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Habitat selection in spatially heterogeneous environments: a test of foraging behaviour in the clonal submerged macrophyte *Vallisneria spiralis*

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SUMMARY

1. To test whether clonal macrophytes can select favourable habitats in heterogeneous environments, clonal fragments of the stoloniferous submerged macrophyte *Vallisneria spiralis* were subjected to conditions in which light intensity and substratum nutrients were patchily distributed. The allocation of biomass accumulation and ramet production of clones to the different patches was examined.
2. The proportion of both biomass and ramet number of clones allocated to rich patches was significantly higher than in poor patches. The greatest values of both clone and leaf biomass were produced in the heterogeneous light treatment, in which clones originally grew from light-rich to light-poor patches, while clones produced the most offspring ramets in the treatments with heterogeneous substratum nutrients. Similarly, root biomass had the highest values in nutrient-rich patches when clones grew from nutrient-rich to nutrient-poor patches.
3. The quality of patches in which parent ramets established significantly influenced the foraging pattern. When previously established in rich patches, a higher proportion of biomass was allocated to rich patches, whereas a higher proportion of ramet number was allocated to rich patches when previously established in poor patches.
4. Results demonstrate that the clonal macrophyte *V. spiralis* can exhibit foraging in submerged heterogeneous environments: when established under resource-rich conditions *V. spiralis* remained in favourable patches, whereas if established in adverse conditions it could escape by allocating more ramets to favourable patches.

Keywords: clonal growth, foraging behaviour, heterogeneous environment, morphological plasticity, submerged macrophyte

Introduction

Essential resources for plants are usually distributed patchily in natural environments (Caldwell & Pearcy, 1994; Hutchings, John & Stewart, 2000). The ubiquity of heterogeneity in natural habitats makes it likely that plasticity will have evolved enabling plants to cope with, and perhaps even benefit from, heterogeneous rather than homogeneous environments. This may be particularly true for clonal species (van Kleunen, Fischer & Schmid, 2000; van Kleunen & Fischer, 2001). Clonal species dominate many natural communities (van Groenendael *et al.*, 1996; Klimes *et al.*, 1997), in which the genets of some species can live for thousands of years and cover many thousands of square metres (Cook, 1985). Therefore, it is highly likely that sites occupied by connected ramets of these species will differ from one another in the availability of essential resources. Many studies of clonal species have described plasticity in the form of localised morphological responses to small-scale differences in growing conditions (Slade & Hutchings, 1987; Dong, 1993; Wijesinghe & Hutchings, 1997; Sampaio *et al.*, 2004).

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One growth strategy for clonal species in heterogeneous environments is the selective (i.e. non-random) placement of resource-acquiring structures in favourable habitats (Salzman, 1985; Sutherland, 1987; Bazzaz, 1991; Kelly, 1992). This is expected to enhance resource acquisition and has been interpreted as foraging behaviour (Silvertown & Gordon, 1989; Hutchings & de Kroon, 1994; Oborny & Cain, 1997). First, clonal architecture (including spacer length, branching intensity and branching angle) may change to position offspring ramets preferentially in favourable habitats or escape unfavourable ones (Sutherland & Stillman, 1988; de Kroon & Hutchings, 1995; Oborny & Cain, 1997). In addition, clonal foraging is often accompanied by localised morphological specialisations that enhance the ability of the plant to acquire resources from habitat patches in which they are abundant (Dong, 1995; Stuefer, de Kroon & During, 1996; Wijesinghe & Hutchings, 1997).

Clonal foraging in heterogeneous environments has been studied extensively in clonal plants from a number of terrestrial habitats such as grasslands, forest understorey, salt marshes, sand dune and disturbed sites (Sutherland & Stillman, 1988; Hutchings & de Kroon, 1994; Oborny & Cain, 1997). Although clonal growth is more frequent in aquatic than in terrestrial habitats (Grace, 1993; Barrett, Echert & Husband, 1993; Philbrick & Les, 1996; van Groenendael *et al.*, 1996), information on the foraging behaviour of clonal aquatic plants is lacking. There are a number of differences in the growth conditions of clonal macrophytes, especially submerged species, compared with terrestrial habitats, associated with water saturation and a lack of transpiration. In addition, other resources such as carbon dioxide may constrain the growth of submerged macrophytes (Vadstrup & Madsen, 1998). Therefore, some differences in foraging behaviour might be expected between aquatic and terrestrial clonal species in heterogeneous environments.

Vallisneria spiralis L. is an important freshwater submerged macrophyte in many regions of the world (Lowden, 1982). It can produce plagiotropic stolons, spread horizontally aboveground and form many ramets at the nodes. These ramets are usually interconnected by stolons and form large clonal system across heterogeneous environments. In this study, the clonal fragments of *V. spiralis* were subjected to spatially heterogeneous environments in terms of light intensity and substratum nutrient concentrations. The aim was to test the following question: Are clones of *V. spiralis* growing in spatially heterogeneous environments able to remain in favourable patches and escape unfavourable ones?

Methods

Plant materials

A clone originated from a single tuber collected from a natural population of *V. spiralis* in Liangzi Lake (30°05′–30°18′N, 114°21′–114°39′E) produced about 200 tubers in an outdoor pond at the Freshwater Ecological Station of Liangzi Lake in 2002. At the end of March 2003, these tubers were dug up and transplanted into sand covered by 10 cm water and kept in a greenhouse. About 6 weeks later the tubers sprouted and produced their parent ramets. Sixty-four single ramets with an initial stolon of uniform size were selected for use in the experiment (15–20 cm height and three to four leaves).

Experimental set-up

Single ramets with a stolon were transplanted into one of two adjoined patches with different light intensity or substratum nutrient content (Fig. 1). There were two levels of light supply and two types of substratum: light-rich conditions (full natural daylight, 100% photosynthetic photon flux density 1800–2300 μmol m^{-2} s^{-1} during the experiment); light-poor conditions (10% of full sunlight, obtained by covering with neutral shading nets); nutrient-rich substratum (full lake sediment, 2.94 mg g^{-1} TN, 0.13 mg g^{-1} TP and 12.85% organic matter); and nutrient-poor substratum (10% of lake sediment, obtained by mixing with clean sand, v/v). Each patch had the same area (53 × 35 cm) and substratum volume (depth of 15 cm). There were eight treatments designed as follows: two light heterogeneous treatments, l_a (parent ramet in a light-rich patch, its primary stolon growing towards a light-poor patch, both patches nutrient-rich) and l_t (parent ramet in a light-poor patch, its primary stolon growing towards a light-rich patch, both patches nutrient-rich); two nutrient heterogeneous treatments, n_a (parent ramet in a nutrient-rich patch, its primary stolon growing towards a nutrient-poor patch, both patches light-rich) and n_t (parent

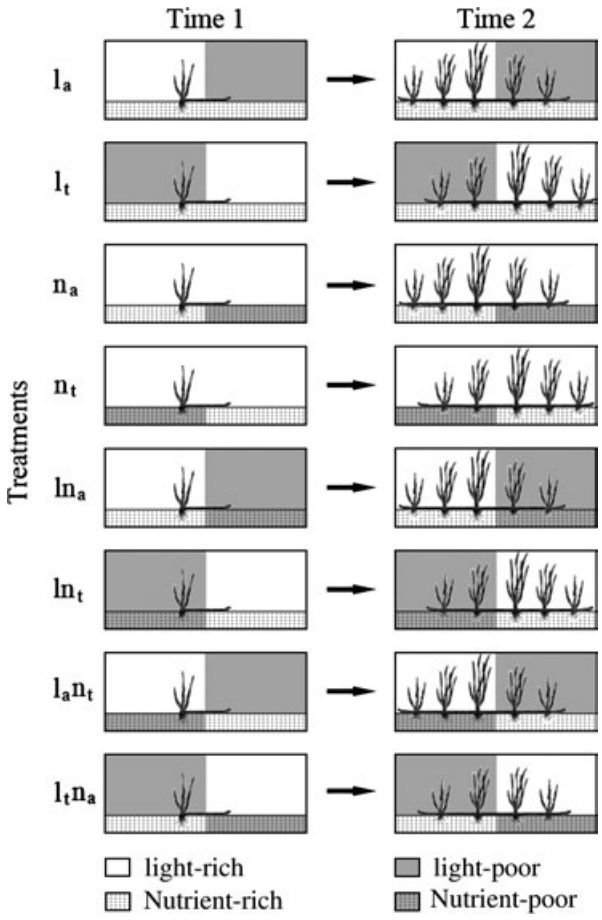

Fig. 1 Experimental scheme, showing eight treatments. Ramets with a stolon were planted into two adjoined patches with different light intensity or substratum nutrient content (time 1). The plants were harvested after 6 weeks (time 2).

ramet in a nutrient-poor patch, its primary stolon growing towards a nutrient-rich patch, both patches light-rich); two light and nutrient additive treatments, ln_a (parent ramet in a light-rich and nutrient-rich patch, its primary stolon growing towards a light-poor and nutrient-poor patch) and ln_t (parent ramet in a light-poor and nutrient-poor patch, its primary stolon growing towards a light-rich and nutrient-rich patch); two light and nutrient reciprocal treatments, l_an_t (parent ramet in a light-rich but nutrient-poor patch, its primary stolon growing towards a light-poor but nutrient-rich patch) and l_tn_a (parent ramet in a light-poor but nutrient-rich patch, its primary stolon growing towards a light-rich but nutrient-poor patch). Each treatment was replicated eight times. All the patches were set up in an outdoor pond. After transplanting the plants, the pond was filled with lake water to a depth of 150 cm. During the experiment, each parent ramet survived and its primary stolon spread into the patch it was initially positioned towards and produced offspring ramets.

Harvest

After 6 weeks of growth, the experimental plants were harvested on 28 June 2003. Before harvest, for each different patch the number of ramets and branches was counted and stolon length was measured. After harvest, all plants were divided into roots, stolons and leaves, oven dried at 80 °C for 72 h, and their weight recorded. The biomass of each clone and the biomass of each clonal part in the different patches were measured. During the experiment, no plants flowered or produced tubers. Here, a clone is defined as a complete unit of ramets connected by stolons, originating from a parent ramet.

Data analysis

The original biomass of transplanted plants was subtracted from the biomass of harvested plants prior to analysis. All data were analysed using fixed-model one-way analyses of variance (ANOVA) after correction for non-normality and heteroscedasticity by logarithmic transformation or, in the case of proportions, by angular transformations. The traits investigated (biomass and ramet number) were compared using Tukey's test (at $P < 0.05$) between treatments overall and also between patches within treatments (e.g. rich versus poor patches). A fixed-model one-way ANOVA was carried out to determine differences between treatments in both rich and poor patches. Statistical comparisons of the proportional distribution of traits between rich and poor patches in each treatment are presented only for the rich patches. Similarly, in the reciprocal treatments (l_an_t and l_tn_a), patch quality is only presented for light, because the data are the reciprocal of those for substratum nutrient.

Results

Biomass accumulation and allocation

Clonal biomass was greater in treatment l_a than in any other treatments, the others being similar (Fig. 2a). The clonal biomass located to both rich and poor patches

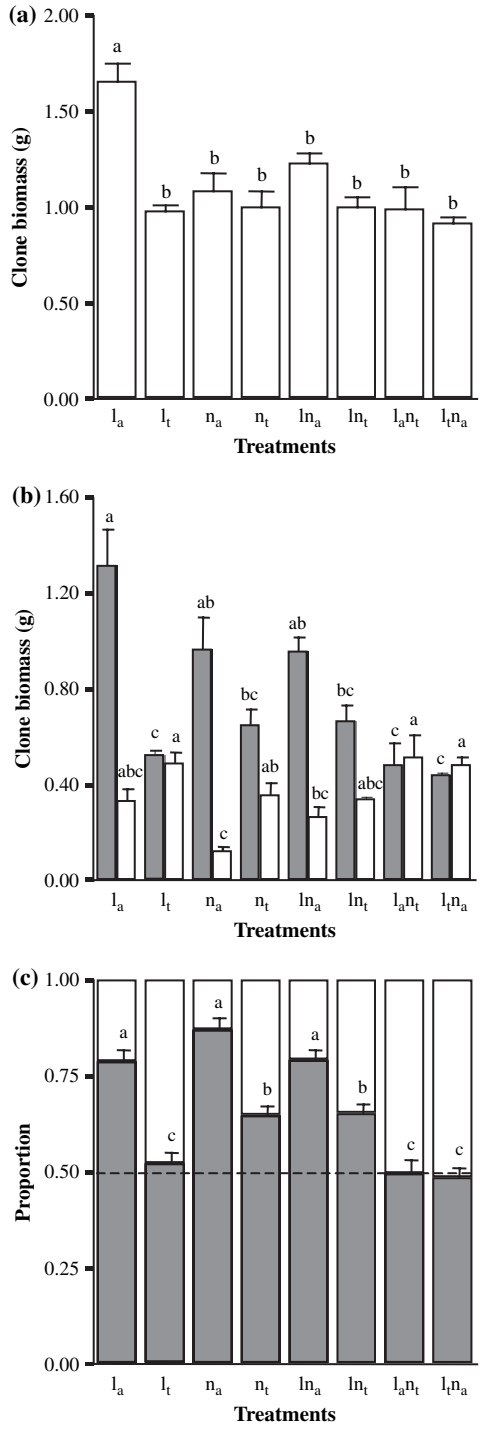

Fig. 2 Biomass (a) per clone in each treatment, biomass (b) of parts of clones in rich patches (shaded bars) and poor patches (open bars) in each treatment, and proportion of clonal biomass (c) partitioned between rich (shaded) and poor (open) patches in each treatment. Values are mean ± SE. Bars sharing the same letters are not significantly different at $P = 0.05$. In panel b significant differences between treatments are calculated separately for rich and poor patches. Treatment codes as in Fig. 1.

differed between treatments ($F = 9.99$, $P < 0.001$ in rich patches; $F = 9.49$, $P < 0.001$ in poor patches; Fig. 2b). The proportion of the clonal biomass allocated to rich patches was significantly higher in l_a, n_a and ln_a than in l_t, n_t and ln_t ($F = 61.58$, $P < 0.001$). In l_t and the two reciprocal treatments l_an_t and l_tn_a, however, clonal biomass in the two patches was almost equal ($F = 0.25$, $P > 0.05$) (Fig. 2c). Leaf biomass and root biomass of clones in each treatment followed a pattern similar to that of overall clonal biomass, showing the higher proportions in rich patches of l_a, n_a and ln_a than in rich patches of l_t, l_an_t and l_tn_a (Fig. 3b,d).

Ramet production and clonal architecture

Ramet number differed between treatments ($F = 30.86$, $P < 0.001$), and clones produced more offspring ramets in the heterogeneous nutrient treatments n_a and n_t than in other treatments (Fig. 4a). There were more ramets in rich than in poor patches in each treatment ($F = 160.62$, $P < 0.001$). The proportion of ramets located in rich patches was lower in l_a, n_a and ln_a than in l_t, n_t and ln_t ($F = 20.61$, $P < 0.001$). In the two reciprocal treatments, foraging direction had a significant effect on the proportion of ramets in the two patches ($F = 250.78$, $P < 0.001$), with more ramets in light-rich patches (Fig. 4b,c).

Branch production was affected by the quality of patches ($F = 137.69$, $P < 0.001$). More branches were produced in rich than in poor patches (Fig. 5a). *Vallisneria spiralis* often failed to produce other branches besides the primary branch under the light-poor condition. In the two reciprocal treatments, the number of branches was higher in the light-rich parent patches of l_an_t than in nutrient-rich parent patches of l_tn_a ($F = 7.35$, $P < 0.001$, Fig. 5a,b). Stolon length of clones in each treatment showed a similar pattern to ramet number (Fig. 5c,d).

Discussion

Numerous environmental and biotic processes contribute to the patchy distribution of resources such as light and nutrients in aquatic habitats. Although clonal plants have little control whether their dispersing propagules arrive in resource-rich or -poor patches, our results indicate that *V. spiralis* exhibits a foraging strategy which allows it to remain in favourable patches and escape unfavourable ones.

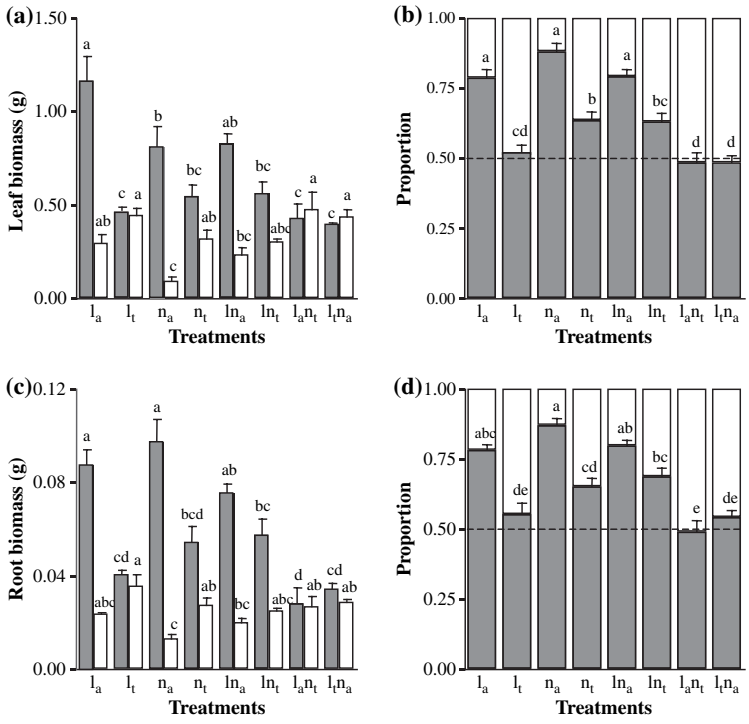

Fig. 3 Leaf biomass (a) and root biomass (c) of parts of clones in rich patches (shaded bars) and poor patches (open bars) in each treatment, and proportion of leaf biomass (b) and root biomass (d) between rich (shaded) and poor (open) patches in each treatment. Values are mean ± SE. Bars sharing the same letters are not significantly different at $P = 0.05$. In panels a and c significant differences between treatments are calculated separately for rich and poor patches. Treatment codes as in Fig. 1.

Hence, it is well placed to exploit patchily distributed resources.

Remaining in favourable habitats

When *V. spiralis* exploited heterogeneous patches by clonal growth, both the absolute values and proportions of biomass and ramets were higher in rich patches than in poor patches. When parent ramets were established in rich patches, a higher proportion of clonal biomass remained in the rich patch. These results indicate that *V. spiralis* which initially established in resource-rich conditions could remain within the favourable habitat. This is consistent with previous observations of terrestrial clonal plants grown in heterogeneous environments (Slade & Hutchings, 1987; Birch & Hutchings, 1994; Evans & Cain, 1995; Stuefer *et al.*, 1996; van Kleunen & Fischer, 2001).

Leaf biomass was highest when the parent was established in a light-rich patch. Similarly, when growing from nutrient-rich to -poor patches, root biomass was highest in nutrient-rich patches. This might represent specialisation of function and division of labour. Division of labour has been demonstrated in a number of clonal plant species (Stuefer *et al.*, 1996; Alpert & Stuefer, 1997). If such division of labour occurs, ramets will specialise functionally in the uptake of a locally abundant resource and support connected ramets positioned where that resource is scarce. As a result, the performance of the whole clone would be enhanced (Alpert & Stuefer, 1997; Hutchings & Wijesinghe, 1997). In our experiment, greater biomass was allocated to leaves in light-rich patches and to roots in nutrient-rich patches, seemingly increasing the uptake of light and nutrients. Consequently, enhancement of ramet performance in resource-rich patches helps *V. spiralis* to remain in favourable patches.

Escaping unfavourable habitats

When clones grew from poor to rich patches, *V. spiralis* invested more biomass and ramets into rich patches. Particularly when growing from light and nutrient-poor patches to light and nutrient-rich patches, *V. spiralis* allocated the highest proportion of ramets to rich patches. This investment in ramets could be envisaged as a means of 'sampling' alternative patches. These results suggest that, if established in adverse conditions, *V. spiralis* could escape into favourable patches by clonal growth. This phenomenon has been reported in some terrestrial clonal

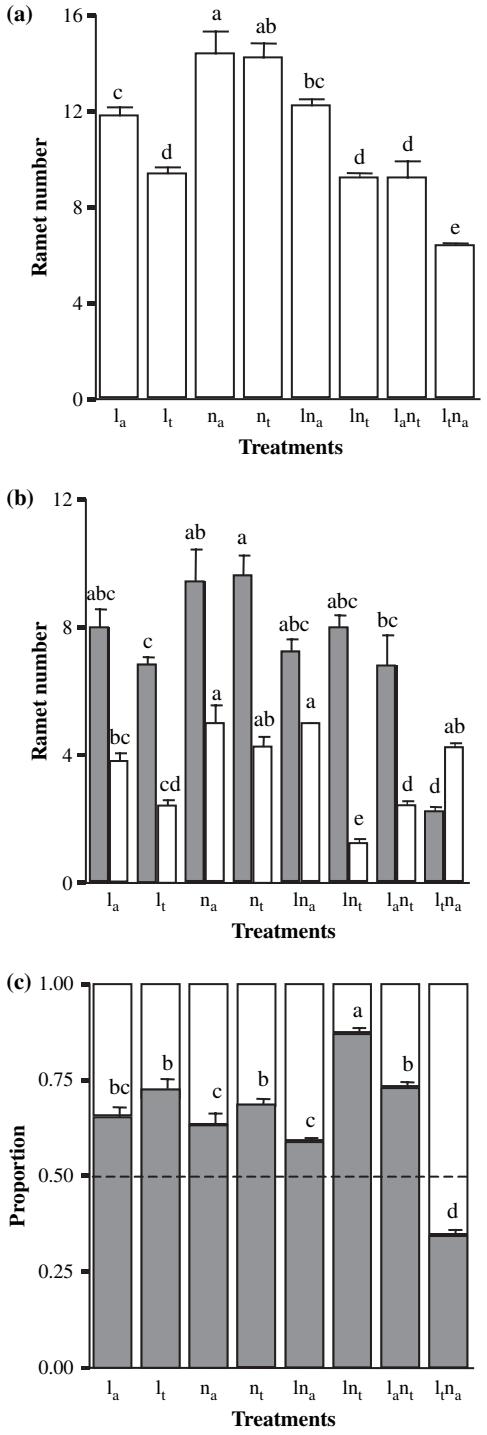

Fig. 4 Ramet number (a) per clone in each treatment, ramet number (b) of parts of clones in rich patches (shaded bars) and poor patches (open bars) in each treatment, and proportion of ramet number (c) between rich (shaded) and poor (open) patches in each treatment. Values are mean ± SE. Bars sharing the same letters are not significantly different at $P = 0.05$. In panel b significant differences between treatments are calculated separately for rich and poor patches. Treatment codes as in Fig. 1.

plants. For instance, some clonal species show a tendency to grow away from vegetation patches towards gaps (Evans & Cain, 1995; Macek & Leps, 2003; Sampaio *et al*., 2004). However, other studies have suggested that detrimental conditions in the parental environment could force the parent ramets to allocate all available resources to their own growth and stop producing offspring ramets (Slade & Hutchings, 1987; Caraco & Kelly, 1991). These different results illustrate that clonal foraging varies between species and environments (Dong, 1995). In submerged habitat, *V. spiralis* initially established under resource-poor conditions did not stop producing offspring ramets, but rather grew towards resource-rich patches. One reason might be that aquatic habitats are suitable for clonal growth even in resource-poor conditions (van Groenendael *et al*., 1996; Santamaria, 2002).

Plasticity in clonal architecture, including internode length, branching intensity and branching angle, has been considered as important for characters associated with clonal foraging (Sutherland & Stillman, 1988; Evans & Cain, 1995; Cain, Dudle & Evans, 1996; Oborny & Cain, 1997). In our experiment, *V. spiralis* produced significantly more branches in rich than in poor patches. Especially in the heterogeneous nutrient treatments, *V. spiralis* produced the most branches both in rich and poor patches, resulting in the most offspring ramets of clones in these treatments. However, a similar pattern of stolon length and ramet number suggests that stolon length reflected the number of stolons and therefore, did not itself show a plastic response to resource availability. This agrees with the theory that the most consistent foraging behaviour is a higher branching intensity in favourable habitats, while stolons or rhizomes act mainly as connections between ramets rather than as foraging organs (de Kroon & Hutchings, 1995).

Vallisneria spiralis produced almost no branches in light-poor conditions while it did so in nutrient-poor conditions. In addition, clonal biomass was greater in treatment l_a than in treatment n_a. Besides clonal foraging, the other advantage of clonal growth is clonal integration, namely translocation of resources between interconnected ramets under conditions of patchy resource conditions (Pitelka & Ashmun, 1985). Clonal integration could enhance performance of *V. spiralis* grown in heterogeneous light environments (K. Xiao & D. Yu, unpublished data). However,

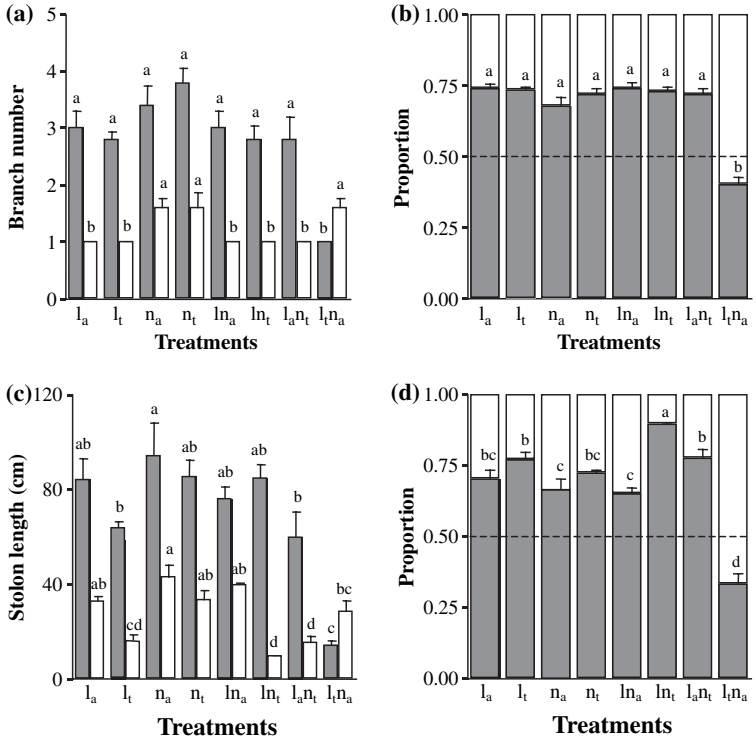

Fig. 5 Branch number (a) and stolon length (c) in rich (shaded bars) and poor (open bars) patches in each treatment, and proportion of branch number (b) and stolon length (d) between rich (shaded) and poor (open) patches in each treatment. Values are mean ± SE. Bars sharing the same letters are not significantly different at $P = 0.05$. In panels a and c significant differences between treatments are calculated separately for rich and poor patches. Treatment codes as in Fig. 1.

because of nutrient uptake by leaves from water-column, the integration of nutrients between ramets might be less important in aquatic plants when growing in heterogeneous sediments than in terrestrial plants (Xiao *et al*., 2006). Therefore, the foraging of *V. spiralis* appeared to be influenced more by light intensity than by soil nutrients. This may be a general difference in foraging between aquatic and terrestrial clonal plants in heterogeneous environments.

This study clearly demonstrates that the clonal macrophyte *V. spiralis* can exhibit foraging in submerged heterogeneous environments. Foraging behaviour can enhance survival and performance of clonal plants and further influence the spatial distribution of aquatic clonal plant species in the field. However, besides abiotic factors, such as light, soil nutrient and water availability, a more important heterogeneity is created by competition, which has a major influence on the structure of communities. Therefore, future studies on aquatic clonal plants should pay more attention to the community level.

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