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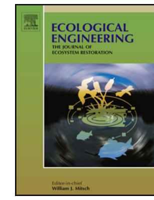

Impacts of water depth and substrate type on *Vallisneria natans* at wave-exposed and sheltered sites in a eutrophic large lake

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ABSTRACT

Water depth, substrate type and wave exposure are major environmental factors influencing the growth and distribution of submerged macrophytes. However, we lack knowledge on the ecological reactions of submerged macrophytes to those factors during an entire growth period in a eutrophic lake with a Secchi depth of less than 50 cm. We investigated the interactive effects of water depth (60, 120 and 200 cm), waves (exposed vs. sheltered) and substrate nutrient level (fertile sludge vs. brown clay) on the survival, growth and morphology of *Vallisneria natans* using a new type of rhizotron in a 252-day field experiment. Plant length, leaf number, ramet number, root length, root number and biomass generally decreased with increased water depth at both wave conditions and in both substrates. When exposed to wave, the biomass of *V. natans* in water at 200 cm depth rapidly declined in both substrates. When sheltered to wave, aboveground biomass at 60 cm water depth first declined to zero with many buried rhizomes remained. The tuber germination rate decreased with increasing water depth during the second year of germination. No plants sprouted at 200 cm water depth except at the case of exposed wave and sludge substrate. Ramet number was influenced most by water depth, followed by aboveground biomass, leaf number, plant length, and survival rate. Wave shelter and brown clay enhanced the impacting strength of the water depth. Wave exposure exhibited no negative influence on survival percentage, whereas sludge had a positive influence on plant survival in deep water after overwintering. Waves negatively affected the rate of increase of plant growth in sludge but positively in clay. The positive joint effects of wave exposure and low-nutrient substrate were mainly on plant length and biomass. Water depth had a negative influence that predominated over substrate and waves regarding plant survival and growth. Moreover, this negative influence may be aggravated by an increasing risk of submersed macrophyte loss caused by decreased belowground growth under high water levels, high wave exposure and high-nutrient conditions. Decreasing the water depth could be an useful measure for submerged macrophyte restoration in freshwater habitats, even in turbid eutrophic water.

1. Introduction

Water depth is a major environmental factor influencing the distribution and growth of submerged macrophytes (Strand and Weisner, 2001; Xu et al., 2016). Human activities are expected to increase the probability of flooding (Blom and Voesenek, 1996), and to alter previous regular water level fluctuation in many lakes (Hu et al., 2010). An increase in water level reduces the light penetration into the lake bottom, especially in eutrophic water. The growth of submerged macrophytes tends to be light limited in most aquatic environments. However, submerged macrophytes exhibit high phenotypic plasticity in response to increasing water depth. Morphological characteristics, such as plant length, ramet number, internodal length and branch number, may react to water depth (Reckendorfer et al., 2013; Zhu et al., 2012). Such adaptations are favoured by differential photosynthetic efficiency at low light intensities (Eusebio Malheiro et al., 2013; Yang et al., 2004). Without plastic changes, a species might not be able to respond adequately to rapidly changing water levels (Clevering and Hundscheid, 1998). It is predicted that global warming will cause extreme events, such as earlier and higher flooding (means the water level increasing earlier and more), to occur more fre-

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quently (Monirul Qader Mirza, 2002), which may have important consequences on plant growth in floodplains because it will lead to a sudden rise of water level.

However, water depth does not affect plant growth in isolation and often influences plant growth in conjunction with other factors, such as mechanical stress from wave action (Madsen et al., 2001; Van Zuidam and Peeters, 2015). The hydrodynamic conditions of waves and currents also-directly and indirectly affect seagrass ecosystems (La Nafie et al., 2012). Macrophytes growing in lakes are frequently subject to hydrodynamic forces resulting from the drag of water passing along the plant. Aquatic plants in moving water experience a force more than 25 times greater than that experienced by terrestrial plant in wind of the same velocity (Denny and Gaylord, 2002). If sufficiently strong, such forces will tend to break the stems or uproot entire plants.

Some studies have shown that organic-rich sediment may be a key factor limiting the growth and distribution of submerged macrophytes in eutrophic shallow lakes (Soana et al., 2012; Yu et al., 2010). In addition, compared to water column nutrients, sediment type has more significant impacts on the growth, nitrogen (N) and phosphorus (P) content of certain plants (Xie et al., 2005). Excessive sediment nutrients and organic matter (OM) are important indicators of shallow lake eutrophication, and may have direct and indirect negative effects on aquatic plant growth (Best et al., 1996; Thiebaut, 2005). Roots are the most important parts of aquatic plants for nutrient uptake and fixing, and primarily occur in the sediment. No long-term culture of submerged plants can be performed successfully without sediments. Therefore, it is important to recognise the influence of sediment type on aquatic plants. Many large lakes have different sediment types with different nutrient levels. However, information about how aquatic plants adjust their root traits to adjust to different sediment environments remains limited (Xie et al., 2007).

Although the individual effects of water depth, substrate type and hydrodynamics on seagrasses have been studied in detail, their interactive effects may be difficult to predict for submerged macrophytes because plant responses to individual stressors are diverse (Xie et al., 2007). Many studies have been conducted on water column with water transparency of more than 1.0 m. However, in the clear-water state in shallow lakes, light penetration through the water column is not influential in regulating submerged vegetation. Currently, most experiments and studies on the growth of submerged macrophytes have covered only a short period (10 days–100 days) of submerged macrophyte life (Jiang et al., 2008). Studies on the growth strategy over the whole one or more life period of submerged macrophytes in a eutrophic lake have rarely been reported, particularly for lakes with <50 cm Secchi depth.

Eel grass, *Vallisneria natans* (Lour.) Hara., is a perennial submerged plant with a wide geographical range that occurs in freshwater lakes, ponds, and rivers. This species produces plagiotropic stolons, which spread horizontally above the ground and form large clonal populations in the field (Xiao et al., 2007). This plant provides food resources and habitats for fish and invertebrates, and has a strong positive influence on water quality. It was chosen for the current study because of its high frequency and adaptive capability in freshwater habitats.

This paper examines the effects of water depth and substrate type on the growth and ramet morphology of *V. natans* under wave-exposed and sheltered case in eutrophic water with a series of in situ experiments. The purpose of the experiments was to (1) investigate changes in the growth and phenotypic characteristics of shoots and roots in response to water depth and substrate type under wave exposure, (2) determine which growth strategy *V. natans* adopts based on its morphological traits, (3) examine plant regeneration and regrowth after winter, and (4) identify the mechanisms that cause a decline in submerged vegetation biomass in shallow eutrophic lakes in a turbid state. The results are expected to contribute helpful information towards enhancing macrophyte restoration projects in freshwater habitats.

2. Materials and methods

2.1. Experimental site and conditions

The experiments were conducted on a floating platform approximately 100 m offshore in Zhushan Bay, located at the northwest part of Lake Taihu, China (Fig. 1). Zhushan Bay has been phytoplankton-dominated zone since 2000. Because of the long-term discharge of OM from the Yincun River and Baidugang River, fertile sludge is present in the sediments, along with brown clay, due to the wind-wave induced erosion of the lake bottom and sediment resuspension. The prevailing wind direction in Lake Taihu is southeast, and thus Zhushan Bay is frequently exposed to strong wind wave. At present, water quality in the bay is worse than class IV standards (National environmental quality standard for surface water, GB3838-2002 of the People's Republic of China). Submerged vegetation covered the majority of Zhushan Bay before 1997. However, by 2012, nearly no submerged plants remained in the bay because of its poor water quality, lake eutrophication and, potentially, the occurrence of increasing water levels in some periods.

In June 2011, a wave-sheltered site was created by constructing a 70-m wave barrier composed of one row of 600 stakes positioned parallel to the shore using a professional pile driving boat (Fig. 1). Wave barriers are effective in reducing wave energy, water velocity and sediment accretion if properly designed and constructed. It reduced wave energy by 70% (Alkhalidi et al., 2015). The wave-sheltered experimental site (the sheltered site) was between the wave barrier and shoreline, 20 m distance from the wave barrier, whereas the wave-exposed experimental site (the exposed site) was in the open water equidistant from the shoreline as the sheltered site. There was no significant difference in water quality between the sheltered site and the exposed site, because the sheltered site was only approximately 80 m from the exposed site. The total N (TN) and total P (TP) concentrations ranged from 2.32 to 5.52 mg L^{-1} and from 0.133 to 0.184 mg L^{-1}, with means of 3.52 and 0.152 mg L^{-1}, respectively (Table 1). The Secchi disc depth was approximately 37.0–76.2 cm, with a mean of 48.8 cm.

2.2. Rhizotrons

Rhizotrons are important instruments to noninvasively study the dynamics of root growth and development of plants through an entire growth cycle (Busch et al., 2004). Rhizotrons have frequently been applied to both terrestrial and wetland plants (Busch et al., 2006), but rarely to submerged macrophytes. A new type of rhizotron was developed to make the traditional rhizotron suitable for the submerged macrophytes (Chinese patent number: 201310731902.8). The rhizotron was in the shape of a cross to increase its stability in water with a strong hydrodynamic disturbance and was made from clear acrylic (Fig. 2), which is one of the most favoured materials for this apparatus because of its low weight and good machinability. It was constructed of 0.4-cm clear acrylic at the front and back and 1.4-cm clear acrylic at the sides and the bottom. Each rhizotron had four arms with same inner cavity dimensions of 25 cm × 50 cm × 3.4 cm. Removable black plastic boards were inserted on the front and back and sides of each rhizotron to create a dark environment for the roots. When the removable black plastic boards were removed from a rhizotron, plant roots in the inner cavity of the rhizotron can be easy to measure and count. This newly developed rhizotron