Ecophysiological acclimation to different soil moistures in plants from a semi-arid sandland

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Abstract

In order to explore the functional significance of ecophysiological heterogeneity among three arid microhabitats (sand dune, lowland and wetland), we investigated the stomatal and photosynthetic acclimation to soil moistures in different plants of highly diversified Hunshandak Sandland, Inner Mongolia, China. Wetland was found to have the highest soil water potential (0–40 cm), while the fixed sand dune had the lowest (P<0.001). The three microhabitats appeared in a similar pattern in leaf water potential ($\Psi_{\text{leaf}}$), stomatal conductance ($g_s$), photosynthetic rate ($P_n$) and photochemical efficiency of photosystem II ($F_v/F_m$) with that of soil water potential, i.e. wetland > lowland > fixed sand dune (p < 0.01). Inversely, however, root depths in both fixed sand dune and lowland was 58% deeper (p < 0.05) than wetland. Photosynthetic characteristics (e.g. $g_s$, $P_n$, and $F_v/F_m$) were found to be linearly correlated with $\Psi_{\text{leaf}}$ in fixed sand dune and lowland (p < 0.05), but no linear relation among these traits were noted in wetland. Such a result indicated that water played an important role in controlling the ecophysiological process. Stomata sensitivity to leaf water potential changes increased with drought. In the microhabitats with contrasting soil water availabilities, plants may display feedback responses to the arid environment through elongating their root lengths and/or reducing their stomatal conductance.

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Keywords: Chlorophyll fluorescence; Leaf water potential; Photosynthetic rate; Root depth; Stomatal conductance

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1. Introduction

Soil surface irregularities can channelize water and thereby create moist as well as dry microhabitats in arid regions (Nobel, 1991). Thus the habitat partitioning between species came into being. Differences in intrinsic traits among plant species and their plasticity could reflect interspecific microhabitat differentiation. Variation in physiological and morphological traits among species has been related to their differences in habitat conditions (Jones, 1996; Nona et al., 2004). The survival and growth of the species will depend on its physiological response to stress, especially in limited resources or structurally poor environments (Zobel, 1992; Leiss and Schärer, 2001). In the process of plants’ acclimation to their habitats, some ecophysiological traits may change to character certain habitats (Villar et al., 1999; Ward et al., 1999), such as the xeromorphy and hydrophyte structure developed in drought and water habitats, respectively. Abundant studies in this field have been conducted. However, past studies on plants acclimations to habitats have primarily concentrated on large spatial scale that belong to different kinds of habitats (Schulze et al., 1996; Jiang et al., 1999). Such a large scale includes multiple environmental factors that makes it difficult to understand the impact of a given factor on plants. Regarding the relationship between plant ecophysiology and their microhabitats formed by the heterogeneous distribution of soil moistures described here, few studies were conducted before.

The extent to which photosynthetic capability is maintained during water stress period plays an important role in plants’ acclimation to drought environments. In order to preserve photosynthesis under drought conditions, plants have evolved a number of physiological traits, such as maintaining some extent of tissue turgor and controlling stomatal opening (Nunes et al., 1989). Although there is no obvious advantage to have low leaf water potential for some species, plants do reduce their leaf osmotic potential to acclimate to drier soil, in order, presumably, to maintain positive cell turgor at lower leaf water condition (Mielke et al., 2000). Leaf water potential is generally and physiologically associated with the stomatal complex (Comstock and Mencuccini, 1998; Nardini and Salleo, 2000), and has been often considered as one of the important factors in determining plants’ growth (Eschenbach and Kappen, 1999). It has been reported that photosynthetic rate is affected by leaf water potential under arid environment (Sen Gupta and Berkowitz, 1987; Meinzer et al., 1990). However, what is the threshold of leaf water potential in limiting gas exchanges? Does the microhabitat or soil water availability influence the pattern of the relationship between leaf water potential and gas exchange? The questions need to be well investigated.

Hunshandak Sandland is one of the four largest sands in China (the other sands are Ke’erqin, Maowusu and Hulun Beier). It is a typical semi-arid sandland with high heterogeneity (e.g. sand dune, lowland and wetland) and thus forms microhabitats with quite different soil water condition (Bai et al., 2000; Cui et al., 2001). Such spatial variation in soil moisture provides a broad range of habitats where distinct niches could co-exist (Sack and Grubb, 2002). The utilization of unevenly distributed soil water is likely to differ among grass species with different
mechanisms of drought tolerance. Therefore, the landscape heterogeneity in Hunshandak Sandland serves an ideal platform to study the responses of plant ecophysiology to water gradient under exact field conditions.

The purposes of this study were to conduct a basic research on the ecophysiological acclimations to heterogeneous soil moistures by some in situ sandy grasses, and to determine the environmental factors that control their growth and distribution at different spatial scales.

2. Materials and methods

2.1. Study site and species

The investigation was conducted at the experiment site (43°56′47″N, 116°08′15″E) of Sandy Ecosystem Research Station of Chinese Academy of Sciences in Hunshandak Sandland, located in the middle of Xilingel league of Inner Mongolia Autonomous Region of China. The prevailing climate here is of the temperate arid and semi-arid type. According to Zhenglan Banner Weather Station based in the centre of Hunshandak, the average annual temperature is about 1.7°C. The mean maximum in July and minimum in January values is 16.6 and −24.1°C, respectively. The annual total radiation time is 3000–3200 h. The above 10°C accumulated temperature is 2000–2600°C. The frostless period lasts approximately for 100 days. It receives an annual precipitation of about 250–350 mm, with uneven distribution throughout the year. The maximum value (30 mm month⁻¹) was observed from June to August and the minimum values (1 mm month⁻¹) from March to May. Additionally, the rainfall fluctuates among years greatly, from 150 mm in drought year to 400 mm in abundant precipitation year. The potential annual evaporation is 2000–2700 mm, six times higher than the total annual precipitation. The main habitats are shifting sand dune, fixed sand dune, lowland and wetland, recognized by their water-table (Table 1). The three typical kinds of landscapes (i.e. fixed sand dune, lowland and wetland) distribute within a small range (ca. 300 × 300 m², difference in elevation <10 m). So, the three microhabitats were so close to each other that they shared highly similar climatic conditions and the same soil type (chestnut soil). The soil information about microhabitats was according to Soil of Inner-Mongolia (Baoin et al., 1994). The name of species was according to Flora of Inner-Mongolia (Ma et al., 1993).

A criterion for the selection of species in the different microhabitats was by either high abundance or a major contribution of species that could stand for the biomass on any of the microhabitats. According to such criteria, 30 species (10 for each site) were selected (Table 1). The growth period extended from the beginning of May to the end of September. Fifteen days before our measurement, there was no rain recorded, so the plants there exhibited drought stress during the ecophysiological measurements.
Table 1
Site description for soil characters and studied species

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<thead>
<tr>
<th></th>
<th>Fixed sand dune</th>
<th>Lowland</th>
<th>Wetland</th>
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<tr>
<td>Water-table</td>
<td>&gt; 10 m</td>
<td>1–2 m</td>
<td>&lt;0.5 m</td>
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<tr>
<td>Soil pH</td>
<td>7.8</td>
<td>8.5</td>
<td>8.6</td>
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<tr>
<td>Soil organic (g kg⁻¹)</td>
<td>1.89</td>
<td>5.4</td>
<td>13.2</td>
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<td>Soil N (g kg⁻¹)</td>
<td>0.26</td>
<td>0.47</td>
<td>1.18</td>
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<td>Soil P (g kg⁻¹)</td>
<td>0.29</td>
<td>0.34</td>
<td>0.46</td>
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<td>Soil K (g kg⁻¹)</td>
<td>18</td>
<td>18.1</td>
<td>21.4</td>
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<td>Vegetation cover</td>
<td>30–40%</td>
<td>60–80%</td>
<td>100%</td>
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<td>Measured species</td>
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<td>1 Thermopsis lanceolata</td>
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<td>2 Calamagrostis epigejos</td>
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<td>3 Leymus chinensis</td>
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<td>4 Artemisia argyi</td>
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<td>5 Silene jenisseensis</td>
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<td>6 Thalictrum petaloideum</td>
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<td>7 Clematis macropetala</td>
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<td>8 Cynanchum thesioides</td>
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<td>9 Polygonum divaricatum</td>
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<td>10 Cnidium salinum</td>
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<td>11 Achnatherum purpurascens</td>
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<td>12 Artemisia annua</td>
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<td>13 Aster alpinus</td>
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<td>14 Leontopodium longifolium</td>
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<td>15 Cirsium esculentum</td>
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<td>16 Medicago falcata</td>
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<td>17 Hedysarum fruticosum</td>
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<td>18 Amaranthus retroflexus</td>
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<td>19 Ephedra equisetina</td>
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<td>20 Urtica cannabina</td>
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Number symbols for species were given ahead of species name. PF, PG, AF and AG represent perennial forb, perennial grass, annual forb and annual grass, respectively.
2.2. Ecophysiological measurements

Five individuals per species were measured using a LCA-4 Portable Photosynthetic System (ADC, Hoddesdon, England) to determine net photosynthetic rate \( (P_n) \), intercellular \( CO_2 \) concentration \( (C_i) \) and stomatal conductance \( (g_s) \). Measurements were conducted at about 10:00 am when photosynthetic photoflux density (PPFD) was above light saturated point \( (Jiang \text{ and } Zhu, 2001) \) on the clear days in July 2001. During operation, air was collected from 6 m above the soil surface and dried (by passing through “drier”) to 20% relative humidity before being pumped into the analyser. Flow rate of air through the leaf cuvette was 375 ml min\(^{-1}\). The central portions of most leaves were maintained approximately horizontally, so that the effect of leaf-angle on incident photon flux was minimized during the measurements. When taking the measurement, only the full-expanded functional leaves in upper shoots were selected. Gas exchange data were soon recorded when readings became stable, usually 30–90 s after leaf insertion into the cuvette. Leaf areas were determined using an Area Meter (AM100, Analytical Development Company Limited, Hoddesdon, England) to re-calculate the gas exchange values in case of measured leaf areas were smaller than the standard area provided by the machine (6 cm\(^2\)).

Meanwhile, Chlorophyll fluorescence was measured using a portable plant efficiency analyzer (PEA, Hansatech, King’s Lynn, UK). \( F_0 \) (minimal fluorescence), \( F_m \) (maximal fluorescence), \( F_v \) (variable fluorescence) and \( F_v/F_m \) (maximal photochemical efficiency of PS II) were measured shortly after keeping the leaves in dark for 30 min. A red irradiance of 3000 \( \mu \text{mol m}^{-2} \text{s}^{-1} \) was applied for measurements. The full-expanded leaves near those with photosynthesis measurement were selected for Chl fluorescence investigation.

Leaf water potential \( (\Psi_{leaf}) \) and soil water potential \( (\Psi_{soil}) \) were recorded with a WP4 Dewpoint Potential Meter (Decagon Devices, Inc., Pullman Washington, USA). Full-expanded leaves (near the top canopy) with their twigs were taken from plants and soil core was extracted from the plant-rooting zone, and were then kept in a sealed plastic bag and stored in an ice-box during transportation. Measurements were done immediately after being brought into laboratory. Five to eight maturing leaves were sampled for each determination. When measuring, small linear leaves or leaf sections were put into chamber for measure. Mature leaf tissue was used to minimize growth effects on leaf water potential. All the ecophysiological measurements were made for one leaf from each of the five individuals per species.

2.3. Statistical analysis

Analysis of variance of leaf traits was carried out on each measurement and the significance of plant mean square determined by testing against the error (species \( \times \) replicate) mean square. The least significant differences (LSD) between the means were estimated at 95% confidence level. The variation (ANOVA) among three microhabitats and the correlation of parameters were analysed for using SPSS statistical software (SPSS 10.0 for Windows, Chicago, USA).
3. Results

Soil water potential at the upper 20 and 20–40 cm soil depth among the three microhabitats were significantly different \((p<0.05)\) (Fig. 1). In the upper layer (0–20 cm), \(\psi_{\text{soil}}\) was in a series of wetland \((-0.05 \, \text{MPa}) > \) lowland \((-0.92 \, \text{MPa}) > \) fixed sand dunes \((-2.56 \, \text{MPa})\). In the lower layer (60–80 cm), however, soil water potential did not display any difference among three microhabitats. Of the three habitats, wetland had a constant \(\psi_{\text{soil}}\) from the top to 80 cm depth, with an average value of \(-0.13 \, \text{MPa}\), whereas in fixed sand dune and lowland, \(\psi_{\text{soil}}\) kept constant from 60 cm downward, which was significantly lower than that of 0–40 cm soil layer.

On an average, \(\psi_{\text{leaf}}\) was 0.85 MPa lower than \(\psi_{\text{soil}}\) at the depth of 0–40 cm and was significantly different among three microhabitats in the order of wetland \((-1.08 \, \text{MPa}) > \) lowland \((-1.43 \, \text{MPa}) > \) fixed sand dune \((-2.07 \, \text{MPa})\) \((p<0.05)\) (Table 2). Similar trends were observed in \(P_n\), \(g_s\) and \(C_i\) among three microhabitats, with the mean values in wetland being 2.4, 2.8 and 2.5 times that in fixed sand dune, respectively \((p<0.01)\) (Table 2). The average \(F_v/F_m\) was 0.69, 0.76 and 0.81 in fixed sand dune, lowland and wetland, respectively (Table 2). Differences in root length among the three microhabitats, however, were just contrary to those physiological characteristics. It was the lowest in wetland with a mean value of 17 cm and was similar in fixed sand dune and lowland (41 cm) (Table 2).

Positive correlations were observed between \(P_n\), \(g_s\) and \(\psi_{\text{leaf}}\) in fixed sand dune and lowland (Fig. 2A and B). The intensity was dependent on the sites, as reflected by the slope variation. The slope was larger in lowland than in fixed sand dune, suggesting that \(P_n\) and \(g_s\) changed greater in lowland per unit change of

![Fig. 1. Soil water potential in 0.2, 0.4, 0.6 and 0.8 m layers below land surface among three microhabitats.](image-url)
The maximum quantum efficiency of photosystem II \( (F_v/F_m) \) was also regulated by the variation of \( \Psi_{\text{leaf}} \) in the range of \(-3 \) to \(-1 \) MPa (Fig. 2C). It was obviously inhibited (with the value less than 0.8) when \( \Psi_{\text{leaf}} \) was \(<-1 \) MPa in fixed sand dune and lowland, indicating that reductions in photochemical capacity (photoinhibition) were responsible for the depression of net photosynthesis in fixed sand dune and lowland. There were no obvious relations between \( \Psi_{\text{leaf}} \) and gas exchange traits in wetland (Fig. 2), which means that the leaf water content did not limit gas exchange there.

Stomatal conductance was found to positively correlate with \( C_i \) in three microhabitats (Fig. 3A). The best fit of net photosynthesis versus stomatal conductance (Fig. 3B) always displayed a positive relationship between the two variables in all the three habitats, indicating strong dependence of the assimilation rate on stomatal aperture. However, the slope was different among three microhabitats with the order of fixed sand dune > lowland > wetland, which means that \( P_n \) changed more greatly per unit \( g_s \) in fixed sand dune and lowland than in wetland.

Both in the fixed sand dune and lowland, plants with a deeper root system had higher \( \Psi_{\text{leaf}} \). Such a pattern can be reflected by the positively linear correlations between leaf water potential and root depth (Fig. 4). The slope and coefficient \((r)\) in fixed sand dune and lowland were pretty similar. However, there was no obvious relation between \( \Psi_{\text{leaf}} \) and root depth in wetland \((p>0.05)\) (Fig. 4).

### 4. Discussion

According to Denmead and Shaw (1962) and Garnier and Berger (1985), a severe soil drought might reach when soil water potential approached \(-0.44 \) MPa at the soil layer of \(0–30 \) cm. We can therefore infer from our study that fixed sand dune and lowland were dry enough to inhibit the plants’ physiological process, because \( \Psi_{\text{soil}} \) at \(0–20 \) cm soil depth was less than \(-1.0 \) MPa (Fig. 1). While in wetland where upper
soil layer (0–20 cm) \( \Psi_{\text{soil}} \) was above \(-0.1 \text{ MPa} \), water availability was enough for plants activity.

Generally, stomatal conductance and net photosynthesis in many species decreased when exposed to low soil moisture conditions (Cornic, 2000). In our study, plants living in fixed sand dune and lowland decreased their stomatal conductance by 150% and photosynthetic rate by 135%, compared to those in wetland (Table 2). This suggests that water limitation to photosynthesis was severe in fixed sand dune and lowland. Soil water availability was apparently the main driving force in controlling gas exchange in Hunshandak Sandland.

Stomatal conductance decreased as leaf water potential declined during drought, which was previously observed in individual plant experiment (Prior et al., 1997; Oren et al., 1999). Our results also suggest that stomatal conductance depended on leaf water potential, especially in habitats of fixed sand dune and lowland (Fig. 2). The lower \( g_s \) there indicated that species in both microhabitats might have the drought escape strategy through which plants could successfully acclimate to the drought condition in Hunshandak Sandland.

Photosynthetic rate and steady-state chlorophyll fluorescence were also closely correlated with leaf water potential in our study (Fig. 2), which was previously reported (Larcher et al., 1981; Abril and Hanano, 1998). This might be owing to the strong dependence of these characteristics on stomatal conductance, which was shown by a more close correlation of \( P_n \) with \( g_s \) than with \( \Psi_{\text{leaf}} \) (Figs. 2A and 3B). The decrease in \( P_n \) as \( \Psi_{\text{leaf}} \) becomes more negative could be explained by a stomatal dependence (lower \( C_i \)) (Figs. 2A and 3A) and by a nonstomatal limitation (lower \( F_v/F_m \), Fig. 2C). The mechanism responsible for such a coordinated regulation of stomatal conductance and photosynthetic apparatus activity was still under discussion (Lawlor and Cornic, 2002; Medrano et al., 2002). It is hard to differentiate whether stomatal or non-stomatal limitation plays a more important role because the same metabolic factor may act on both stomata and the photosynthetic apparatus.

Though gas exchange traits were closely related to leaf water potential, the slope and correlation coefficient (\( r \)) of the relationship between \( \Psi_{\text{leaf}} \) vs. \( g_s, P_n, F_v/F_m \) was site-related. In wetland, no significant linear relationship between \( \Psi_{\text{leaf}} \) and other physiological parameters was noted, if any, the slope was very low. In contrast, the slope and \( r \) were higher in fixed sand dune and lowland where soil water were deficit, indicating that \( g_s, P_n, \) and \( F_v/F_m \) were much more dependent on and sensitive to \( \Psi_{\text{leaf}} \).

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**Fig. 2.** Relationships between leaf water potential vs. photosynthetic rate (A), stomatal conductance (B) and photochemical efficiency of photosystem II (C) in fixed sand dune, lowland and wetland (Means±S.E.). The number symbols were listed in Table 1. Correlation and \( p \) values were as follows: (A) fixed sand dune \( P_n = 6.61\Psi_{\text{leaf}} + 22.23, r^2 = 0.716, p<0.01 \); lowland \( P_n = 9.69\Psi_{\text{leaf}} + 28.33, r^2 = 0.810, p<0.001 \); (B) fixed sand dune \( g_s = 0.072\Psi_{\text{leaf}} + 0.29, r^2 = 0.628, p<0.01 \); lowland \( g_s = 0.177\Psi_{\text{leaf}} + 0.486, r^2 = 0.747, p<0.001 \); (C) fixed sand dune \( F_v/F_m = 0.074\Psi_{\text{leaf}} + 0.844, r^2 = 0.904, p<0.001 \); lowland \( F_v/F_m = 0.062\Psi_{\text{leaf}} + 0.852, r^2 = 0.612, p<0.01 \).
Root plasticity is an ability to exploit available natural resources by increasing root length and/or physiological activity in enriched micro sites or horizons of the soil profile (Eissenstat and Caldwell, 1988; Pregitzer et al., 1993; Huang, 1999). Drought resistant plants are generally characterized as having extensive, well-branched, deep rooted systems (Kramer, 1983). Our results agree with conventional

![Graph A](image)

![Graph B](image)

Fig. 3. Relationships between intercellular CO₂ concentrations (A), photosynthetic rate (B) vs. stomatal conductance in fixed sand dune, lowland and wetland (Means ± S.E.). The number symbols were listed in Table 1. Correlation and p values were as follows: (A) fixed sand dune $C_i = 978g_s - 16.909$, $r^2 = 0.6199$, $p < 0.05$; lowland $C_i = 563.47g_s + 57.994$, $r^2 = 0.5371$, $p < 0.05$; wetland $C_i = 666.27g_s - 25.932$, $r^2 = 0.4717$, $p < 0.05$; (B) fixed sand dune $P_n = 79.453g_s - 2.685$, $r^2 = 0.856$, $p < 0.001$; lowland $P_n = 47.037g_s + 3.482$, $r^2 = 0.798$, $p < 0.001$; wetland $P_n = 36.558g_s + 7.232$, $r^2 = 0.524$, $p < 0.01$.

Root plasticity is an ability to exploit available natural resources by increasing root length and/or physiological activity in enriched micro sites or horizons of the soil profile (Eissenstat and Caldwell, 1988; Pregitzer et al., 1993; Huang, 1999). Drought resistant plants are generally characterized as having extensive, well-branched, deep rooted systems (Kramer, 1983). Our results agree with conventional
generalization on the relationship between root length and soil water content. Along our water gradient among microhabitats, where the soil water potential was higher (wetland) the root depth there was shallow (Fig. 4). This might because the shallow depth of root could meet their water absorption. Whereas in lowland and fixed sand dune that had lower soil water potential, plants had longer root in order to reach the permanently wet layer to absorb deeper water (Batanouny, 2001). In addition, low C leaf in the fixed sand dune and lowland will support the maintenance of a potential gradient for water uptake at low soil water potential. However, within the same microhabitat, the relationships between root depth and leaf water potential were contrary to that across-microhabitats. Within the fixed sand dune or lowland, plants that have a deeper root system could maintain higher leaf water potential and then keep the normal photosynthesis (Fig. 4). The positive correlations between root depth and leaf water potential in fixed sand dune and lowland (p<0.01) indicated that plants with deeper root always had better leaf water condition than the plants with shallow roots in the same habitats where soil water was stressed.

5. Conclusions

Soil water availabilities among three microhabitats in Hunshandak Sandland have great impacts on the plants ecophysiological characters. Our results agree with the previous report about the correlation between leaf water potential and gas exchange characters. This suggests that the general correlations of gas exchange to declining water potential were relatively similar in magnitude, and water deficit was the main
factor limiting the plant growth in fixed sand dune and lowland in Hunshandak Sandland. In addition, soil water availability regulates the sensitivity of gas exchange to leaf water potential. The critical value of this function was about $-1.0 \text{ MPa}$, above which, the leaf water potential was not the limiting factor for gas exchange. The main control of photosynthesis apparently is through stomata limitation trigged by variation in water availability, and the photoinhibition of PSII. However, plant could feedback to the arid environment by acclimation response such as closing their stomata and elongating their root length, thus the root depth niche was obviously shaped among three microsites.

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