Aquatic Botany 119 (2014) 51–56

Contents lists available at ScienceDirect

Aquatic Botany

journal homepage: www.elsevier.com/locate/aquabot

Responses of the invasive aquatic plant water hyacinth to altered nutrient levels under experimental warming in China

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ARTICLE INFO

Article history:
Received 5 August 2013
Received in revised form 11 June 2014
Accepted 13 June 2014
Available online 23 June 2014

Keywords:
Aquatic plant
Biological invasion
Climate warming
Eichhornia crassipes
Eutrophication

ABSTRACT

Global warming and eutrophication may interact and increase the invasiveness of certain aquatic plants. To test this hypothesis, a mesocosm experiment was conducted to investigate the growth, biomass allocation and carbon/nitrogen balance of the invasive aquatic plant *Eichhornia crassipes* (Mart.) Solms in response to three nutrient levels representing oligotrophic to eutrophic water under simulated warming in a greenhouse. The growth and clonal propagation of *E. crassipes* were significantly promoted by simulated warming and elevated nutrient levels. The mean relative growth rate and mean clonal propagation rate of the plants increased 32% and 152% due to elevated nutrient levels, whereas those values increased 18.3% and 14.9% due to warming. The shoot/root ratio of *E. crassipes* was also greatly improved by simulated warming (50.2% increase) and elevated nutrient levels (475% increase). Moreover, the leaf and stembase N concentrations increased and C/N mass ratios decreased with elevated temperature and nutrient levels. These results suggest that the ecological invasion of the highly invasive aquatic plant *E. crassipes* will be exacerbated by increasing eutrophication under future climate warming in China.

1. Introduction

Climate change and invasive species are arguably two of the most important global change factors (Hellmann et al., 2008; Walther et al., 2009). In China, the average temperature has increased markedly by approximately 0.4 °C every 10 years in the past 40 years (Ding et al., 2007). Water temperature warming, followed by elevated air temperature, is expected to have profound effects on the growth, distribution and phenology of aquatic species and the productivity of aquatic ecosystems (Carpenter et al., 1992; Parmesan, 2006), as temperature is an important abiotic factor influencing macrophyte growth and production (Santamaria and van Vierssen, 1997; Brian et al., 2003). Many studies have investigated the effects of warming, separately or combined with other factors, on plants (e.g., CO_2 concentration, precipitation, nutrient, light; Jonasson et al., 1999; Usami et al., 2001; Shaw et al., 2002). However, such research on aquatic plants, and especially invasive aquatic plants, has lagged far behind that on terrestrial plants, with the exception of rice and marsh species (Brian et al., 2003; Yan et al., 2006).

Nutrient loadings (N and P) by human activities have accelerated the eutrophication of water bodies, resulting in declines in macrophyte diversity and changes in community structure (Vitousek et al., 1997; Tracy et al., 2003). Approximately one third to more than half of all lakes worldwide are considered eutrophic (Chorus and Bartram, 1999; Wang et al., 2012). Previous studies have demonstrated that P concentrations are more important in determining the eutrophication of lakes than those of N because N fixation by nitrogen-fixing cyanobacteria is sufficient to allow biomass to be produced in proportion to P (Kobayashi et al., 2008; Schindler et al., 2008). Currently in China, 65% of lakes are eutrophic, and more than 29% of lakes are becoming eutrophic, with most of these lakes having high P concentration (Xie, 2003; Le et al., 2010). In the years ahead, climate warming will exacerbate eutrophication in lakes by increasing evaporation and decreasing water movement, both of which can contribute to lake eutrophication (Schindler, 2006).

In addition, plant invasion has become a great threat to biodiversity and global ecosystem stability (Mack et al., 2000). A key component in the plant invasion process may be the increased availability of nutrients (Wersal and Madsen, 2011), as some species possess the ability to increase their growth rates in response to enhanced nutrient availability, suppressing native species that cannot respond in a similar way (Vitousek et al., 1997; Kennedy et al., 2009; Wersal and Madsen, 2011). Therefore, these invasive species that are capable of higher growth rates may have profound negative impacts on native community structure (Kennedy et al., 2009; Wersal and Madsen, 2011).

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http://dx.doi.org/10.1016/j.aquabot.2014.06.004
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In aquatic ecosystems, biomass allocation is a fundamental aspect of the competitiveness of aquatic invasive plants, which often allocate a large fraction of their biomass to form canopies and to support the rapid spring growth that allows them to suppress other species (Madsen, 1991; Sytsma and Anderson, 1993; You et al., 2013a). Changes in patterns of resources allocation have been regarded as one reason for natural declines in aquatic plant abundance and an important mechanism by which plants adapt to resource imbalance. Therefore, understanding biomass allocation in response to altered resources may be crucial for the development of effective management methods (Xie et al., 2004). Moreover, variation in nutrient availability in the environment may result in changes in nutrient concentrations and ratios in plant tissues (Lambers et al., 1998), which may be closely related to invasion by aquatic plants (Wersal and Madsen, 2011).

Water hyacinth (*Eichhornia crassipes*), a mat-forming aquatic plant originating from tropical South America, is one of the world's most prevalent invasive aquatic plants and causes severe ecological and socio-economic changes where it invades (Center, 1994; Villamagna and Murphy, 2010). Nutrient concentrations and water temperature (air and water) are two key factors for determining its growth and reproduction (Wilson et al., 2005). Moreover, *E. crassipes* performance and clonal propagation are positively correlated with nutrient levels, especially with the P concentration, in the water column (Reddy et al., 1990; Xie et al., 2004). Water hyacinth was introduced into China as an ornamental plant in the early 1900s and is now widely distributed in 17 provinces or cities, causing severe damage in more than 10 provinces (Ding et al., 1995). However, water hyacinth is also often used as a phytoremediation agent for pollutant removal because of its high capability of assimilating nutrients, metal ions and organic pollutants (Malik, 2007; Wang et al., 2012). Because of this dual status, increasing attention is being given to water hyacinth's biological and ecological characteristics, environmental impacts and management, as well as its bioremedial efficiency (Liu et al., 2010; Villamagna and Murphy, 2010). Regardless, to our knowledge, little experimental information exists on the response of water hyacinth to altered nutrient levels in the water column under climate warming.

We conducted a mesocosm experiment to investigate the growth, biomass allocation and carbon/nitrogen balance of *E. crassipes* in response to three nutrient levels representing oligotrophic to eutrophic water under experimental warming in the greenhouse. Our objectives were to determine: (1) how warming and altered nutrient levels interact and affect the growth of water hyacinth, (2) whether biomass allocation to the shoots of this invasive aquatic plant increases to support its rapid propagation in response to these two factors and (3) whether its nutrient (C, N) concentration and mass ratio (C/N) change with altered nutrient levels under experimental warming.

2. Materials and methods

2.1. Plant material

In early August 2009, source material of *E. crassipes* was collected from Liangzi Lake in Hubei Province of China (N 30°05′–30°18′, E 114°21′–114°39′) and then propagated in a greenhouse with lake water (TN 0.6 mg L^{-1}, TP 0.05 mg L^{-1}) at an air temperature of 25 ± 2 °C during the day and 15 ± 2 °C at night under a light regime of approximately 80% of full sun (640–960 μmol m^{-2} s^{-1}) and a light:dark cycle of 14:10 h. To avoid the impact of population differentiation, all the plants were collected from the same clone. Ten days later, 36 homogeneous primary ramets (15 ± 1.21 g, fresh weight) with 6–8 leaves generated by the source plants were selected for the experiment.

2.2. Experimental design

A simulated warming system was set up using a south-north quadrate glassy greenhouse with the south door open to produce a temperature gradient from the south to the north in The National Field Station of Lake Ecosystem of Liangzi Lake, Wuhan University (see You et al., 2013b). This system was passively warmed by solar radiation, and a thermal current flowed from the north of the greenhouse to the south due to the opened south door through the exchange of indoor warm air with outdoor cool air. A temperature gradient of approximately 3.5 °C (mean air temperature) from south to north (from outdoor to indoor, marked Low, Medium and High, with Low treated as ambient temperature) was simulated, rising by approximately 1.5 °C at 8 m intervals during the experiment. The elevated temperature was within the average temperature increase amplitude (1.4–5.8 °C) in 2100 predicted by IPCC. Microclimate parameters including temperature (air and water), light intensity and air CO_2 concentration were monitored every hour using a weather station (PC-3, Jinzhou Sunshine Technology, China), and none of the above mentioned parameters exhibited significant differences, with the exception of temperature during the experimental period. The mean air temperature was 25.3 ± 0.2 °C, 27.3 ± 0.2 °C and 28.8 ± 0.1 °C (mean ± SE, $F_{2,35} = 123.24$, $P < 0.001$, one-way ANOVA), and the mean water temperature (10 cm below water surface) was 24.1 ± 0.1 °C, 25.7 ± 0.2 °C, 27.0 ± 0.2 °C ($F_{2,35} = 166.73$, $P < 0.001$, one-way ANOVA) for the three temperature treatments marked as A, B and C, respectively. Therefore, the microclimate in the greenhouse can be treated as a homogeneous condition, and the simulated warming system is reliable.

A mesocosm experiment was conducted in this simulated warming system in the greenhouse for 6 weeks from August 20 to October 2, 2009. The study was conducted in 36, 100-L aquaria ($L \times W \times H$, 50 cm × 50 cm × 45 cm) with a 3 by 3 factorial arrangement of treatments arranged in a two-way factorial design, with 4 replicates per treatment combination. The two factors were nutrient addition in the water column and simulated warming. There were three levels of nutrient supply (lake water for oligotrophic water (OW), eutrophic water (EW) and high P eutrophic water (HPEW)) for the nutrient addition treatment. The warming treatment was applied with the temperature gradient produced by the simulated warming system (form outdoor to indoor). According to world eutrophication standards, in the nutrient addition treatment, lake water (TN 0.6 mg L^{-1}, TP 0.05 mg L^{-1}) without nutrient addition was a low-nutrient treatment representing oligotrophic water; eutrophic water and high P eutrophic water were applied with two levels of P (NaH_2PO_4) supply (eutrophic water, 0.5 mg L^{-1}; high P eutrophic water, 1.0 mg L^{-1}) and with 5 mg L^{-1} N (NH_4NO_3) (Liu et al., 2010). There was one young plant (15 ± 1.21 g, fresh weight) in each tank in the initial experiment. The culture solution was refreshed weekly after measuring the fresh weight of the plant to avoid the influence of algae blooms on the growth of *E. crassipes* and to maintain a relatively constant concentration of the culture solution. The pH value of the culture was adjusted to approximately 7.0 with weak acids and bases.

2.3. Data collection

During the experiment, the ramet number at all levels (primary ramets, secondary ramets, third ramets and total ramets) and the clonal length was recorded weekly. The fresh weight of the entire plant was determined after draining for 10 min (the plant was carefully taken out of the tank using a nylon mesh and laid on the floor), and then the plants were placed back into their respective tanks. Six weeks later, all the plants were harvested after occupying the entire surface of the tank to avoid the interference of density effects.