Postprint: Light Response of PSII Fluorescence Parameters of Vallisneria natans and Potamogeton malaianus to Water Depth Variation in Poyang Lake

Authors: Gao Guiqing, Lü Shunhua, Lü Nianze, Lulong, Li Wei, Yong Ji, You Jikang, Wan Peng, Lulong County

Date: 2018-06-19T00:00:00+00:00

Abstract

Using typical submerged macrophytes Vallisneria natans and Potamogeton malaianus from Poyang Lake wetlands as experimental materials, water levels were controlled through bucket suspension experiments, and an underwater pulse-amplitude-modulated chlorophyll fluorometer (Diving-PAM) was employed to investigate the effects of different water depths (0.5, 1.0, 1.5, 2.0, 2.5 m) on leaf fluorescence parameters including minimum fluorescence Fo, maximum fluorescence Fm, PSII maximum photochemical efficiency Fv/Fm, effective quantum yield Y(II), photochemical quenching coefficient qP, non-photochemical quenching coefficient qN, and quantum yield of non-regulated energy dissipation Y(NO), and to explore the variation patterns of each parameter with water depth. The results showed that: Vallisneria natans achieved maximum biomass at 1.5-2.0 m water depth, while Potamogeton malaianus achieved maximum biomass at 1.0-1.5 m water depth; Fo of both species first decreased and then increased, whereas fluorescence parameters (Fm, Fv/Fm, Fv/Fo, Y(II), qP) exhibited a trend of first increasing and then decreasing; Fv/Fm and Fv/Fo of Vallisneria natans reached their maxima at 2.0 m, while those of Potamogeton malaianus reached their maxima at 1.5 m; at the same water depth, qN of Potamogeton malaianus was lower than that of Vallisneria natans, showing a trend opposite to qP; the maximum Y(II) of Vallisneria natans occurred within the 1.5-2.0 m depth range, while the maximum Y(II) of Potamogeton malaianus occurred at 1.5 m; both species showed significant differences in Y(NO) with varying water depths, and both excessively high and low water depths inhibited plant growth; relative photosynthetic electron transport rate ETR showed significant differences among different water depth treatments, and the maximum ETR of Vallisneria natans was lower than that of Potamogeton malaianus, indicating its stronger tolerance to low light conditions. In conclusion, plant leaf fluorescence characteristics can be used to reflect water depth variations, providing a reference for lake water level regulation. Under the experimental conditions, Vallisneria natans exhibited the strongest photosynthetic capacity and was most suitable for growth at 1.5-2.0 m water depth, while 1.0-1.5 m water depth was most suitable for Potamogeton malaianus growth.

Full Text

Light-Response of PSII Fluorescence Parameters in *Vallisneria natans* and *Potamogeton malaianus* to Various Water Depths in Poyang Lake

GAO Gui-qing[1],[2], LÜ Shun-hua[2], LÜ Nian-ze[2], LU Long[1]*, LI Wei[2], JI Yong[2], YOU Ji-kang[2], WAN Peng[2]

[1] School of Resource Environment and Chemical Engineering, Nanchang University, Nanchang 330031, China
[2] School of Civil and Architecture Engineering, Nanchang Institute of Technology, Nanchang 330099, China

Abstract

This study investigated the effects of water depth on chlorophyll fluorescence characteristics of two typical submerged macrophytes, *Vallisneria natans* and *Potamogeton malaianus*, in the Poyang Lake wetland. Water levels were controlled at five depths (0.5, 1.0, 1.5, 2.0, and 2.5 m) using bucket experiments. A submersible pulse-amplitude-modulated chlorophyll fluorometer (Diving-PAM) was employed to measure key fluorescence parameters in leaf tissues, including minimum fluorescence (Fo), maximum fluorescence (Fm), maximum photochemical efficiency of PSII (Fv/Fm), effective quantum yield (Y(II)), photochemical quenching coefficient (qP), non-photochemical quenching coefficient (qN), and quantum yield of unregulated energy dissipation (Y(NO)). The variation patterns of these parameters with water depth were systematically analyzed.

The results demonstrated that maximum biomass for *V. natans* occurred at 1.5–2.0 m depth, while *P. malaianus* achieved peak biomass at 1.0–1.5 m. Both species exhibited an initial decrease in Fo followed by an increase with depth, whereas fluorescence parameters (Fm, Fv/Fm, Fv/Fo, Y(II), qP) showed the opposite trend—increasing initially then decreasing. The Fv/Fm and Fv/Fo ratios for *V. natans* peaked at 2.0 m, whereas those for *P. malaianus* peaked at 1.5 m. At equivalent depths, *P. malaianus* exhibited lower qN values than *V. natans*, with qP showing an inverse relationship. The maximum Y(II) for *V. natans* occurred at 1.5–2.0 m, while *P. malaianus* reached its maximum at 1.0–1.5 m. Both species showed significant differences in Y(NO) across depth treatments, with growth inhibition observed at both excessively high and low water depths. Relative electron transport rate (ETR) differed significantly among depth treatments, with *V. natans* showing lower maximum ETR than *P. malaianus*, indicating stronger tolerance to low-light conditions. In summary, leaf fluorescence characteristics effectively reflect water depth variations and can inform lake water level management strategies. Under experimental conditions, *V. natans* exhibited optimal photosynthetic capacity and growth at 1.5–2.0 m depth, while *P. malaianus* thrived best at 1.0–1.5 m.

Keywords: *Vallisneria natans*; *Potamogeton malaianus*; water depth; chlorophyll fluorescence; light-response curve

Introduction

Submerged macrophytes serve as crucial primary producers in lake ecosystems and play a key role in maintaining ecological functions. With increasing water pollution, the restoration and reconstruction of submerged macrophyte communities have become major priorities in aquatic ecology research. Water depth represents a critical factor influencing the successful establishment and survival of submerged macrophytes in shallow lakes, alongside substrate, light intensity, transparency, and nutrient availability. Previous studies have documented significant differences in biomass and viability among different plant species under varying hydrological conditions. For instance, research on *V. natans* has shown that plant density, leaf length, and leaf thickness vary significantly with depth, with optimal planting depths of 0.5–1.0 m under transparency conditions of 1.0–1.5 m. Other work indicates that 1.3 m depth is suitable for *V. natans* growth, while depths of 1.0–1.4 m are appropriate for population restoration in clear waters. Studies on *P. malaianus* in Lake Taihu suggest optimal growth occurs at 0.6–1.2 m, with both greater and lesser depths inhibiting growth and reproduction due to light limitation or photodamage.

These findings demonstrate that submerged macrophytes adapt to different water depths through morphological and physiological responses. However, research on submerged macrophytes in Poyang Lake remains limited, particularly regarding chlorophyll fluorescence characteristics. Since Kautsky discovered chlorophyll fluorescence induction and linked it to photosynthesis, chlorophyll fluorescence techniques have been increasingly applied in plant ecophysiology research due to their ability to reflect intrinsic properties of the photosynthetic system. The development of modulated fluorometers enabled measurements under all physiological states, including strong ambient light, transitioning chlorophyll fluorescence from traditional "black box" measurements to field applications. The advent of submersible fluorometers (Diving-PAM) has made in situ measurements of photosynthesis in submerged macrophytes feasible.

Poyang Lake, the largest freshwater lake in China, covers 9% of the Yangtze River basin area and provides multiple functions including water regulation, climate moderation, and environmental enhancement. The health of the Poyang Lake ecosystem is critical for water quality and ecology in the middle and lower

Yangtze River regions. The second scientific expedition to Poyang Lake in 2013 revealed a significant decline in submerged macrophyte distribution area. While *P. malaianus* was once widespread across the lake in the 1980s, it now occurs only in small patches in shallow areas of some butterfly-shaped lakes, with low water levels identified as the primary cause of wetland vegetation degradation. Currently, *V. natans* is the most widely distributed submerged macrophyte in Poyang Lake, with *P. malaianus* as a companion species. This study examined these two species through in situ measurements of leaf fluorescence characteristics across different water depths, combined with biomass analysis, to determine optimal growth depths and provide scientific guidance for water level regulation and submerged macrophyte restoration in Poyang Lake.

Materials and Methods

Plant Collection and Cultivation

In early June 2016, healthy *V. natans* and *P. malaianus* specimens were collected from Dahuchi in the Poyang Lake Nature Reserve. Prior to experiments, uniformly sized plants were acclimated for two weeks in plastic buckets (120 cm × 80 cm × 110 cm). Healthy, consistently sized individuals were then selected from the acclimated stock and transplanted into smaller buckets containing sediment from Poyang Lake. Each bucket contained six *V. natans* plants with an average wet weight of (0.86 ± 0.03) g, approximately six leaves per plant, and height of (11.25 ± 0.34) cm. *P. malaianus* was cultivated from cuttings, with six plants per bucket, average wet weight of (0.52 ± 0.02) g, approximately three leaves per plant, and height of (30.12 ± 0.46) cm.

Experimental Design

An outdoor controlled simulation experiment was conducted by suspending the planted buckets in a concrete pool (12.0 m × 6.0 m × 2.8 m) at the Poyang Lake Wetland Observation Station (Xingzi Station). Water was sourced directly from Poyang Lake, with water quality parameters monitored weekly (Table 1). Water depth was controlled using a bucket suspension system with five treatment levels: 0.5, 1.0, 1.5, 2.0, and 2.5 m, each with three replicates (Figure 1 [Figure 1: see original paper]).

Light intensity represents the primary limiting factor for photosynthesis in submerged macrophytes. Underwater light attenuation followed Beer' s Law: $I_h = I_0 e^{-kh}$, where I_0 is light intensity at 1 cm below the water surface (lx), h is water depth (cm), and k is the light attenuation coefficient. Light distribution in the experimental water body was fitted as $y = 2.8716e^{-1\times10^{-4}x}$, showing significant attenuation with increasing depth (Figure 2 [Figure 2: see original paper]).

Biomass Measurement

Plant height was measured using a ruler. For each depth treatment, all plants from three replicate buckets were harvested, surface attachments were removed with filter paper, and wet weight was recorded.

Chlorophyll Fluorescence Parameter Measurement

After 30 days of cultivation, chlorophyll fluorescence characteristics were measured using a Diving-PAM fluorometer (WALZ, Germany). Prior to measurement, dark-adaptation clips were attached to leaves for 20 minutes. After opening the clips and activating the measuring light, induction curves were obtained to determine minimum fluorescence (Fo) and maximum fluorescence (Fm) over approximately 5 minutes. PSII maximum photochemical efficiency (Fv/Fm), effective quantum yield (Y(II)), photochemical quenching coefficient (qP), non-photochemical quenching coefficient (qN), and quantum yield of unregulated energy dissipation (Y(NO)) were automatically calculated by the system. Rapid light curves were then measured at PAR gradients of 0, 100, 200, 300, 500, 700, 900, 1100, and 1250 $\text{mol} \cdot \text{m}^{2} \cdot \text{s}^{1}$ over approximately 2 minutes. All measurements were completed before 9:00 AM to avoid direct solar radiation on measured leaves.

Data Analysis

Data processing and graphing were performed using Excel 2016. One-way ANOVA was conducted using SPSS 19.0 to analyze differences in chlorophyll fluorescence parameters between species across depth treatments, with Duncan' s multiple range test applied at a significance level of $P < 0.05$.

Results

Effects of Water Depth on Plant Height and Biomass

For *V. natans*, plant height increased significantly with depth in the 0.5–1.5 m range, reaching a maximum of 24.73 cm at 1.5 m, with no significant difference between 1.5 and 2.0 m ($P > 0.05$). At 2.5 m, height decreased to a minimum of 17.57 cm (Figure 3 [Figure 3: see original paper]). Biomass followed a similar pattern, though no significant difference was observed between 0.5 and 1.0 m due to increased new leaf production in shallow water, representing a morphological plasticity response to depth variation.

For *P. malaianus*, both height and biomass increased significantly with depth in the 0.5–1.5 m range, peaking at 83.37 cm at 1.5 m, with no significant difference between 1.0 and 1.5 m. Beyond 1.5 m, both parameters declined significantly, indicating that greater depths inhibited biomass accumulation (Figure 4 [Figure 4: see original paper]).

Responses of Fo, Fm, Fv/Fm, and Fv/Fo to Water Depth

Measurements across the five depth treatments revealed distinct patterns in fluorescence parameters (Figure 5 [Figure 5: see original paper]). Fo decreased initially then increased with depth in both species, reaching minima at 1.5 m for *V. natans* and showing no significant difference between 2.0 and 2.5 m ($P > 0.05$). *P. malaianus* showed a similar trend but with significant differences between 2.0 and 2.5 m. In the 0.5–1.5 m range, *V. natans* exhibited higher Fo than *P. malaianus*, while the opposite was true at depths > 2.0 m, indicating differential PSII reaction center openness between species.

Fm values for *V. natans* showed no significant differences between 1.0 and 2.0 m. In contrast, *P. malaianus* Fm increased then decreased with depth (except at 1.5 m), peaking at 2.0 m. *V. natans* consistently showed higher Fm values, indicating greater maximum electron transport potential through PSII. Both species displayed similar patterns for Fv/Fm and Fv/Fo, increasing initially then decreasing with depth, with maxima at 2.0 m for *V. natans* and 1.5 m for *P. malaianus*.

Overall, *V. natans* exhibited significantly higher Fm, Fv/Fm, and Fv/Fo values across all depths, indicating superior PSII primary light energy conversion efficiency compared to *P. malaianus*.

Responses of qP and qN to Water Depth

Photochemical quenching coefficient (qP) reflects the proportion of light energy absorbed by PSII antenna pigments used for photochemical electron transport. For *V. natans*, qP showed no significant difference between 1.0 and 2.0 m ($P > 0.05$) but decreased sharply at 2.5 m. *P. malaianus* also exhibited its minimum qP at 2.5 m, suggesting photochemical quenching inhibition similar to that observed in emergent plants under high nitrogen conditions. Across all depths, *V. natans* showed lower qP than *P. malaianus*, indicating a smaller proportion of absorbed light energy participating in electron transport.

Non-photochemical quenching coefficient (qN) reflects the capacity to dissipate excess light energy as heat and serves as a sensitive indicator of early plant stress, showing an inverse trend to qP. At equivalent depths, *P. malaianus* exhibited lower qN than *V. natans*, indicating weaker photoprotective capacity (Figure 6 [Figure 6: see original paper]).

Responses of Y(II), Y(NO), and Y(NPQ) to Water Depth

Both species showed an initial increase then decrease in Y(II) with depth, with maxima at 1.5–2.0 m for *V. natans* and 1.0–1.5 m for *P. malaianus*. *V. natans* consistently showed lower Y(II) than *P. malaianus*, indicating lower actual photosynthetic efficiency.

Y(NO) in *V. natans* differed significantly across depths ($P < 0.05$), with maxima at depths < 1.0 m and > 2.0 m, indicating damage at both excessively shallow and deep conditions. *P. malaianus* showed no significant differences in Y(NO). Both species exhibited significant differences in Y(NPQ) ($P < 0.05$), with *V. natans* showing higher values, indicating greater excess light energy reception at equivalent depths (Figure 7 [Figure 7: see original paper]).

Rapid Light Curve Responses to Water Depth

Rapid light curves were generated by measuring relative electron transport rate (ETR) across PAR gradients at different depths (Figure 8 [Figure 8: see original paper]). ETR initially increased then decreased with increasing PAR, rising rapidly below 300 mol·m^{2}·s^{1} and declining more gradually above this threshold. Both species reached maximum ETR saturation at 300 mol·m^{2}·s^{1}. *V. natans* peaked at 32.6 mol·m^{2}·s^{1} at 2.0 m, while *P. malaianus* peaked at 35.9 mol·m^{2}·s^{1} at 1.5 m, with both showing photoinhibition at higher irradiances. The lower maximum ETR in *V. natans* indicates stronger tolerance to low-light conditions and suitability for deeper waters.

Discussion

Water depth is a critical limiting factor for aquatic plant growth and distribution, affecting not only light availability but also gas and nutrient exchange between plants and water, thereby altering photosynthetic performance. This study demonstrates that water depth significantly influences chlorophyll fluorescence characteristics in both *V. natans* and *P. malaianus* from Poyang Lake.

Minimum fluorescence (Fo) is related to PSII pigment density, thylakoid structure, and chlorophyll content, but not photochemical reactions. The observed initial decrease then increase in Fo for both species suggests that extreme depths (> 2.0 m or < 1.0 m) elevate pigment density and alter thylakoid membranes as an adaptive response. Depths of 1.5–2.0 m may enhance protein complex activity on thylakoid membranes, strengthening electron transport and photophosphorylation. The similar patterns of Fv/Fm and Fv/Fo in both species, increasing then decreasing with depth, align with previous research. Higher values in *V. natans* indicate that both shallow and deep water reduce primary light energy conversion efficiency and PSII reaction center potential activity in both species. At depths > 2.0 m, reduced light intensity may provide insufficient excitation energy for PSII reaction centers, while limited CO availability may constrain dark reactions. In shallow water (< 1.0 m), strong light may damage photosynthetic machinery and inhibit PSII activity. The superior photochemical efficiency of *V. natans* at equivalent depths may reflect lower light compensation and saturation points compared to *P. malaianus*, enabling photosynthesis under lower irradiance.

Photochemical quenching (qP) in both species increased then decreased with depth, while qN was significantly higher in shallow water (< 1.0 m) than at 1.0–

2.0 m. This suggests that excess light energy in shallow conditions caused photoinhibition, exceeding the self-regulation limits of PSII protective mechanisms and reducing actual photosynthetic rates. In deep water (> 2.0 m), low qP and high qN likely resulted from weak light, high pressure, compressed leaf stomata, and insufficient CO , causing more absorbed light energy to be dissipated as heat for photoprotection. At equivalent depths, *P. malaianus* showed higher Y(II) and qP but lower qN than *V. natans*, indicating stronger photosynthetic activity but weaker photoprotective capacity.

Light quanta absorbed by PSII reaction centers are primarily allocated among three processes: Y(II), Y(NPQ), and Y(NO), with the sum approaching 1 [Y(II) + Y(NPQ) + Y(NO) 1]. The observed patterns suggest that to adapt to varying light intensities at different depths, both species must dissipate unusable quantum energy as heat to minimize damage to reaction centers, representing a self-protection mechanism.

Relative electron transport rate (ETR) reflects apparent electron transport under actual light conditions and carbon fixation via photochemical reactions. Both species showed rapid ETR increase followed by gradual decline with increasing PAR, reaching maximum saturation at 300 mol·m^{2}·s^{1}. This indicates significant photoinhibition of electron transport above 300 mol·m^{2}·s^{1}, with excess absorbed energy dissipated as heat to minimize damage. ETR was highest at 1.0–2.0 m depth for both species, peaking at 2.0 m for *V. natans* and 1.5 m for *P. malaianus*, consistent with biomass measurements. These differences reflect distinct adaptive strategies and light use efficiencies between the two species.

Both shallow and deep water reduce primary light energy conversion efficiency and PSII reaction center potential activity. Shallow water (< 1.0 m) may cause photodamage from strong light, while deep water (> 2.0 m) provides insufficient light for PSII excitation, minimizing biomass. The lower maximum ETR in *V. natans* indicates stronger low-light tolerance and suitability for deeper waters. Fluorescence analysis reveals that 1.5-2.0 m depth is optimal for *V. natans*, while 1.0–1.5 m is optimal for *P. malaianus*.

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