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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.

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^{-2}. The initial planting 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: $B_{II}V$ (stolons spreading from bare to vegetated habitats were severed), B–V (stolons spreading from bare to vegetated habitats remained intact), $V_{II}B$ (stolons spreading from vegetated to bare habitats were severed), and V–B (stolons spreading from vegetated to bare habitats remained intact) (Fig. 1).

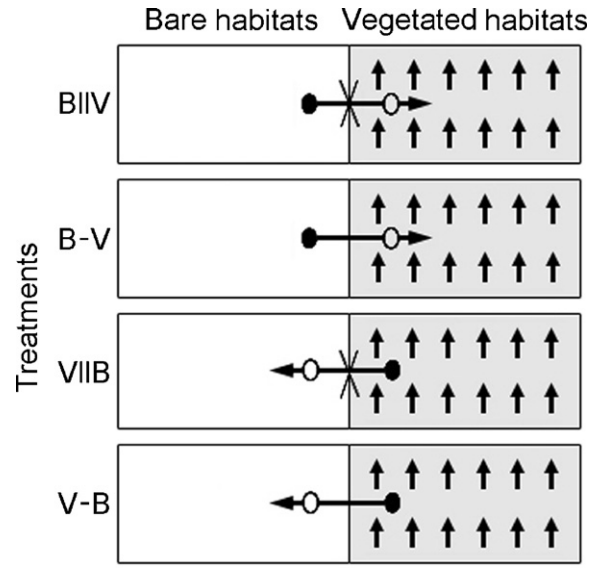

Fig. 1. Schematic representation of the experimental design. Clonal fragments of *Vallisneria spiralis*, each consisting of one mother ramet (filled circles) and one offspring ramet (open circles) with a stolon apex (horizontal arrow), were grown either with (vegetated habitats) or without (bare habitats) 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: $B_{II}V$ (stolons spreading from bare to vegetated habitats were severed), B–V (stolons spreading from bare to vegetated habitats remained intact), $V_{II}B$ (stolons spreading from vegetated to bare habitats were severed), and V–B (stolons spreading from vegetated to bare habitats remained intact).

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

V. spiralis ramets originating from the initially transplanted ramet was defined as one whole clonal fragment. At a cloudless midday before the final harvest, we used a solar monitor to measure irradiance at the sediment surface in each bare and vegetated patch. The measured photosynthetic photon flux density was $1512 \pm 21\,\mu mol\,m^{-2}\,s^{-1}$ (means ± SD) in bare habitats and $453 \pm 14\,\mu mol\,m^{-2}\,s^{-1}$ in vegetated habitats. The average biomass and density of *M. spicatum* in vegetated habitats was 117 ± 18 g (mean ± SD) and 131 ± 12 shoots m^{-2} (mean ± SD) at the final harvest, respectively.

2.4. Data analysis

Prior to analysis, variables were transformed as necessary to meet the assumptions of normality and homoscedasticity for ANOVA. Block effects (the position effect of four treatments in each pond) had been examined in the analysis. Two-way ANOVA was used to investigate the effects of clonal growth direction, stolon connection and their interaction on dry weight and ramet number of the whole clonal fragments, the mother and offspring ramets of *V. spiralis* at the last harvest time, respectively. A post-hoc test (Duncan) at the 0.05 significance level was performed for difference between size of clonal fragments among the four treatments at the last harvest time. All statistical tests were performed with SPSS 15.0 (SPSS, Chicago, IL, USA).

3. Results

During the experimental period, *V. spiralis* showed a strong capacity for acropetal stolon growth. Substantial biomass and ramets were produced in offspring ramets of the clonal fragment whether or not it was in vegetated habitats (Fig. 2). Severing the stolon resulted in an increase in biomass and number of ramets in the mother ramets of the clonal fragments at the expense of offspring ramets. When *V. spiralis* grew from vegetated to bare habitats, the biomass and ramet number of the whole clonal fragment were not significantly changed by severing stolon. Harvest time had a noticeable and significant interaction with stolon connection on the growth of ramets in vegetated habitats (for dry weight: $F = 12.698$, $P < 0.001$; for ramet number: $F = 77.177$, $P < 0.001$). Especially when separated from ramets in bare habitats, the biomass and number of ramets in vegetated habitats, even the offspring ramets of the clonal fragment, significantly decreased from 12 July to 4 August (Fig. 2).

The clonal direction and stolon connection had significant interaction on the growth of *V. spiralis* (Table 1). When *V. spiralis* invaded vegetated habitats, the stolon connection significantly enhanced the biomass and number of ramets of the whole clonal fragment, especially the offspring ramets in vegetated habitats (for biomass: $F = 56.716$, $P < 0.001$; for ramet number: $F = 212.268$, $P < 0.001$; Fig. 3). In comparison to severing the stolon, the stolon connection eventually facilitated a 49% increase in the total biomass and a 27% increase in number of ramets allocated to vegetated habitats. However, no significant effect of stolon connection was observed with regard to the size of whole clonal fragment in the opposite direction. When *V. spiralis* grew from vegetated to bare habitats, the biomass and number of ramets in bare habitats were not significantly changed by the stolon connection (for biomass: $F = 3.044$, $P = 0.088$; for number of ramets: $F = 0.808$, $P = 0.374$; Fig. 3). The stolon connection only helped *V. spiralis* a 5% increase

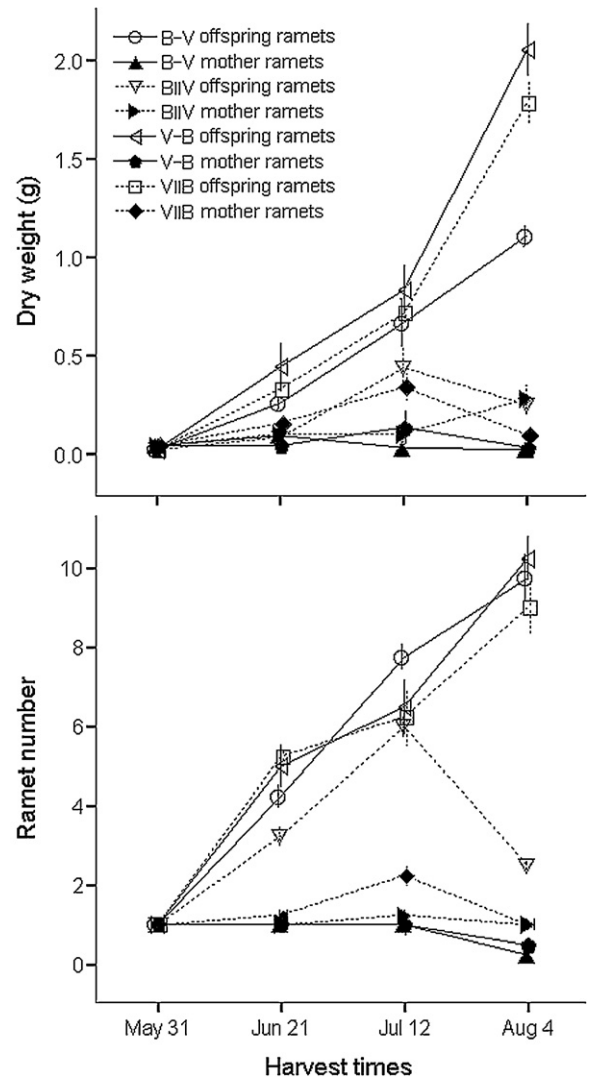

Fig. 2. Dry weight (means ± SE) and ramet number (means ± SE) of the mother and offspring ramets of *Vallisneria spiralis* over the four harvest times in the four treatments. See Fig. 1 for the treatment codes.

Table 1
F-vaules and their significance for effects of clonal growth direction, stolon connection and their interaction on dry weight and ramet number of the whole clonal fragments, the mother ramets, and the offspring ramets at the last harvest time.

Source of variation	d.f.	Whole clonal fragments		Mother ramets		Offspring ramets	
		Dry weight	Ramet number	Dry weight	Ramet number	Dry weight	Ramet number
Block	3,31	1.696^{ns}	0.993^{ns}	2.130^{ns}	2.333^{ns}	0.732^{ns}	0.785^{ns}
Clonal direction (*D*)	1,31	77.147^{***}	31.015^{***}	5.510^{*}	1.000^{ns}	123.296^{***}	34.449^{***}
Stolon connection (*C*)	1,31	24.065^{***}	62.246^{***}	19.810^{***}	25.000^{***}	47.162^{***}	92.654^{***}
$D \times C$	1,31	0.075^{ns}	42.215^{***}	7.088^{*}	1.000^{ns}	2.882^{ns}	40.181^{***}

ns, not significant.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

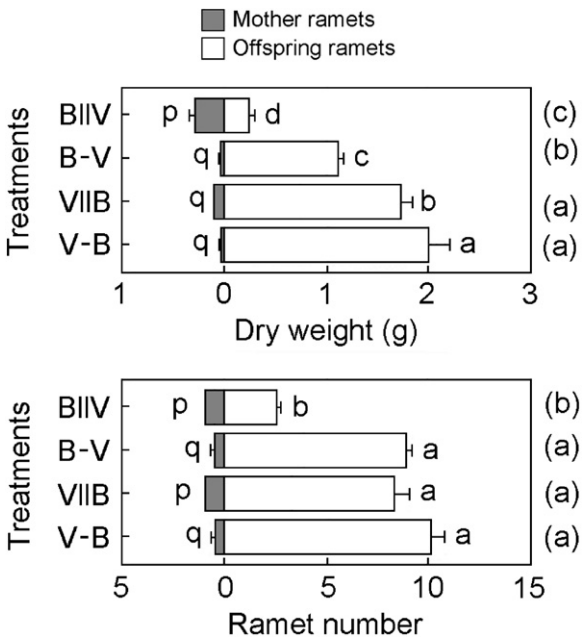

Fig. 3. Dry weight (means ± SE) and ramet number (means ± SE) of the mother and offspring ramets of *Vallisneria spiralis* at the last harvest time in the four treatments. See Fig. 1 for the treatment codes. The values of whole clonal fragments are the sum of those of the mother and offspring ramets. The same letter (a, b, c, d) among the four offspring ramets and the same letter (p, q) among the four mother ramets are not different at $P = 0.05$. The same letter in parenthesis are not different at $P = 0.05$ comparing the values of whole clonal fragments among the four treatments.

in its total biomass and a 6% increase in its number of ramets into bare habitats at the end of experiment.

4. Discussion

4.1. Neighbour competition

When separated from ramets in bare habitats, the biomass and number of ramets of *V. spiralis* in vegetated habitats significantly decreased at the end of experiment. Even though the connection significantly increased the biomass and number of ramets in vegetated habitats, their values were still smaller than those observed for bare habitats, especially for the final biomass. These results suggest that competition with *M. spicatum* suppressed the clonal growth of *V. spiralis*. The reason might be that the competition between *M. spicatum* and *V. spiralis* was asymmetrical because of the low density of *V. spiralis* in this experiment. In addition, larger individuals may reduce the light available to smaller individuals and thus suppress their growth (Weiner, 1990; de Kroon et al., 1992). The loss in biomass and number of *V. spiralis* in vegetated habitats from 12 July to 4 August might be due to the suppression by *M. spicatum*. As we measured, reduced light levels resulting from *M. spicatum* over-topping could be the main reason for the reduction in growth parameters of *V. spiralis* in vegetated habitats.

4.2. Effects of physiological integration

When *V. spiralis* invaded the vegetated habitats occupied by *M. spicatum*, stolon connection significantly enhanced the biomass and number of ramets in vegetated habitats and resulted in a larger-sized clonal fragment. This may be due to promotion of photosynthetic capacity of ramets in bare habitats by the strong carbon demand of sinks created by connected ramets in vegetated habitats. Furthermore, more material was produced and transported to offspring ramets in vegetated habitats (Stuefer et al., 1994; Roiloa and Retuerto, 2005; Xiao et al., 2007). Therefore, clonal integration enhanced the performance and tolerance of ramets in vegetated habitats. This result confirms the first hypothesis.

When *V. spiralis* grew from vegetated to bare habitats, the stolon connection did not significantly help offspring ramets escaping from vegetated habitats at the beginning of experiment, and that the growth of mother ramets in vegetated habitats was not improved by connections with offspring ramets in bare habitats at the end of experiment. Therefore, the second hypothesis was not confirmed. These results imply that the reciprocal physiological integration did not occur or was too small to have a significant effect on growth. This is consistent with the author's former study, in which *V. spiralis* only benefited from acropetal clonal integration in heterogeneous light environments (Xiao et al., 2007). However, several studies demonstrated extensive physiological integration in some clonal plants such that, regardless of the direction of clonal growth, ramets in a disadvantageous environment can be supported by those in a favourable environment (Jónsdóttir and Watson, 1997; D'Hertefeldt and Falkengren-Grerup, 2002). Stuefer and Hutchings (1994) considered acropetal transport to be the predominant reason for the loss of reciprocal physiological integration. Although no transpiration occurs underwater, submerged plants still have the ability of acropetal transport (Terrados et al., 1997; Marbà et al., 2002). Some studies have shown that material transfer between interconnected ramets of clonal plants is closely related to water transport (de Kroon et al., 1998; D'Hertefeldt and Falkengren-Grerup, 2002). Because basipetal integration is often observed in clonal plants located in very dry environments, basipetal transport might result from the uneven distribution of water. Since water transport is acropetal in submerged plants (Pedersen and Sand-Jensen, 1993), we presume that physiological integration would also be acropetal underwater, although this hypothesis requires further study.

4.3. Habitat selection in heterogeneous communities

One growth strategy for clonal species in heterogeneous environments is the selective placement of ramets in favourable habitats. This is expected to enhance resource acquisition and has been interpreted as habitat selection or foraging behaviour (Hutchings and de Kroon, 1994). When spread from vegetated to bare habitats, *V. spiralis* placed more ramets into bare habitats in spite of severing connections with basal ramets. This indicates that *V. spiralis* can escape an adverse environment through clonal growth. This habitat selection has been demonstrated in some terrestrial clonal plants (Evans and Cain, 1995; Macek and Lepš, 2003; Sampaio et al., 2004), and in some aquatic clonal plants (Titus and Stephens, 1983; Xiao et al., 2006). Because resource availability in bare habitats was sufficient for offspring ramets, they no longer depended on support from mother ramets. Therefore, clonal integration between connected ramets in different habitats contributed little to escape of *V. spiralis* away from vegetated habitats occupied by *M. spicatum*. In the process of competition between *V. spiralis* and *M. spicatum*, physiological integration greatly increased the interaction between *V. spiralis* and *M. spicatum*. We speculate that *V. spiralis* can continually invade into the area occupied by *M. spicatum*, leading to coexistence.

In conclusion, the present study showed that clonal integration did not facilitate *V. spiralis* to escape away from vegetated habitats at the temporal resolution of this study, but significantly helped *V. spiralis* invasion into vegetated habitats. This provides evidence that clonal integration is important for survival and tolerance of ramets in competitively stressful environments and can help clonal plants to coexist with other species.

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References

Alpert, P., Holzapfel, C., Slonimski, C., 2003. Differences in performance between genotypes of *Fragaria chiloensis* with different degrees of resource sharing. J. Ecol. 91, 27–35.
Alpert, P., Mooney, H.A., 1986. Resource sharing among ramets in the clonal herb, *Fragaria chiloensis*. Oecologia 70, 227–233.
Amsberry, L., Baker, M.A., Ewanchuk, P.J., Bertness, M.D., 2000. Clonal integration and the expansion of *Phragmites australis*. Ecol. Appl. 10, 1110–1118.
Březina, S., Koubek, T., Münzbergová, Z., Herben, T., 2006. Ecological benefits of integration of *Calamagrostis epigejos* ramets under field conditions. Flora 201, 461–467.
de Kroon, H., Hara, T., Kwant, R., 1992. Size hierarchies of shoots and clones in clonal herb monocultures: do clonal and non-clonal plants compete differently? Oikos 63, 410–419.
de Kroon, H., van Der Zalm, E., van Rheenen, J.W.A., van Dijk, A., Kreulen, R., 1998. The interaction between water and nitrogen translocation in a rhizomatous sedge (*Carex flacca*). Oecologia 116, 38–49.
D'Hertefeldt, T., Falkengren-Grerup, U., 2002. Extensive physiological integration in *Carex arenaria* and *Carex disticha* in relation to potassium and water availability. New Phytol. 156, 469–477.
Evans, J.P., Cain, M.L., 1995. A spatially explicit test of foraging behavior in a clonal plant. Ecology 76, 1147–1155.
Grace, J.B., 1993. The adaptive significance of clonal reproduction in angiosperms: an aquatic perspective. Aquat. Bot. 44, 159–180.
Hutchings, M.J., de Kroon, H., 1994. Foraging in plants: the role of morphological plasticity in resource acquisition. Adv. Ecol. Res. 25, 159–238.
Hutchings, M.J., Wijesinghe, D.K., 1997. Patchy habitats, division of labor and growth dividends in clonal plants. Trends Ecol. Evol. 12, 390–394.
Jónsdóttir, I.S., Watson, M.A., 1997. Extensive physiological integration: an adaptive trait in resource-poor environments? In: de Kroon, H., van Groenendael, J. (Eds.), The Ecology and Evolution of Clonal Plants. Backhuys Publishers, Leiden, pp. 109–136.
Lovett Doust, L., 1981. Population dynamics and local specialisation in a clonal plant (*Ranunculus repens*): I. The dynamics of ramets in contrasting habitats. J. Ecol. 69, 743–755.
Lowden, R.M., 1982. An approach to the taxonomy of *Vallisneria* L (Hydrocharitaceae). Aquat. Bot. 13, 269–298.
Macek, P., Lepš, J., 2003. The effect of environmental heterogeneity on clonal behaviour of *Prunella vulgaris* L. Plant Ecol. 168, 31–43.
Marbà, N., Duarte, C.M., 1998. Rhizome elongation and seagrass clonal growth. Mar. Ecol. Prog. Ser. 174, 269–280.
Marbà, N., Hemminga, M.A., Duarte, C.M., 2006. Resource translocation within seagrass clones: allometric scaling to plant size and productivity. Oecologia 150, 362–372.
Marbà, N., Hemminga, M.A., Mateo, M.A., Duarte, C.M., Mass, Y.E.M., Terrados, J., Gacia, E., 2002. Carbon and nitrogen translocation between seagrass ramets. Mar. Ecol. Prog. Ser. 226, 287–300.
Nielsen, S.L., Pedersen, M.F., 2000. Growth, photosynthesis and nutrient content of seedling and mature plants of *Cymodocea nodosa*—the importance of clonal integration. Aquat. Bot. 68, 265–271.
Oborny, B., Kun, A., Czaran, T., Bokros, S., 2000. The effect of clonal integration on plant competition for mosaic habitat space. Ecology 81, 3291–3304.
Pedersen, O., Sand-Jensen, K., 1993. Water transport in submerged macrophytes. Aquat. Bot. 44, 385–406.
Peltzer, D.A., 2002. Does clonal integration improve competitive ability? A test using aspen (*Populus tremuloides* [Salicaceae]) invasion into prairie. Am. J. Bot. 89, 494–499.
Pennings, S.C., Callaway, R.M., 2000. The advantages of clonal integration under different ecological conditions: a community-wide test. Ecology 81, 709–716.
Roiloa, S.R., Retuerto, R., 2005. Presence of developing ramets of *Fragaria vesca* L. increases photochemical efficiency in parent ramets. Int. J. Plant Sci. 166, 795–803.
Sampaio, M.C., Araújo, T.F., Scarano, F.R., Stuefer, J.F., 2004. Directional growth of a clonal bromeliad species in response to spatial habitat heterogeneity. Evol. Ecol. 18, 429–442.
Santamaria, L., 2002. Why are most aquatic plants widely distributed? Dispersal, clonal growth and small-scale heterogeneity in a stressful environment. Acta Oecol. 23, 137–154.
Sosnová, M., van Diggelen, R., Macek, P., Klimesová, J., 2011. Distribution of clonal growth traits among wetland habitats. Aquat. Bot., doi:10.1016/j.aquabot.2011.04.001.
Stuefer, J.F., During, H.J., de Kroon, H., 1994. High benefits of clonal integration in two stoloniferous species, in response to heterogeneous light environments. J. Ecol. 82, 511–518.
Stuefer, J.F., Hutchings, M.J., 1994. Environmental heterogeneity and clonal growth: a study of the capacity for reciprocal translocation in *Glechoma hederacea* L. Oecologia 100, 302–308.
Titus, J.E., Adams, M.S., 1979. Coexistence and the comparative light relations of the submersed macrophytes *Myriophyllum spicatum* L. and *Vallisneria americana* Michx. Oecologia 40, 273–286.
Titus, J.E., Stephens, M.D., 1983. Neighbor influences and seasonal growth patterns for *Vallisneria americana* in a mesotrophic lake. Oecologia 56, 23–29.
Terrados, J., Duarte, C.M., Kenworthy, W.J., 1997. Is the apical growth of *Cymodocea nodosa* dependent on clonal integration? Mar. Ecol. Prog. Ser. 158, 103–110.
Wang, N., Yu, F., Li, P., He, W., Liu, F., Liu, J., Dong, M., 2008. Clonal integration affects growth, photosynthetic efficiency and biomass allocation, but not the competitive ability, of the alien invasive *Alternanthera philoxeroides* under severe stress. Ann. Bot. 101, 671–678.
Weiner, J., 1990. Asymmetric competition in plant populations. Trends Ecol. Evol. 5, 360–364.
Xiao, K., Yu, D., Wang, J., 2006. Habitat selection in spatially heterogeneous environments: a test of foraging behavior in the clonal submerged macrophyte *Vallisneria spiralis* L. Freshwater Biol. 51, 1552–1559.
Xiao, K., Yu, D., Xu, X., Xiong, W., 2007. Benefits of clonal integration between interconnected ramets of *Vallisneria spiralis* in heterogeneous light environments. Aquat. Bot. 86, 76–82.
Xiao, Y., Tang, J., Qing, H., Ouyang, Y., Zhao, Y., Zhou, C., An, S., 2010. Clonal integration enhances flood tolerance of *Spartina alterniflora* daughter ramets. Aquat. Bot. 92, 9–13.
Yu, F., Wang, N., Alpert, P., He, W., Dong, M., 2009. Physiological integration in an introduced, invasive plant increases its spread into experimental communities and modifies their structure. Am. J. Bot. 96, 1983–1989.
Zhan, C., Yu, D., Wu, Z., Liu, C., Li, Z., 2001. The community ecology of aquatic plant in the water-land ecotone of Liangzi Lake. Acta Phytoeco. Sin. 25, 573–580.