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Foraging responses of clonal plants to multi-patch environmental heterogeneity: spatial preference and temporal reversibility

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Abstract

Background and aims Plant root placement is highly plastic in order to acquire patchily distributed nutrients and to ensure their survival, growth and reproduction. Considering the spatial extension of clonal organs, we selected two clonal plants (*Leymus chinensis* (Trin.) Tzvel. and *Hierochloa glabra* Trin.) to determine the spatio-temporal effects of environmental heterogeneity on belowground organs and newly-born ramets.

Methods Small-scale and multi-patch heterogeneous environments were manipulated by creating four patches filled with different types of soil in a same pot. The four patches were composed of sandy soil, sandy loam, loam soil and humus soil, respectively.

Ramet number, bud number, mean spacer length, rhizome length, and biomass allocation within each patch were measured to identify plant foraging responses.

Results The preferential patch of *L. chinensis* was humus soil patch which was the highest in nutrient availability, whereas *H. glabra* preferred to place ramets in sandy loam and loam soil patches. When growing in homogeneous environments, both species randomly rooted their offspring ramets in the four compartments. In heterogeneous environments, foraging responses were detected in ramet placement, aboveground biomass and total rhizome length. However, there were no differences in bud number or belowground biomass among four types of patches in heterogeneous environments, which might suggest that there would be no inter-patch differences in seedling establishment in the next year.

Conclusions Plants show selective allocation of offspring ramets to preferential patches in the presence of multi-patch environmental heterogeneity. Responses of *H. glabra* to multi-patch heterogeneity were faster than those of *L. chinensis*, demonstrating that the foraging patterns are species-specific. Clonal plants can rapidly respond to environmental heterogeneity, whereas foraging responses are potentially reversible over a longer temporal scale.

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Keywords Nutrient heterogeneity · Plant plasticity · Resource allocation · Ramet placement · Temporal change

Introduction

Plants can exhibit ability to respond rapidly and reversibly to environmental stimuli and thus result in differential fitness (Silvertown and Gordon 1989). These responses to external stimuli are most often examined in the context of morphologically plastic growth, secondary metabolite production, and the expression of other adaptive traits (Braam 2005; Ballaré 2009; Metlen et al. 2009). Plant plasticity in morphology and physiology is considered as the adaptation to environmental stimuli (Dong 1996; Hodge 2004; Mommer et al. 2011). These environmental stimuli include abiotic factors such as patchily-distributed resources and biotic factors such as competition, herbivory, and mycorrhiza (Croft et al. 2011; Schiffers et al. 2011).

In natural ecosystems, spatial and temporal variation in resource distribution is a very common feature of environments (Farley and Fitter 1999). Resource availability in natural communities can vary widely both in space and over time (Wijesinghe and Hutchings 1997). Considerable temporal variation in soil nutrient concentration has been well recorded throughout the year (Farley and Fitter 1999). Additionally, the study on spatial variation in soil resources has demonstrated that nutrient availability can vary significantly at a scale of 10 cm (Lechowicz and Bell 1991). The quality of grassland soils in North China shows obvious variation at a scale of 20 cm (Zhu 2004). Neighbor relations in pastures can also vary at very fine spatial scales (Turkington and Harper 1979; Wijesinghe and Hutchings 1997). Heterogeneity can also result in rapid changes to plant morphology and physiology at very small spatial scales. Plants can respond dramatically to small-scale spatial variation in habitat quality (Roiloa and Retuerto 2006).

A number of studies have shown that some plant species can increase resource capture through morphological and physiological adjustments in order to adapt to heterogeneous environments (Hodge 2004; Hodge 2006; Stephens et al. 2007). During recent 30 years, plant foraging responses in heterogeneous environments have been the subject of intense research interest and several reviews (Karban 2008; de Kroon et al. 2009; McNickle et al. 2009). Many relevant researches mainly focus on the analysis and interpretation of plant phenotypic plasticity in patchy habitats and their consequences for resource acquisition (Hutchings and de Kroon 1994). It was concluded that plants prefer to

inhabit high-quality patches in heterogeneous environments and that plant species can develop morphological and physiological plasticity as their efficient foraging strategies in order to increase plant fitness (Welham et al. 2002; Day et al. 2003; Wang et al. 2011).

However, the experimental design of most related studies hitherto involves only two contrasting types of patches (high or poor quality habitats). Their main concerns of these studies are the phenotypic plasticity of plants growing in high- or poor-quality patches and their capacity to obtain more resources (Slade and Hutchings 1987; Stuefer et al. 1996; Price and Marshall 1999). Actually, the natural environments are often extremely heterogeneous with patchy resource distribution and different total amount of resources. Thus, heterogeneous habitats composed of only two contrasting types of patches represent a great simplification of natural environmental heterogeneity. In natural environments, plants must often cope with complex habitats with multi-patch spatial segregation of resources at small spatial scales, rather than the environments with the nutrient gradient of only two levels. However, little is known about the influence of more realistic scenarios of heterogeneity on plant foraging strategies. Thus, in the present work, we investigated plant foraging responses to small-scale and multi-patch patterns of habitats. This heterogeneous design would more closely mimic the soil environments that plants experience in nature.

Clonal plants depend on asexual reproduction to produce offspring ramets and expand the population, and thus dominate many natural communities. Genetically distinct individuals (genets) of clonal species are composed of potentially independent units (ramets) with potential of physiological integration. Each ramet of a clonal plant is, at least potentially, capable of developing all the organs necessary for the survival and reproduction. This reproduction mode enables clonal plants to have more opportunities to experience small-scale spatial heterogeneity in natural environments. Moreover, physiological integration of clonal plants allows the transport of photosynthates, water and nutrients between established ramets and thereby buffers clonal plants against heterogeneous habitats (Wijesinghe and Hutchings 1997; Saitoh et al. 2002). The patterns of ramet placement in heterogeneous environments, incorporating rapid morphological and physiological acclimation to patchy habitats, could be adaptive strategies of clonal plants to efficiently

harvest essential resources (Karban 2008). It is important to know about the spatial and temporal changes of root foraging responses in clonal plants. The central objective of our research was to determine the spatio-temporal effects of small-scale and multi-patch heterogeneity on the foraging responses of clonal plants, including effects on ramet establishment, biomass allocation and phenotypic plasticity of root system.

Clonal plants can respond to varied environments by adjusting their morphological and physiological characteristics to match current conditions. Special regeneration mode depending on asexual reproduction can increase root plasticity of clonal plants in patchy nutrient environments to acquire more resources. Specifically, our first hypothesis was that clonal plants could preferentially root their ramets in favorable patches for capturing more available resources. Although many species respond to nutrient heterogeneity through root plasticity, the magnitude of these foraging responses varies substantially among species (James et al. 2009; Croft et al. 2011; Mommer et al. 2011). Species-specific patterns might demonstrate that clonal plants possess multiple strategies to establish offspring ramets in multi-patch heterogeneous habitats at small spatial scales. Second, we hypothesized that the foraging strategies in heterogeneous environments would vary among plant species, including variation in the selectivity of patches colonized and in colonization rate in new patches. Environmental heterogeneity widely exists in natural habitats, whereas nutrient uptake and leaching might lead to resource removal and depletion in natural patches and thus affect plant responses related to root proliferation and ramet production in the heterogeneous environments. Therefore, the relatively rapid responses of perennial plants also might be non-permanent and disappear in the long run. Further, we hypothesized that clonal plants would rapidly respond to multi-patch environments through the morphological adjustment, but the plastic responses would be potentially reversible over time.

Materials and methods

Study site and plant species

The experiment was conducted in a greenhouse at the Grassland Ecological Research Station of Northeast Normal University, Jilin Province, PR China (44° 45' N, 123° 45' E). The station is located in the southern part of the

Songnen Plain in the eastern Eurasian steppe region. The mean temperature of our study area is 6.2°C in 2009. The annual precipitation is 353 mm in that year.

We selected two clonal species, *Leymus chinensis* (Trin.) Tzvel. and *Hierochloa glabra* Trin., to be our experimental subjects. These two species are both herbaceous perennial species with extensive plasticity in morphological and physiological characteristics, and have a naturally widespread distribution in the meadow soils and sandy loam of northern China and eastern Mongolia. *L. chinensis* is a dominant species in arid to semi-arid steppes in northern China, and *H. glabra* is often found in communities as a companion species in these areas (Bai et al. 2009; Yang and Zheng 1997).

Both species are typical perennial rhizomatous grasses and their rhizomes lie horizontally 5–15 cm under the soil surface and are highly branched (Wang and Ba 2008). For both two species, rhizome growth plays a major role in spatial expansion and colonization by offspring ramets. Rhizome buds can be dormant, and grow upward to form new ramets or grow horizontally to form new rhizomes (Zhu 2004). We selected *L. chinensis* and *H. glabra* as the study species for this experiment because of their well documented phenotypic plasticity and foraging responses (Dong 1996; Fan et al. 2006; Wang et al. 2004; Wang et al. 2008). Their foraging responses are likely to have profound effects on the community structure, plant-plant interactions, plant-animal interactions and ultimately ecosystem functioning.

Experimental design

The greenhouse experiment was a completely randomized design with thirty replicates, and sixty plastic pots were used for each species. Two types of environments (homogeneous and heterogeneous conditions) were created in large plastic pots (65 cm in diameter and 20 cm in depth). Every pot was divided into 4 equal compartments by plastic partitions, with the central area (0.1 × 0.1 m²) of each pot used for seedling transplantation (Fig. 1). The plastic partitions were firmly attached to the sides of the pots using plastisol so that the soil in the four compartments could not mix. A 2-cm diameter circular hole at the bottom of each patch was covered with window screening to ensure breathability but prevent rhizomes from growing out of the pot. The homogeneous environment was created by adding the same loam soil to all the four

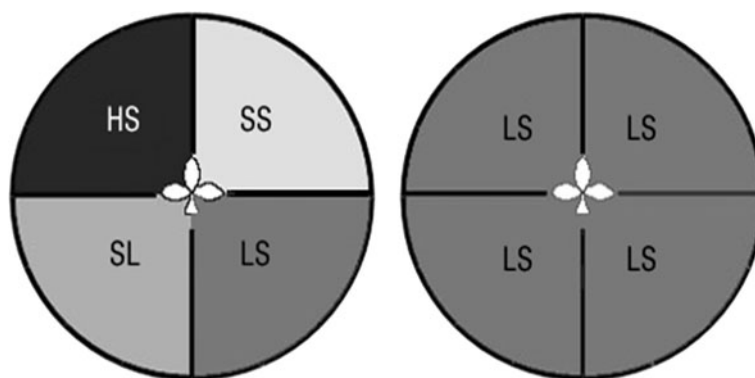


Fig. 1 Schematic representation of heterogeneous and homogeneous environments used in our experiment. The heterogeneous habitat was composed of four different patches (sandy soil (SS); sandy loam (SL); loam soil (LS); and humus soil (HS)).

compartments. Loam soil was chosen as the substrate for the homogeneous environments because it is the common farmland soil in this region. Four patch types in the heterogeneous treatment were created by assigning different soil types to the four compartments of the pot. The four soil types in the heterogeneous environments were as follows: sandy soil (a mixture of 80% sand and 20% loam), sandy loam (a mixture of 35% sand and 65% loam), loam soil (100% local farmland loam), and humus soil (a mixture of 50% loam and 50% humus). The sand was sieved and washed to remove non-sand materials, and the impurities were removed from the loam and humus substrates.

In early May 2009, 60 *L. chinensis* and 60 *H. glabra* seedlings with no offspring ramets were selected for size uniformity from the same field site and then were randomly assigned to heterogeneous or homogeneous habitat types. The plants were then planted in the center area of each pot, giving each compartment a priori equal chance of being colonized. Every parent ramet was transplanted with 1-cm rhizomes on each side (with no buds) to avoid artifactual directional growth, and ramets were further clipped to a 2-cm height to increase survival rate. The plants were allowed to grow for 5 months (May 10th to September 20th). All pots were watered when necessary (frequent shorter watering was preferred).

Measurements and data analysis

Once every 5 days during the experiment (14 times in total), we recorded the number of offspring ramets in each patch to identify possible colonization preferences.

Nutrient availability gradually increases along the gradient $SS < SL < LS < HS$. The four compartments of the homogeneous habitat were composed of a single soil type (loam soil)

All of the plant materials within homogeneous and heterogeneous treatments were harvested at the end of the growing season. The aboveground parts of all ramets in each patch were cut at the soil surface and dried to a constant mass at 80°C in the oven. The underground parts in each patch were dug out and were separated into buds, rhizomes and fibrous roots. We measured bud number, spacer length, total rhizome length and primary rhizome length in each patch. We defined rhizome length as the absolute length of all rhizomes. All of the underground parts were also dried to measure biomass. Because rhizome clonal plants mainly depend on rhizomes to survive the winter and recover in the spring of the following year, we used bud number and underground biomass to infer the effects of heterogeneity on clonal plant populations at the second growing season.

Prior to analyses, all variables were tested for normality and homoscedasticity of variance. We used mixed MANOVA with profile analysis to determine whether heterogeneity-induced variation in ramet placement changed over time, with heterogeneity used as the between-subject factor and patch type (four soil types) and time used as the within-subject factors. Non-parametric statistics, with patch type serving as the between-subject factor, were used to analyze differences in the number of ramets established in the different patches on each date, and analyses were conducted separately for homogeneous and heterogeneous environments. When significant violations of sphericity were found, non-parametric statistical analyses of K related samples were conducted to determine the differences in spacer length, rhizome length, aboveground and underground biomass, bud number, and primary

rhizomes within the four patches. Multiple comparison analysis within the four nutrient patches in the heterogeneous environment was also conducted using the significance level $p \leq 0.05$. Differences in total biomass and biomass allocation between heterogeneous and homogeneous treatments were compared using one-way analyses of variance (ANOVA) with heterogeneity as the factor to determine the effects of heterogeneity treatments on total productivity. All statistical tests were performed with SPSS 19.0 software.

Results

Spatial habitat selection — ramet establishment and spacer length

The significant interaction between heterogeneity, patch type and time indicated an obvious difference in ramet placement between homogeneous and heterogeneous treatments over time both in *L. chinensis* (profile analysis: $F_{(39, 20)} = 57.28$, $P = 0.036$) and in *H. glabra* (profile analysis: $F_{(39, 17)} = 238.14$, $P = 0.000$). Generally, both species randomly placed offspring ramets in homogeneous environments, with no difference in ramet number among the four homogeneous compartments (Fig. 2a). Ramet number of *L. chinensis* showed significant differences among four types of patches in heterogeneous environments after July 30th, with more ramets in the humus soil patch, but did not before the date. The numbers of *H. glabra* ramets in the four types of patches in heterogeneous treatment were different prior to August 20th, with the highest number of ramets in the patches of sandy loam and loam soil. However, this difference disappeared on the last four sampling dates (Fig. 2b).

Phenotypic plasticity in spacer length within the multi-patch heterogeneous nutrient patches was detected in *L. chinensis* ($F_{(2.17, 26.05)} = 3.30$, $P = 0.049$), but not in *H. glabra* ($F_{(1.57, 9.43)} = 0.940$, $P = 0.402$). The mean spacer length of *L. chinensis* in the humus soil patch was significantly greater than that in the sandy loam patch, and slightly greater than that in the sandy soil and loam soil patches (Fig. 3a).

Temporal change of the reproductive potential — bud propagation and rhizome length

We found no significant difference in bud number among the four heterogeneous nutrient patches,

indicating that there was no effect of patch type on dormant buds at the end of the growing season in *L. chinensis* ($F_{(2.49, 72.19)} = 0.96$, $P = 0.405$) or *H. glabra* ($F_{(1.96, 56.92)} = 0.53$, $P = 0.587$) (Table 1). For the heterogeneous treatment, the total rhizome length of *H. glabra* significantly differed among the four patches ($F_{(2.67, 50.76)} = 3.29$, $P = 0.025$), whereas that of *L. chinensis* did not (Table 1). The primary rhizome length of *H. glabra* was slightly higher in sandy loam and loam soil patches than in sandy soil and humus soil patches. Similarly, primary rhizome length of *L. chinensis* was appreciably greater in the humus soil patch than in the other three patches (Fig. 4).

Biomass allocation

Ramets of *L. chinensis* growing in heterogeneous environments showed significantly lower investment in photosynthetic biomass (aboveground/total biomass, AB : TB) (ANOVA: $P = 0.046$) than ramets growing in homogeneous environments (Table 2). Such difference was not observed for *H. glabra* (ANOVA: $P = 0.061$) (Table 2). In the heterogeneous treatments, significant effects of patch type were found for the aboveground biomass of ramets in *L. chinensis* (ANOVA: $F = 9.70$, $P = 0.000$) and *H. glabra* (ANOVA: $F = 2.99$, $P = 0.045$). The aboveground biomass of *L. chinensis* and *H. glabra* was highest in the humus soil patch and in the sandy loam patch, respectively (Fig. 5a and c). Multiple range test revealed no differences in belowground biomass among the four types of patches in either species, suggesting that patch type had no effect on belowground biomass at the end of the growing season (Table 1, Fig. 5b and d).

Discussion

Spatial expansion and morphological plasticity of clonal plants

Clonal plants can plastically respond to environmental heterogeneity by placing ramets in favorable sites. The influence of multi-patch heterogeneity on the foraging responses of clonal plants was similar for *L. chinensis* and *H. glabra*, with both species preferentially inhabiting particular patches in heterogeneous environments. Facing multi-patch heterogeneous habitats, the offspring ramets of *L. chinensis* were established

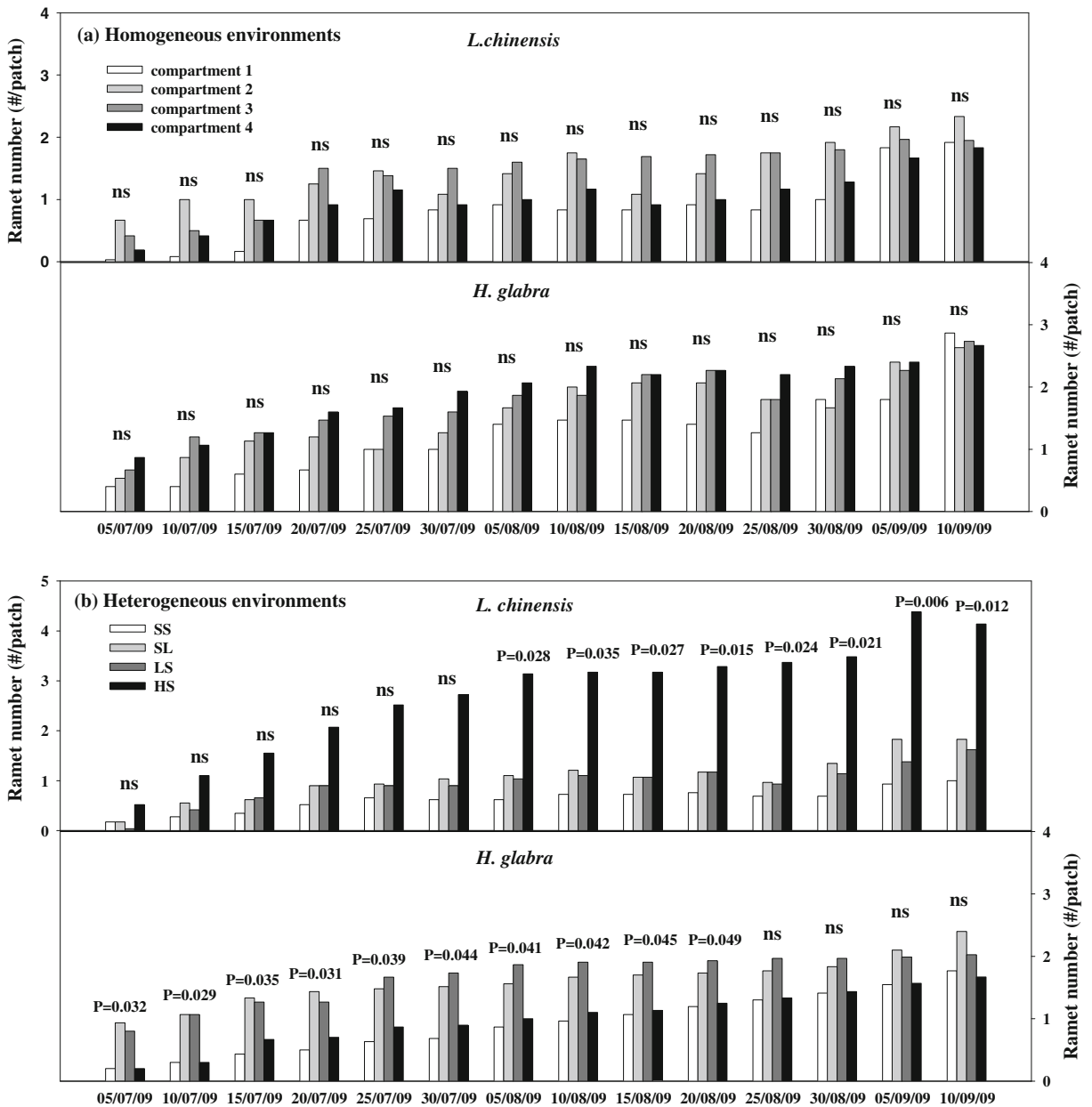


Fig. 2 Time course of patch colonization in homogeneous and heterogeneous environments by ramets of two clonal plants (*Leymus chinensis* and *Hierochloa glabra*). The heterogeneous habitat was composed of four different patches (sandy soil (SS); sandy loam (SL); loam soil (LS); and humus soil (HS)). The four compartments of the homogeneous habitat were composed of a single soil type (loam soil). For each date, columns show the average number of offspring ramets established in the different patches comprising the homogeneous (a) and heterogeneous (b)

habitats. Non-parametric statistical results for each date are shown (* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; ns = not significant). Profile analysis with heterogeneity (two levels: heterogeneous and homogeneous treatments) as a between-subject factor and patch type and time as within-subject factors produced the following results: $F_{(39, 20)} = 57.28, P = 0.036$ for the heterogeneity \times patch type \times time interactive effects on *L. chinensis*; $F_{(39, 17)} = 238.14, P = 0.000$ for the heterogeneity \times patch type \times time interactive effects on *H. glabra*

in its most favorable patch (humus soil patch), and *H. glabra* quickly inhabited the sandy loam and loam soil

patches (Fig. 2b). This confirms our prediction that plants would select particular patches as preferential

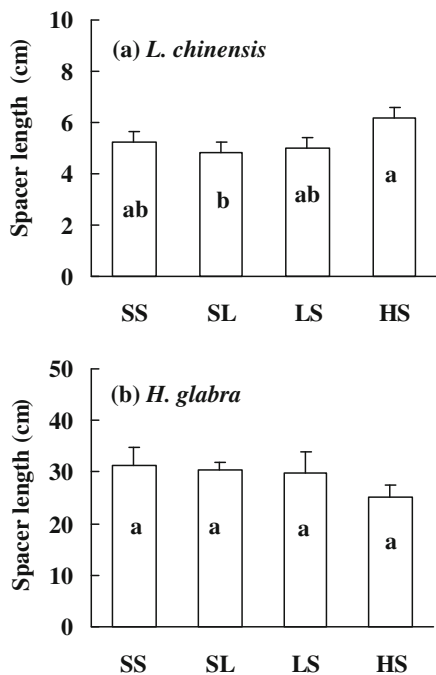


Fig. 3 Mean spacer length of *Leymus chinensis* (a) and *Hierochloa glabra* (b) in sandy soil (SS), sandy loam (SL), loam soil (LS), and humus soil (HS) patches under heterogeneous conditions. Habitats not sharing the same letters were significantly different at $p \leq 0.05$. Values represent means \pm S.E

locations for ramets under heterogeneous conditions. This selective ramet establishment in clonal plants has sometimes been attributed to enhancing the acquisition of essential resources (Oborny 1994). Clonal plants respond to high local resource availability by morphological plasticity, such as decreasing internode length and/or increasing branching frequencies. Such a pattern would enable the plants to accumulate more ramets in favourable microsites and increase resource efficiency. Other studies also suggested that clonal

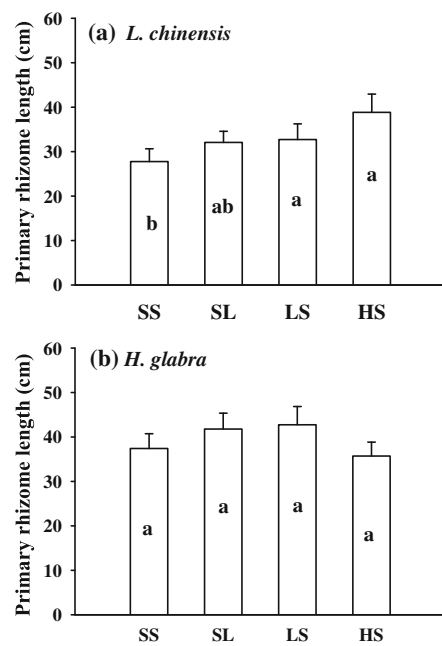


Fig. 4 Primary rhizome length of *Leymus chinensis* (a) and *Hierochloa glabra* (b) in sandy soil (SS), sandy loam (SL), loam soil (LS), and humus soil (HS) patches under heterogeneous conditions. Habitats not sharing the same letters were significantly different at $p \leq 0.05$. Values represent the means \pm S.E

plants might respond to patchy distribution and total amount of resources in heterogeneous environments, and thereby increase the probability of placing ramets in high-quality patches (Schellner et al. 1982; Eriksson 1986). The most preferred habitat of *L. chinensis* was the humus soil patch in which nutrient availability was higher than in other three types of patches. However, *H. glabra* preferentially placed more ramets in sandy loam and loam soil patches, not in the humus soil patch with the highest nutrient availability. Therefore, nutrient availability is not the only factor that explains

Table 1 Non-parametric statistics results of bud number, total rhizome length, aboveground biomass and belowground biomass of *Leymus chinensis* and *Hierochloa glabra* growing in

Parameter	<i>L. chinensis</i>			<i>H. glabra</i>		
	df	F-values	P-values	df	F-values	P-values
Bud number	3	0.96	0.405 ^{NS}	3	0.53	0.587 ^{NS}
Total rhizome length	3	1.13	0.342 ^{NS}	3	3.29	0.025*
Aboveground biomass	3	9.70	0.000***	3	2.99	0.045*
Belowground biomass	3	0.31	0.822 ^{NS}	3	0.37	0.746 ^{NS}

* $p \leq 0.05$; ** $p \leq 0.01$; *** $p \leq 0.001$; NS no significance

heterogeneous environments. P-values showed effects of ‘patch type’ in heterogeneous environments (values with * are significant at $p \leq 0.05$)

Table 2 Mean values (\pm SE) and non-parametric statistics for aboveground biomass (AB), belowground biomass (BB), aboveground: total biomass ratio (AB:TB) of two clonal species

(*Leymus chinensis* and *Hierochloa glabra*) in heterogeneous and homogeneous environments

	Parameter	Heterogeneity	Homogeneity	P-values
<i>L. chinensis</i>	AB	3.30 \pm 0.81	3.68 \pm 0.45	0.668 ^{NS}
	BB	7.67 \pm 1.21	6.61 \pm 0.75	0.478 ^{NS}
	AB:TB	0.27 \pm 0.04	0.36 \pm 0.03	0.046*
<i>H. glabra</i>	AB	2.86 \pm 0.52	2.42 \pm 0.16	0.312 ^{NS}
	BB	8.78 \pm 1.71	8.02 \pm 0.46	0.582 ^{NS}
	AB:TB	0.27 \pm 0.02	0.23 \pm 0.01	0.061 ^{NS}

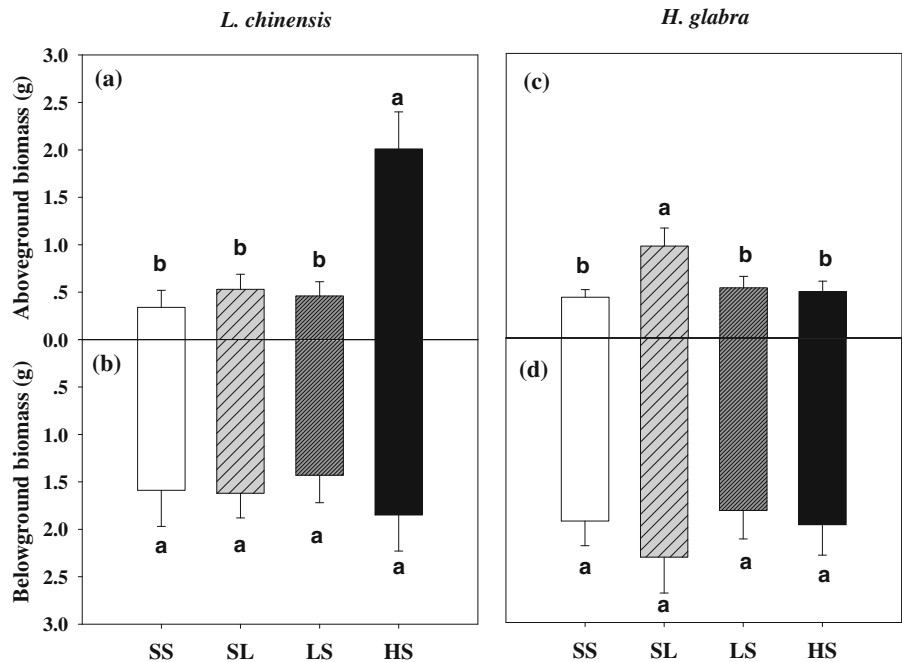
* $p \leq 0.05$; NS no significance

the variation in initial ramet placement. Other physical and chemical characteristics of soils related to gas exchange and water humidity are also plausible mechanisms affecting selective ramet establishment of clonal plants (Roiloa and Retuerto 2006).

Selective ramet placement is the main characteristic of clonal plant foraging (Evans and Cain 1995). Indeed, many clonal species would produce more ramets within favorable patches than within unfavorable ones (de Kroon and Knops 1990; Alpert 1991; Evans 1992; Evans and Cain 1995). Internode length, spacer length and rhizome length have been used to describe plant foraging responses in some studies. However, Dong and de Kroon (1994)

showed that rhizome length and internode length of *Cynodon dactylon* (L.) Pers. did not show significant variation in relation to nutrient availability. Dong and Alaten (1999) also suggested that internode length was not affected by variation in water or nutrient supply. Similarly, morphological plasticity in spacer length and primary rhizome length was not detected in *L. chinensis* and *H. glabra* in the present study, with the exception that the spacer length of *L. chinensis* increased in the humus soil patch (Figs. 3 and 4). Because of the greater plasticity of root distribution, short-time response of plant roots to patchily distributed nutrient is mainly in growth direction, not in root length.

Fig. 5 Mean aboveground and underground biomass in 4 patch types (sandy soil-SS, sandy loam-SL, loam soil-LS, and humus soil-HS) for two species (*Leymus chinensis* and *Hierochloa glabra*) in heterogeneous habitats. Habitats not sharing the same letters were significantly different at $p \leq 0.05$. Values represent the means \pm S.E



Species-specific patterns of foraging responses

The heterogeneous environments resulted in a decrease in the relative aboveground biomass in *L. chinensis*, demonstrating a decrease in plant investment in photosynthetic biomass. However, *H. glabra* did not respond to nutrient heterogeneity in the same manner (Table 2). Moreover, environmental heterogeneity also induced the preferential selection of patches for placing new ramets in *L. chinensis* and *H. glabra*, but the two species displayed different modes of ramet establishment. Ramet number of *L. chinensis* differed significantly among patches after July 30th. In contrast, for *H. glabra*, ramet number was significantly different in the four heterogeneous patches before August 20th, but turned out to be similar after August 25th (Fig. 2b). These results support our hypothesis that the two clonal species would show species-specific patterns and have different foraging strategies in their responses to patchy nutrient distribution. We found that *H. glabra* showed a faster change in response to multi-patch heterogeneous conditions than *L. chinensis*. This result suggests that the foraging response of *H. glabra* in response to small-scale spatial heterogeneity is more sensitive than that of *L. chinensis*. The difference in patch selection of plant ramet placement and the speed of plant foraging responses is also likely to be related to osmotic changes in ionic concentrations or electrical signals, their phenological rhythms, bud development, and other biological characteristics and processes (Karban 2008). Compared with *L. chinensis*, *H. glabra* has more and longer rhizomes, which could result in more extensive spread of clones (Table 1). The species-specific foraging patterns of *L. chinensis* and *H. glabra* are probably associated with the difference in their root structure and function (Fan et al. 2006).

Rapid and reversible foraging responses of clonal plants at a long temporal scale

Plants usually respond to external stimuli very rapidly, like leaflets of legumes can quickly fold up in response to herbivory (Braam 2005). Our results also demonstrated that the foraging responses of *L. chinensis* and *H. glabra* to heterogeneous environments were very rapid in ramet placement (Fig. 2). For both species, the number of newly produced ramets in different patches was significantly different during the first growing season (Fig. 2b). However, most studies on physiological or morphological foraging of clonal

plants have focused on short-term effects and have not determined whether such effects can be maintained over a longer term (Hutchings and de Kroon 1994; Dong 1996; de Kroon et al. 2009; Cahill Jr and McNickle 2010). The responses of *H. glabra* to heterogeneity reversed very quickly, but we did not find this reversion in *L. chinensis* during the course of this experiment (Fig. 2b). We further determined the long-term foraging responses of the two species according to ramet placement in the four types of patches at the beginning of the second growing season.

Neither species showed significant difference in bud number among four types of patches, suggesting that patch type had no effect on the number of dormant buds at the end of the growing season (Table 1). For perennial clonal plants depending on asexual reproduction, dormant buds are the important sources and reserve for the production of new ramets, and determine the population dynamics over a long period (Charpentier et al. 1998; Gao et al. 2008; Wang et al. 2008). Multiple comparison analysis showed that there was no difference in belowground biomass among the four different patches in either *L. chinensis* or *H. glabra* (Fig. 5). Therefore, we inferred that there would be no difference in ramet number among the four types of patches at the next growing season. This means that these species exhibited no obvious foraging responses that persisted at the longer-term time scale, which confirms our third hypothesis. In general, plant species display the preference for occupying the patches with high quality. However, nutrient availability in nutrient-rich patches would also decrease more quickly due to higher root turnover rates, leaching and exudation (Vázquez de Aldana et al. 1996). In nature, the effects of patch depletion, the absorbability of root system, root turnover and the spatial competition of existing ramets might result in the disappearance of the long-term foraging responses of plants to environmental heterogeneity (Fransen and de Kroon 2001; Roiloa and Retuerto 2006).

In general, the present study supports the premise that clonal plants present rapid plastic responses in small-scale, multi-patch heterogeneous environments. The rapid foraging response is the important adaptive strategy for clonal plants and plays a substantial role in their long-term persistence in heterogeneous environments. The speed of plant foraging is quick and obvious at a short time scale. However, foraging responses are reversible over the long run, possibly due to the

quick decrease in nutrient heterogeneity over time, the increase of root density per unit area, or spatial competition among ramets. Our study has detected the species-specific foraging patterns of *L. chinensis* and *H. glabra* in response to patchy nutrient environments, which might be associated with the modular structure and function of the species. Future consideration would aim to make clear the mechanisms underlying foraging responses in clonal plants, especially when competition for resource acquisition in different species affects the plasticity of foraging responses under the field conditions.

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