Fertile islands under *Artemisia ordosica* in inland dunes of northern China: Effects of habitats and plant developmental stages

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Abstract

Plants may induce small-scale heterogeneity in soil nutrients, forming fertile islands. However, this process may depend on plant developmental stages and habitat conditions. We address whether fertile islands are formed under semi-shrubs of *Artemisia ordosica* in Ordos Plateau, a semiarid region in northern China, and how they are affected by developmental stages and habitat conditions. We selected young, mature and senescent individuals of *A. ordosica* from three habitats, i.e. the fixed dune, leeward and windward slopes of the mobile dune. At the location of each individual, we took soil samples beneath, at the edge of and outside canopies from 0–10 to 10–20 cm depth, and measured total organic carbon (TOC) and total nitrogen (TN). Soil TOC and TN were highest beneath and lowest outside the canopies. The differences in TOC and TN between soil beneath and outside the canopies were larger in the fixed than in the mobile dune, at the surface than at the deeper layer, and under the mature and senescent than under the young individuals. We conclude that fertile islands were formed under *A. ordosica* semi-shrubs, and that they are more strongly developed in fixed than in mobile dunes, in the surface soils than in the deeper soils, and under the mature and senescent individuals than under the young individuals.

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1. Introduction

Plant-induced nutrient-rich zones, resulting from a range of interacting physical and biotic concentrating mechanisms, are named “fertile islands”, “resource islands”, or “islands of fertility” (Coppinger et al., 1991; Schlesinger et al., 1996; Reynolds et al., 1999; Stock et al., 1999; Camargo-Ricalde and Dhillion, 2003). Formation of fertile islands is very common in arid and semiarid ecosystems (Belsky et al., 1989; Schlesinger et al., 1990; Hook et al., 1991; Vinton and Burke, 1995). It increases spatial heterogeneity in soil resources, and affects not only seedling establishment (Maestre et al., 2003) and plant–plant interactions (Aguiar and Sala, 1999) but also species distribution (Pan et al., 1998), diversity (Anderson et al., 2004) and productivity (Mou et al., 1995) of plant communities.

Many studies have investigated the phenomena of plant-induced fertile islands, but little is known about the effects of plant developmental stages, especially in dune ecosystems (Fransen et al., 1999). The accumulation of litter and nutrients under the canopy of an individual plant may be affected by its developmental stage because the temporal scale may affect the accumulation of nutrients (Robinson, 1994; Maestre and Reynolds, 2006) and be an important factor determining the formation of fertile islands (Vinton and Burke, 1995). At earlier stages when a plant is young and its canopy size is small, the fertile island may be very weak or non-existent, because litter and other nutrients may not be efficiently trapped under the small canopy within a relatively short time (Ludwig et al., 1975; Reynolds et al., 1999). With increasing developmental stage of the individual plant, however, the canopy size and duration of nutrient accumulation increase, so that more litter and nutrient resources may be accumulated and the bare inter-shrub spaces may become increasingly nutrient-poor (Charley and West, 1975; Ludwig et al., 1975; Reynolds et al., 1999). It is, therefore, hypothesized that fertile islands under individuals become stronger with increasing plant developmental stages. On the other hand, how fertile islands are formed with the developmental stage may give insight into how small-scale heterogeneity in soil resources is developed with time (Maestre and Reynolds, 2006).

It is evident that the intensity of fertile islands may differ among habitats (Charley and West, 1975; Derner et al., 1997; Su et al., 2004). However, few studies have investigated the difference in the intensity of fertile islands under shrubby species between fixed and mobile dunes in the semiarid ecosystems. In sandy areas, accumulation rate of litter and soil nutrients under plants may be different between fixed and mobile dunes because vegetation cover and soil nutrients are higher in fixed than in mobile dunes (Su et al., 2004; Wen and Zhao, 2004; Cakan and Karatas, 2006; He et al., 2006). Fixed dunes are associated with higher biomass, more litter, more active soil microorganisms and more stable environmental conditions than mobile dunes (Charley and West, 1975; Jackson and Caldwell, 1993). Consequently, it is expected that the intensity of shrub-induced fertile islands on fixed dunes differs from that on mobile dunes.

Intensity of fertile islands may also vary with soil depth (Charley and West, 1975; Soriano et al., 1987; Caldwell and Manwaring, 1994; Zaady et al., 1996; Derner et al., 1997). In sandy ecosystems, because the sand is less stable in mobile than in fixed dunes (Charley and West, 1975; Kieft et al., 1998), the formation of fertile islands may be expressed differently in surface and deeper soils in these habitats. On fixed dunes, we expect that fertile islands are more pronounced near the surface soil than in the deeper soil layers, because the surface soil traps most litter and nutrients which are less disturbed by
strong wind (Charley and West, 1975; Cakan and Karatas, 2006). On mobile dunes, in contrast, we expect that the vertical gradient is weaker because the surface soil is more frequently disturbed by wind-driven sand deposition or erosion (Cakan and Karatas, 2006).

The southeastern Ordos Plateau is one of the most severely desertified areas in the semiarid region in northern China (Zhang, 1994), where fixed dunes and mobile dunes are widely distributed (Dong et al., 1999; Chen et al., 2001). The semi-shrub, *Artemisia ordosica*, is one of the most dominant species and occurs in various habitats, including fixed and mobile dunes (Cui, 1991). To address the impact of *A. ordosica* on the formation of fertile islands, we sampled soils under *A. ordosica* individuals of different developmental stages in both fixed and mobile dunes. Specifically, we addressed the following questions: (1) Does *A. ordosica* induce fertile islands in the habitats in question? (2) If it does, how do plant developmental stages, habitats, and soil depths affect the extent of the phenomenon?

2. Materials and methods

2.1. Plant species

*A. ordosica* Krasch., a medicinal and sand-binding semi-shrub of Asteraceae, is a dominant species in Ordos Plateau and widely distributed in northern and northwestern China. As a perennial semi-shrub with an average lifespan of 10 years, *A. ordosica* forms thick stems with many clustered wooden branches and well-developed root systems (Cui, 1991). They are mostly 60–100 cm tall and have a canopy of up to 2 m in diameter. In the study area, mature individuals of *A. ordosica* are generally spatially separated from one another (Cui, 1991).

2.2. Study area

The study area is located in southeastern Ordos Plateau in Inner Mongolia, China. This is a semiarid area with a typical temperate continental climate and a mean annual precipitation of 260–450 mm, occurring mostly (60–80%) between June and August. Historically, this area was highly productive grassland. However, overgrazing, mining, and other human-mediated activities led to severe desertification, and nowadays the landscape is characterized by fixed and moving sand dunes with patchy vegetation dominated by psammophytic shrubs and herbs, including *A. ordosica*, *A. sphaerocephala*, *A. frigida*, *Caragana intermedia*, *Hedysarum laeve*, *Sabina vulgaris*, *Thymus serpyllum*, *Psammochloa villosa*, *Agropyron cristatum*, and *Agriophyllum pungens* (Zhang, 1994; Wu and Ci, 1998).

For field sampling, we selected three habitats dominated by *A. ordosica* near Ordos Sandland Ecological Station (39°02′N, 109°51′E; Institute of Botany, Chinese Academy of Sciences). One habitat was located on a fixed dune, and the other two were on the leeward and the windward slope of a mobile dune, respectively. The vegetation cover on the fixed dune is about 64.3 ± 3.8% (mean ± SE), which is much higher than that on the leeward (4.8 ± 0.7%) or on the windward slope (5.4 ± 0.6%) of the mobile dune. Each habitat was covered by a mixture of *A. ordosica* of different developmental stages (see the following paragraph).
2.3. Sampling design and measurements

Field work was carried out between late July and mid-August of 2005. Based on size and vitality we distinguished the following three developmental stages of *A. ordosica*: (i) young (canopy diameter <100 cm and leaf cover >20%), (ii) mature (canopy diameter >120 cm and >30% leaf cover), and (iii) senescent (canopy diameter >150 cm and leaf cover <15%). In each habitat and for each developmental stage of *A. ordosica*, we randomly selected 10 individuals. On average, the young, mature and senescent individuals had canopy diameters of 79.4 (±2.1, SE), 164.9 (±4.7), and 170.2 (±4.0) cm, respectively, and leaf cover of 30.0 (±2.2)%, 50.8 (±3.3)%, and 6.7 (±1.2)%, respectively. To minimize potential shrub–shrub interactions, we made sure that the canopies of the nearest neighbors were separated from the selected individuals by a gap of at least 50 cm.

Starting at the main stem of the selected *A. ordosica*, we drew three transects on the soil surface separated by about 120°. On every transect, we took a soil core (5.0 cm in diameter and 20 cm in depth): (i) beneath the canopy and next to the main stem of *A. ordosica*, (ii) at the edge of the canopy, and (iii) 20 cm outside the edge of the canopy. Each soil core was divided into a surface (0–10 cm) and deeper (10–20 cm) part. The three cores collected in the same location (stem, edge, and outside) on the three transects were pooled to reduce variability.

The soil samples were air-dried and passed through a 2-mm sieve to remove plant material. Subsequently, the samples were pulverized in a grinder and passed through a 0.2-mm sieve. Sub-samples were analyzed for total organic carbon (TOC) and total nitrogen (TN). TOC was measured using the H$_2$SO$_4$–K$_2$Cr$_2$O$_7$ wet oxidation followed by titration with FeSO$_4$ with the Walkley–Black procedure (Liu, 1996; Nelson and Sommers, 1996), and TN was determined using micro-Kjeldahl digestion (Nelson and Sommers, 1980) followed by colorimetric analysis (Hook et al., 1991; Katherinel et al., 1995).

2.4. Statistical analysis

We used four-way repeated-measures ANOVA to test effects of the habitat, plant developmental stage, sampling location, and soil depth on TOC and TN, with the sampling location and soil depth as repeated factors (von Ende, 2001). For each *A. ordosica* individual, we derived the data on differences in TOC and TN, respectively, between soils beneath and outside the canopy. We then used three-way repeated-measures ANOVA to investigate effects of the habitat, plant developmental stage, and soil depth on such difference data, with soil depth as a repeated factor (von Ende, 2001). When a significant effect of habitats or plant developmental stage was detected, an S–N–K test was used to compare the grand means among the three treatments. SPSS v. 11.0 software package was used for all analyses.

3. Results

3.1. Effects of habitats and developmental stages on TOC and TN

Soil TOC and TN were about two times higher in the fixed dune than in the leeward or windward slope of the mobile dune (Fig. 1; Table 1). TOC was higher in the leeward slope than in the windward slope of the mobile dune (P<0.01), but TN did not differ significantly (P = 0.66, Fig. 1). TOC and TN of the surface soils (0–10 cm) were higher than those of the deeper soils (10–20 cm), especially in the fixed dune (Fig. 1). In the fixed dune, TOC and TN at
both soil depths increased with increasing the developmental stage of *A. ordosica* (Table 1; Fig. 1A, D). In the mobile dune, TOC and TN of the surface soils increased with the developmental stage, but those of the deeper soils did not change significantly (Fig. 1B–C, E–F).

### 3.2. Formation of fertile islands under *A. ordosica*

TOC and TN were significantly higher in soils beneath than outside canopies of *A. ordosica*, irrespective of the habitats, developmental stages or soil depths (Fig. 1; Table 1), suggesting that fertile islands were formed under *A. ordosica*. 
3.3. Effects of developmental stages on the intensity of fertile islands

The developmental stages of *A. ordosica* significantly influenced the intensity of fertile islands under *A. ordosica* (Table 1, the significant L × DS effect; Table 2, the significant DS effect). With increasing developmental stages (from the young, mature to the senescent stage), differences in TOC and TN between soils beneath and outside the canopies of the *A. ordosica* plants increased significantly (Fig. 2). Effects of the developmental stage on the differences in soil TOC did not change with habitats (Table 2; Fig. 2), but those effects on the differences in soil TN were more significant in the fixed dune than in the mobile dune (Table 1, L × H × DS effect; Table 2, H × DS effect; Fig. 2).

3.4. Effects of habitats on the intensity of fertile islands

The habitat significantly affected the intensity of fertile islands under *A. ordosica* (Table 1, L × H effect; Table 2, H effect). Differences in TOC and TN between soils beneath and outside the canopies of the *A. ordosica* plants were the highest in the fixed dune, smallest in the windward slope of the mobile dune and intermediate in the leeward

**Table 1**
Effects of habitat, plant developmental stage, soil depth, sampling location, and interactions on soil traits

<table>
<thead>
<tr>
<th>Effect</th>
<th>DF</th>
<th>Total organic matter</th>
<th>Total nitrogen</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>F</em></td>
<td><em>P</em></td>
</tr>
<tr>
<td><strong>Between-subject effect</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Habitat (H)</td>
<td>2</td>
<td>87.40</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>Developmental stage (DS)</td>
<td>2</td>
<td>5.18</td>
<td>0.008</td>
</tr>
<tr>
<td>H × DS</td>
<td>4</td>
<td>1.92</td>
<td>0.115</td>
</tr>
<tr>
<td>Error</td>
<td>81</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><strong>Within-subject effect</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Soil depth (SD)</td>
<td>1</td>
<td>59.75</td>
<td>&lt;0.001</td>
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<tr>
<td>SD × H</td>
<td>2</td>
<td>13.42</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>SD × DS</td>
<td>2</td>
<td>4.19</td>
<td>0.019</td>
</tr>
<tr>
<td>SD × H × DS</td>
<td>4</td>
<td>1.13</td>
<td>0.349</td>
</tr>
<tr>
<td>Error (SD)</td>
<td>81</td>
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<td></td>
</tr>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sampling location (L)</td>
<td>2</td>
<td>111.68</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>L × H</td>
<td>4</td>
<td>19.69</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>L × DS</td>
<td>4</td>
<td>6.32</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>L × H × DS</td>
<td>8</td>
<td>1.36</td>
<td>0.217</td>
</tr>
<tr>
<td>Error (L)</td>
<td>162</td>
<td></td>
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</tr>
<tr>
<td></td>
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<td></td>
</tr>
<tr>
<td>SD × L</td>
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<td>14.85</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>SD × L × H</td>
<td>4</td>
<td>5.99</td>
<td>&lt;0.001</td>
</tr>
<tr>
<td>SD × L × DS</td>
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<td>1.33</td>
<td>0.263</td>
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<tr>
<td>SD × L × H × DS</td>
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<td>0.39</td>
<td>0.926</td>
</tr>
<tr>
<td>Error (SD × L)</td>
<td>162</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

*F*, *P*, and degree of freedom (DF) were based on four-way repeated-measures ANOVA with soil depth and sampling location as two repeated factors.
slope (Fig. 2). But such effects of habitats were more significant in the surface soils than in the deeper soils (Table 1, SD $\times$ L effect; Table 2, SD $\times$ H effect; Fig. 2).

### 3.5. Effects of soil depths on the intensity of fertile islands

The intensity of fertile islands also differed among the soil depths (Table 1, SD $\times$ L effect; Table 2, SD effect). Differences in TOC and TN between soils beneath and outside the canopies of *Artemisia ordosica* plants were more pronounced in the surface layer than than the deeper layer (Fig. 2). But such effects of soil depths were more significant in the fixed dune...
than in the leeward of windward slope of the mobile dune (Table 1, SD × L × H effect; Table 2, SD × H effect; Fig. 2).

4. Discussion

In both fixed and mobile dunes on Ordos Plateau, A. ordosica individuals accumulated soil nutrients and formed fertile islands under their canopies. Fertile islands have been found in many other shrubby species, including Larrea tridentata in Chihuahuan Desert of USA (Schlesinger et al., 1996), Ruschia cyathiformis and Stoeberia utilis in the desert in northern Namaqualand of South Africa (Stock et al., 1999), and L. tridentata and Prosopis glandulosa in Jornada Basin of USA (Reynolds et al. 1999).

4.1. Developmental stages and intensity of fertile islands

Differences in TOC and TN between soils beneath and outside the A. ordosica plants increased significantly from the young to the mature and the senescent stages, supporting the hypothesis that the intensity of fertile islands increases with the developmental stages of a plant. It has been found that the canopy size of a shrubby plant is positively correlated with the amount of litter accumulation under its canopy (Ludwig et al., 1975; Belsky et al., 1989; Reynolds et al., 1999). The large canopies of the mature and the senescent A. ordosica individuals thus may have trapped more litter and more nutrients than the small canopies of the young individuals. It has also been suggested that shrubs with a long life span may form fertile islands and those with a short one may not, because nutrients accumulated by short-lived shrubs, especially those with small canopies, will fade away quickly (Schlesinger et al., 1990; Stock et al., 1999; Cheng et al., 2004). Thus, more litter accumulation with a longer time may have contributed to the higher intensity of fertile islands in the mature and senescent individuals of A. ordosica than in the young ones. However, fertile islands may quickly fade away after the death of the senescent individuals.

Effects of the developmental stages on the intensity of TOC islands did not change with habitats, but those effects on that of TN islands were more pronounced in the fixed than in the mobile dune (Table 2; Fig. 2). The reason might be the different accumulation mechanisms between organic carbon and nitrogen. Previous studies showed that TOC islands developed more quickly than TN islands because TOC was derived mainly from decomposition of plant material and TN was provided by biological nitrogen fixation and mineralization (Charley and West, 1975; Cheng et al., 2003). Cheng et al. (2004) suggested that nitrogen accumulation needed better conditions than accumulation of carbon. On the relatively more stable and thus less harsh fixed dune, organic carbon may start to accumulate from the establishment of A. ordosica; accumulation of nitrogen may start later but increase relatively quickly with the development of A. ordosica. However, on the less stable mobile dunes, both carbon and nitrogen accumulation were slowed down, and the decrease of nitrogen accumulation may be at a less degree than that of carbon accumulation (see also Derner et al., 1997).

4.2. Habitats and intensity of fertile islands

The intensity of fertile islands under A. ordosica was larger in the fixed dune than in the mobile dune. It has also been reported that fertile islands developed more quickly or
strongly along a precipitation gradient (Charley and West, 1975), at the later than at the earlier stages of artificial forestation on mobile dunes (Su et al., 2004; Wang et al., 2005; He et al., 2006), and in the mid-grass habitat than in the shortgrass or tallgrass communities (Derner et al., 1997). In the present study, the difference between the fixed dune and the mobile dune may be caused by their different rates in accumulating and decomposing litters and also the different disturbance regime by wind. Higher rates in litter accumulation and decomposition lead to larger heterogeneity (Garcı´a-Moya and McKell, 1970; Scholes and Archer, 1997). Under the canopies of A. ordosica, litter was accumulated and decomposed relatively more easily on the fixed than on the mobile dune because surface soils on both windward and leeward slopes of the mobile dune were more disturbed by wind than those on the fixed dune. After heavy disturbance by wind, both soils blown to the leeward slope and deeper soils of the windward slope of the mobile dune became surface soils. This process may have reduced the heterogeneity between soils outside and beneath the shrub canopies on the mobile dune.

4.3. Soil depths and intensity of fertile islands

The intensity of fertile islands under A. ordosica was larger in the surface than in the deeper soils, agreeing with the former findings (Charley and West, 1975; Derner et al., 1997; Su et al., 2004). However, in the desert in northern Namaqualand of South Africa, Stock et al. (1999) found that the intensity of fertile islands under R. cyathiformis, S. utilis, or Ruschia sp. nov. did not differ between surface and the deeper soils. The desert in northern Namaqualand is characterized by many short-lived perennials that produce copious quantities of seeds and seedlings (Jürgens et al., 1999; Stock et al., 1999). This is in contrast to most of the other dune systems such as Ordos sandy land, where recruitment is lower and plants are generally long-lived. Thus, it is likely that the shrubs in northern Namaqualand were not long-lived enough to cause the vertical heterogeneity.

Effects of soil depths on the intensity of fertile islands under A. ordosica were more pronounced in the fixed dune than on the leeward or windward slope of the mobile dune. After establishment, shrubs accumulated carbon and nitrogen derived from photosynthesis and/or other mechanisms. The stability of fixed dunes favored this process and the spatial heterogeneity gradually strengthened with the development of shrubs because nutrients were transferred from the surface to the deeper soils and from the beneath areas to the openings gradually with the time went on (Charley and West, 1975; Wang et al., 2005).

5. Conclusions

We conclude that the modification of soil traits by A. ordosica is more significant with the development of the plant and this effect increases with the fixation of the dunes. As the most widely distributed species on Ordos Plateaus, A. ordosica may have played an important role in the fixation of dunes and the environmental melioration. This process will also contribute much to the following succession stages of this area.

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