

# Physiological integration helps a clonal macrophyte spread into competitive environments and coexist with other species

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## ABSTRACT

Physiological integration may help clonal macrophytes invade or escape from existing communities. No studies have tested the above hypothesis in aquatic plants. In an outdoor pond experiment, we subjected clonal fragments of the submerged macrophyte *Vallisneria spiralis* L. to heterogeneous environments in which *V. spiralis* spread from bare habitats towards vegetated habitats occupied by *Myriophyllum spicatum* L. or *V. spiralis* spread from vegetated habitats towards bare habitats. *V. spiralis* stolons between ramets in bare habitats and in vegetated habitats were either intact or severed. We investigated the habitat selection of *V. spiralis* by examining the allocation of biomass and ramets to heterogeneous habitats during its vegetative spread phase. Results showed that the stolon connection had different effects on the habitat selection of *V. spiralis* with regard to invasion and escape. When *V. spiralis* spread from bare to vegetated habitats, in comparison to severing the stolon, the stolon connection eventually facilitated a 49% increase in biomass and a 27% increase in number of ramets allocated to vegetated habitats. However, when *V. spiralis* spread from vegetated to bare habitats, biomass and ramets allocated to bare habitats were not significantly changed by the stolon connection (only a 5% increase in biomass and a 6% increase in number of ramets). These results indicate that clonal integration facilitated *V. spiralis* not to escape from but invade into vegetated habitats. The study provides evidence that physiological integration is important for survival and tolerance of ramets in competitively stressful environments and can help clonal macrophytes coexist with other species.

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## 1. Introduction

A great number of studies have shown that connected ramets of clonal plants can share photosynthate, water, and nutrients through clonal integration (Alpert and Mooney, 1986; Stuefer and Hutchings, 1994; de Kroon et al., 1998; Alpert et al., 2003; Marbà et al., 2006). Clonal integration can improve the survival, growth, and reproduction of ramets in stressful environments and help genets occupy open space (Hutchings and Wijesinghe, 1997; Amsberry et al., 2000; Wang et al., 2008). These positive effects of clonal integration may provide clonal plants with a competitive advantage by improving the performance of ramets in communities and reducing the growth and reproduction of their competitors. Therefore, clonal integration may influence species coexistence and community structure (Pennings and Callaway, 2000; Peltzer, 2002; Březina et al., 2006; Yu et al., 2009).

Genets or fragments of clonal plants can be established initially in bare or vegetated habitats because of the mosaic structures of natural communities (Hutchings and Wijesinghe, 1997; Oborny et al., 2000). When clonal plants, especially the guerrilla growth forms (i.e. clonal plants with relatively long stolons or rhizomes and a strong tendency to grow in a single direction with little branching, see Lovett Doust, 1981), begin their vegetative spread across borders in heterogeneous communities, two possible directions exist: escape away from or invasion into interspecific neighbours. However, previous experiments dealing with the physiological integration of clonal plants during competition with neighbours have not considered the direction of clonal growth as an important variable. Whether invasion into a competitive habitat or escape to an open habitat is more dependent on clonal integration remains to be clarified.

Clonal growth is very common in wetland and aquatic plant species (Grace, 1993; Sosnová et al., 2011). After initial colonization of a site by seedlings or asexual propagules, clonal growth seems to be the primary method of maintaining and expanding natural populations for aquatic clonal species (Marbà and Duarte, 1998; Santamaria, 2002). For understanding the role of clonal growth of aquatic plants, it is necessary to research the clonal integration, one of the important characteristics of clonal growth. There are

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some studies that have tested the effects of clonal integration on growth of aquatic macrophytes (Terrados et al., 1997; Nielsen and Pedersen, 2000; Marbà et al., 2002; Xiao et al., 2007, 2010). However, no study has reported the effect of clonal integration on the spatial distribution of submerged macrophytes when they compete with neighbours.

To assess how clonal integration affects the invasion or escape of clonal macrophytes in heterogeneous communities, ramets having a stolon apex of the stoloniferous macrophyte *Vallisneria spiralis* L. were subjected to heterogeneous environments in which *V. spiralis* spread from bare habitats towards vegetated habitats occupied by *Myriophyllum spicatum* L. or *V. spiralis* spread from vegetated habitats towards bare habitats. Furthermore, stolons between ramets in bare habitats and vegetated habitats were either intact or severed. Our hypotheses were: (1) when *V. spiralis* grows from bare to vegetated habitats, clonal integration will facilitate *V. spiralis* invasion into vegetated habitats and further support survival and tolerance of its offspring ramets in vegetated habitats; (2) when *V. spiralis* grows from vegetated to bare habitats, mother ramets will help offspring ramets escape away from vegetated habitats at the beginning of experiment, but this process might be reversed when the offspring ramets in bare habitats grown up, i.e. mother ramets in vegetated habitats might be improved by connections with offspring ramets in bare habitats at the end of experiment.

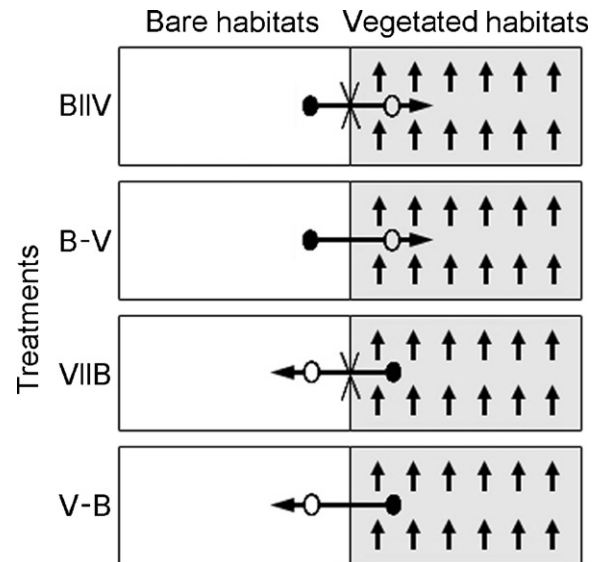
## 2. Materials and methods

### 2.1. Plant materials

*V. spiralis* is an important freshwater submerged macrophyte in many regions of the world (Lowden, 1982). It can produce plagiotropic stolons, spread horizontally above the sediment surface, and form ramets at the nodes. Each ramet has a basal rosette of leaves which may extend to the surface but do not form a canopy. These ramets are interconnected by stolons and form a large clonal system across heterogeneous environments (Xiao et al., 2007). At the study site, *V. spiralis* generally began clonal growth in April and continued to September, flowered and fruited in autumn, and overwintered by tubers. Its leaves died down at the end of autumn. In the field, *V. spiralis* and its congener *Vallisneria americana* Michx. often coexist with *M. spicatum* (Titus and Adams, 1979; Zhan et al., 2001). Whereas, *V. spiralis* occupies horizontal space over the sediment by clonal growth, *M. spicatum* generally occupies vertical space in the water column by shoot branching.

### 2.2. Experimental design

Two hundred tubers of *V. spiralis* were buried into pots with sand covered by 10 cm water in a greenhouse and sprouted in mid-April. After approximately 3 weeks, each sprout formed a ramet and began producing a stolon. Ninety-six ramets having an initial stolon and uniform size were selected as testing plants (15–20 cm in height and three to four leaves). At the same time, about 800 shoots of *M. spicatum*, each 40–50 cm high, were collected from Liangzi Lake. On 8 May, we conducted the experiment in 24 outdoor concrete ponds in the National Field Station for Lake Ecosystem in Liangzi Lake, Hubei Province, China (30°15'N, 114°33'E; 17 m asl.). The ponds were the same size (200 cm in length, 200 cm in width, 120 cm in height), were oriented equivalently towards the sun, and each of them was filled with a 20 cm depth of lake clay. The lake clay was homogenized before being placed in the ponds. Each pond was divided into four strips of equal size (200 cm in length, 50 cm in width), and *M. spicatum* was then transplanted into half of each strip (100 cm in length, 50 cm in width, vegetated habitats) at a density of 16 shoots m<sup>-2</sup>. The initial planting



**Fig. 1.** Schematic representation of the experimental design. Clonal fragments of *Vallisneria spiralis*, each consisting of one mother ramet (filled circles) and one offspring ramet (open circles) with a stolon apex (horizontal arrow), were grown either with (vegetated habitats) or without (bare habitats) competitors (*Myriophyllum spicatum*, vertical arrows) and with stolon connections between mother ramet and offspring ramet that were either intact or severed (fork). Four treatments were utilised as follows: B<sub>11</sub>V (stolons spreading from bare to vegetated habitats were severed), B–V (stolons spreading from bare to vegetated habitats remained intact), V<sub>11</sub>B (stolons spreading from vegetated to bare habitats were severed), and V–B (stolons spreading from vegetated to bare habitats remained intact).

density of *M. spicatum* shoots was consistent with shoot density in the field. The other half of the strip was left bare (100 cm in length, 50 cm in width, bare habitats). The four vegetated habitats or four bare habitats were located side by side in the same side of each pond (Fig. 1). One *V. spiralis* ramet having an initial stolon was then transplanted into each strip. Of the four strips in each pond, two ramets were transplanted randomly into two bare habitats with their initial stolons pointing towards two vegetated habitats, and the other two ramets were transplanted randomly into two vegetated habitats with their initial stolons pointing towards two bare habitats. After transplanting the plants, all of the ponds were filled with lake water and maintained full water during the experiment. On 31 May, we found that all transplanted plants survived. Each *V. spiralis* initial ramet had elongated its stolon and produced rooted offspring ramets in the other habitats. We then randomly selected one of the two *V. spiralis* plants oriented in the same growth direction in each pond and severed the stolons between the mother ramets and the offspring ramets in different habitats. Therefore, there were four treatments were set up randomly in each pond, which were designated as follows: B<sub>11</sub>V (stolons spreading from bare to vegetated habitats were severed), B–V (stolons spreading from bare to vegetated habitats remained intact), V<sub>11</sub>B (stolons spreading from vegetated to bare habitats were severed), and V–B (stolons spreading from vegetated to bare habitats remained intact) (Fig. 1).

### 2.3. Measurements

The experiment were harvested on 21 June, 12 July, and 4 August. Eight ponds were used for each harvest, and each treatment was replicated with eight *V. spiralis* clones for each harvest. For each part of the *V. spiralis* clonal fragment in different habitats, we counted the number of ramets, oven-dried the plants at 80 °C for 72 h, and measured their weight. A complete unit of

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