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The contribution of seeds to the recruitment of a *Nymphoides peltata* population

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A B S T R A C T

The *Nymphoides peltata* population expands quickly in Lake Taihu, China. One question addressed in this study is whether the seeds of *N. peltata* contribute to this expansion. The buoyancy and germination of *N. peltata* seeds and the development of *N. peltata* seedlings were studied, using seeds collected from Lake Taihu. The results indicated that a low wind velocity of 2.4–3.0 m s^{-1} had a slightly negative effect on seed buoyancy. After 19 and 67 h of gentle stirring, 50% and 90%, respectively, of the *N. peltata* seeds had sunk. Few seeds floated again after sinking, but these refloating seeds sank soon with the disturbance. The *N. peltata* seeds did not germinate without stratification, but the stratification of seeds for a two-week period resulted in a high germination rate (63.3%) at a light intensity of 20 μmol photons m^{-2} s^{-1}. Both the light and stratification treatments stimulated the seeds germination. The seeds did not germinate in sediment at depths greater than 0.25 cm. A high germination rate (74%) was observed for the seeds that laid on the water–sediment interface; however, nearly all of the germinated seeds floated on the water surface after germination. Only a small fraction (14%) of the buoyant seedlings could re-establish in shallow water (less than 3 cm). In the eighth week of the experiments, the buoyant seedlings that failed to re-establish rotted. When grown in low light intensity conditions, the *N. peltata* seedlings had smaller cotyledons, shorter primary roots, and weak development of adventitious roots. Sufficient light was important for both seed germination and seedling development. It was found that sexual reproduction is likely to have little direct contribution to the rapid expansion of *N. peltata* towards the centre of this large shallow lake.

Introduction

Nymphoides peltata (Menyanthaceae) is a wide-spread aquatic species that occurs in a wide range of climates and habitats, especially in temperate regions of the northern hemisphere (Li et al. 2010). In the past few decades, the distribution of *N. peltata* has drastically changed. This species is now listed as ‘vulnerable’ in the national Red Data Book of Japan (Ministry of the Environment, Japan 2002). In contrast, *N. peltata* is an invasive species of North America and New Zealand (Champion and Clayton 2003; Darbyshire and Francis 2008), and it is considered a nuisance in these areas. In China, this native species is expanding rapidly in waterways and lakes, such as Lake Taihu, in Jiangsu Province. *N. peltata* often grows in dense patches and competes with other species. This growth habit leads to stagnant areas with low oxygen levels (Caraco et al. 2006) and threatens commercial shipping and recreational vessels. Therefore, a study of the establishment and propagule dispersal of *N. peltata* is needed.

Lake Taihu is a shallow lake with a surface area of 2338 km^2 and a mean depth of 1.9 m. In the 1950s, the lake was oligotrophic; however, since then, the water quality has decreased, and the lake is now eutrophic. Blue-green algae dominate the west basin of Lake Taihu, whilst the east basin is generally covered by vascular plants (Rose et al. 2004; Qin et al. 2007; Ye et al. 2007). Multi-temporal satellite imagery reveals that Lake Taihu area is dominated by floating-leaved macrophytes; the population of hydrophytes has been increasing rapidly since 2001 (Ma et al. 2008). According to a field survey conducted in the summer of 2010, the floating-leaved macrophytes of Lake Taihu were dominated by *N. peltata* plants.

The *N. peltata* plants colonise by vegetative means (i.e., by vegetative fragments) and by germination of seeds (Cook 1990). The structure of *N. peltata* seeds and the biology of its seed dispersal have been described in detail by van der Velde and van der Heijden (1981), Smits et al. (1989), and Cook (1990). The results reported by these authors are in agreement, but some aspects have not been addressed. For instance, quantitative description of seed buoyancy is lacking. Danvind and Nilsson (1997) proposed a method which can be used for assessing quantitatively the seed buoyancy of *N. peltata*. Furthermore, seed germination is a vital step in the process of population expansion. Takagawa et al. (2005) reported that safe-sites for *N. peltata* seeds germination were those less prone to inundation on bare ground exposed to sufficient light during the spring water-level drawdown. However, seeds located far from the shoreline might be faced with different conditions, such as

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low light intensity and high sediment deposition rate. Successful seedling establishment could lead to the recruitment of *N. peltata* population and contribute to its rapid expansion. In the centre of large, shallow, eutrophic lake, seeds are usually buried by sediment and exposed to low light intensity. However, seed germination and seedling development responses to these environmental stresses have seldom been considered, but are important for refining models of population recruitment and expansion.

In this paper, we hypothesise that seeds are a major contributor to the recruitment and rapid expansion of the *N. peltata* population. The successful recruitment of *N. peltata* from seeds in population expansion depends on three main characteristics: (1) long-distance seed dispersal capacity; (2) successful seed germination; and (3) survivorship of seedlings (establishment and development). Therefore, the aims of this paper are focused on examining these three characteristics to determine whether sexual reproduction plays an important role in the expansion of *N. peltata* populations in the centre of Lake Taihu. A detailed understanding of the reproduction and dispersal patterns will lead to the development of better models of vegetation dynamics and more predictable management results.

Materials and methods

Seed collection and storage

In October 2011, more than 950 ripe fruits were collected from several localities in a *N. peltata* stand of eastern Lake Taihu (31.112° N, 120.366° E). The fruits were stored in an open, plastic container filled with tap water (changed weekly) at room temperature (approximately 20 °C). The fruits were collected randomly from different colonies to minimise the bias for specific plants. In the laboratory, the seeds were released from the fruits naturally. According to Smits et al. (1989), when the fruits become detached from the mother plants at maturity in nature, the seeds within the fruits are stacked upon one another in a fashion analogous to piles of coins. When the stacked seeds are disturbed, they slide away from one another and rest on the water surface. The seeds used for our experiments are randomly selected from 100 fruits, and pre-treatment of seeds were described in every experiment below.

Seed buoyancy

For each experiment, 50 seeds were released from the 5 random fruits and immediately put into a glass beaker (1.5-L) filled with 1-L tap water (four replicates), gently stirred for 5 s, and then the number of floating seeds was counted. The number of floating seeds was counted every 4 min during the first hour, every hour for the next 7 h, thereafter every 12 h for another 15 days (Boedeltje et al. 2003). The beakers were placed in an unheated room in natural daylight. Before each count, a beaker was stirred for 5 s to reduce the influence of water surface tension (Danvind and Nilsson 1997). The effect of stirring beaker was similar to the action of flapping of leaves and wave. The time periods after which 50% (t_{50}) and 90% (t_{90}) of the seeds had sunk were recorded.

In a different treatment, the effect of wind of the seed buoyancy was assessed. The wind was simulated using an electric fan (2.4–3.0 m s^{-1}, AN400 Wind Anemometer, Extech Instruments, New Hampshire, USA) per container. Each experiment utilised 100 seeds in plastic containers (45 cm × 40 cm × 20 cm), with a water depth of 15 cm. Seed buoyancy was monitored for 2 months.

The control was 100 seeds that were left floating on the water surface in plastic containers without any treatment. This experiment was performed for 3 months from October 10, 2011 to January 10, 2012 in triplicate.

Seed germination

The three factors studied were the following: light intensity, stratification (here defined as storage in demineralised water at 4 °C), and seed depth in sediment. The experimental design consisted of the two following treatments:

(a) *Light intensity and stratification interaction*: After being stratified for 0, 1, 2, 3, or 4 weeks, the seeds were incubated in a petri dish and submerged by fresh tap water to a depth of approximately 0.2 cm. Seeds length and width were 2.37 ± 0.13, and 4.19 ± 0.29 mm (n = 389, mean ± S.D.), respectively. All the seeds used were submerged in 0.2 cm of the water. The light was provided by a fluorescent white tube for a photoperiod of 14 h. Each treatment was performed in the following three light regimes: 0, 5, and 20 μmol photons m^{-2} s^{-1}. The maximum light intensity of the light gradient in the area slightly above the sediment of the *N. peltata* stand in Lake Taihu in May was similar to the light intensity used in the laboratory experiments (LI-189, LI-COR, Inc., Lincoln, NE, USA). Batches of 30 seeds were used in each Petri dish for each experiment, and the experiments were performed in triplicate at 25 °C in a climate-controlled room. The experiment lasted four weeks. During the period, the water was replenished, and the germinated seeds were counted and removed every other day.

(b) *Light intensity and seed depth interaction*: The seeds that were stratified for 4 weeks were used in the experiments. The substrates were collected from the *N. peltata* stand in Lake Taihu (31.112° N, 120.366° E). The average size of the particles in suspension was close to 9.5 ± 0.0 μm (n = 3, mean ± S.D.), measured by a laser diffraction instrument (Mastersize 2000, Malvern, UK). A stable weight of 4.5 ± 0.3% (n = 3, mean ± S.D.) was obtained by performing loss on ignition to estimate sediment organic matter at 550 °C for 4 h. The concentration of total nitrogen and total phosphorus were 1.24 ± 0.09, and 0.33 ± 0.02 g kg^{-1} (n = 3, mean ± S.D.), respectively. The sediment was passed through a 1.5-mm sieve to remove the *N. peltata* seeds and then stirred in a mixer. The substrates were collected in 1-L black cylindrical polyethylene containers or 1-L rectangular glass containers that were filled to a height of 15 cm. Seed germination was examined using the two following experimental designs: (I) The seeds were horizontally sown (cotyledons emerged parallel to the water–sediment interface) at depths of 0, 0.25, 0.5, 1.0, and 1.5 cm in the black polyethylene containers. Each depth treatment was placed in a new container. The light was provided at the top of the containers by a fluorescent white tube at an intensity of 20 μmol photons m^{-2} s^{-1}; (II) The seeds were vertically sown (cotyledons emerged perpendicular to the water–sediment interface) along the wall of the rectangular glass containers at depths of 0, 0.25, 0.5, 1.0, and 1.5 cm with reference to the longitudinal axis of the seeds. The light was provided by a laterally positioned, fluorescent white tube at an intensity of 20 μmol photons m^{-2} s^{-1}. This approach allowed us to determine the effect of light on seed germination at different depths. All containers were placed in continuously circulating water at 25 °C, and performed in triplicate. For each experiment, 30 seeds were planted in each container; the water was replaced with aerated tap water once a week. If the radicle protruded at least 1 mm from the seed, the seed was scored as germinated.