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Do plants explore habitats before exploiting them? An explicit test using two stoloniferous herbs

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We tested whether the processes of exploration and exploitation can be explicitly distinguished as plants grow and develop within a habitat using two stoloniferous clonal herbs, *Hydrocotyle sibthorpioides* (Umbelliferae) and *Potentilla anserina* (Rosaceae). Ramets were planted in four circular trays differing in diameter. One replicate from each diameter-group was sampled at intervals corresponding to plant coverage of the trays, and plant biomass allocation to leaves, stolons, and roots and internode length were quantified. For both species, at early sampling times (when the smallest trays were full), total plant biomass and ramet number were larger in the smaller trays than in the larger trays. However, this trend was reversed for plants collected at later times. For *H. sibthorpioides*, leaf mass ratios (leaf mass to total plant mass) were significantly greater, but stolon mass ratios (stolon mass to total plant mass) were less in the small trays than in the larger ones, particularly during the early stages of the experiment. Similarly, for *P. anserina*, leaf mass ratios decreased in the smaller trays but increased in the larger ones as the experiment progressed. Root mass ratios showed contrasting pattern to leaf mass ratios for both species; stolon mass ratios were significantly smaller in the smaller trays than in the larger ones, although there were no obvious patterns during the course of the experiment. In addition, for both species, internode length was shorter but the number of ramets was greater in the smaller trays at early sampling times. We conclude that plants invest greater biomass in resource-exploring organs (stolons) than in resource-exploiting organs (leaves or roots) as they initially establish in a habitat. The relatively lower plant productivity in the largest trays at early sampling times presumably reflects the cost of exploration prior to resource exploitation and utilization.

clonal plant, foraging behavior, exploring and exploiting behavior, biomass allocation, life history tradeoff

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Although plant behavior has been defined in many different ways [1–4], the majority of metaphors for this phenomenon have been borrowed from observations of animal behavior [5]. This practice is particularly true for the phenomenon of plant "foraging", which has been defined as the selective placing of resource-acquiring organs into resource-rich patches within heterogeneous habitats [6]. For example, just as animals often forage longer in favorable sites than in less favorable ones, plants tend to increase branching intensity (the number of ramets) and decrease internode length in high-quality sites compared to low-quality sites [7–10]. This foraging behavior has been interpreted to reflect a strategy to enhance future resource uptake rather than a simple growth process resulting from current resource availability [2,11]. It is also thought to foster clonal expansion and offspring establishment [12,13]. Regardless of its strategic significance, this form of plant foraging occurs widely among clonal plant species [2,14–18]. It has also been reported for plant roots [5,11,19].

Continuing in the metaphorical spirit, botanists often di-

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vide foraging in a site into two processes: exploration and exploitation. The time allocated to these two processes is theorized to maximize energy gain per unit time, depending on which "prey" is selected and the length of time the "predator" stays within a patch [7,20–22]. Longer exploration is often associated with low-quality prey or less exploitation time (e.g., handling), whereas a shorter exploration time is associated with high-quality prey or longer exploitation time [21,22].

Numerous authors have drawn attention to the ways in which clonal plant species explore and exploit their habitats [7,16,23,24] by comparing clonal architecture among contrasting patches of resource quality, and a recent study compared social insect colonies to plant root foraging [5]. Clonal plants tend to produce longer but fewer spacers (e.g., stolons or rhizomes) in poor versus rich habitats [2,17], thereby permitting them to escape from poor sites into rich ones. Similarly, clonal plants tend to produce short but numerous spacers in rich habitats [25], which allows them to persist in favorable habitats and thus capture and exploit resources. These and other observations allow us to explicitly define (or at least quantify) plant exploration in the context of the production and growth of spacers and to define plant exploitation in terms of resource-capturing organs (e.g., roots and leaves), respectively. However, because most plants produce spacers and resource-capturing organs more or less simultaneously as they grow in size, the ability to explicitly distinguish between the two processes remains a significant experimental challenge.

Here, we propose that the exploration and exploitation processes can be distinguished by examining the effect of spatial scale on clonal plant growth. If the foraging behavior of plants involves both processes, at any given time, increased exploration will delay exploitation (and associated resource capture). That is, there is likely a cost associated with exploration before exploitation is initiated. Assuming a single plant enters a new resource patch, it would spend more time exploring before exploiting a resource in (relatively) large as opposed to small patches. Therefore, at any given time, plants living in large patches would gain fewer resources and accumulate less biomass than plants living in small patches. If this hypothesis is correct, the cost of exploration is expected to be dependent on the spatial scale that must be explored to acquire adequate resources to initiate the exploitation process.

We evaluated the hypothesis that the cost of exploration in plant foraging is a spatially-dependent variable using two clonal herbaceous species, *Hydrocotyle sibthorpioides* (Umbelliferae) and *Potentilla anserina* (Rosaceae). We placed equivalently-sized plants in circular trays with diameters ranging between 5 and 20 cm for *H. sibthorpioides* and between 18 and 50 cm for *P. anserina*. Trays were sampled at different times, depending on the extent of plant coverage, to determine the effect of spatial scale on biomass accumulation, biomass allocation, and spacer internode length. If the investment cost in exploration is positively correlated with patch size, individuals in smaller trays should initiate the exploitation process earlier than those in larger trays. Likewise, plants in smaller trays should have larger total biomass and leaf mass ratios (leaf mass/total mass) and/or root mass ratios (root mass/total mass) than those in larger trays, particularly at earlier sampling times, because they should spend less time exploring and more time acquiring resources.

The motivation underlying this study was different from that of previous studies addressing the effect of spatial scale on clonal plant growth; those studies focused on determining either the scale of habitat heterogeneity to which plants might respond or the manner in which plants respond to heterogeneity scales [7,26,27]. In contrast, our experimental design focused on homogenous habitats to determine whether exploration and exploitation processes during plant foraging could be distinguished quantitatively.

1 Materials and methods

1.1 Plant species

Two common wild clonal herbaceous species were used to carry out the experiment. *Hydrocotyle sibthorpioides* (Umbelliferae) is a creeping perennial clonal species that can grow under a wide variety of conditions, ranging from relative dryness to full submergence, in habitats as diverse as forests, mountain slopes, and grasslands to wet valleys and stream banks. This species normally grows to a height of 1–2 cm. Leaves are reniform, about 0.5–1.5 cm × 0.8–2.5 cm; stolon length ranges between 6 and 30 cm. In contrast, *Potentilla anserina* (Rosaceae) is a stoloniferous perennial rosette plant. This species is native throughout the temperate northern hemisphere and found in meadows and grasslands on mountain slopes, river and ditch banks, and roadsides across altitudes ranging from 500 to 4100 m above sea level (a.s.l.). Its stolons are able to grow up to 80 cm in length and form networks with rooting nodes. The leaves are 10–20 cm long, evenly pinnate with crenate leaflets 2–5 cm long and 1–2 cm wide. Compared to *H. sibthorpioides*, the stolons of *P. anserina* are visibly longer but less branched. In these respects, *H. sibthorpioides* and *P. anserina* represent two contrasting types of clonal growth (i.e., a phalanx-type and a guerrilla-type, respectively). An additional reason for selecting these two species is that both are ecologically wide-spread and representative of many other species with similar growth forms.

The plants used in this study were propagated from four specimens (genets) collected in April, 2008 from the suburbs of Chengdu City (500 m a.s.l.; E104°05′, N30°39′; for *H. sibthorpioides*) and from Hongyuan County (3500 m a.s.l., E102°33′, N31°48′; for *P. anserina*) of Sichuan Province, southwestern China. Cuttings from the four original genets were cultivated for two months to produce a suffi-

cient number of healthy ramets for this experiment.

1.2 Experiments

A nested experimental design was used. For each species, 64 individual ramets (0.02–0.03 g fresh weight) were randomly separated into four groups, each consisting of four replicates derived from a single genet and similar in size. Each replicate consisted of four trays differing in diameter (5, 10, 15 and 20 cm for *H. sibthorpioides* and 18, 25, 35, and 50 cm for *P. anserina*) and made of 10 cm-high steel screen (with 7 cm below the soil and 3 cm above) with a 0.5-mm mesh size. The tray diameters were generally but not exactly correlated to average internode length for young seedlings of the two species (ca. 1.5 and 3 cm for *H. sibthorpioides* and *P. anserina*, respectively). The areas of the smaller trays were approximately 1/2, 1/4 and 1/8 that of the largest tray for both species.

Each set of four different-sized trays was placed in a large flat-bottomed pot that prevented water and nutrient run-off. All the trays were filled with homogenized soil with uniform nutrient and water content. The soil was relatively rich in nutrients (organic matter content was 20.6 g/kg, total N concentration was 1.8 g/kg, with available N, P and K at 163.6, 16.9 and 100.6 mg/kg, respectively). The soil was disinfected with 40% formaldehyde before use. The space among trays was filled with the same soil. Plants were regularly watered. Prior to the experiment, that average soil moisture varied from 37% to 66% (v/v) during sunny days. The moisture was homogeneous among trays with different diameters at any given time of day ($P < 0.001$; Figure S1). Additionally, we measured the temperature of different-sized trays throughout the experiment and found no statistical differences in temperature among the trays during typical sunny, cloudy, and rainfall days (Figure S2). Likewise, mean temperatures were not correlated with tray size, and there was no obvious diurnal variation pattern associated with tray size (Table S1).

The ramets were planted in a greenhouse on February 1, 2009. Plants were sampled and measured four times from March 3, 2009 to May 9, 2009 for each species. At each time, one replicate was randomly selected from each group; 16 trays were sampled in total. The first sampling was conducted when the smallest trays were visibly full (about 30% vertical edge was contacted but not wholly covered by plants), the second sampling occurred when the second smallest trays were visibly full, etc. However, because not all the replicates were fully covered at exactly the same time, we sampled trays ranging between 25% and 35% edge contact. The sampling intervals were about 15 d, with 1 (*P. anserina*) or 2 d (*H. sibthorpioides*) of variation. For each sampling, we excavated whole plants with their entire root systems and measured morphological parameters (including ramet number and stolon length) after washing and removing the substrate from roots. Harvested plants were then dissected and their leaves, stems, and roots weighed after being dried to constant weight. Root mass, stolon mass, and leaf mass ratios (RMR, SMR and LMR, respectively) were calculated as ratios to total plant dry mass and used to characterize plant biomass allocation patterns. Internode length was calculated as total stolon length divided by the ramet number.

1.3 Data analysis

The data for each variable of interest were tested for normality before additional statistical analysis. Because the effect of sampling time could override the morphological or biomass variables for either or both species (all $P < 0.001$) (Table S2), we analyzed the spatial size effect separately for each sampling time. For each species, one-way randomize-blocked ANOVA was employed to estimate the difference in total dry mass, number of ramets, biomass allocation, total stolon length, and internode length among the different tray sizes at each sampling time. Tukey tests were subsequently used whenever a significant difference was detected. The random block factor was taken to be differences in genets resulting from morphological plasticity. In addition, correlation analyses were conducted to determine the relationships among plant size, ramet number, biomass allocation, total stolon length, and internode length. All statistical analyses were performed using STATISTICA for Windows [28].

2 Results

2.1 Overall plant performance

For any specific tray size, total biomass and the number of ramets increased over time for each species. Total plant biomass and ramet number in smaller trays (e.g., 5 and 10 cm diameter for *H. sibthorpioides* and 18 cm diameter for *P. anserina*) generally increased more slowly than in the larger trays. Plant biomass was positively correlated with ramet number when the data were pooled ($P < 0.001$ for both species; Table 1). The effect of tray size was significant on plant biomass and ramet number for each sampling time in both species (Figure 1). At early sampling times, when only small trays were full, plants in the smaller trays had accumulated more biomass than those in the larger trays (e.g., 15 and 20 cm or 35 and 50 cm in diameter) ($P < 0.05$). As the experiment progressed, however, plants in the larger trays had larger plant biomass and ramet number than plants in the smaller trays (Figure 1; $P < 0.001$). Although a general tendency was apparent, the differences in total biomass were not always significant for each sampling time (Figure 1).

2.2 Biomass allocation

For *H. sibthorpioides* over time, the LMR increased and the

Table 1 Matrix *of Pearson*'s correlation coefficients for the relationships among plant biomass (PB), ramet number (RN), root mass ratio (RMR), stolon mass ratio (SMR), leaf mass ratio (LMR), total stolon length (TSL), and internode length (IL) in *Hydrocotyle sibthorpioides* (below the diagonal) and *Potentilla anserina* (above the diagonal)[a)]

	PB	RN	RMR	SMR	LMR	TSL	IL
PB		0.837***	–0.127	0.138	–0.060	0.837***	0.400**
RN	0.955***		–0.016	0.470**	–0.263	0.973***	0.418**
RMR	–0.283*	–0.371**		–0.167	–0.87***	–0.079	–0.142
SMR	–0.297**	–0.334**	–0.062		–0.223	0.471**	0.237
LMR	0.182	0.261*	–0.447***	–0.736***		–0.199	–0.045
TSL	0.968***	0.982***	–0.338**	–0.300**	0.186		0.566***
IL	0.655***	0.612***	–0.220	–0.219	0.018	0.717***	

a) *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

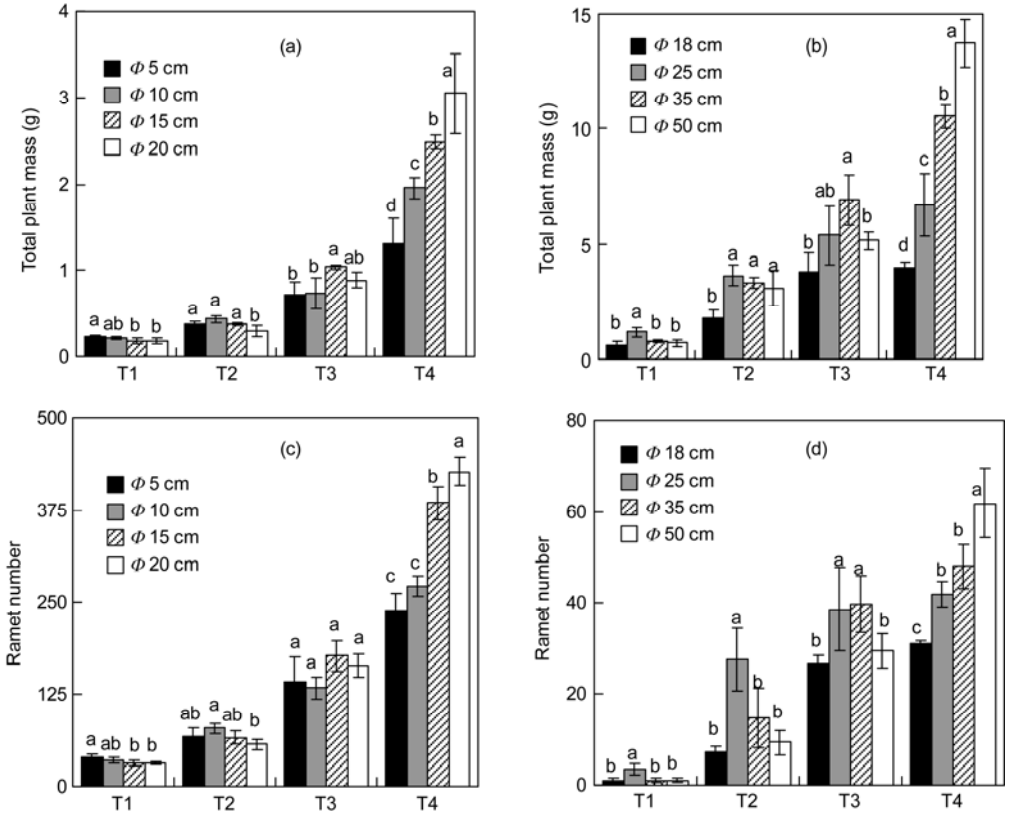

Figure 1 Variation in plant biomass ((a) and (b)) and ramet number ((c) and (d)) among different trays during the course of the experiment in *H. sibthorpioides* ((a) and (c)) and *P. Anserina* ((b) and (d)). T1, T2, T3 and T4 denote sequential sampling times. Different letters above the error bars indicate significant differences among trays differing in size for each sampling time ($P < 0.05$).

SMR decreased in larger trays but remained relatively constant for plants in smaller trays (Figure 2). At early sampling times, plants in the smaller trays (5 and 10 cm diameters) had larger LMR but smaller SMR than plants grown in the larger trays (Figure 2). RMR did not show an obvious pattern among trays during the course of the experiment.

For *P. anserina*, LMR decreased over time in the smaller trays (with 18 cm diameters) but increased in the large trays (e.g. with 50 cm diameters). In contrast, RMR increased over time in the smaller trays but decreased over time in the large trays (Figure 2). During the first sampling, RMR was significantly greater while LMR was slightly but not significantly larger in the smaller trays than in the larger ones. SMR were significantly less in the smaller trays than in the larger ones at the first sampling, although there was no consistent pattern of variation for SMR during the entire course of the experiment.

2.3 Internode length

For both species, internode length increased gradually during the course of the experiment for any given tray size and

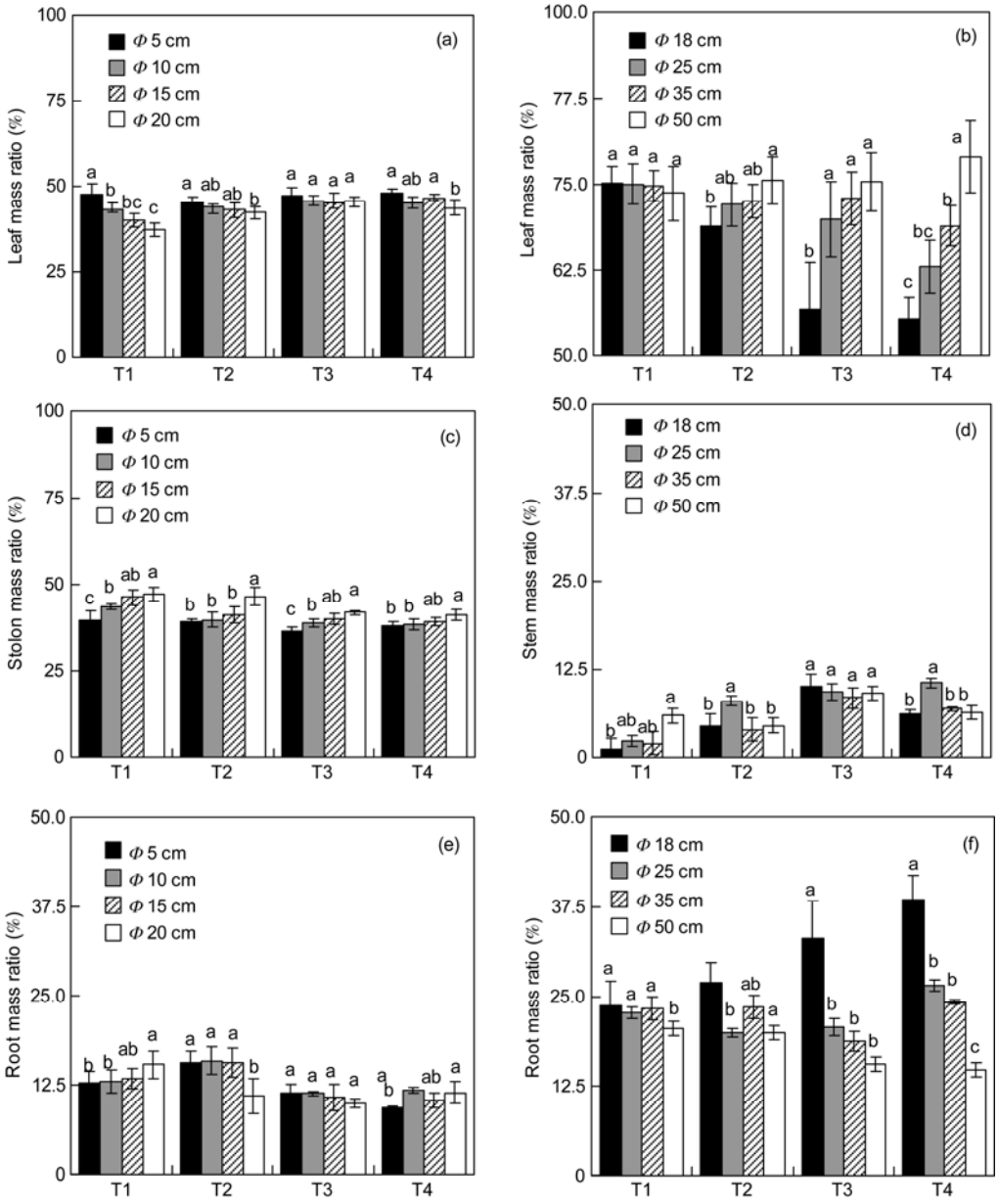

Figure 2 Variation in leaf mass ratio (LMR) ((a) and (b)), stolon mass ratio (SMR) ((c) and (d)), and root mass ratio (RMR) ((e) and (f)) among different trays during the course of the experiment in *H. sibthorpioides* ((a), (c) and (e)) and *P. Anserina* ((b), (d) and (f)). T1, T2, T3 and T4 denote sequential sampling times. Different letters above the error bars indicate significant differences among trays differing in size for each sampling time ($P<0.05$).

was generally significantly greater in the larger than in the smaller trays, although no significant differences were found in the earliest sampling times (Figure 3). Furthermore, ramet number and internode length were negatively correlated with one another during the earliest sampling times ($r=-0.480$, $P<0.05$ for *H. sibthorpioides* and $r=-0.513$, $P<0.05$ for *P. anserina*). In contrast, ramet number and internode length were positively correlated at the last sampling time ($r=0.532$, $P<0.05$ for *H. sibthorpioides* and $r=0.739$, $P<0.05$ for *P. anserina*).

Finally, for both species, total plant biomass, number of ramets, total stolon length, and internode length were significantly positively correlated with one another ($P<0.001$), whereas total biomass, ramet number, and stolon length were negatively correlated with SMR, but positively correlated with LMR (Table 1).

3 Discussion

To our knowledge, this study provided the first experimental data that explicitly distinguish between the exploration and exploitation processes of plant foraging and that show that exploration comes at a "cost" in terms of biomass

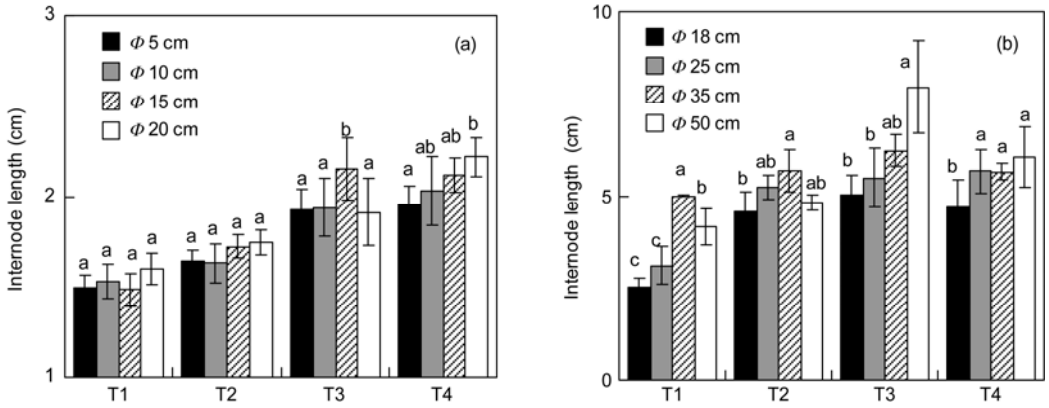

Figure 3 Variation in internode length among different trays during the course of the experiment in *H. sibthorpioides* (a) and *P. Anserina* (b). T1, T2, T3 and T4 denote sequential sampling times. Different letters above the error bars indicate significant differences among trays differing in size for each sampling time ($P<0.05$).

accumulation and allocation. Our observations support the hypothesis that there exists a cost associated with occupying larger spatial scales and that this cost takes the form of investing more biomass in constructing resource-exploring organs as opposed to resource-capturing or exploiting ones (i.e., stolons versus leaves and/or roots). Importantly, this "cost" is measureable even when plants are grown under completely homogeneous conditions (but at different spatial scales), which removes the possibility that non-linear growth responses to different light or nutrient levels statistically confounded the effect of tray size on biomass accumulation or allocation patterns.

The proximate mechanisms responsible for the responsiveness of biomass allocation patterns to different spatial scales nevertheless remain unclear. As noted, the abiotic factors attending plant growth in our experiment were carefully maintained at the same levels for all tray sizes. Yet, plants growing in smaller trays allocated a larger proportion of their biomass to the production of leaves and/or roots and less to the formation of stolons. Such a bias favoring larger LMRs is known to increase relative growth rates [29,30]. In this context, we note that during early sampling times, LMRs were generally smaller while SMRs were generally larger in the largest trays compared to the smaller ones, consistent with the observation that total plant biomass and ramet number were smaller in the larger than in the smaller trays. In the case of *P. anserina*, LMRs were higher in the smaller trays during the earliest sampling times. With *H. sibthorpioides*, LMRs increased whereas SMRs decreased with increasing total biomass for any given tray size (but especially in the largest trays) possibly because of physical limitation by the trays. These observations suggest to us that, for any spatial scale, whether large or small, plants may initially invest more in the production of exploring organs and only subsequently invest in the construction of resource-exploiting organs.

Our data also indicate that the time at which biomass allocation shifts is dependent on habitat spatial scales. Plants grown in small trays allocated more biomass to the construction of leaves earlier than plants grown in larger trays, possibly because plants in larger trays initially spent more time exploring (before capturing and utilizing) resources. For both species during the earliest sampling times, ramet number was negatively correlated with internode length, and the larger trays had relatively fewer ramets (but with longer internodes) than the smaller trays. However, the differences in the time at which biomass allocation patterns change cannot be attributed simply to the differences in total plant size. For both species, the scaling exponent for leaf mass with respect to stem mass, root mass, and total plant mass was approximately 1.0 (Table S3). This numerical value is consistent with the numerical values of scaling exponents reported for other herbaceous species [31,32], which suggests that spatial scale does not affect to a significant degree the allometry of biomass allocation patterns.

Identifying the immediate physiological mechanisms underlying the response of plants to different spatial scales is beyond the scope of this study. However, we note that numerous studies indicate that plants have the ability to sense physical barriers (and thus spatial scales) using specialized cell, tissue, or organ types [33–35]. For example, climbing plants can sense and respond to supports differing in diameter [36–38], and plants grown on identical substrates with the same nutrient conditions produce disproportionately more roots in larger than smaller soil volumes [35,39,40]. Clearly, plant stems and roots can sense and respond to differences in the spatial scales of the habitats they occupy. Plant roots might have detected the physical limits of the trays before the above-ground parts reached the tray verge. Perhaps *H. sibthorpioides* and *P. anserina* possess tactile mechanisms capable of sensing and responding to the tray walls. This hypothesis will be explored in future experiments.

We speculate that the cost of exploring resources during the early stages of plant growth and establishment in a habitat may bring benefits later in plant growth or reproduction,

depending on environmental conditions. Plants usually live in heterogeneous habitats and only rarely in homogeneous ones [16,24]. Therefore, long-term evolutionary adaptations to heterogeneity might have selected for individuals that initiated and extended the exploration phase of foraging before engaging in exploitation, thereby increasing foraging efficiency over the course of its lifetime. Certainly, studies have shown that some species grow better in heterogeneous habitats than in homogeneous ones that provide the same overall amounts of resources [10,41]. Although our study of two clonal species involves short-term observations in homogeneous environments, the responses of both species suggest a strategy that can facilitate the exploration and exploitation of resources in patchy and heterogeneous environments [42,43].

Likewise, the cost of exploration during plant foraging may confer subsequent benefits in occupying space and gaining competitive dominance later in a plant's lifetime, as suggested by other studies. For example, when plants of the same species are grown to competitively "share" the same space, some increase their root proliferation in shared as opposed to unshared soil-root regions [44,45]. This kind of behavior has been interpreted to be a strategy for guarding a species' territory [19,46], although it may also reflect intraspecific competition (particularly since it appears to come at the cost of reproductive fitness).

In conclusion, we have demonstrated that ramets of *H. sibthorpioides* and *P. anserina* explore a habitat before exploiting resources during the course of their foraging and that this exploring behavior is sensitive to spatial scale and incurs a short-term cost in biomass accumulation. Future avenues of research include extending our experimental design to test other species with different growth forms and to observe our two experimental species over longer timespans to measure the tradeoff between the cost of exploration and possible long-term dividends.

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Supporting Information

Figure S1 Daily variation in soil water content of the trays differing in size. No significant differences were observed among tray sizes sampled at the same time (all $P > 0.05$). The moisture was not measured at night because the trays were watered at 19: 00 (Beijing time) each day during the measurements.

Figure S2 Daily variation in soil temperature of the trays differing in size for three typical weather conditions: (a) sunny, (b) rainy, and (c) cloudy days.

Table S1 Descriptive statistics of temperature variation of the trays differing in diameter for three typical weather conditions (sunny, rainy, and cloudy days)

Table S2 Effects of sampling times and spatial scale on plant traits for the two species. Two-way ANOVAs were performed for pooled data for each species

Table S3 The SMA regression parameters for the scaling relationships among root mass, stem mass, leaf mass and total plant mass. The data were pooled from all sampling times for each species. All the relationships are significant ($P < 0.001$)

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