

## GROWTH CHARACTERISTICS OF *POTENTILLA ANSERINA* DETERMINED BY ANALYZING SMALL-SCALE PATCHY HABITATS

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### Abstract

Patchy distribution of plant populations is a hallmark of saline grassland ecosystem at Weiyuan, YouYu County, Shanxi Province, north China. According to species composition and community dominance, the grassland was divided into 8 patches. First, we investigated and analyzed community characteristics, including  $\alpha$  diversity and soil properties (soil moisture, bulk density, pH value, basicity) of the 8 patches of the grassland and found that the 8 patches were obviously divided into 2 categories. Patches I, II, and III formed group 1, and the other patches were included in group 2. The soil moisture, bulk density, pH value, and basicity in group 1 were lower than those in group 2 ( $p < 0.05$ ). Next, we selected *Potentilla anserina* as a representative species and measured its growth characteristics in each patch and found its root length ( $df = 46$ ,  $|t| = 5.84$ ,  $p < 0.0001$ ), spacer length ( $df = 118$ ,  $|t| = 3.61$ ,  $p = 0.0005$ ), and stolon length ( $df = 118$ ,  $|t| = 2.53$ ,  $p = 0.0127$ ) were significantly greater in group 1 than in group 2. We concluded that under relatively good habitat conditions, *Potentilla anserina* adopted breadth foraging strategy, increased its stolons number, which reduced the risk of death and promoted valid survival by spreading in the available space. On the contrary, under relatively poor habitat conditions and in a highly competitive environment, *Potentilla anserina* adopted the strength foraging strategy to acquire resource from farther places by increasing its spacer and stolon lengths or rapidly explore new habitats to avoid unfavorable environments.

**Key words:** Patchy habitat, *Potentilla anserina*, Plasticity, Patches, Clonal plants.

### Introduction

In natural environment, spatial and temporal variation in resource distribution is a common environmental feature (Farley & Fitter, 2001). Essential resources for plant growth and reproduction (such as water and mineral nutrients), as well as environmental conditions (such as temperature, humidity, and interference) have a heterogeneous distribution in time and space. This heterogeneity existed even at a very small scale (Frankland *et al.*, 1963; Janeček *et al.*, 2008; Kelly & Canham, 2009), namely, resource heterogeneity and habitat heterogeneity. Patchiness is a manifestation of the spatial and temporal heterogeneity of resource and habitat (Hutchings & de Kroon, 1994) and contents of the resources are relatively consistent within a patch, while they obviously vary from patch to patch (Dong, 1996a).

Some plants could change their biomass allocation pattern in response to actual environmental conditions (Ikegami *et al.*, 2008; Eilts *et al.*, 2011). Clonal and non-clonal plants have different biomass allocation patterns in heterogeneous environments because clonal plants depended on asexual propagation to produce offspring ramets and expanded the population, and that connections among ramets of clonal plants by stolons or rhizome internodes allowed transport of photosynthate, water, and nutrients from established ramets (parent ramets) to developing ramets (offspring ramets) (Hartnett & Bazzaz, 1983; Slade & Hutchings, 1987a). This propagation pattern enabled clonal plants to have more opportunities to experience small-scale spatial heterogeneity in natural environments. Thus, clonal plants could perform well under heterogeneous patches or adapt to diverse environmental conditions (Alpert & Mooney,

1986; Wijesinghe & Handel, 1994; Hutchings & Shulman, 1999); while a non-clonal plant could grow only in a single environment.

Over the last 30 years, plant foraging behavior has been the subject of intense research interests (De Kroon *et al.*, 2009; Karban, 2008; McNickle *et al.*, 2009). Many relevant researches mainly focused on analysis of plant phenotypic plasticity in patchy habitats (Stuefer & Huber, 1998), their consequences for resource acquisition and pattern of biomass allocation (Eriksson, 1985; Hutchings & de Kroon, 1994; Wang *et al.*, 2011). Moreover, most studies investigating the responses of clonal plants to environmental heterogeneity have used simple heterogeneity models with only 2 types of patches (Price & Marshall, 1999; Salzman & Parker, 1985; Slade & Hutchings, 1987b; Stuefer, 1996). They concluded that plants prefer inhabiting high-quality patches in heterogeneous environments and develop morphological and physiological plasticity as their efficient foraging strategy in order to increase ecological fitness. A single factor was used to determine nutrition patches and barren patches in previous studies. However, in the case of natural ecosystems, several factors exert mutual or negative effects (Stuefer *et al.*, 1994), so patches cannot be simply classified as favorable or unfavorable. Comprehensively considering mutual influence of several abiotic (nutrition, water, and light) and biological (intraspecific and interspecific competition) factors, we defined an environment with abundant resources and less competition as favorable, and an environment with contrast features as adverse.

As a typical stoloniferous and rosulate clonal plant (Zhou *et al.*, 2002), *Potentilla anserina* is a dominant species in many grasslands across north China and is

considered as a key indicator species of degraded grasslands (Eriksson, 1988). Patchy distribution of plant populations is a hallmark of saline grassland ecosystem at Weiyuan, Youyu County, Shanxi Province, north China. However, *Potentilla anserina* perform well in this patchy habitat compared to other species. However, little is known about the cause of patchy habitats formation and mechanism of *Potentilla anserina* adapted to this patchy habitats. In the present study, we investigated growth behavior of *Potentilla anserina* in 8 groups patches to address the following questions. (1) Does *Potentilla anserina* respond to multi-patch environments through its morphological plasticity? (2) Can individuals of *Potentilla anserina* strategically develop their stolons to increase ramets in favor of adapting to patchy habitat?

## Materials and Methods

**Description of the study site:** The study site is located at Weiyuan, Youyu County, Shanxi Province, north China, and the geographic coordinates are 40.18° N, 112.33° E; the site is located 1,348 m above sea level (Fig. 1). The annual average temperature is 4°C; the minimum temperature in January ranges from -11°C to -15°C, and the maximum temperature in July ranges from 19°C to 20°C. The first frost usually occurs in early to middle September and the last frost in early May. The frost-free period is from 100 to 120 days. The average annual solar radiation is 598 KJ/cm<sup>2</sup>, and the annual sunshine hours range from 2,600 to 2,700. Average annual precipitation is 450 mm. The soil type is light chestnut soil. The grassland type is classified as temperate meadow steppe, which is dominated by *Leymus secalinus* and *Potentilla anserina*.

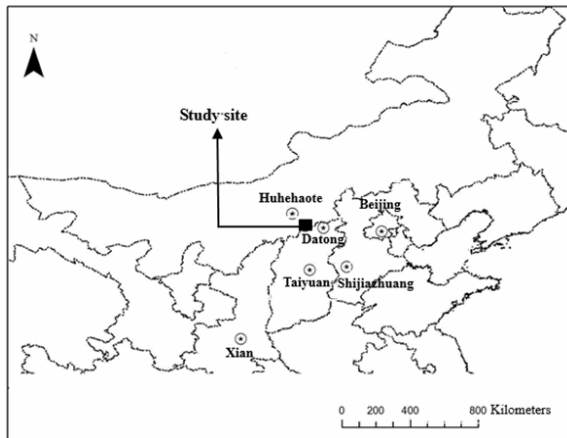


Fig. 1. Study site.

**Patch identification:** There are very clear landscape features of patchy distribution in this grassland, which species composition in each patches were significantly different from the surrounding grassland. A 500 m × 500 m region of the grassland was enclosed for the study, and grazing was completely prohibited for 2 years in this region. The region was selected such that it had obvious characteristics of natural and flat grassland. First, the area was divided into 8 patches (namely, I--VIII) according to

species composition and community dominance by visual inspection. From patches I to VIII: *Potentilla anserina* and *Leymus secalinus*, *Leymus secalinus* and *Potentilla anserina*, *Leymus secalinus* and *Taraxacum mongolicum*, *Artemisia lavandulaefolia* and *Potentilla anserina*, *Casuarina cunninghamiana* and *Potentilla anserina*, *Halerpestes lancifolia* and *Potentilla anserina*, *Leymus secalinus* and *Halerpestes lancifolia*, and *Potentilla anserina* and *Halerpestes lancifolia* were respectively the dominant species and second dominant species. *Leymus secalinus* was common dominant species in patches II, III, and VII, and *Potentilla anserina* was common dominant species in patches I, IV, V, VI, and VIII.

Subsequently, we sampled 10 quadrats (1 m × 1 m) in each patch and recorded the species composition and cover (needle punching method), frequency (quadrat method) (Zhang, 1995). In addition to *Potentilla anserina*, the density of other species were recorded in each quadrat of each patch. Each species within the quadrats were separately cut, transferred to the laboratory and dried at 65°C for the measurement dry matter of above-ground biomass. Finally, the dominance of each species and  $\alpha$  diversity of each patches were calculated.

## Population characteristics and measurement methods:

The genets were defined as a parent that originated from a seed or through asexual reproduction, all clonal fragment were to expand around it as the centre. The clonal ramets was defined as the collection of clones derived from the same genets (Liu & Zhong, 1995). The stolons of *Potentilla anserina* produced adventitious roots and sprouted adventitious buds that formed new ramets. The new ramets remained attached to the stolon until space was available to expand; once the stolons fractured, new individuals were formed.

From each patch, 50–60 plants of *Potentilla anserina* were randomly sampled. When sampling, if a stoloniferous clonal fragment was found, we traced its all clonal ramets connected together by stolons, dug complete roots of each ramet, included all stolons and clonal ramets as one. The height and root length of each genet, stolon number and each stolon length of genets, and spacer length in each stolons (gap length between adjacent ramets) were measured and recorded (Fig. 2). The number of stolons was counted using the method of Zhou *et al.* (2004) for typical stolon plants such as *Halerpestes cymbalaris*, the longest stolon was identified as the first, and the next longest as the second, and so on. If a clonal fragment having no stolons was found, it was considered as one. The samples were obtained from a location that was at least 2 m away from the edge of the patch to avoid simultaneous sampling of stolons from the same genet across 2 patches.

We randomly selected 5 points and sampled soil (0–30 cm) in 10 quadrats of each patch, transferred to the laboratory for the measurement of soil moisture (oven-drying method), bulk density (core cutter method), pH value, and soil basicity. The methods described in the Soil Agricultural Chemistry Analysis book were used (Bao, 2000).

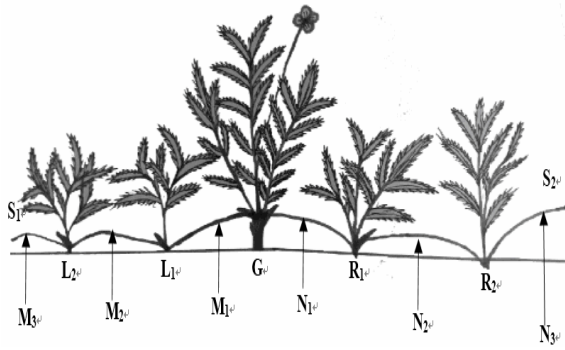


Fig. 2. Diagrammatic clonal architecture and stolon spread for *P. anserina*.

Note: G represents genet; L<sub>1</sub>~L<sub>2</sub>, R<sub>1</sub>~R<sub>2</sub> represent ramets in the first and second stolons, respectively; M<sub>1</sub>~M<sub>3</sub>, N<sub>1</sub>~N<sub>3</sub> represent the spacers in the first and second stolons, respectively; S<sub>1</sub>, S<sub>2</sub> respectively represent the first and second stolons.

**Population density:** Three 4 m<sup>2</sup> quadrats were randomly selected in each patch. The population density was measured in each patches as the proportion of *Potentilla anserina* found in 2 cm × 2 cm squares of 2 m × 2 m quadrats and was denoted by P. Assuming that the number of *Potentilla anserina* found in the squares was X, the population density for the genets and asexual strains was defined as follows:

$$P = \frac{X}{(100 \times 100)}$$

**Data processing**

$$(1) \quad H' = H_A / \sum_{i=1} H_i, \quad C' = C_A / \sum_{i=1} C_i, \quad D' = D_A / \sum_{i=1} D_i, \\ W' = W_A / \sum_{i=1} W_i, \quad SDR = (H' + C' + D' + W') / 4$$

where H<sub>A</sub>, C<sub>A</sub>, D<sub>A</sub> and W<sub>A</sub> are the frequency, cover, density, and biomass of species A, respectively; H', C', D', and W' are the relative frequency, relative cover, relative density, and relative biomass, respectively. Species dominance (SDR) in each quadrat was calculated using the following equation (Zhang, 1995).

(2) α diversity (Magurran, 1988), was measured using the following equation:

Margalef index (Ma)

$$M a = (S - 1) / \ln N$$

Shannon–Wiener index

$$H = - \sum_{i=1} P_i \ln P_i$$

Pielou index

$$E = H' / \ln S$$

Simpson index

$$P = 1 - \sum_{i=1}^S P_i^2$$

where S represents the number of species in the sample, and N represents the number of species in the community.

**Statistical analysis:** The surveyed data from the sampling area were converted into data per unit area of 1 m × 1 m. The data were calculated and analyzed using Excel software and represented as mean (M) ± standard deviation (SD), where M represented the data composition, and SD accounted for the degree of variation between repeated samples. The α diversity (including Margalef abundance index, Shannon–Wiener community diversity index, Pielou evenness coefficient, and Simpson dominance index), above-ground biomass, population density, and soil properties (including soil moisture, soil bulk density, pH value, soil basicity) across the 8 groups patches were analyzed using one-way analysis of variance (ANOVA) by using SAS 9.0 software and Duncan’s multiple range tests. This approach was used to test whether there was a significant difference (Schmid *et al.*, 2002). The regular pattern of stolons in different patches was determined by analyzing the data for genets height, root length, spacer length, and stolon length across the 8 groups patches. Chi-square test was used to analyze the diversity in stolon number for *Potentilla anserina* among the 8 patches. Next, *t*-test was used to analyze genets height, root length, spacer length, and stolon length of *Potentilla anserina* between groups 1 and groups 2. The relationship between the species found in a patch and environmental conditions was analyzed using principal components analysis using CANOCO for Window 4.5 software. The statistical fitting of stolon and sample numbers of *Potentilla anserina* was analyzed using SPSS 17.0 software.

**Results**

**Characteristics of communities in the patches:** In all, 17 species were detected in the 8 groups patches; each patch had about 8–12 species, accounting for an overall rate of 47.06% to 70.59%. There were obvious differences in the dominant and sub-dominant species in the 8 patches (Table 1). *Leymus secalinus* was the common dominant species in patches I, II, III, and VII, and *Potentilla anserina* was the common dominant species in patches IV, V, VI, and VIII.

The α diversity of patches II and III was significantly lower than that of the other patches (Fig. 3). The soil moisture and soil basicity was significantly lower in patches I to III than in the other patches (Fig. 4A, D). The soil bulk density was significantly lower in patches II and III than in patches VI to VIII (Fig. 4B). The pH value was significantly lower in patches I to V than in patches VI to VIII (Fig. 4C).

**Table 1. The dominance of species in the 8 patches.**

Species	Patch number (I–VIII)							
	I	II	III	IV	V	VI	VII	VIII
<i>Potentilla ansrina</i>	0.2805	0.1536	0.0508	0.1885	0.1646	0.1526	0.1767	0.2278
<i>Halerpestes lancifolia</i>	0.0881	0.0474	0.0709	0.1041	0.1340	0.1954	0.1990	0.1727
<i>Polygonum sibiricum</i>	0.0713	0.0331	0.0401	0.0342	0.0367	0.0572	0.0592	0.0615
<i>Puccinellia floorida</i>	----	----	----	----	0.0750	0.0604	0.0766	0.0829
<i>Plantago asiatica</i>	0.0314	0.0174	----	0.0712	0.0441	0.0603	0.0810	0.0442
<i>Leymus secalinus</i>	0.2458	0.5306	0.4355	0.1685	0.1262	0.1439	0.2557	0.1375
<i>Casuarina cunninghamiana</i>	----	----	----	0.0674	0.2260	0.0685	0.0928	0.2128
<i>Taraxacum mongolicum</i>	0.0648	0.1087	0.1303	0.0357	0.0575	0.0821	0.0699	0.0808
<i>Artemisia lavandulaefolia</i>	0.0916	0.0556	0.0646	0.2187	0.0812	0.0104	0.0270	0.0453
<i>Phragmites australis</i>	----	0.1190	----	0.0371	----	0.1122	0.0756	0.0711
<i>Saussurea amara</i>	0.0554	----	0.0453	----	----	0.0322	0.0087	0.0278
<i>Potentilla eriocarpa vartsarongensis</i>	0.0273	----	0.0299	0.0481	----	----	----	----
<i>Astragalus melilotoides</i>	----	----	----	0.0317	0.0479	----	----	----
<i>Leontopodium leontopodioides</i>	----	----	----	----	0.0346	0.0514	0.0596	----
<i>Setaria viridis</i>	0.0149	----	----	----	----	----	----	----
<i>Salsola collina</i>	0.0831	----	----	----	----	----	----	----
<i>Artemisia dalailamae</i>	0.0902	----	----	----	----	----	----	----
the number of species	12	8	9	11	12	12	12	11

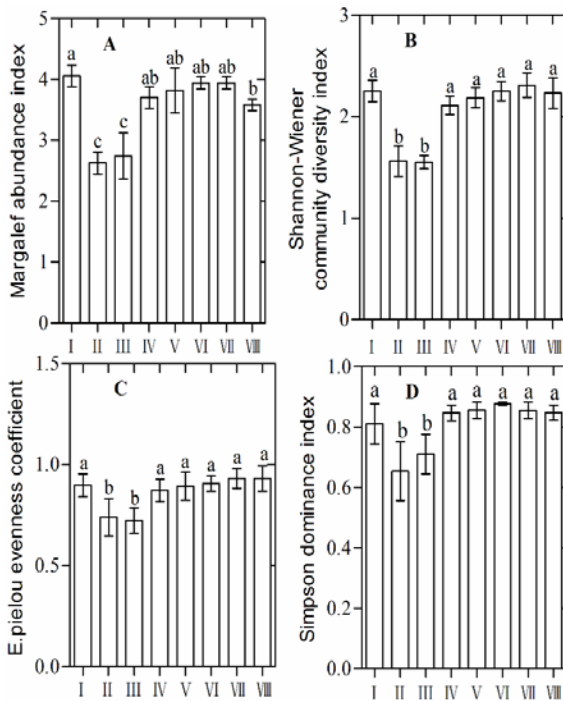


Fig. 3. The  $\alpha$  diversity analysis of the 8 patch communities. Note: A, B, C, and D represent Margalef abundance index, Shannon–Wiener community diversity index, Pielou evenness coefficient, and Simpson dominance index, respectively, of the 8 patch community. Different lowercase letters represent significant differences at  $p = 0.05$ .

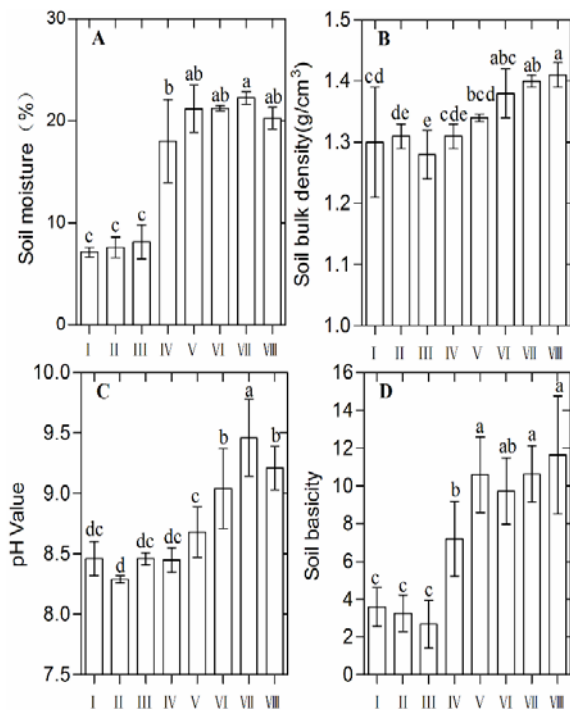


Fig. 4. Soil properties (soil moisture, soil bulk, pH value, soil basicity) of the 8 patches.

Note: different lowercase letters represent significant differences at  $p = 0.05$ .

**Relationship between species, patches, and environment:**

The eigenvalue of the 4 coordination axes (Fig. 5) were 0.621, 0.169, 0.094, and 0.052; the cumulative variance contribution rates of axis 1 and axis 2 reached 79.0%. A negative correlation existed between axis 1, axis 2, and environmental factors (including pH value, soil moisture, bulk density, and soil basicity, Fig. 5). The correlations among the 8 patches, environmental factors, and species were determined by performing PCA considering species and soil properties as variable factors. The distance was the shortest between patches I and IV; patches II and III; and among patches V, VI, VII, and VIII, suggesting that there was a strong similarity between these patches. There was a positive correlation among soil moisture, basicity, bulk density, and pH value. The correlation of environmental factors with patches V to VIII was stronger than that with patches I to IV. Unlike *Leymus secalinus*, *Casuarina cunninghamiana*, *Halerpestes lancifolia*, and *Puccinellia florida* showed a strong positive correlation with environmental factors, suggesting that these plants preferably grew under moist conditions. The correlation between the clonal plants, *Potentilla anserina* and *Phragmites australis*, and environmental factors was poor, showed their strong adaptability to current environment (Fig. 5); This suggested that most species are strongly dependent

on environmental factors; however, clonal plants showed different adaptation strategies to current environments.

**The plasticity of *Potentilla anserina*:** Characteristics of *Potentilla anserina* population.

The cover (Fig. 6A), frequency (Fig. 6B), above-ground biomass (Fig. 6C), and population density (Fig. 6D) were significantly lower in patches II and III than in the other patches. This may be associated with the low soil moisture in patches I to III.

**Distribution of *Potentilla anserina* stolons number**

There was a significant difference in the number of stolons of *Potentilla anserina* among the 8 patches ( $df = 42$ ,  $X^2 = 85.52$ ,  $p < 0.0001$ ). The relationship between stolon number and sample number was determined by performing fitting analysis for *Potentilla anserina* in the 8 patches and the entire plot. The results suggested that a negative linear relationship existed in patches I ( $Y = 13.036 - 1.964X$ ,  $R^2 = 0.826$ ,  $p < 0.01$ ; Fig. 7A) and III ( $Y = 12.179 - 1.679X$ ,  $R^2 = 0.832$ ,  $p < 0.01$ ; Fig. 7C). The other patches showed a curve (II and V) and parabolic (IV, VI, VII, VII and entire plot) relationship. The equations for the remaining patches are as follows:

$$\begin{aligned} \text{II:} & \quad Y = 13.052\exp^{-0.276X}, & (R^2 = 0.647, p < 0.05; \text{Fig. 7B}) \\ \text{IV:} & \quad Y = -0.679X^2 + 3.75X + 4.7143, & (R^2 = 0.817, p < 0.05; \text{Fig. 7D}) \\ \text{V:} & \quad Y = 58.948\exp^{-1.336X}, & (R^2 = 0.764, p < 0.05; \text{Fig. 7E}) \\ \text{VI:} & \quad Y = -0.774X^2 + 3.964X + 5.310, & (R^2 = 0.867, p < 0.05; \text{Fig. 7F}) \\ \text{VII:} & \quad Y = -1.179X^2 + 6.750X + 2.214, & (R^2 = 0.633, p = 0.135; \text{Fig. 7G}) \\ \text{VIII:} & \quad Y = -1.095X^2 + 6.071X + 3.167, & (R^2 = 0.670, p = 0.109; \text{Fig. 7H}) \end{aligned}$$

In the entire plot, a significant parabolic relationship was found; the equation for the same is as follows:  $Y = -4.131X^2 + 14.89X + 66.16$ , ( $R^2 = 0.9236$ ,  $p < 0.01$ ; Fig. 7I).

In a word, *Potentilla anserina* having less stolons (0–2) dominated in patches I to III ( $df = 13$ ,  $|t| = 2.98$ ,  $p = 0.0107$ ), while those having more stolons ( $\geq 2$  and 5) dominated in patches IV–VIII ( $df = 23$ ,  $|t| = 1.56$ ,  $p = 0.1329$ ). Characteristics of genets and stolons of *Potentilla anserina*.

The genet height and root length of *Potentilla anserina*, the spacer length and length of *Potentilla anserina* stolon were no obvious difference across patches I–VIII (Table 2 - Table 5). But, the t-test results showed that the root length ( $|t| = 5.84$ ,  $p < 0.0001$ ), spacer length ( $|t| = 3.61$ ,  $p = 0.0005$ ), and stolon length ( $|t| = 2.53$ ,  $p = 0.0127$ ) of *Potentilla anserina* were significantly greater in patches I to III than in the other patches; however, the height of *Potentilla anserina* was not significantly different between patches I to III and the other patches ( $|t| = 1.31$ ,  $p = 0.1978$ ). Besides, there was a significant positive correlation between spacer length and stolon length for *Potentilla anserina* in the entire survey plot ( $R^2 = 0.6287$ ,  $p < 0.0001$ ; Fig. 8). This suggested that spacer length of *Potentilla anserina* was related to stolon length, i.e., longer the stolons, longer were the spacers.

Comprehensive analysed above results, the 8 patches were obviously divided into 2 categories (2 extreme environments) on the basis of soil property and

community characteristics. Patches I, II, and III were included in one group, and the other patches were included in the other group. However, the soil moisture, bulk density, pH value, and basicity was significantly lower in groups 1 than in groups 2, *Potentilla anserina* having less stolons dominated in groups 1, while those having relatively more stolons dominated in groups 2.

**Discussion****The factors that influence patchy distribution patterns:**

The changes of soil moisture is one of the important factors that effect the heterogeneity in plant distribution and evolution of patch community structure in the habitat (Su *et al.*, 2008). In grasslands, relatively low light intensity under tall grasses or shrubs is usually associated with relatively high availability of water due to the effect of litter, while the high light intensity in the absence of tall grasses and shrubs is usually associated with relatively low water availability (Yu *et al.*, 2002; Roilola *et al.*, 2007). The population distribution patterns were formed by the long-term mutual adaptation and interaction between the species and environment. Small-scale patterns are known to be determined by the biological characteristics of species, such as asexual reproduction of roots and modes of seed dispersal causing small-scale aggregated distribution, whereas large-scale patterns were primarily prompted by environmental factors (Fu & Nan, 1992).

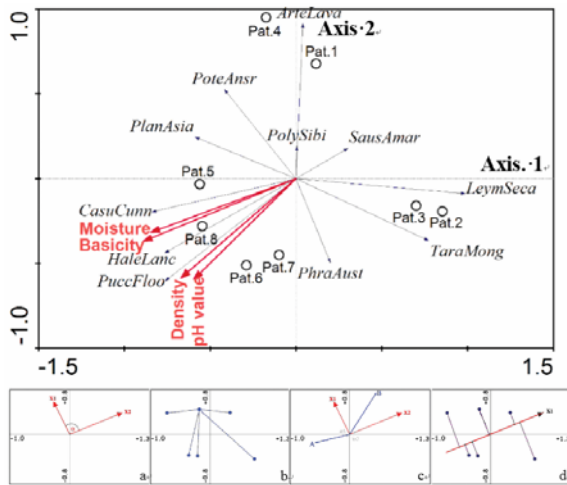


Fig. 5. The PCA ordination diagram of species, environmental factors, and 8 patch communities.

Note: Ordination diagram [axis 1, axis 2] with species, patches, and environmental factors. The letters a, b, c, and d represent the relationship interpretation among environment factors, patches, and species.

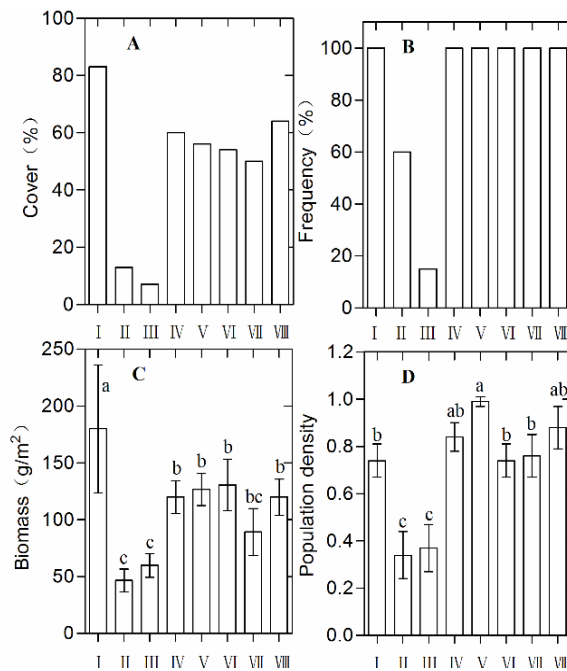


Fig. 6. The population characteristic of *Potentilla anserina* in 8 patches (including cover, frequency, biomass and population density).

Note: different lowercase letters represent significant differences at  $p = 0.05$ .

Due to the different ways of population growth and propagation, the expansion of population was mainly parent-centered for aggregated distribution causing grassland habitats to decompose to patch communities (Silvertown, 2009). There were 6 dominant populations (*Potentilla anserina*, *Halerpestes lancifolia*, *Polygonum sibiricum*, *Leymus secalinus*, *Taraxacum mongolicum*, and *Artemisia lavandulaefolia*) in the 8 patchy communities of

northern Shanxi salinization grassland; *Taraxacum mongolicum* had become a part of this habitat due to seed multiplication, and the other populations had high capacity of nutrition acquisition, such as *Potentilla anserina* and *Halerpestes lancifolia*. These plants found it difficult to complete their growth period because of grazing disturbance. Moreover, if seeds were produced, the distance of seed dispersal was short because these are dwarf species; hence, a small-scale aggregated distribution pattern developed. *Potentilla anserina* and *Halerpestes lancifolia* had stolons as reproductive organs. After the stolons invaded, diffused, and successfully settled in the form of seeds, they started population growth via asexual reproduction; eventually, they became the dominant species in the patches. The other reason for their dominance could be that grazing inhibited the growth of other plants and relatively increased the space for *Potentilla anserina*. Thus, clonal growth was the primary way in which *Potentilla anserina* population regenerated and developed, followed by sexual reproduction. After habitat fragmentation and changes in community structure due to environmental factors, the micro-habitat of populations, including soil moisture, bulk density, pH value, and basicity, affected the distribution of the population, leading to diverse population composition and dominance across different patches.

Many clonal plants in a heterogeneous environment obtained more resources via the foraging behavior of rhizomes and stolons and showed favorable growth compared to others. The clonal plants had 2 foraging strategies: strength foraging and breadth foraging. Strength foraging of clonal plants led to the generation of a large number of stolons within the small habitat under good environmental conditions that were linked by short spacer ramets within the occupied habitats. Breadth foraging led to the formation of longer spacer ramets under poor environmental conditions that helped in rapidly escaping the unfavorable environment and increased the opportunity to settle in a better environment (Slade & Hutchings, 1987b). Due to the lower soil moisture in patches I, II, and III, *Potentilla anserina* adapted breadth foraging strategy, occupied larger spaces, and searched for water to avoid competition among internal clone ramets; simultaneously, this strategy allowed the clonal plants to cross patches having adverse habitats and increased the probability of ramets to grow under favorable habitats (He *et al.*, 2007). Oppositely, when the soil moisture was high as in patches IV–VIII, *Potentilla anserina* adapted the strength foraging strategy and developed many short stolons to occupy patches with favorable habitats and improved the ability of clonal plants to inhibit the invasion of other plant species. *Potentilla anserina* are known to change their reproductive strategies according to the specific changes in habitat conditions; they can increase their numbers morphologically and physiologically by clonal growth and effectively occupy larger habitat areas. This finding was supported by the fact that *Potentilla anserina* had less stolons in patches I, II, and III and had more stolons in patches IV–VIII; moreover, the stolon length of *Potentilla anserina* in patches I, II, and III was greater than those in other patches. The foraging behavior theory (i.e., clonal plants obtain the necessary resources for heterogeneous distribution) of clonal plants also indicated that clonal ramets had higher density (Liu & Zhong, 1995) and shorter spacers (Dong, 1996 b) under better habitat conditions.

**Table 2. The genet height of *Potentilla anserina* having different number of stolons in the 8 patches (cm).**

	The number of stolons						F value	p value
	No stolon	1 stolon	2 stolons	3 stolons	4 stolons	5 stolons		
I	10.67 ± 1.16	10.80 ± 1.31	9.53 ± 0.49	9.73 ± 0.31	9.93 ± 2.40	12.03 ± 1.27	1.44	0.280 <sup>NS</sup>
II	13.57 ± 0.95	14.67 ± 2.00	17.37 ± 2.60	9.37 ± 2.65	10.53 ± 2.02	8.83 ± 1.27	8.34	0.001 <sup>**</sup>
III	12.10 ± 1.54	12.47 ± 1.33	8.67 ± 1.56	8.27 ± 1.72	8.57 ± 0.42	10.50 ± 0.70	6.18	0.005 <sup>**</sup>
IV	10.00 ± 0.36	10.40 ± 0.70	16.63 ± 1.57	8.40 ± 1.55	8.70 ± 0.60	7.60 ± 0.87	29.22	0.000 <sup>***</sup>
V	9.30 ± 1.71	4.90 ± 1.85	16.63 ± 1.57	15.63 ± 5.53	10.10 ± 2.25	7.57 ± 0.87	8.38	0.001 <sup>**</sup>
VI	13.30 ± 2.08	16.37 ± 2.52	17.17 ± 0.99	13.33 ± 1.17	14.73 ± 2.16	9.90 ± 1.57	6.04	0.005 <sup>**</sup>
VII	11.50 ± 1.06	17.17 ± 3.11	16.63 ± 1.57	19.60 ± 1.31	11.90 ± 2.12	9.27 ± 1.76	12.89	0.000 <sup>***</sup>
VIII	10.13 ± 3.91	11.77 ± 1.45	12.57 ± 6.03	12.03 ± 4.11	11.17 ± 2.40	11.97 ± 1.72	0.20	0.958 <sup>NS</sup>
F value	1.43	12.41±	5.78	6.07	3.10	5.26		
p value	0.011 <sup>*</sup>	0.000 <sup>***</sup>	0.001 <sup>**</sup>	0.001 <sup>**</sup>	0.029 <sup>*</sup>	0.003 <sup>**</sup>		

Note: Mean ± Standard Deviation (M ± SD); \*, 0.01 < p < 0.05; \*\*, 0.001 < p < 0.01; \*\*\*, p < 0.001; NS, not significant p > 0.05

**Table 3. The root length of *Potentilla anserina* having different number of stolons in the 8 patches (cm).**

	The number of stolons						F value	p value
	No stolon	1 stolon	2 stolons	3 stolons	4 stolons	5 stolons		
I	9.70 ± 1.37	9.61 ± 1.14	12.86 ± 2.73	11.40 ± 2.29	12.03 ± 2.38	11.83 ± 1.35	1.34	0.314 <sup>NS</sup>
II	13.68 ± 0.65	12.77 ± 0.45	10.98 ± 2.25	9.77 ± 1.59	10.47 ± 2.38	11.13 ± 1.81	2.27	0.113 <sup>NS</sup>
III	11.50 ± 1.35	12.07 ± 1.45	12.12 ± 0.76	12.51 ± 1.01	12.23 ± 1.16	12.83 ± 0.35	0.52	0.757 <sup>NS</sup>
IV	9.80 ± 1.25	8.47 ± 1.30	10.78 ± 1.48	10.07 ± 0.23	9.73 ± 1.50	12.07 ± 1.96	2.23	0.118 <sup>NS</sup>
V	9.83 ± 1.19	9.85 ± 2.51	11.59 ± 3.71	11.03 ± 2.06	11.77 ± 2.22	10.10 ± 1.82	0.41	0.832 <sup>NS</sup>
VI	8.23 ± 0.45	8.77 ± 0.51	9.09 ± 0.37	9.36 ± 0.60	10.20 ± 0.95	9.80 ± 0.40	4.42	0.016 <sup>*</sup>
VII	7.47 ± 0.58	7.43 ± 0.47	8.28 ± 0.99	8.97 ± 0.31	10.13 ± 0.80	9.30 ± 0.46	8.32	0.001 <sup>**</sup>
VIII	8.98 ± 0.80	10.00 ± 1.06	10.17 ± 0.15	9.98 ± 1.55	9.10 ± 1.01	8.97 ± 1.42	0.81	0.562 <sup>NS</sup>
F value	10.93	5.82	1.85	2.08	1.44	3.24		
p value	0.000 <sup>***</sup>	0.001 <sup>**</sup>	0.146 <sup>NS</sup>	0.107 <sup>NS</sup>	0.258 <sup>NS</sup>	0.024 <sup>*</sup>		

Note: Mean ± Standard Deviation (M ± SD); \*, 0.01 < p < 0.05; \*\*, 0.001 < p < 0.01; \*\*\*, p < 0.001; NS, not significant p > 0.05

In summary, the spatial distribution pattern of plants was affected by many factors. The driving force prompting the formation and evolution of patch communities, directly or indirectly, was human activities. In the salinization natural grassland, the distribution was determined on the basis of the performance of the species to adapt to long-term environmental variations. The non-uniform distribution of soil moisture and basicity was the main reason for the formation of population patches. After communities developed in patches, the biological characteristics and competition (intraspecific and interspecific) among the species were the factors that determined the direction of community succession.

**The plasticity of *Potentilla anserina*:** Because of the heterogeneity of resources and habitat, plants could not easily acquire resources (Hutchings & de Kroon, 1994). During long-term growth and evolution, plants may adopt certain strategies, accordingly, change the morphological and physiological characteristics; this phenomenon is known as plant plasticity (Slade & Hutchings, 1987b). Adaptation of clonal growth characteristics, configuration,

and plasticity were the ecological adaptive strategies that clonal plants used to obtain resources in a heterogeneous environment (Hutchings & de Kroon, 1994). The morphological plasticity of plants to partially specialize was one of the important ways in which plants overcame environmental heterogeneity (Bazzaz & Grace, 1997). The changes in plant morphology in different habitats manifested the characteristic changes in leaf area, root to shoot ratio, and plant height. In addition to the above features, clonal plants also showed clonal growth and morphological changes such as stolon length and the number and length of spacers. These characteristics reflected and indicated the ecological adaptive strategies of clonal plant ramets. The root length of *Potentilla anserina* in patches I to III was significantly greater than that in the other patches ( $|t| = 5.84, p < 0.0001$ ). This could be due to the lower soil moisture in patches I to III; lower soil moisture compelled plant roots to run deeper into the soil to absorb more water. Further, when the local shortage of resources limited plant growth, plants allocated more biomass to the organ that needed to acquire the most limiting resource (Hutchings & de Kroon, 1994; Aung, 1974; Shipley & Meziane, 2002).

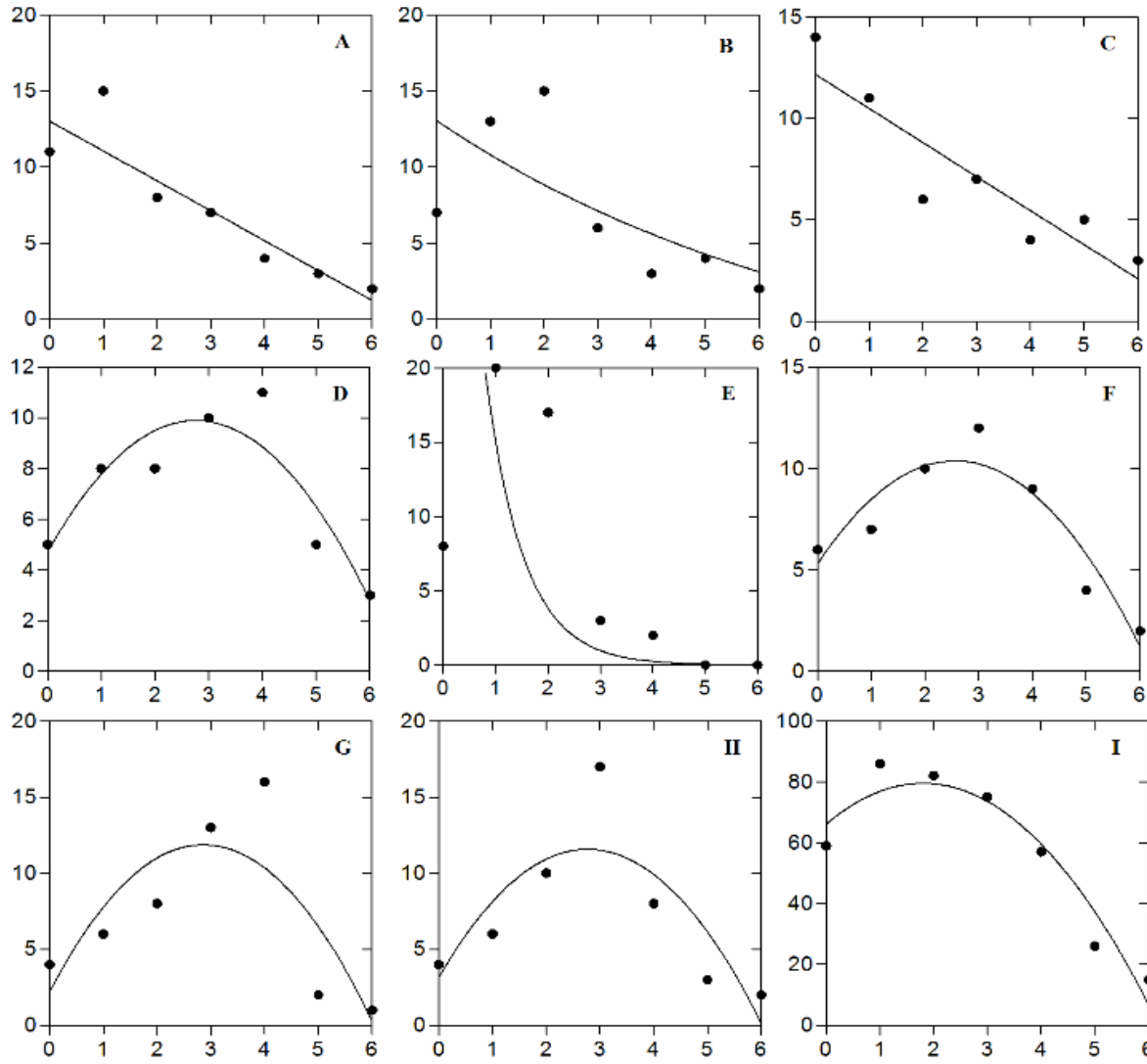


Fig. 7. The fitting analysis of *Potentilla anserina* between stolon number and sample number across different patches. Note: A–H show the fitting analysis of *Potentilla anserina* between stolon number and sample number in patches I–VIII, while I represents the fitting analysis of *Potentilla anserina* between stolon number and sample number in the entire plot.

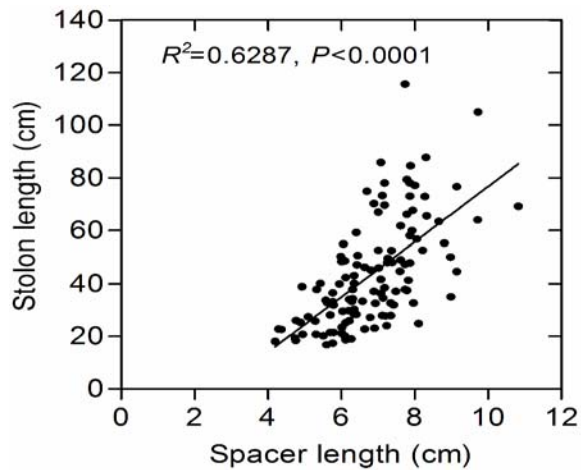


Fig. 8. The correlation analysis between stolon length and spacer length of *Potentilla anserina*.

When plants compete for resources, their growth and ability to reproduce are affected (Ma *et al.*, 2006). Since *Potentilla anserina* showed clonal growth, it had more access to resources compared to the other plant species (Ge & Xing, 2012) and hence could survive in a highly competitive environment. This suggested that the growth (including height, root length, stolon length, and spacer length) of *Potentilla anserina* was influenced by both the nature of the habitat (mainly soil moisture and basicity) and species competition in the heterogeneous habitats (Xiao *et al.*, 2006; Zou *et al.*, 2007). Clonal plants show features of clonal growth patterns and manifest a foraging behavior for obtaining resources, which was found in species such as *Potentilla angelica* and *Potentilla reptans* (Ren, 1998). This kind of behavior was shown to ensure the breeding and survival of offspring and reduce the risk of death; this also ensured that the plants escaped adverse habitats and had access to resources (Horn, 1966; Ma *et al.*, 1995). Hence, the diversity of clonal growth and morphological characteristics was the response of *Potentilla anserina* to comprehensive environmental factors.



Table 4. The spacers length of *Potentilla anserina* having different stolon numbers in the 8 patches (cm).

	I	II	III	IV	V	VI	VII	VIII	F value	p value
1 stolons	1 <sup>st</sup> 7.34 ± 1.38	8.66 ± 1.36	8.80 ± 1.85	7.43 ± 1.87	6.27 ± 0.49	6.11 ± 1.14	7.2 ± 1.11	7.13 ± 3.10	0.98	0.476 <sup>NS</sup>
2 stolons	1 <sup>st</sup> 7.79 ± 0.96	7.94 ± 0.5	7.86 ± 1.69	7.18 ± 0.95	10.42 ± 1.6	7.73 ± 0.46	7.97 ± 1.2	6.28 ± 2.02	2.48	0.063 <sup>NS</sup>
	2 <sup>nd</sup> 7.89 ± 1.05	7.74 ± 0.76	7.39 ± 1.12	6.12 ± 0.75	6.4 ± 1.35	7.34 ± 1.3	5.30 ± 0.75	4.36 ± 0.14	5.03	0.003 <sup>**</sup>
3 stolons	1 <sup>st</sup> 9.71 ± 2.41	8.98 ± 1.43	8.28 ± 1.63	7.82 ± 0.08	6.89 ± 0.38	8.21 ± 1.36	6.10 ± 0.45	6.22 ± 1.30	2.77	0.044 <sup>*</sup>
	2 <sup>nd</sup> 7.26 ± 1.32	7.49 ± 1.2	7.00 ± 0.58	4.28 ± 0.64	6.34 ± 0.94	6.12 ± 0.30	7.11 ± 0.97	6.22 ± 0.85	3.84	0.012 <sup>*</sup>
	3 <sup>rd</sup> 5.57 ± 0.1	5.62 ± 0.56	6.31 ± 1.57	4.19 ± 0.60	5.79 ± 1.14	6.92 ± 1.09	7.24 ± 2.1	4.94 ± 0.95	2.20	0.091 <sup>NS</sup>
4 stolons	1 <sup>st</sup> 9.72 ± 4.02	9.15 ± 0.68	9.14 ± 0.9	7.08 ± 0.8	7.73 ± 1.86	7.00 ± 1.39	8.30 ± 1.63	10.83 ± 2.57	1.31	0.306 <sup>NS</sup>
	2 <sup>nd</sup> 8.33 ± 0.92	8.99 ± 0.78	8.05 ± 1.48	5.98 ± 0.08	6.69 ± 0.59	6.34 ± 0.46	7.62 ± 1.72	7.61 ± 1.60	2.65	0.050 <sup>*</sup>
	3 <sup>rd</sup> 7.78 ± 0.28	8.11 ± 0.63	7.25 ± 1.52	5.42 ± 0.12	6.06 ± 0.53	6.91 ± 2.34	6.40 ± 1.1	6.64 ± 0.87	1.81	0.154 <sup>NS</sup>
	4 <sup>th</sup> 4.93 ± 1.3	5.7 ± 0.43	5.79 ± 0.71	4.76 ± 0.28	5.94 ± 2.18	6.10 ± 2.38	5.33 ± 0.9	6.78 ± 1.18	0.68	0.684 <sup>NS</sup>
5 stolons	1 <sup>st</sup> 7.92 ± 1.84	8.00 ± 1.76	7.87 ± 1.88	7.87 ± 1.88	7.11 ± 0.41	6.63 ± 0.38	7.18 ± 0.22	6.45 ± 0.88	0.63	0.727 <sup>NS</sup>
	2 <sup>nd</sup> 7.78 ± 1.93	7.86 ± 1.86	7.36 ± 2.29	7.01 ± 0.34	6.00 ± 0.00	6.42 ± 0.35	7.60 ± 2.12	5.77 ± 0.23	0.93	0.508 <sup>NS</sup>
	3 <sup>rd</sup> 5.77 ± 0.47	7.18 ± 1.03	6.80 ± 0.4	6.88 ± 1.29	7.07 ± 1.14	6.30 ± 0.27	7.07 ± 1.14	5.28 ± 0.02	2.00	0.119 <sup>NS</sup>
	4 <sup>th</sup> 5.10 ± 0.47	6.34 ± 1.33	6.35 ± 0.18	6.02 ± 1.37	6.58 ± 0.86	6.20 ± 0.33	6.02 ± 1.37	4.88 ± 0.25	1.35	0.291 <sup>NS</sup>
	5 <sup>th</sup> 4.75 ± 0.15	6.02 ± 1.62	5.69 ± 0.54	5.77 ± 1.56	6.03 ± 1.34	5.50 ± 0.67	5.60 ± 1.73	4.73 ± 0.13	0.59	0.757 <sup>NS</sup>

Note: Mean ± Standard Deviation (M ± SD); \*, 0.01 < p < 0.05; \*\*, 0.001 < p < 0.01; \*\*\*, p < 0.001; NS, not significant p > 0.05

Table 5. The stolon length of *Potentilla anserina* in the 8 patches (cm).

	I	II	III	IV	V	VI	VII	VIII	F value	P value
1 stolons	1 <sup>st</sup> 32.73 ± 6.24	63.53 ± 5.56	55.35 ± 3.15	31.97 ± 5.43	19.03 ± 5.42	18.67 ± 5.02	27.80 ± 7.33	34.60 ± 9.91	19.70	0.000 <sup>***</sup>
2 stolons	1 <sup>st</sup> 79.40 ± 14.33	67.67 ± 2.60	73.10 ± 15.72	69.70 ± 28.50	64.67 ± 27.16	37.90 ± 3.38	32.73 ± 11.53	33.33 ± 23.79	3.29	0.0231 <sup>*</sup>
	2 <sup>nd</sup> 84.63 ± 15.02	47.43 ± 7.97	48.10 ± 6.04	25.30 ± 11.50	28.43 ± 6.99	27.90 ± 3.12	20.77 ± 3.77	22.67 ± 5.03	20.06	0.000 <sup>***</sup>
3 stolons	1 <sup>st</sup> 64.15 ± 15.45	50.13 ± 8.08	72.93 ± 9.38	41.40 ± 33.78	70.32 ± 22.17	52.67 ± 8.54	48.71 ± 7.01	34.13 ± 11.52	1.99	0.120 <sup>NS</sup>
	2 <sup>nd</sup> 49.66 ± 12.14	37.20 ± 3.42	67.03 ± 5.92	22.80 ± 7.54	28.44 ± 5.53	42.40 ± 9.58	27.91 ± 2.26	25.97 ± 7.62	12.30	0.000 <sup>***</sup>
	3 <sup>rd</sup> 33.74 ± 3.30	32.87 ± 3.40	34.40 ± 15.70	18.10 ± 8.94	21.54 ± 5.40	32.60 ± 6.16	24.13 ± 4.77	20.83 ± 8.02	2.19	0.093 <sup>NS</sup>
4 stolons	1 <sup>st</sup> 105.05 ± 26.72	44.63 ± 12.05	76.70 ± 44.02	85.89 ± 33.06	115.63 ± 10.50	52.63 ± 13.40	87.80 ± 39.60	69.20 ± 38.00	1.96	0.125 <sup>NS</sup>
	2 <sup>nd</sup> 65.64 ± 15.67	35.03 ± 15.45	56.90 ± 22.73	50.30 ± 9.50	75.00 ± 11.84	40.20 ± 5.57	61.90 ± 21.10	49.00 ± 31.60	1.57	0.216 <sup>NS</sup>
	3 <sup>rd</sup> 66.25 ± 16.25	24.90 ± 11.07	48.00 ± 30.21	40.20 ± 4.00	55.00 ± 25.37	23.17 ± 5.60	59.35 ± 23.15	22.85 ± 9.65	2.76	0.0438 <sup>*</sup>
5 stolons	4 <sup>th</sup> 38.90 ± 16.30	21.53 ± 10.11	31.87 ± 20.21	26.02 ± 6.00	39.93 ± 16.40	20.07 ± 6.00	37.85 ± 17.35	27.20 ± 14.80	0.91	0.522 <sup>NS</sup>
	1 <sup>st</sup> 60.00 ± 2.15	77.20 ± 36.61	58.20 ± 2.97	78.10 ± 35.84	73.30 ± 40.62	46.30 ± 8.30	78.10 ± 35.84	50.70 ± 8.30	0.71	0.661 <sup>NS</sup>
	2 <sup>nd</sup> 37.50 ± 3.50	47.90 ± 7.11	52.50 ± 2.55	46.00 ± 6.39	48.50 ± 10.16	47.20 ± 3.40	44.70 ± 7.41	33.20 ± 0.80	3.39	0.020 <sup>*</sup>
	3 <sup>rd</sup> 36.60 ± 3.60	38.60 ± 10.72	45.20 ± 8.91	37.20 ± 7.32	41.70 ± 11.92	37.90 ± 8.95	36.40 ± 8.69	25.80 ± 7.20	1.22	0.347 <sup>NS</sup>
	4 <sup>th</sup> 27.50 ± 5.70	30.30 ± 10.41	43.10 ± 8.84	32.53 ± 2.50	33.40 ± 16.64	29.75 ± 12.35	23.53 ± 2.50	25.35 ± 7.85	1.39	0.275 <sup>NS</sup>
5 <sup>th</sup> 18.50 ± 5.00	21.20 ± 7.70	28.20 ± 15.57	17.40 ± 6.44	29.60 ± 13.27	20.20 ± 6.35	16.90 ± 6.86	19.40 ± 4.15	0.87	0.550 <sup>NS</sup>	

Note: Mean ± Standard Deviation (M ± SD); \*, 0.01 < p < 0.05; \*\*, 0.001 < p < 0.01; \*\*\*, p < 0.001; NS, not significant p > 0.05

We identified that the spacer lengths and stolon lengths of *Potentilla anserina* were significantly greater in patches I to III than in the other patches. This could be due to the lower soil moisture and basicity in patches I to III than in other patches. According to the risk sharing principle of clonal plant genets (Huai *et al.*, 2004), under relatively good habitat conditions, the number of *Potentilla anserina* stolons increased, which reduced the risk of death, promoted valid survival, and allowed plants to occupy space using the clone characteristics. In contrast, under relatively poor habitat conditions and in a highly competitive environment, the spacer and stolon lengths were increased to acquire resources from farther places or rapidly explore new habitats to avoid unfavorable environment or reduced the impact of the adverse environment (Dong, 1993). Moreover, a significantly positive correlation between stolon and spacer length suggested that *Potentilla anserina* placed ramets on suitable habitats by synchronizing stolon and spacer lengths to allow clones to spread rapidly and promote survival chances after the ramets became independent. This was one of the mechanisms that *Potentilla anserina* used to adapt to the adverse environment and maintain its population.

A large number of studies about foraging behaviour of clonal plants, including phenotypic plasticity and physiological integration of clonal plants, resource heterogeneity and adaptability of habitat, supported the two hypotheses (Sultan, 1995; Lortie & Aarssen, 1996). (1) Limit hypothesis, explains that the phenotypic plasticity of clonal plants associated with the form of clonal growth in their evolution (Dong, 1994). (2) Habitat adaptation hypothesis, explains that the morphological plasticity of clonal plants is adapted to their habitat resources condition (Van der Hoeven *et al.* 1990). In our study, the stolons of *Potentilla anserina* performed morphological plasticity and modularity differences in order to overcome and reduce intake difficulties caused by heterogeneous distribution of necessary resources, which reached high fitness to resource status under different habitats. Compared with previous studies, we found that the placement pattern of clonal plants resources absorption structure (clone strains) coordinated with habitat resources heterogeneity, provided a evidence for habitat adaptation hypothesis of the foraging behavior of clonal plants.

**Patch points:** The distance between the hollow dots in the diagram approximate the dissimilarity of their species composition, measured using their Euclidean distance. Pat.1–Pat.8 represent patches I–VIII (Fig. 5b).

**Species arrows:** Thin arrows point in the direction of the steepest increase in the values for the corresponding species. The angles between the arrows indicate correlations (or covariance) between the species (Fig. 5c).

**Environment arrows:** Thick arrows point in the expected direction of the steepest increase of values of environmental variables. The angles between the arrows indicate correlations between individual environmental variables (Fig. 5a).

**The relationship between the species:** The angle

representing the correlation between 2 species. The smaller the angle, the larger is the correlation.

**The relationship between species and the environment:** The correlation is represented by the cosine of the angle between species and the environmental variables (Fig. 5c).

**The correlation between patches:** The length of a straight line between 2 patches represented the correlation. The shorter the length of the straight line, smaller was the difference between the 2 patches (Fig. 5b).

**The correlation between patches and environmental factors:** The patches were vertically projected on the extended rays of the environment factors; the correlation between them increased along the direction of the arrows representing environmental factors (Fig. 5d).

#### The letters in the figure

*PoteAnsr*—*Potentilla anserina*, *HaleLanc*—*Halerpestes lancifolia*, *PolySibi*—*Polygonum sibiricum*, *PuccFloo*—*Puccinellia florida*, *PlanAsia*—*Plantago asiatica*, *LeymSeca*—*Leymus secalinus*, *CasuCunn*—*Casuarina cunninghamiana*, *TaraMong*—*Taraxacum mongolicum*, *ArteLava*—*Artemisia lavandulaefolia*, *PhraAust*—*Phragmites australis*, *SausAmar*—*Saussurea amara*

#### Conclusions

The grassland was excessively disturbed (by grazing activities), and the vegetation composition and soil properties had changed. During the 2 years when the grassland was fenced, distinctive patches of diverse habitats developed under the long-term and mutual interaction of plants and environmental factors. There was well performance only for *Potentilla anserina*, which could utilize heterogeneous resources, in such an environment. When *Potentilla anserina* occupied the dominant position in grassland, which suggested the grassland was a severe degradation state.

Under relatively good habitat conditions, *Potentilla anserina* adapted breadth foraging strategy, its stolons number increased, which reduced the risk of death and promoted valid survival by spreading in the available space using the clone characteristics. On the other hand, under relatively poor habitat conditions and in a highly competitive environment, *Potentilla anserina* adapted the strength foraging strategy to acquire resource from farther places by increasing its spacer and stolon lengths or rapidly exploring new habitats to avoid unfavorable environments or reduce the impact of the adverse environment.

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