of the sediment was measured with an ORP meter (OM-68, Takemura Electric Works LTD, Japan). For chlorophyll (a + b) content, carbohydrate content, peroxidase activity of the plants, and nitrogen and phosphorus content of the water and plants, three individuals of each treatment were mixed and ground, results of two sub-samples were then averaged. Carbohydrate was determined by phenol-sulfuric acid method for total sugar plus soluble starch (Johan et al. 1956). POD activity was measured in unit ($U = \Delta\text{A}470 \text{ min}^{-1} \text{ g}^{-1}\text{FW}$) after Kal and Miskra (1976). Total and reactive N and P contents were after Golterman et al. (1969).

RESULTS

Nutrient and organic contents in the sediment supplied to the plants were high (TN = 4.8%, TP = 3.2%, organic content = 11.2% of dry weight). Sediment redox potentials (Eh) ranged -60 to -190 mv (mean -141, Figure 1), were inversely related to water nutrient levels. Total shoot length (main plus lateral shoot lengths, TL), ranged from 90 to 190 cm (mean 132.8, Figure 1) among individuals, and was closely related to sediment redox potential ($r = 0.98$, $p < 0.05$, Figure 2A). Tissue peroxidase activities were negatively correlated to their sediment redox potential ($r = -0.99$, $p < 0.01$, Figure 2B), and with TL ($r = -0.98$, $p < 0.01$). The plant showed reduced shoot development at reducing sediment.

As shown in Figure 1, tissue N content of the plant ranged 62.5 to 255.4 mg g^{-1} (mean 173.9) and P content 3.5 to 5.6 mg g^{-1} (mean 4.9), all exceeded the critical contents of 13 $\text{mg N g}^{-1}\text{DW}$ and 3 $\text{mg P g}^{-1}\text{DW}$ regarded for growth requirements (Gerloff 1969). The N and P increased with water trophic levels.

Biomass accumulation in dry weight (DW) ranged from 0.23 to 0.73 g DW ind.^{-1} (mean 0.44) in three water nutrient

levels, varied by three fold. Biomass accumulation was inversely related to the plant tissue N and P contents ($r = -0.85$, $p < 0.05$ and $r = -0.87$, $p < 0.05$, respectively, Figure 2C), showing an inhibitory effect of tissue excess nutrients on biomass accumulation of the plant. Plant tissue carbohydrate contents ranging from 65.9 to 78.2 mg l^{-1} did not show any correlation with its tissue N and P concentrations.

Biomass accumulation rates of *P. maackianus* increased at light intensities corresponding to 0.6 and 0.8 m vertical depths of the lake, then declined from 0.8 to 1.4 m (Figure 3A), indicating that photosynthetic light saturation point (L_s) of the plant was near 0.9 m. Negative shoot growth rates were observed at ≥ 1.6 m depth (Figure 3A), indicating that photosynthetic light compensation point (L_c) of the plant was around 1.5m depth and the range of 1.0 to 1.4 m depths was the photosynthetic low light stress zone. In the stress zone, negative regression between the growth rate and the light intensities was significant ($y = -3.41x + 5.36$ for DW, $r = 0.99$, $p < 0.05$).

Chlorophyll (a + b) content, the growth of the main (L) and total shoot lengths (TL) of the plant all increased initially with the increase of the stress and peaked at light intensities corresponding 1.2 to 1.3 m depth (Figure 3B to 3C), growth of TL then declined steeply toward the highest end of the stress zone from 1.2 to 1.4 m (Figure 3C), showing the adaptation to the low light stress by this plant was limited at the low through medium stress levels and was ineffective at high stress condition.

DISCUSSION

Effects of Low Sediment Redox Potential on Shoot Development

Sediment redox potentials have been correlated with the loading of both organic matter and phosphorus into the sediment (Sondergaard 1990). Dissolved reactive phosphorus (DRP) in the sediment interstitial water was much higher than that of the open water (Patterson and Brown 1979). Therefore, oxygen demand is very high for the sedimenta-

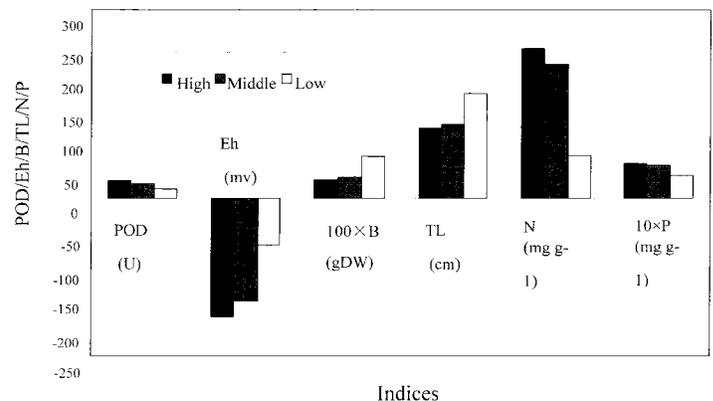


Figure 1. Changes in sediment redox potential, (Eh), growth indices (B, TL), tissue Nitrogen and phosphorus contents (N and P) and peroxidase activity (POD) of *P. maackianus* grown in fertile sediment and low to high nutrient waters.

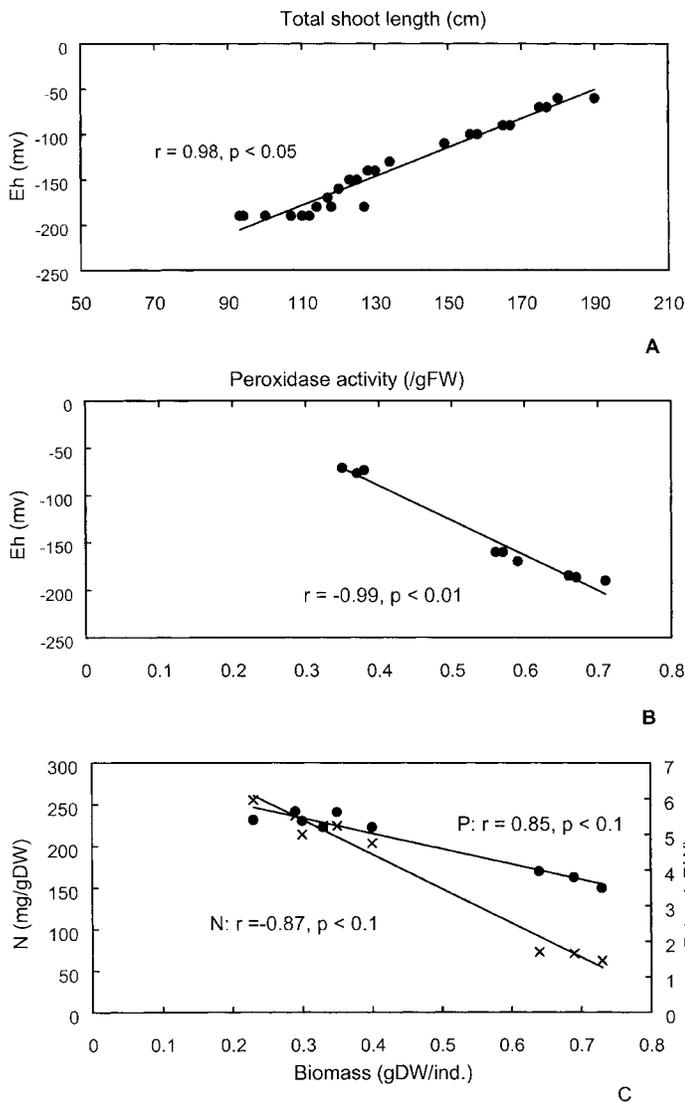


Figure 2. Regressions between the plant (shoot and biomass) growth, and the stresses of eutrophication (sediment redox potential, excessive tissue N and P contents). A. Regression between sediment redox potential and the growth of total shoot length; B. Regression between sediment redox potential and the tissue peroxidase activity; C. Regression between plant biomass growth, and the tissue N and P contents.

tion of phosphorus and the decomposition of organic matter in sediment of nutrient enriched waters of high primary production. The resulting negative Eh (reducing condition) sediment is potentially phytotoxic (Ponnamperuma 1972, Sanderson and Armstrong 1980). Although submersed macrophytes are reportedly capable of aerating their rhizosphere by transporting oxygen of photosynthetic origin through the intercellular lacunae to their roots (Armstrong 1978), or forming nontoxic end products in anaerobic respiration of roots (Penhale and Wetzel 1983), these mechanisms seem to be ineffective in fertile sediment of eutrophic waters (Carpenter et al. 1983, Chen and Barko 1988). In the present study, increase of peroxidase activity in plants was probably induced by phytotoxins in the reducing sediment. Wound reducible POD has been widely reported in crops (Catala et al.

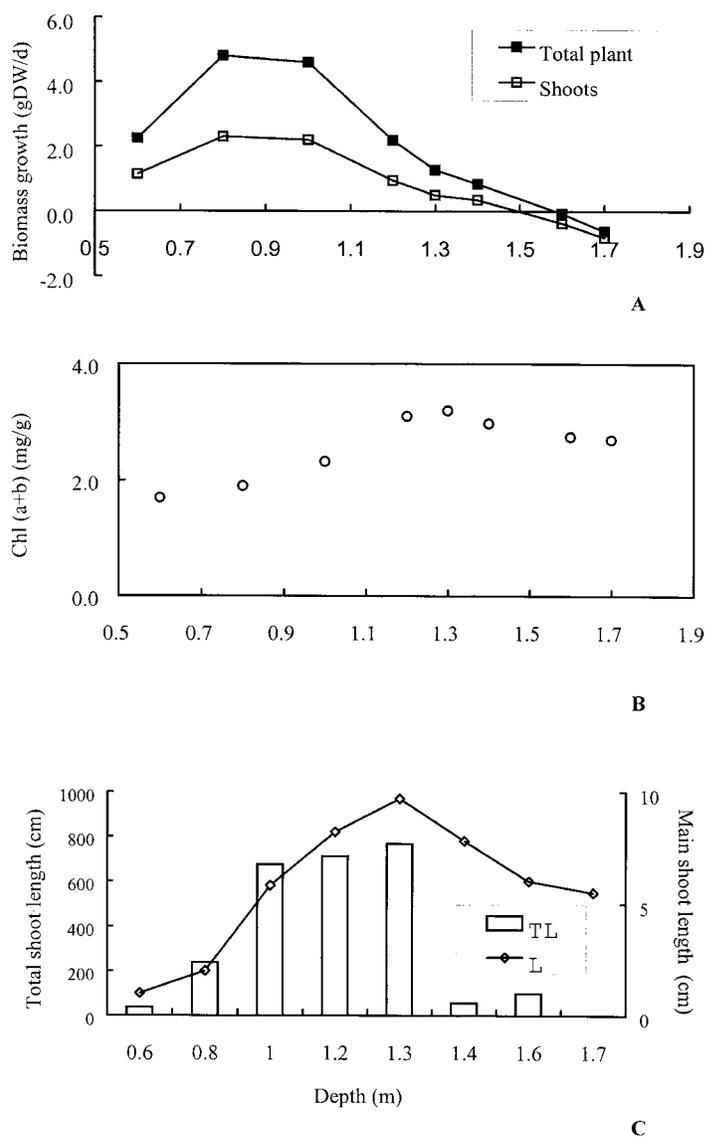


Figure 3. Changes of the plant (biomass and total shoot length) growth and chlorophyll content against the simulated depths of light intensities of Lake Donghu. A. Biomass growth rates at different depths of light intensities; B. Chlorophyll (a + b) contents at different depths of light intensities; C. Main and total shoot (main plus lateral shoots) growth at different depths of light intensities.

1994, Kato et al. 2000, Kawaoka et al. 1994). Decrease in shoot development at reducing sediment has not been reported in submersed macrophyte up to date. However, similar shoot and biomass reduction occurred in anoxic or hypoxic treatments performed on roots of emergent macrophytes (Donovan 1985, Pearce et al. 1992, Everard et al. 1991). In seagrasses, reduction in leaf length was observed in plants grown on fertile sediment (Thursby 1984). A mechanism accounting for this response is currently unknown. It has been suggested that ethylene might be induced by stresses of a wound and or H_2S treatment, or by the increase of tissue peroxidase. However, ethylene was found to promote elongation of submersed petiole of floating-leaved macrophyte (Horton 1992).

TABLE 1. COMPARISON OF BIOMASS ACCUMULATION, CARBOHYDRATE RESERVE, PEROXIDASE, SHOOT DEVELOPMENT AND ELONGATION RATE OF FOUR SUBMERSED MACROPHYTES GROWN IN NUTRIENT ENRICHED WATER AND FERTILE SEDIMENT. DATA SOURCE IS NI AND XIE, 2000, UNPUBLISHED DATA

Species name	<i>Potamogeton maackianus</i>	<i>Myriophyllum spicatum</i>	<i>Vallisneria natans</i>	<i>Ceratophyllum demersum</i>
Biomass accumulation (g DW ind. ⁻¹)	0.19	0.16	0.27	0.24
Carbohydrate (mg g ⁻¹ FW)	66.7	66.9	91.8	82.5
Stress peroxidase (U)	27.4	1.5	11.8	24.3
TL (cm)	110.6	48.7	469	126.7
Main shoot elongation (cm)	27	38.7	8.7	39

Effects of Excess Nitrogen and Phosphorus in Tissue on Plant Biomass Accumulation and Carbohydrate Reserve

Luxury consumption of nutrients is characteristic of submersed macrophytes, and thus they accumulate excess nutrients in their tissue when it grown in eutrophic water (Wetzel 1983). Although no information has been found regarding the direct inhibitory effects of excess nutrients on the growth of submersed macrophyte, it is a common ecological role that any growth condition may turn into stress factor when it is far above the optimum level. In the present study, both N and P concentration of the plant are much higher than the critical level to saturate its optimum growth. Biomass accumulation was strongly inhibited by nutrient accumulation in *P. maackianus* in the present study, demonstrating that to maintain excess nutrient is energy consuming.

Carbohydrate is an index of reserve, remaining low at high biomass growth rate accelerated by the increased nutrient supply (Best and Dassen 1987). In nutrient enriched water, reduced biomass accumulation of excess N and P concentration might result in the rise of carbohydrate reserve of the plant. This gain may be counteracted by the relatively large loss of energy through anaerobic respiration of the root in a reducing sediment (Armstrong and Armstrong 2001).

Effects of Low Light Stress on the Plant Growth

An earlier experiment showed that the L_c of *P. maackianus* was intermediate among eight tested submersed macrophyte species (Chen 1990), suggesting that the plant is unlikely to experience more low light stress than the other submersed macrophytes. In submersed macrophytes, morphological and pigment adaptations of plants to shading by shoot elongation and increased chlorophyll contents have been well documented as an effective strategy to escape from low light stress through shoot elongation and canopy development (Barko and Smart 1981, Barko et al. 1981). However, in these studies, photosynthetic low light stress zone was not defined and the limit of the low light adaptation by submersed macrophyte was not tested. Thus it is unknown whether or not the adaptive range of *P. maackianus* to low-light stress is narrower than those of the other submersed macrophytes. Besides this, *P. maackianus* was limited more by low light in eutrophic water due to its slower elongation rate than those of the other species such as *M. spicatum*, *C. demersum* and *V. natans* which presently grow in Lake Donghu (Ni and Xie 2000, unpublished data).

Mechanism Accounting for the Decline and Disappearance of *P. maackianus* from Lake Donghu

From the results of the present experiment presented in Table 1, it is clear that many stresses of eutrophication have caused the decline of *P. maackianus* from Lake Donghu. Moreover, this plant is found to be more fragile than are the other major submersed macrophytes in nutrient enriched water, e.g., it is high in stress induced peroxidase activity but low in reserves, low in shoot development and slow in main shoot elongation. It is probably less adaptive to low light due to its narrow adaptive range to stress and slow elongation rate. These disadvantages may act according to a basic ecological "Law of Tolerance" (Sun 1998). One factor among these may be critical for the survival of the plant, while the others depress the resistance of the plant against the main stress. Therefore, decline and disappearance of *P. maackianus* in Lake Donghu during 1970s can be considered as a result of several coincident stresses of eutrophication. Additionally, grazing of herbivorous fish on the plant may also contribute considerably to the disappearance as the fish yield of the lake increased from 60 to 180 tons during 1970s in which grass carp comprised 2% (Huang, unpublished data).

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