Journal of
Plant Ecology

VOLUME 8, NUMBER 1,
PAGES 91–100

FEBRUARY 2015

doi:10.1093/jpe/rtu003

Advance Access publication
19 April 2014

available online at
www.jpe.oxfordjournals.org

Soil heterogeneity affects ramet placement of *Hydrocotyle vulgaris*

Bi-Cheng Dong[1,#], *Jiu-Zhong Wang*[2,#], *Rui-Hua Liu*[1,3], *Ming-Xiang Zhang*[1], *Fang-Li Luo*[1,*], and *Fei-Hai Yu*[1]

[1] *School of Nature Conservation, Beijing Forestry University, Qinghua East Road 35, Haidian District, Beijing 100083, China*
[2] *School of Forestry, Beijing Forestry University, Qinghua East Road 35, Haidian District, Beijing 100083, China*
[3] *Research Center for Eco-Environmental Sciences, Chinese Academy of Sciences, Shuangqing Road 18, Haidian District, Beijing 100085, China*
*Correspondence address. School of Nature Conservation, Beijing Forestry University, Qinghua East Road 35, Haidian District, Beijing 100083, China. Tel/Fax: +86-10-62-33-61-73; E-mail: ecoluofangli@163.com
[#]These authors contributed equally to this work.

Abstract

Aims
Soil heterogeneity is common in natural habitats. It may trigger foraging responses (placing more ramets and/or roots in nutrient-rich patches than in nutrient-poor patches) and further affect the growth of plants. However, the impact of soil heterogeneity on competitive interactions has been little tested.

Methods
We conducted a greenhouse experiment to investigate the effects of soil heterogeneity on intraspecific competition with a stoloniferous herb *Hydrocotyle vulgaris*. We grew one (without competition) or nine ramets (with competition) of *H. vulgaris* under a homogeneous environment and two heterogeneous environments differing in patch size (large or small patches). In the heterogeneous treatment, the soil consisted of the same number of nutrient-rich and nutrient-poor patches arranged in a chessboard manner, and in the homogeneous treatment, the soil was an even mixture of the same amount of the nutrient-rich and the nutrient-poor soil.

Important Findings
Irrespective of intraspecific competition, *H. vulgaris* showed foraging responses to soil heterogeneity in the large patch treatment, e.g. it produced significantly more biomass, ramets, aboveground mass and root mass in the nutrient-rich patches than in the nutrient-poor patches. In the small patch treatment, foraging responses were observed when intraspecific competition was present, but responses were not observed when there was no competition. However, we find a significant effect of soil heterogeneity on neither overall growth nor competitive intensity of *H. vulgaris*. Our results suggest that foraging responses to soil heterogeneity may not necessarily be adaptive and intraspecific competition may not be influenced by soil heterogeneity.

Keywords: clonal plant, competition, environmental heterogeneity, foraging response, patch size, physiological integration

Received: 4 December 2013, Revised: 5 March 2014, Accepted: 23 March 2014

INTRODUCTION

Spatial heterogeneity in soil nutrients potentially creates difficulty for plants to exploit soil resources (Gross *et al.* 1995; Jackson and Caldwell 1993a, 1993b; Lechowicz and Bell 1991). To efficiently capture heterogeneously distributed soil resources, clonal plants can show foraging responses, e.g. placing more nutrient-absorbing organs (e.g. roots or ramets) in high-quality patches than in low-quality ones (de Kroon *et al.* 2005; Gao *et al.* 2012; Hodge 2004; Hutchings and de Kroon 1994; Hutchings and John 2004; Peng *et al.* 2013). Meanwhile, physiological connection *via* stolons or rhizomes allows the transport of carbohydrates, water and minimal nutrients from ramets growing in high-quality patches to those in low-quality ones (Alpert and Stuefer 1997; He *et al.* 2010, 2011; Price and Marshall 1999; Stuefer 1996). A number of studies have revealed that physiological integration can contribute to the fitness of ramets growing in low-quality patches and further enhance the development of the whole plant (Hutchings and Wijesinghe 1997, 2008; see Song *et al.* 2013 for a review).

Soil heterogeneity is also an important factor influencing the outcome of competition between plants (Fransen *et al.* 2001; Janecek *et al.* 2004; Mommer *et al.* 2012; van der Waal *et al.* 2011). In heterogeneous environments, preferential ramet or root placements can cause overgrowth of ramets in high-quality patches and little growth of ramets in low-quality ones. In high-quality patches, competitive intensity between ramets may be aggravated due to densely packed ramets and roots, and the reverse is the case in low-quality patches (Casper *et al.* 2000). Therefore, we predict that in heterogeneous environments intraspecific competitive interactions between the whole plants (genets) will be determined by interactions of ramets in both high- and low-quality patches (Bliss *et al.* 2002; Casper *et al.* 2000; Schwinning and Weiner 1998). Because the majority of biomass, ramets and roots may be produced in high-quality patches, we predict further that soil heterogeneity will intensify intraspecific competition of whole plants.

The spatial scale of soil heterogeneity can influence foraging responses of clonal plants, individual performance and outcome of competition (Day *et al.* 2003a; Fransen *et al.* 2001). If patch size is too small, clonal plants may be hard to sense soil heterogeneity and no effect will be shown (Hutchings and John 2004; Wijesinghe and Hutchings 1997, 1999). If patch size is too large, then plants in most cases will meet only one type of patches and effects of soil heterogeneity will be small (Hutchings *et al.* 2003). Only at some scales, preferential ramet and root placements can happen, and fitness and competitive interactions of clonal plants can be affected (Day *et al.* 2003a; Fransen *et al.* 2001).

To investigate the responses of clonal plants to soil heterogeneity and intraspecific competition, we conducted a greenhouse experiment with a stoloniferous, clonal plant *Hydrocotyle vulgaris*. We grew one (without intraspecific competition) or nine ramets (with competition) of *H. vulgaris* under a homogenous environment or two heterogeneous environments differing in patch scale (large patch and small patch). We predicted that (i) in heterogeneous environments, like many clonal plants, *H. vulgaris* can show foraging responses, i.e. it will place more ramets and biomass in the nutrient-rich patches than in the nutrient-poor ones, (ii) such foraging responses will depend on patch scale, (iii) soil heterogeneity will intensify intraspecific competition of *H. vulgaris* and (iv) competitive intensity will be affected by patch size.

MATERIALS AND METHODS

The species

Hydrocotyle vulgaris L. (Araliaceae), a perennial clonal herb, is widely distributed in tropical and temperate regions such as Southeast Asia, Europe and North America (Murphy *et al.* 1990). The species is introduced in China as a garden species in the 1990s and recently considered potentially invasive in China (Miao *et al.* 2011; Murphy *et al.* 1990). It can grow in a broad range of habitats, from semi-moist to wet conditions (Haslam 1987), and form large clones by producing plagiotropic stems, i.e. stolons (Miao *et al.* 2011). Each node along stolons has the potential to produce an independent ramet that consists of a simple leaf and adventitious roots. *Hydrocotyle vulgaris* produces flowers and fruits from May to August (Lacey and Herr 2005; Miao *et al.* 2011).

Plants of *H. vulgaris* were collected from a wetland (30°16′N; 120°05′E) in the suburb of Hangzhou in Zhejiang Province, China. They were propagated vegetatively in a greenhouse at Forest Science Co. Ltd of Beijing Forestry University in Beijing. We selected 320 ramets of *H. vulgaris*, each having a node, a leaf and a few roots. Of them, 150 ramets were used for the experiment and 20 ramets for the initial measurement. The average initial petiole length was 15.95 ± 0.97 cm (mean ± standard error, $n = 20$).

Experimental design

The experiment was a 2 × 3 factorial design, consisting of two intraspecific competition treatments (without or with intraspecific competition, i.e. each container was planted with one or nine ramets of *H. vulgaris*) and three heterogeneous treatments (homogeneous, heterogeneous with large patches or heterogeneous with small patches; Fig. 1). There were five replicates of containers (32 cm long× 32 cm wide × 18 cm deep) for each of the six treatments and thus 30 containers in total. Of the 30 containers, 10 (five with and five without competition) assigned to the large patch treatment were each divided into four large patches (each measuring 16 cm × 16 cm), 10 assigned to the small patch treatment were each divided into 16 small patches (each measuring 8 cm × 8 cm) and the remaining 10 were assigned to the homogeneous treatment. For the two heterogeneous treatments, each container had two types of patches arranged in a checkerboard pattern. In each container, half patches were filled to a depth of 15 cm with a mixture of sand and commercial compost (Meishimei Bio-Tech Co. Ltd, Beijing, China) at a 1:9 volume ratio (termed 'nutrient-rich patches'; 8.70 mg total N g^{-1} and 4.64 mg total P g^{-1}) and the other half with a mixture of sand and commercial compost at a 9:1 ratio (termed 'nutrient-poor patches'; 0.79 mg total N g^{-1} and 1.03 mg total P g^{-1}). For the homogeneous treatment, each container was filled with an even mixture of sand and commercial compost at a 1:1 volume ratio. The total amount of soil nutrients was the same in all treatments. There were no physical barriers between patches, and thus, plant roots could grow through different patches.

For the treatments without intraspecific competition, one ramet of *H. vulgaris* was grown in the center of each container (Fig. 1). For the treatments with intraspecific competition, nine ramets were grown in each container, positioned at the corners of nutrient patches in the heterogeneous, small patch treatment, and the corresponding places in the homogeneous treatment and in the heterogeneous, large patch treatment (Fig. 1).

The experiment was conducted from 1 August to 1 November 2012 in the greenhouse. During the experiment, the mean temperature and mean relative humidity in the greenhouse were 22.0°C and 73.9%, respectively (measured by iButton DS1923; Maxim Integrated Products, Sunnyvale, CA, USA). Water was added to the containers when the surface soil became dry. To avoid mass flow of water and thus soil nutrients between adjacent patches,

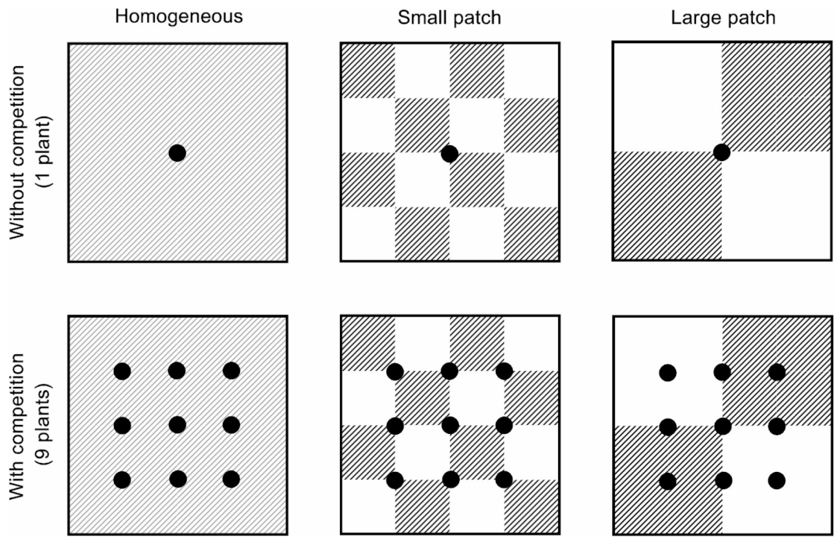

Figure 1: schematic representation of the experimental design. One (without competition) or nine (with competition) ramets of *H. vulgaris* (black dots) were grown under a homogeneous environment or two heterogeneous environments differing in patch scale (large patch and small patch). In the large patch treatment, each container was divided into four large patches, two of which were filled with nutrient-rich soil and the other two with nutrient-poor soil. In the small patch treatment, each container was divided into 16 small patches, eight of which were filled with nutrient-rich soil and the other eight with nutrient-poor soil. In the homogeneous treatment, each container was filled with an even mixture of the nutrient-rich and nutrient-poor soil. The total amount of soil nutrients in a container was the same in all the treatments.

water was added slowly to the soil. During the experiment, the containers were randomly repositioned three times to avoid potential effects of environment patchiness in the greenhouse.

Measurements

At the end of the experiment, for the two heterogeneous treatments, we counted total number of ramets of *H. vulgaris* in nutrient-rich patches and nutrient-poor patches separately. The plants in the homogeneous treatment were harvested in a similar fashion, i.e. plants in the imagined, nutrient-rich patches (hereafter also referred to as 'nutrient-rich patches') and the imagined, nutrient-poor patches (hereafter also referred to as 'nutrient-poor patches') were harvested separately. The plants were then separated into petioles, leaf blades, stolons and roots, dried at 70°C for 72 h and weighed. Total biomass was the sum of dry mass of petioles, leaf blades, stolons and roots; aboveground mass was the sum of dry mass of petioles, leaf blades and stolons.

Data analysis

We calculated biomass, number of ramets, aboveground mass and root mass per initial ramet of *H. vulgaris* in each container. We also calculated biomass, number of ramets, aboveground mass and root mass per initial ramet in nutrient-rich patches and nutrient-poor patches separately. These data (thereafter we omitted 'per initial ramet' for simplicity) were used in the following analyses.

We used two-way analysis of variance (ANOVA) to test the effects of soil heterogeneity (homogeneous vs. heterogeneous with large patches vs. heterogeneous with small patches) and intraspecific competition (with vs. without competition) on biomass, number of ramets, aboveground mass and root mass of *H. vulgaris* at the whole plant (container) level. We also employed ANOVA with repeated measures to test the effects of patch type (nutrient-rich patches vs. nutrient-poor patches), heterogeneity and intraspecific competition on the variables at the patch level (Roiloa and Retuerto 2006). In this model, patch type was treated as a repeated variable because the nutrient-rich and the nutrient-poor patches in each container were not independent (Roiloa and Retuerto 2006). Differences between nutrient-rich patches and nutrient-poor patches within each treatment were tested by paired *t*-tests and differences between soil heterogeneity within competition treatments at the patch level were tested by *post hoc* Tukey honest significant difference tests.

To measure the intraspecific competitive intensity, we calculated the log response ratio (LnRR) as LnRR = $\ln(B_o/B_w)$, where B_o is the mean value of a growth measure (biomass, number of ramets, aboveground and root mass) per initial ramet without competition across the five replicate containers, and B_w is the value of the corresponding growth measure per initial ramet with competition in each replicate container. Values of LnRR are symmetrical around zero (Armas *et al.* 2004; Hedges *et al.* 1999). Positive values indicate competition, negative values indicate facilitation and zero indicates neutral. We used one-way ANOVA to test the effect of soil heterogeneity on LnRR at the patch level and at the whole plant level, respectively. All analyses were conducted using SPSS 16.0 (SPSS, Chicago, IL, USA).

Table 1: **ANOVA results for effects of soil heterogeneity (homogeneous vs. large patch vs. small patch) and intraspecific competition (without vs. with competition) on growth measures of *H. vulgaris* at the whole plant level**

Effect	*df*	Biomass	Number of ramets	Aboveground mass	Root mass
H	2,24	2.1*	2.2*	2.2*	0.6*
C	1,24	474.2*****	482.7*****	472.0*****	202.1*****
H × C	2,24	1.4*	1.5*	1.5*	0.6*

Abbreviations: C = competition, H = heterogeneity.
Significance levels: *****$P < 0.001$ and *$P \geq 0.1$ (not significant).

RESULTS

Effects at the whole plant level

We found a significant effect of soil heterogeneity on none of the four growth measures (biomass, number of ramets, aboveground mass or root mass) of *H. vulgaris* (Table 1, Fig. 2). Intraspecific competition dramatically decreased all growth measures of *H. vulgaris* (Table 1, Fig. 2). There were significant interactive effects between intraspecific competition and soil heterogeneity on none of the four growth measures (Table 1), and we did not find a significant effect of soil heterogeneity on the LnRR (Fig. 3). These results suggest that there is little effect of soil heterogeneity on intraspecific competition of *H. vulgaris* at the whole plant level.

Effects at the patch level

Patch type significantly affected biomass, aboveground mass and root mass (Table 2). There were interactive effects of patch type by soil heterogeneity on all the four measures (Table 2; significant effects of patch type × heterogeneity). Without competition, biomass, number of ramets and aboveground mass were greater in the nutrient-rich patches than in the nutrient-poor patches in the large patch treatment, but not in the homogeneous or the small patch treatment (Fig. 4a, c and e). With competition, biomass, number of ramets and aboveground mass were greater ($P < 0.05$) or tended to be greater ($P < 0.1$) in the nutrient-rich patches than in the nutrient-poor patches in both the small patch and the large patch treatments, but not in the homogeneous treatment (Fig. 4b, d and f). With competition, root mass was also significantly greater in the nutrient-rich than in the nutrient-poor patches in the small patch treatment (Fig. 4h).

Irrespective of competition, none of the four growth measures in the nutrient-rich patches in the large and small patch treatments differed significantly from that in the corresponding areas in the homogeneous treatment (Fig. 4). Similarly, there was a significant effect of soil heterogeneity on none of the growth measures in the nutrient-poor patches, except number of ramets (Fig. 4). Number of ramets in the nutrient-poor patches in the large patch treatment was significantly smaller than that in the corresponding areas in the homogeneous treatment (Fig. 4c and d).

There were significant effects of patch type × soil heterogeneity × intraspecific competition on none of the four growth measures except number of ramets (Table 2). Also, there was no significant effect of soil heterogeneity on the LnRR of ramets growing in nutrient-rich patches or in nutrient-poor patches (Fig. 5). These results suggest that there is little effect of soil heterogeneity on intraspecific competitive intensity of *H. vulgaris* at the patch level.

DISCUSSION

Irrespective of intraspecific competition, *H. vulgaris* showed foraging responses in the heterogeneous environment with large patches, i.e. it produced higher total mass, number of ramets and aboveground mass in the nutrient-rich patches than in the nutrient-poor ones. Also, such foraging responses existed in the heterogeneous, small patch treatment when intraspecific competition was present, but did not when there was no competition. Thus, our results partly support the first and second predictions, and suggest that foraging responses of *H. vulgaris* may depend on the spatial scale of soil heterogeneity (Wijesinghe and Hutchings 1997, 1999). These results also indicate that foraging responses of *H. vulgaris* in the small patch treatment can be triggered by the presence of intraspecific neighbors. The plausible reason can be the existence of a negative correlation between plant growth rate and foraging precision (Cahill *et al.* 2010; Campbell *et al.* 1991; Wijesinghe *et al.* 2001). If *H. vulgaris* grows alone, high ramet production rate (~62.6 ramets per week) may decrease its foraging precision. Because of such high ramet production rate, when growing alone, *H. vulgaris* may ignore the heterogeneous resource distribution in the small patch environment. On the other hand, if *H. vulgaris* grows with intraspecific neighbors, low ramet production rate (~8.0 ramets per week) caused by intraspecific competition may enable *H. vulgaris* to have a higher foraging precision in response to nutritious cues in the small patch environment (Cahill *et al.* 2010; Campbell *et al.* 1991; Wijesinghe *et al.* 2001).

Previous studies have shown that preferential ramet and root placements in nutrient-rich patches may greatly increase the efficiency and amount of resource capture of these ramets and further increase their local growth (Roiloa and Retuerto 2006; Wang *et al.* 2012, 2013). Furthermore, the efficiency of resource capture by these ramets in nutrient-rich patches can also benefit growth of the whole plant, partly due to physiological integration (He *et al.* 2011; Song *et al.* 2013; Zhou *et al.* 2012). However, foraging responses of *H. vulgaris* to soil

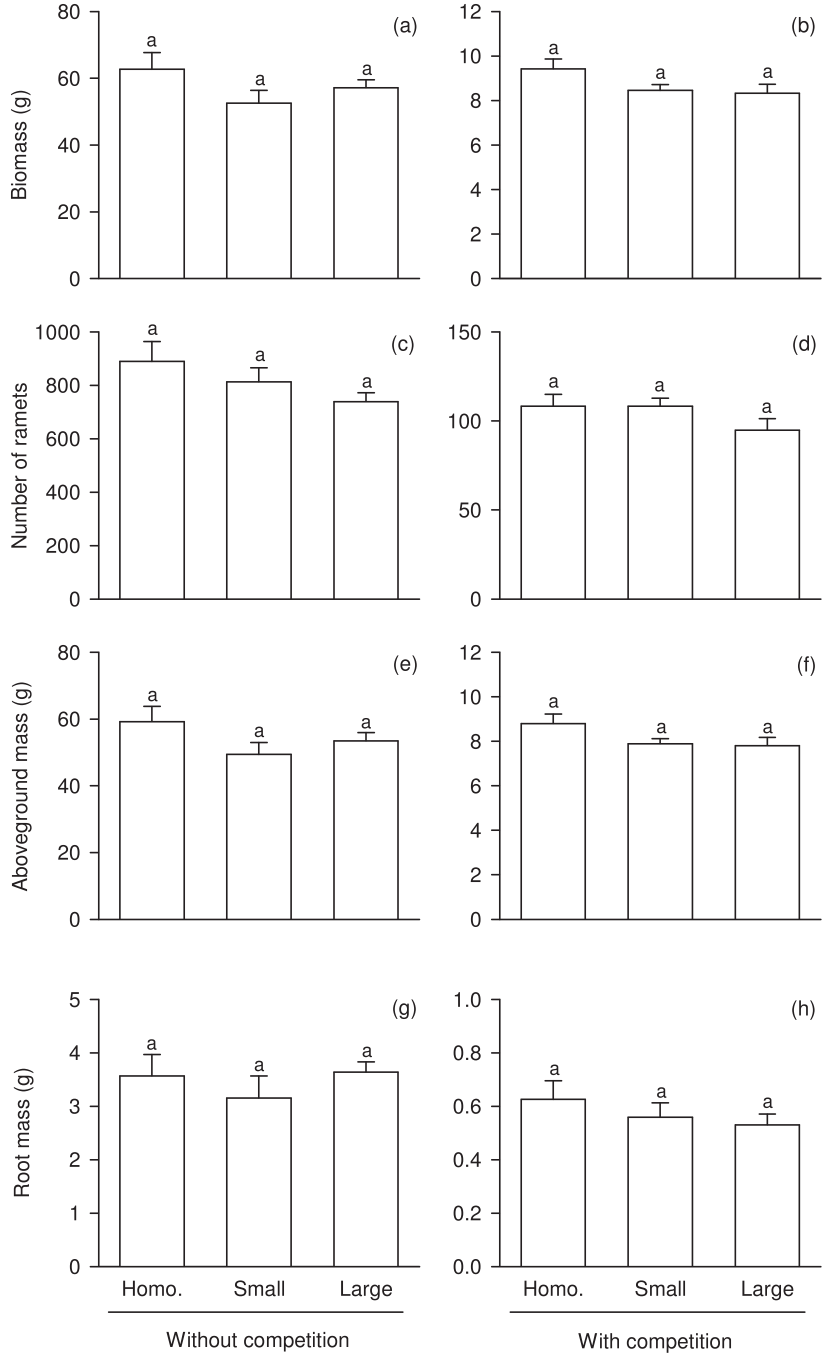

Figure 2: effects of soil heterogeneity (homogeneous vs. large patch vs. small patch) and intraspecific competition (without vs. with competition) on biomass (**a** and **b**), number of ramets (**c** and **d**), aboveground mass (**e** and **f**) and root mass (**g** and **h**) of *H. vulgaris* at the whole plant level. Error bars show +1 SE. Bars sharing the same letters are not different at $P = 0.05$ (Tukey tests).

nutrient heterogeneity did not increase the growth of ramets growing in nutrient-rich patches compared with that in the homogeneous treatment. Moreover, the growth of ramets growing in nutrient-poor patches was also little affected by soil heterogeneity. Consequently, the growth of the whole plants was statistically the same in the homogeneous and the heterogeneous treatments.

The positive effect of soil heterogeneity on plant growth may be transitory, and such effect may be eliminated if resource becomes limited (Casper and Cahill 1996; Day *et al.* 2003a; Peng *et al.* 2013; Roiloa and Retuerto 2006; Zhang and He 2009). For example, Day *et al.* (2003a, 2003b) reported that soil nutrient heterogeneity could increase the yield of the *Cardamine hirsute* population at the early stage of growth

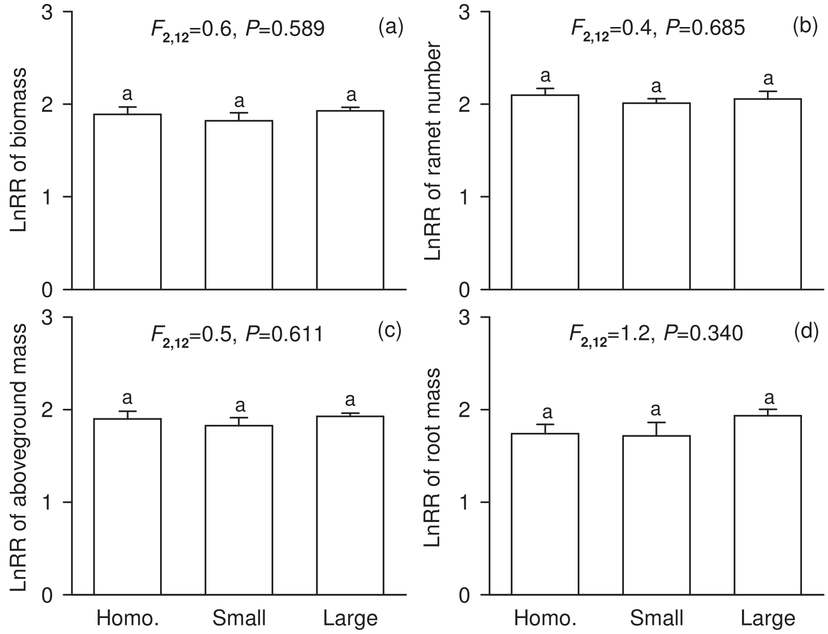

Figure 3: effects of soil heterogeneity (homogeneous vs. large patch vs. small patch) on the LnRR of *H. vulgaris* at the whole plant level. Degree of freedom, *F* and *P* values are given. Error bars show +1 SE. Bars sharing the same letters are not different at $P = 0.05$ (Tukey tests).

Table 2: repeated-measure ANOVA results for effects of patch type (nutrient-rich vs. nutrient-poor patches), soil heterogeneity (homogeneous vs. large patch vs. small patch) and intraspecific competition (without vs. with competition) on growth measures of *H. vulgaris* at the patch level

Effect	*df*	Biomass	Number of ramets	Aboveground mass	Root mass
Between-subject effect					
H	2,24	2.1*	2.2*	2.2*	0.6*
C	1,24	474.2*****	482.7*****	472.0*****	202.1*****
H × C	2,24	1.4*	1.5*	1.5*	0.6*
Within-subject effect					
Pt	1,24	9.3****	2.4*	8.1****	5.2***
Pt × H	2,24	4.7***	13.8*****	4.4***	3.4***
Pt × C	1,24	2.4*	0.08*	2.0*	1.7*
Pt × H × C	2,24	2.9**	9.5*****	2.8**	0.9*

Abbreviations: C = competition, H = heterogeneity, Pt = patch type.
Significance levels: *****$P < 0.001$, ****$P < 0.01$, ***$P < 0.05$, **$P < 0.1$ and *$P \geq 0.1$ (not significant).

(in ~31 days), but not in the long run (in ~60 days). In this study, the density of newly produced ramets of *H. vulgaris* reached up to ~85.4 ramets dm^{-2} at harvest, and in the container, nearly all space was overloaded. Due to the continuous increase of new ramets, the nutrient-rich patches could not always maintain equal suitability and might gradually decline to the same level of suitability as the nutrient-poor patches. As a result, foraging responses could not eventually increase to the growth of *H. vulgaris* in the heterogeneous environments.

Intraspecific competition strongly inhibited the growth of *H. vulgaris* (e.g. biomass declined by 85% and ramet number by 86%). However, we did not find a significant effect of soil heterogeneity on competitive interactions of *H. vulgaris* and such an effect also did not depended on patch scale. Previous studies have shown that soil heterogeneity increased intraspecific competition of *Briza media*, but it did not affect that of *Festuca rubra* or *Alternanthera philoxeroides* (Day *et al.* 2003c; Zhou *et al.* 2012). It has also been shown that light heterogeneity increased intraspecific competition of *Duchesnea indica* and such an effect occurred at both large and small patch scale (Wang *et al.* 2012). It has been suggested that a significant effect of soil heterogeneity on competition may be caused by the differences between plants in their ability to concentrate ramets and/or roots where nutrient levels are high (Bliss *et al.* 2002; Fransen *et al.* 2001; Zhou *et al.* 2012). In this study, although *H. vulgaris* showed the ability to concentrate ramets

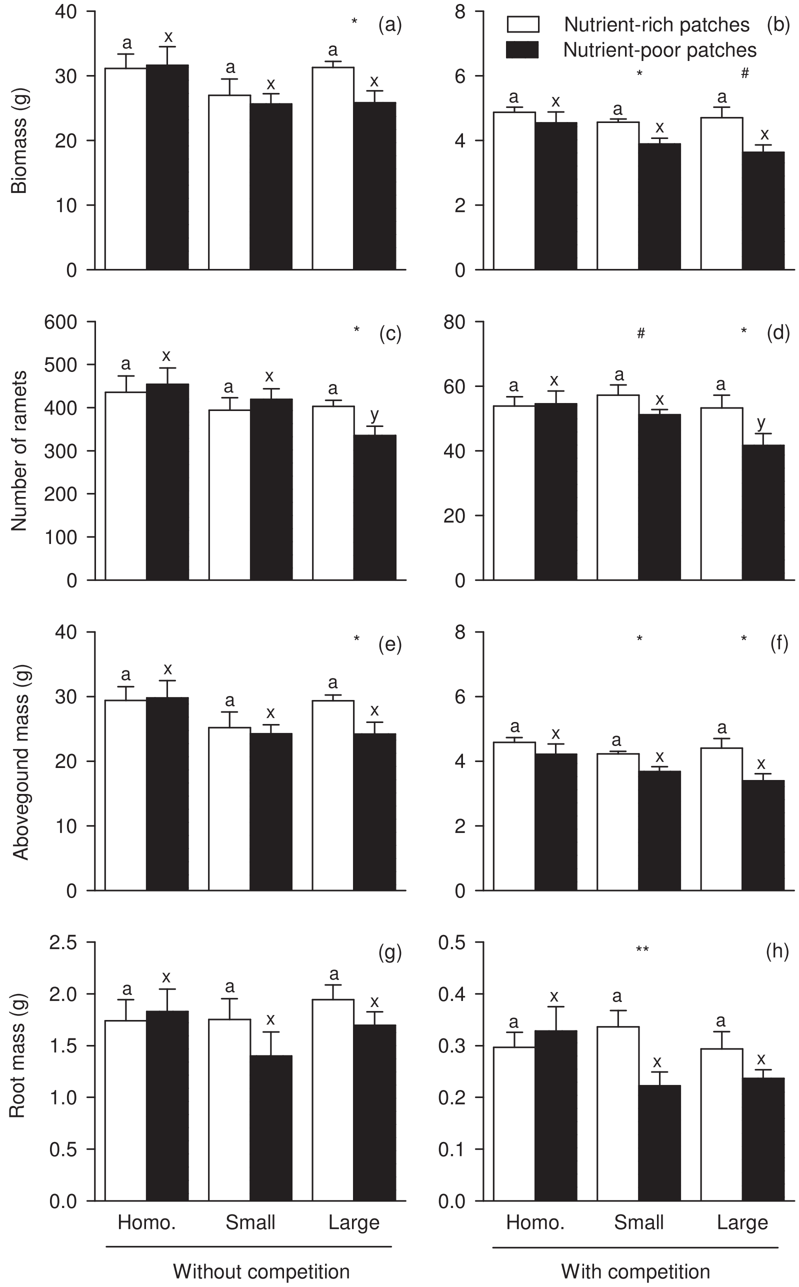

Figure 4: effects of patch type (nutrient-rich vs. nutrient-poor patches), soil heterogeneity (homogeneous vs. large patch vs. small patch) and intraspecific competition (without vs. with competition) on biomass (**a** and **b**), number of ramets (**c** and **d**), aboveground mass (**e** and **f**) and root mass (**g** and **h**) of *H. vulgaris* at the patch level. Error bars show +1 SE. Letters at ends of bars show which means differed between heterogeneity treatments within patch-type treatments (Tukey tests, $P = 0.05$); symbols at ends of bars show which means differed between patch-type treatments (paired *t*-tests): no symbol, $P \geq 0.1$; $^{\#}P = 0.05$–0.1; $^{*}P = 0.01$–0.05; $^{**}P = 0.001$–0.01.

and root mass in nutrient-rich patches, the differences in the ability to respond to soil nutrient heterogeneity between the *H. vulgaris* individuals may be little. Consequently, a significant effect soil heterogeneity on the intraspecific interactions was not observed.

Another possible reason is that physiological integration may weaken the influence of soil heterogeneity on plant competition (Fransen *et al.* 2001; Rajaniemi and Reynolds 2004). Physiological integration may alleviate the severe competition between ramets in nutrient-rich patches by allowing internal re-distribution of resources acquired by ramets in the nutrient-rich patches to support spreading of new ramets in the nutrient-poor patches, avoiding overgrowth of ramets in the nutrient-rich patches (Novoplansky 2009).

We conclude that there is little effect of soil heterogeneity on intraspecific competition of *H. vulgaris*. We hypothesize that

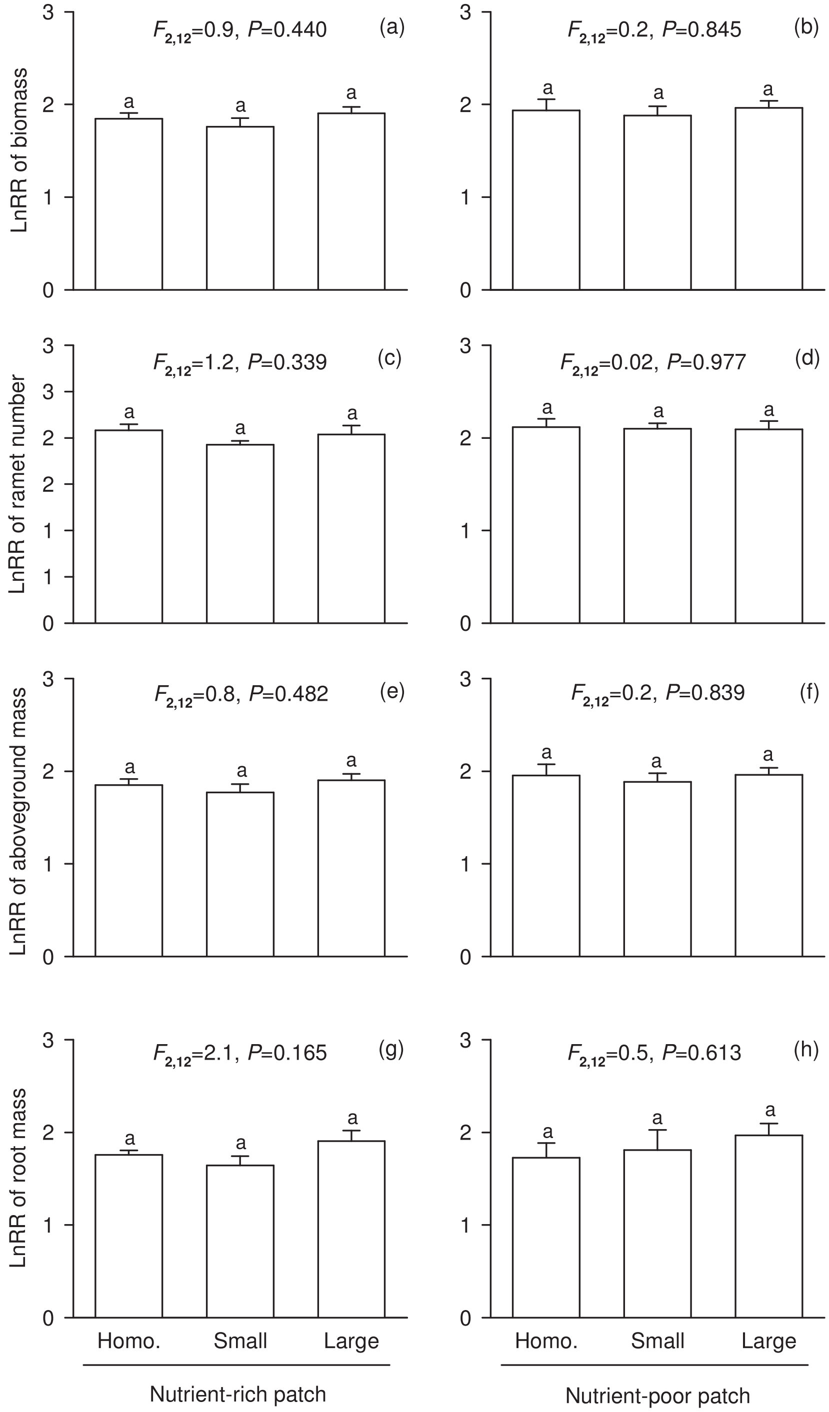

Figure 5: effects of soil heterogeneity (homogeneous *vs*. large patch *vs*. small patch) on the LnRR of *H. vulgaris* at the patch level. Degree of freedom, F and P values are given. Error bars show +1 SE. Bars sharing the same letters are not different at $P = 0.05$ (Tukey tests).

effects of intraspecific neighbors on foraging responses of *H. vulgaris* to soil heterogeneity at small scales may be closely related to the trade-off between ramet production rate and foraging precision. Our results suggest that foraging responses to soil heterogeneity may not necessarily be adaptive and intraspecific competition may not be influenced by soil heterogeneity.

FUNDING

Specific Programs in Graduate Science and Technology Innovation of Beijing Forestry University (BLYJ201204); the Fundamental Research Funds for the Central Universities (TD-JC-2013-1); the Program for New Century Excellent

Talents in University (NECT-10–0234); the National Natural Science Foundation of China (31200314).

Conflict of interest statement. None declared.

REFERENCES

Alpert P, Stuefer JF (1997) Division of labour in clonal plants. In de Kroon H, van Groenendael J (eds). *The Ecology and Evolution of Clonal Plants*. Leiden, The Netherland: Backbuys Publishers, 137–54.

Armas C, Ordiales R, Pugnaire FI (2004) Measuring plant interactions: a new comparative index. *Ecology* **85**:2682–6.

Bliss KM, Jones RH, Mitchell RJ, *et al.* (2002) Are competitive interactions influenced by spatial nutrient heterogeneity and root foraging behavior? *New Phytol* **154**:409–17.

Cahill JF Jr, McNickle GG, Haag JJ, *et al.* (2010) Plants integrate information about nutrients and neighbors. *Science* **328**:1657.

Campbell B, Grime J, Mackey JML (1991) A trade-off between scale and precision in resource foraging. *Oecologia* **87**:532–8.

Casper BB, Cahill JF (1996) Limited effects of soil nutrient heterogeneity on populations of *Abutilon theophrasti* (malvaceae). *Am Bot* **83**:333–41.

Casper BB, Cahill JF, Jackson RB (2000) Plant competition in spatially heterogeneous environments. In Hutchings MJ, *et al.* (eds). *The Ecological Consequences of Environmental Heterogeneity*. London: Blackwell Science, 111–30.

Day KJ, Hutchings MJ, John EA (2003a) The effects of spatial pattern of nutrient supply on the early stages of growth in plant populations. *J Ecol* **91**:305–15.

Day KJ, Hutchings MJ, John EA (2003b) The effects of spatial pattern of nutrient supply on yield, structure and mortality in plant populations. *J Ecol* **91**:541–53.

Day KJ, John EA, Hutchings MJ (2003c) The effects of spatially heterogeneous nutrient supply on yield, intensity of competition and root placement patterns in *Briza media* and *Festuca ovina*. *Funct Ecol* **17**:454–63.

de Kroon H, Huber H, Stuefer JF, *et al.* (2005) A modular concept of phenotypic plasticity in plants. *New Phytol* **166**:73–82.

Fransen B, de Kroon H, Berendse F (2001) Soil nutrient heterogeneity alters competition between two perennial grass species. *Ecology* **82**:2534–46.

Gao Y, Xing F, Jin YJ, *et al.* (2012) Foraging responses of clonal plants to multi-patch environmental heterogeneity: spatial preference and temporal reversibility. *Plant Soil* **359**:137–47.

Gross KL, Pregitzer KS, Burton AJ (1995) Spatial variation in nitrogen availability in three successional plant communities. *J Ecol* **83**:357–67.

Haslam SM (1987) *River Plants of Western Europe: The Macrophytic Vegetation of Watercourses of the European Economic Community*. New York, NY: Cambridge University Press.

He W-M, Alpert P, Yu F-H, *et al.* (2011) Reciprocal and coincident patchiness of multiple resources differentially affect benefits of clonal integration in two perennial plants. *J Ecol* **99**:1202–10.

He W-M, Yu F-H, Zhang L-L (2010) Physiological integration impacts nutrient use and stoichiometry in three clonal plants under heterogeneous habitats. *Ecol Res* **25**:967–72.

Hedges LV, Gurevitch J, Curtis PS (1999) The meta-analysis of response ratios in experimental ecology. *Ecology* **80**:1150–6.

Hodge A (2004) The plastic plant: root responses to heterogeneous supplies of nutrients. *New Phytol* **162**:9–24.

Hutchings MJ, de Kroon H (1994) Foraging in plants: the role of morphological plasticity in resource acquisition. *Adv Ecol Res* **25**:159–238.

Hutchings MJ, John EA (2004) The effects of environmental heterogeneity on root growth and root/shoot partitioning. *Ann Bot* **94**:1–8.

Hutchings MJ, John EA, Wijesinghe DK (2003) Toward understanding the consequences of soil heterogeneity for plant populations and communities. *Ecology* **84**:2322–34.

Hutchings MJ, Wijesinghe DK (1997) Patchy habitats, division of labour and growth dividends in clonal plants. *Trends Ecol Evol* **12**:390–4.

Hutchings MJ, Wijesinghe DK (2008) Performance of a clonal species in patchy environments: effects of environmental context on yield at local and whole-plant scales. *Evol Ecol* **22**:313–24.

Jackson RB, Caldwell MM (1993a) Geostatistical pattern of soil heterogeneity around individual perennial plants. *J Ecol* **81**:683–92.

Jackson RB, Caldwell MM (1993b) The scale of nutrient heterogeneity around individual plants and its quantification with geostatistics. *Ecology* **74**:612–4.

Janecek S, Janeckova P, Leps J (2004) Influence of soil heterogeneity and competition on growth features of three meadow species. *Flora* **199**:3–11.

Lacey EP, Herr D (2005) Phenotypic plasticity, parental effects, and parental care in plants? I. An examination of spike reflectance in *Plantago lanceolata* (Plantaginaceae). *Am J Bot* **92**:920–30.

Lechowicz MJ, Bell G (1991) The ecology and genetics of fitness in forest plants. II. Microspatial heterogeneity of the edaphic environment. *J Ecol* **79**:687–96.

Miao L-H, Ji M-C, Wang Y-Y, *et al.* (2011) Study on invasion risk of *Hydrocotyle vulgaris* as an alien species in wetlands. *J Zhejiang Univ-Agric and Life Sci* **37**:425–31.

Mommer L, van Ruijven J, Jansen C, *et al.* (2012) Interactive effects of nutrient heterogeneity and competition: implications for root foraging theory? *Funct Ecol* **26**:66–73.

Murphy KJ, Rørslett B, Springuel I (1990) Strategy analysis of submerged lake macrophyte communities: an international example. *Aquat Bot* **36**:303–23.

Novoplansky A (2009) Picking battles wisely: plant behaviour under competition. *Plant Cell Environ* **32**:726–41.

Peng Y-K, Luo F-L, Li H-L, *et al.* (2013) Growth responses of a rhizomatous herb *Bolboschoenus planiculmis* to scale and contrast of soil nutrient heterogeneity. *Chinese J Plant Ecol* **37**:335–43.

Price EAC, Marshall C (1999) Clonal plants and environmental heterogeneity. *Plant Ecol* **141**:3–7.

Rajaniemi TK, Reynolds HL (2004) Root foraging for patchy resources in eight herbaceous plant species. *Oecologia* **141**:519–25.

Roiloa SR, Retuerto R (2006) Small-scale heterogeneity in soil quality influences photosynthetic efficiency and habitat selection in a clonal plant. *Ann Bot* **98**:1043–52.

Schwinning S, Weiner J (1998) Mechanisms determining the degree of size asymmetry in competition among plants. *Oecologia* **113**:447–55.

Song Y-B, Yu F-H, Keser LH, *et al.* (2013) United we stand, divided we fall: a meta-analysis of experiments on clonal integration and its relationship to invasiveness. *Oecologia* **171**:317–27.

Stuefer JF (1996) Potential and limitations of current concepts regarding the response of clonal plants to environmental heterogeneity. *Vegetatio* **127**:55–70.

van der Waal C, de Kroon H, Heitkönig IMA, *et al.* (2011) Scale of nutrient patchiness mediates resource partitioning between trees and grasses in a semi-arid savanna. *J Ecol* **99**:1124–33.

Wang P, Lei JP, Li MH, *et al.* (2012) Spatial heterogeneity in light supply affects intraspecific competition of a stoloniferous clonal plant. *PLoS One* **7**:e39105.

Wang Z, van Kleunen M, During HJ, *et al.* (2013) Root foraging increases performance of the clonal plant *Potentilla reptans* in heterogeneous nutrient environments. *PLoS One* **8**:e58602.

Wijesinghe DK, Hutchings MJ (1997) The effects of spatial scale of environmental heterogeneity on the growth of a clonal plant: an experimental study with *Glechoma hederacea*. *J Ecol* **85**:17–28.

Wijesinghe DK, Hutchings MJ (1999) The effects of environmental heterogeneity on the performance of *Glechoma hederacea*: the interactions between patch contrast and patch scale. *J Ecol* **87**:860–72.

Wijesinghe DK, John EA, Beurskens S, *et al.* (2001) Root system size and precision in nutrient foraging: responses to spatial pattern of nutrient supply in six herbaceous species. *J Ecol* **89**:972–83.

Zhang L-L, He W-M (2009) Consequences of ramets helping ramets: no damage and increased nutrient use efficiency in nurse ramets of *Glechoma longituba*. *Flora* **204**:182–8.

Zhou J, Dong B-C, Alpert P, *et al.* (2012) Effects of soil nutrient heterogeneity on intraspecific competition in the invasive, clonal plant *Alternanthera philoxeroides*. *Ann Bot* **109**:813–8.