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ORIGINAL ARTICLE

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Leaf osmotic potentials of 104 plant species in relation to habitats and plant functional types in Hunshandak Sandland, Inner Mongolia, China

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Abstract Leaf osmotic potentials (ψ_s) of 104 plant species from different habitats, i.e., fixed sand dunes, lowland and wetlands in Hunshandak Sandland, Inner Mongolia, China, were investigated. The values of ψ_s were strongly species-specific, and varied from −6.54 MPa (*Caragana microphylla*), to −0.44 MPa (*Digitaria ischaemum*); 75% of plants investigated had ψ_s from −1.01 to −3.0 MPa. Shrubs were found to have the lowest ψ_s, with an average value of −3.19 MPa, while grasses showed the highest ψ_s. The order of plant ψ_s is shrubs<trees<grasses. The result may relate to anatomical features of shrubs. C_4 photosynthetic pathway plants showed lower ψ_s values. The ψ_s values of 104 species were negatively correlated with their rooting depths (r^2=0.42; P <0.001). High hydraulic pressure resulting from the deep roots may well explain this trend. The value of ψ_s increased as the environment became wetter, ranging from −0.79 MPa in wetlands to −2.09 MPa in fixed sand dunes. Although soil salt content was higher in wetlands, we did not find any effect on ψ_s.

Keywords Osmotic potential · Habitats · Plant functional types · Root depth · Hunshandak Sandland

Introduction

Perennial plants in arid areas have to tolerate many environmental stresses such as extreme drought (Batanouny 2001; Wicken 1998), harsh irradiation (Peltier et al. 1997; Jiang and Zhu 2001; Aranda et al. 2001), high temperature (Sánchez-Blanco et al. 1998), and even severe cold in winter (Weiser 1970; Hurme et al. 1997; Repo et al. 2000; Kontunen-Soppela 2001). Different plants have developed different mechanisms to cope with threatening habitats; for example, annual plants can utilize much shorter growth periods to complete their life cycles than perennials, which enables them to escape more stresses (Gutterman 1993).

Osmotic potential (ψ_s) represents the potential ability of plants to absorb water from environments, which is an important indicator of drought tolerance. The value of ψ_s can be regulated by many factors, which characterize the plant's attempt to minimize difference in water potential between the plant body and its environment (Batanouny 2001). To cope with the prolonged annual dry period, which occurs in most arid areas, different plant functional types (PFTs) have evolved different survival mechanisms, which might be reflected by the leaf ψ_s (Walter 1963; Evenavi et al. 1971). Plants exhibiting osmotic regulation can normally lower their own internal water potentials by the synthesis or accumulation of osmotically active substances, e.g., carbohydrates (Oleksyn et al. 2000; Lawlor and Cornic 2002), lipid composition (Sutinen 2000), and protein accumulation (Taulavuori et al. 1999; Kontunen-Soppela et al. 2000).

Although the simple osmotic potential is regarded as a good criterion of the ability of desert plants to extract water (Fernández and Reynolds 2000), it is quite difficult to quickly measure many samples in a natural habitat or for some particular species such as grasses or mosses. Before the invention of the Dewpoint PotentiaMeter, the comparison of a large number of species in a short time was almost impossible. It has been suggested that there is a wide range of ψ_s values in the leaves of desert plants (Abdel and Batannouny 1964), but the real situation of many species in different habitats and PFTs is poorly understood.

Therefore, in this study, with help of a Dewpoint PotentiaMeter (WP4, Decagon Devices, Pullman, Washington, USA), we have studied osmotic potentials in more than 100 species in Hunshandak Sandland, one of the five large sand areas in China. The species we measured belong to different PFTs, which colonize different

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habitats. By doing so, we tried to discover (1) whether or not perennial plants have lower ψ_s than annuals, (2) whether or not deep rooted species have lower ψ_s in the same habitat with their complex soil-plant-atmosphere continuums, and (3) which are the habitats in which plants have characteristic ψ_s and the possible reasons for such discrimination.

Materials and methods

Study area

The investigation was conducted at Hunshandak Sandland Ecosystem Research Station (43°56′47″N, 116°08′15″E) of the Chinese Academy of Sciences, based in Xilingel League of Inner Mongolia Autonomous Region, China (Fig. 1). The prevailing climate is the temperate arid and semi-arid type, with temperatures of average annual, July and January being respectively 1.7°C, 16.6°C and −24.1°C. The area receives an annual precipitation about 350 mm, with uneven distribution throughout the year. Rainfall fluctuates in different years, from 150 mm in a drought year to 450 mm in the wettest year. The year of 2001 was a drought year, with a total precipitation 201 mm. However, the annual potential transpiration is from 2,000 to 2,700 mm and is 7 times the total precipitation (Zhu 1980). The main habitats are shifting sand dune, fixed sand dune, lowland and wetland. Here, the main soil types include brown calcareous soil in lowland, deep sandy soil in shifting sand dune and fixed sand dune, and dark meadow soil in wetland. The detailed background of the four habitats is given in Table 1.

The woody components of the vegetation are dominated by *Ulmus pumila* var. *sabulosa* (native species), *Salix gordejevii* (native species), and *Salix matsudana* (exotic species). Grass components are primarily *Corispermum heptapotamicum*, *Salsola collina*, and *Leymus chinensis* in fixed sand dune. In lowland and wetland, mesophyte plants such as *Plantago cornuti*, *Inula britanica*, and *Stemmacantha uniflora* are predominant. All the plants were measured in terms of their leaf osmotic potentials, root depths, growth forms and other characteristics that are listed in Table 2.

Sampling

Plants

The experiment was conducted from 8 to 14 July 2001. There was no rain for 10 days before measurement and it did not rain during the experiment. All the plant samples were collected between 0900 and 1000 hours on each clear day. Five to eight fully expended leaves from the top of shrubs and grasses, and the lower canopy of trees, with their twigs, sheaths or petioles, were sampled. Therefore, none of the leaves were injured and were kept as whole leaves. Samples were kept in a sealed plastic bag and stored in an ice-box after being collected, then were transported to the laboratory 1,500 m away from the sampling sites, and measured as soon as possible. Samples awaiting measurement were kept in a refrigerator with temperature controlled at about 3°C. Usually the longest waiting time was 2 h, which satisfied the 3-h recommended maximum storage period. Pre-testing also showed that there was little difference between the fresh samples and 3-h samples. Three replications were made for each species. The root depths in this study were referenced from Chen (1986) or measured directly by us.

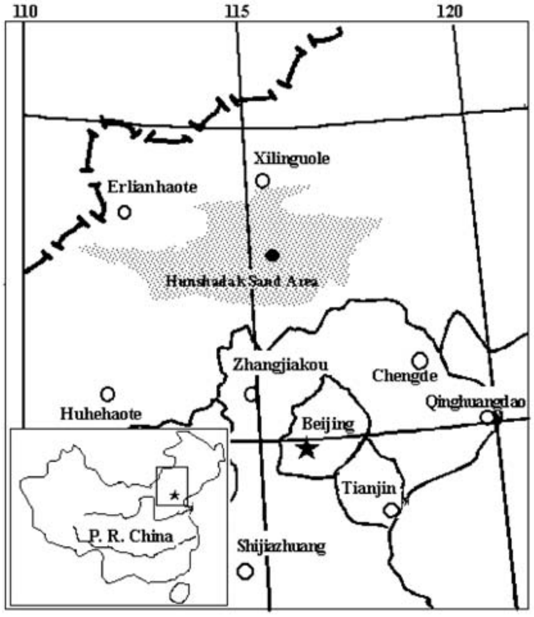

Fig. 1 Location of the experimental site in Hunshandak Sandland

Soils

Soil sample collections were performed just after all the plant samples were collected at each habitat. Samples were taken with a soil drill from 0–20 cm, 20–40 cm, 40–60 cm and 60–100 cm beneath the surface, and were then stored in a soil box sealed by adhesive plaster, and taken to the laboratory for measurements. Soil moisture contents at the four different habitats were determined by a Delta-T Device Moisture Meter (Profile Probe, Type PR1/6). The test depths comprised 20 cm, 40 cm, 60 cm, and 100 cm (not shown in the present paper). In addition to the osmotic potential measurements, monthly rainfall values and temperature values in 2001 were taken from the closest meteorological station located 2 km from the site.

Osmotic potential measurement

Osmotic potential measurements were taken immediately after the leaf samples were brought into laboratory, with a WP4 Dewpoint PotentiaMeter (Decagon Devices, Pullman Washington, USA). It

Table 1 Soil description of experimental sites of shifting sand dunes, fixed sand dunes, lowland and wetland in Hunshandak Sandland

Soil characteristics	Habitats			
	Shifting sand dunes	Fixed sand dunes	Lowland	Wetland
Organism (g/kg)	0.3	1.89	5.4	13.2
Total N (g/kg)	0.03	0.26	0.47	1.18
Total P (g/kg)	0.09	0.29	0.34	0.46
Total K (g/kg)	15.0	18.0	18.1	21.4
Total salt content (g/kg)	0.23	0.44	0.78	0.86
pH value	6.6	7.8	8.5	8.6

Table 2 Leaf osmotic potentials (ψ_s) and roots depth of different plant species with different growth forms (*G* grasses, *S* shrubs, *T* trees), different photosynthetic pathway (*C_3*, *C_4* and *CAM*) on different habitats (*F* fixed sand dunes, *L* lowland, *W* wetland) in the Hunshandak Sandland in summer 2001. The means of three measurements are reported ±SD

Family	Species	Growth form	Photosynthetic way	Habitats	Roots depth (cm)	ψ_s (MPa)
Juncaceae	*Juncus bufonius* L.	G	C_3	L	5	–0.73±0.10
Gramineae	*Digitaria ischaemum* Schreb.	G	C_3	W	8	–0.44±0.21
Ranunculaceae	*Anemone silvestris* L.	G	C_3	L	8	–0.88±0.12
Crassulaceae	*Orostachys malacophyllus* (Pall.) Fisch.	G	CAM	L	9	–0.79±0.28
Plantaginaceae	*Plantago cornuti* Gouan	G	C_3	W	9	–0.66±0.27
Gramineae	*Eragrostis poaeoides* L.	G	C_4	L	9	–1.57±0.14
Liliaceae	*Allium mongolicum* Regel	G	C_3	L	10	–0.73±0.04
Gentianaceae	*Nymphoides peltata* S.G.Gmel.	G	C_3	W	10	–0.87±0.17
Scrophulariaceae	*Linaria vulgaaris* Mill.	G	C_3	L	10	–1.20±0.07
Gramineae	*Leymus chinensis* (Trin.) Tzvel.	G	C_4	F	10	–2.24±0.14
Chenopodiaceae	*Suaeda glauca* (Bunge.) Bunge	G	C_4	L	10	–2.43±0.26
Compositae	*Inula britanica* L.	G	C_3	F	12	–1.32±0.13
Gramineae	*Echinochloa crusgalli* (L.) Beauv.	G	C_4	W	13	–1.38±0.20
Campanulaceae	*Campanula rotumdifolia* L.	G	C_3	L	14	–1.24±0.11
Compositae	*Taraxacum dissectum* (Ledeb.) Ross.	G	C_3	L	15	–0.99±0.32
Ranunculaceae	*Ranunculus intramongolicus* Y.Z.Zhao	G	C_3	L	15	–1.34±0.58
Gramineae	*Calamagrostis epigejos* (L.) Beauv.	G	C_3	F	15	–2.24±0.08
Gramineae	*Setaria viridis* (L.) Beauv.	G	C_4	F	15	–2.34±0.20
Polygonacaceae	*Polygonum hydripiper* L.	G	C_3	F	16	–0.79±0.29
Dipsacaceae	*Scabiosa comosa* Fisch.ex Roem	G	C_3	F	17	–1.41±0.21
Solanaceae	*Solanum tuberosum* L.	G	C_3	F	18	–0.96±0.25
Compositae	*Leontopodium leontopodioides* Willd.	G	C_3	F	18	–1.08±0.26
Compositae	*Echinops gmelini* Turcz.	G	C_3	F	18	–1.76±0.57
Chenopodiaceae	*Corispermum heptapotamicum* Iljin	G	C_3	F	20	–0.98±0.25
Liliaceae	*Allium ramosum* L.	G	C_3	L	20	–1.08±0.45
Cyperaceae	*Scirpus yagara* Ohwi	G	C_3	W	20	–1.09±0.17
Compositae	*Sonchus oleraceus* L.	G	C_3	L	20	–1.16±0.04
Cyperaceae	*Carex duriuscula* C.A.Mey	G	C_3	W	20	–1.39±0.05
Asclepiadaceae	*Cynanchum thesioides* (Freyn.) Schum	G	C_3	F	20	–1.65±0.10
Chenopodiaceae	*Chenopodium glaucum* L.	G	C_4	F	20	–2.06±0.32
Rosaceae	*Potentilla Strigoas* Pall.	G	C_3	F	20	–2.30±0.14
Polygonacaceae	*Polygonum manshuricola* Kitag.	G	C_3	F	23	–0.86±0.09
Ranunculaceae	*Halerpests ruthenica* (Jacq.) Ovcz.	G	C_3	L	24	–1.54±0.03
Rosaceae	*Potentilla sericea* L.	G	C_3	F	24	–1.68±0.14
Gramineae	*Agropyron cristatum* (L.) Gaertn.	G	C_4	F	25	–2.02±0.14
Rosaceae	*Potentilla anserine* L.	G	C_3	F	25	–2.27±0.35
Chenopodiaceae	*Salsola collina* Pll.	G	C_4	F	25	–2.36±0.65
Compositae	*Xanthium sibiricum* Patrin	G	C_3	L	26	–0.97±0.10
Moraceae	*Cannabis sativa* L.	G	C_3	F	26	–1.70±0.29
Leguminosae	*Vicia amoena* Fisch.	G	C_3	F	28	–1.21±0.35
Compositae	*Artemisia annua* L.	G	C_4	F	28	–1.82±0.19
Plantaginaceae	*Plantago major* L.	G	C_3	F	29	–1.10±0.05
Umbolliferae	*Ferula bungeana* Kitag.	G	C_3	F	30	–0.84±0.09
Labiatae	*Thymus serpyllum* L.var.*mongolicus* Roem	G	C_3	F	30	–0.87±0.27
Compositae	*Aster tataricus* L.	G	C_3	F	30	–1.06±0.37
Compositae	*Artemisia demissa* L.	G	C_3	F	30	–1.22±0.23
Rosaceae	*Sanguisorba officinalis* L.	G	C_3	L	30	–1.36±0.10
Loganiaceae	*Buddleja alternifolia* Maxim.	G	C_3	L	30	–1.77±0.66
Compositae	*Heteropapus hispidus* Willd.	G	C_3	F	30	–1.81±0.78
Chenopodiaceae	*Bassia dasyphylla* (Fisch.) O. Kuntze	G	C_3	F	30	–2.48±0.12
Compositae	*Saussurea japonica* (Thunb.) DC.	G	C_3	F	32	–0.80±0.09
Compositae	*Stemmacantha uniflora* (L.) Dittrich	G	C_3	L	34	–0.56±0.05
Leguminosae	*Oxytropis glabra* (Lam.)DC.	G	C_3	L	34	–1.84±0.18
Compositae	*Cirsium japonicum* Fisch.ex DC.	G	C_3	L	35	–0.98±0.12
Crassulaceae	*Rhodiola dumulosa* S.H.Fu.	G	C_3	L	35	–2.38±0.18
Compositae	*Cirsium esculentum* (Sievers)C.A.Mey	G	C_3	L	36	–1.33±0.11
Umbolliferae	*Cnidium monnieri* (L.) Cuss.	G	C_4	F	38	–1.89±0.05
Compositae	*Saussurea runcinata* DC.	G	C_3	L	39	–0.76±0.12
Equisetaceae	*Equisetum ramosissimum* Desf.Fl.	G	C_3	F	39	–1.35±0.30
Rosaceae	*Potentilla flagellaris* L.	G	C_3	L	39	–2.63±0.37
Compositae	*Taraxacum mongolicum* Hand.	G	C_3	F	40	–1.12±0.09
Amaranthaceae	*Amaranthus retroflexus* L.	G	C_3	F	40	–1.47±0.18
Compositae	*Artemisia ordosica* Krasch.	S	C_4	F	40	–1.67±0.14
Gramineae	*Leymus secalinus* (Georgi) Tzvel.	G	C_4	F	40	–3.05±0.18

Table 2 (continued)

Family	Species	Growth form	Photosynthetic way	Habitats	Roots depth (cm)	ψ_s (MPa)
Leguminosae	*Gueldenstaedtia multiflora* Bunge.	G	C_3	F	41	–2.01±0.07
Polygonacaceae	*Polygonum divaricatum* L.	G	C_3	F	42	–1.47±0.07
Leguminosae	*Melilotus suaveolens* Ledeb.	G	C_3	L	45	–1.48±0.19
Caryophyllaceae	*Dianthus chinensis* L.	G	C_4	F	45	–2.75±0.15
Chenopodiaceae	*Chenopodium aristatum* L.	G	C_4	F	45	–3.04±0.14
Urticaceae	*Urticaceae cannabina* L.	G	C_3	F	46	–1.92±0.47
Polygonacaceae	*Polygonum sibiricum* Laxm.	G	C_3	F	50	–1.52±0.08
Gramineae	*Phragmites australis* (Cav.) Trin.	G	C_3	L	50	–1.56±0.24
Ranunculaceae	*Thalictrum squarrosum* Steph.ex Willd	G	C_3	F	50	–1.67±0.73
Caryophyllaceae	*Silene repens* var.*angustifolia* Turcz.	G	C_4	F	50	–2.29±0.36
Leguminosae	*Thermopsis lanceolata* R.Br.	G	C_4	F	50	–2.58±1.04
Umbolliferae	*Bupleurum sibiricum* Vest.	G	C_3	F	55	–2.30±0.73
Liliaceae	*Asparagus schobcrioides* Kunth	G	C_3	F	56	–2.98±0.08
Salicaceae	*Salix matsudana* Koidz	G	C_3	L	60	–1.61±0.17
Gramineae	*Cleistogenes squarrosa* (Trin.) Keng	G	C_3	F	60	–1.96±0.22
Leguminosae	*Sphaerophysa salsula* (Pall.) DC.Prodr.	G	C_3	F	60	–2.08±0.43
Saifragaceae	*Ribes pulchellum* Turez.	S	C_3	F	60	–2.16±0.62
Compositae	*Artemisia argyi* Lévl. et Van.	G	C_3	F	60	–2.52±0.27
Cruciferae	*Thellungiella salsuginea* (Pall.) Schulz	G	C_3	F	64	–2.08±0.33
Leguminosae	*Hedysarum scoparium* Fisch. et Mey.	S	C_3	F	70	–1.76±0.10
Leguminosae	*Medicago falcate* L.	G	C_3	F	70	–1.97±0.28
Gramineae	*Bromus inermis* Leyss.	G	C_3	F	80	–1.76±0.21
Iridaceae	*Iris lactea* Pall.var.*chinensis* Fisch.	G	C_3	L	80	–2.16±0.07
Chenopodiaceae	*Agriophyllum pungens* (Vahl) Link	G	C_3	F	90	–1.40±0.08
Salicaceae	*Salix gordejevii* L.	S	C_3	F	90	–2.62±0.15
Ranunculaceae	*Clematis aethusifolia* Turcz.	G	C_4	F	90	–3.94±0.42
Solanaceae	*Lycium chinense* Mill.	S	C_3	F	96	–1.98±0.15
Rosaceae	*Malus baccata* (L.) Borkh.	T	C_3	F	100	–2.99±0.09
Rosaceae	*Spiraea trilobata* L.	S	C_3	F	100	–4.83±0.71
Gramineae	*Psammochla villosa* (Trin.) Bor	G	C_3	F	100	–2.12±0.17
Caprifoliaceae	*Lonicera chrysantha* Turcz.	S	C_4	F	100	–2.66±0.17
Leguminosae	*Amorpha frnticosa* L.	T	C_3	F	100	–1.96±0.20
Compositae	*Artemisia frigida* Willd.	G	C_4	F	100	–3.34±0.26
Ranunculaceae	*Thalictrum petaloideum* L.	G	C_3	F	100	–3.29±0.28
Leguminosae	*Astragalus efoliolatus* Pall.	G	C_3	F	100	–1.55±0.53
Salicaceae	*Salix microstachya.*	S	C_3	F	120	–2.6±0.15
Betulaceae	*Betula fruticosa* Pall.	T	C_3	F	120	–1.51±0.17
Gramineae	*Achnatherum splendens* (Trin.) Nevski.	G	C_3	L	150	–2.33±0.03
Ulmaceae	*Ulmus pumila* L. var. *sabulosa* Zhao.	T	C_3	F	200	–2.28±0.38
Leguminosae	*Caragana microphylla* Lam.	S	C_3	F	250	–6.54±0.29

measures osmotic potential by equilibrating the temperature of the liquid phase water of plant tissues, i.e. discs cut from the leaf samples, with the vapor phase water in the headspace of a closed chamber, then measuring the vapor pressure of that headspace. The dew point sensor measures the dew point temperature of the air, and the infrared thermometer measures the sample temperatures. The sample osmotic potential could be calculated by a formula automatically on the basis of the sample's temperature and the vapor pressure of that headspace. It measures the sum of the osmotic and matric potentials in a sample. Osmotic potential depends on the concentration of dissolved substance in the water, while matric potential depends on the absorptive forces binding water to a matric. Therefore the plants' tissues, such as leaves, roots, branches, osmotic potential, can be determined during measurement. Soil has a mainly matric component. When measurements were changed from plant materials to soils, the calibration of WP4 should be carried out with the standard KCI solution (0.5 mol l^{-1}).

Data analysis

All the original data of leaf osmotic potentials of different species and soil matric potentials in different habitats were entered into SPSS for the preliminary statistic. The correlation between osmotic potentials and rooting depth was calculated using the non-parametric Kendall's correlation test. Patterns were performed using the SIGMAPLOT, and program and tabulations were produced using EXCELL.

Results

Changes of osmotic potentials among species

The results showed (Table 2) that the 104 species measured had quite different osmotic potentials values, ranging from −0.44 MPa in *Digitaria ischaemum* to −6.54 MPa in *Caragana microphylla*. *Spiraea trilobata*, *Clematis aethusifoli* a and *Artemisia frigid* had relative lower values of osmotic potential, with −4.83 MPa, –3.94 MPa and −3.34 MPa respectively. However, 75% of species had ψ_s from −1.01 MPa to −3.0 MPa. Some species (18%) showed ψ_s higher than −1.0 MPa, with only 7% of the species in Hunshandak possessing ψ_s lower than −3.0 MPa.

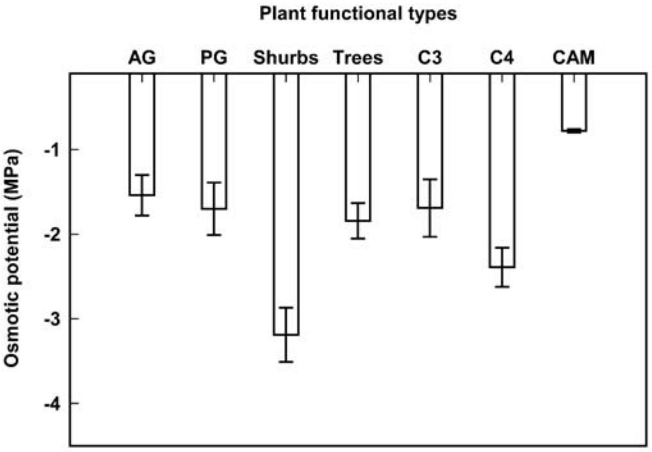

Fig. 2 Osmotic potentials of different plant functional types (PFTs) in Hunshandak (*AG* annual grasses, *PG* perennial grasses). The mean values of all plants with the same PFT are presented

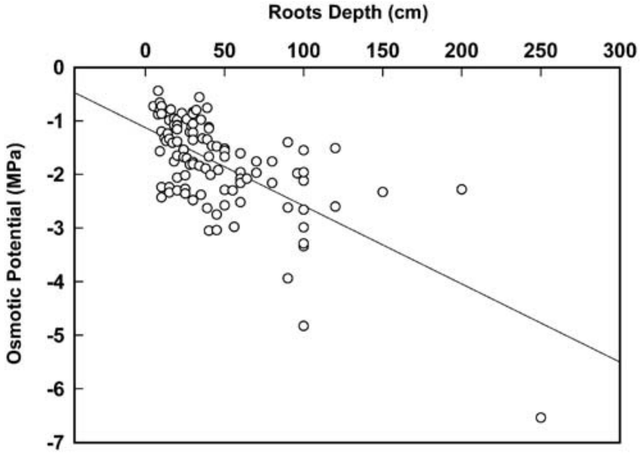

Fig. 3 Regression relationship between rooting depth and osmotic potential of all tested plants in three different habitats in Hunshandak Sandland. The relationship is correlate significant at P <0.001 level and equation is expressed as Y=−0.0146 X−1.1289 (r^2=0.42, n=104). The osmotic potential values were obtained through three replications of each plant

Variations in different plant functional types

Among trees, shrubs and grasses, shrubs were found to have the lowest osmotic potential, with an average value being −3.19 MPa, while grasses showed the highest ψ_s. In terms of ψ_s the order is as follows: shrubs<trees<grasses (Fig. 2). Plants with different photosynthetic pathways showed different values of ψ_s. The lowest and the highest ψ_s appeared in C_4 plants and CAM plants (Fig. 2). Deep rooted plants had relatively low leaf osmotic potentials. Further, we have observed that leaf ψ_s was significantly negatively correlated to rooting depth in all habitats (r^2=0.42, P <0.001) (Fig. 3).

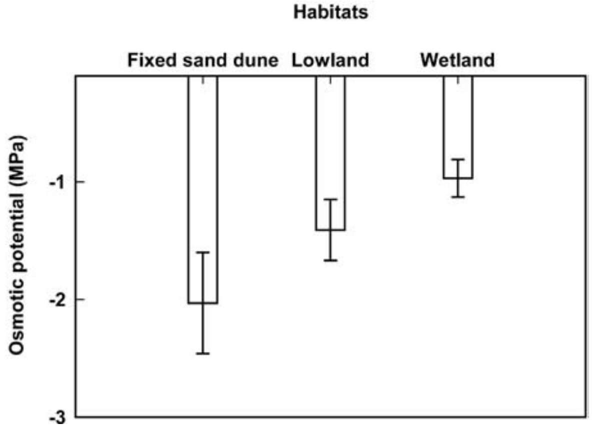

Fig. 4 The average leaf osmotic potential of all species in three habitats in the Hunshandak Sandland. The mean values of all plants in the same habitats are presented

Leaf osmotic potentials in different habitats

Leaf osmotic potentials increased along with the elevation of soil salt content from fixed sand dune, to lowland to wetland. Plants living in the wetland showed the highest ψ_s, while those in the fixed sand dune had the lowest ones. There was a great fluctuation in the ψ_s values of species distributed in different habitats, with the average value changing from −0.85 MPa in wetland, to −2.43 MPa in fixed sand dune (Fig. 4).

Discussion

Although leaf osmotic potentials could be affected by many eco-physiological features of plants, e.g., leaf longevity (Kontunen-Soppela and Laine 2001), and leaf water content (Esch and Mengel 1998), it is an innate physiological characteristic of plants and shows the ability of plants' tissues to absorb water moisture from soil. Furthermore, environmental factors such as precipitation (Matos et al. 1997; Terwilliger and Zeroni 1994), temperature (Laroche et al. 2001), light intensity (Marcelo et al. 2000) and soil salt content (Sánchez-Blanco et al. 1998; Zimmermann et al. 2002), can impact leaf ψ_s, so the value of ψ_s reflects the capability of plants to resist unfavorable environmental conditions.

In the present study, we have found that perennial shrubs showed the lowest ψ_s, followed by trees (Fig. 2). The result may indicate that perennial woody plants possess lower ψ_s than annual plants through which strong resistance to drought stress could be developed (Sarvas 1974; Ismael et al. 2000; Andrea and Sebastiano 2000; García-Plazaola and Becerril 2000). This may also be due to xeric characteristics such as small leaf area (Li 1996), few stomata (Meinzer 2002), thick leaves (Liu 1986), high osmoprotectant (Hare et al. 1998) and extensive root systems (Batanouny 2001). For instance, the woody species *Caragana microphylla* with small leaf area in the present study showed extensive roots as well as low ψ_s (Table 2). The relationship between leaf ψ_s and rooting depth will be discussed later.

Compared with those of C_3 and CAM, the lower osmotic potentials in C_4 plants (Fig. 2) may be associated with high photosynthetic rates (Jiang et al. 1999) and accumulation of photosynthesis-soluble sugars (Walter 1974; Lawlor and Cornic 2002). It has been well documented that accumulated osmolytes derived from photosynthesis-soluble sugars induce low osmotic potential in some species (Guicherd et al. 1997; Alarcón et al. 1993; Mendes et al. 2001). Further experiments need to demonstrate this phenomenon.

The CAM photosynthetic pathway plant, *Orostachys malacophyllus* , possessed a higher osmotic potential in the present research (Fig. 2). The probable reason may be due to the water status of its cell protoplasts that is largely independent of the water status of the environment (Smith and Lüttge 1985; Wicken 1998; Herrera et al. 2000).

The deep rooting systems of plants are particularly important in maximizing water absorption from deep soils. The results obtained by several researchers confirmed that the rooting depth of seedlings might increase significantly in response to drought (Reader et al. 1992; Serraj and Sinclair 2002). In our experiment, we found that the deepest rooting plants presented lowest ψ_s (Fig. 3). The negative linear correlation between leaf ψ_s and rooting depth observed in both habitats (r^2=0.42; P <0.001) (Fig. 3) indicated the strong effect of plant root's depth on ψ_s, mediated either by hydraulic pressure (Etherington 1975) or drought (Shalhevet 1993). Low ψ_s in leaves will support the maintenance of a potential gradient for water uptake at low soil water potential under high evaporative demands causing deficits in the plant (Kassas and Batanouny 1984; Daudet et al. 2002). The relationship between rooting depth and osmotic potential is interactive. Even as for annual grasses, species with lower ψ_s usually had deeper root systems (Fig. 3), indicating that the plants escape progressive desiccation of the upper soil layers through rapid root growth reaching the permanently wet layer (Migahid and Abdel 1953; Levitt 1980; Batanouny 2001).

The osmotic potentials of some plants, i.e. *Atriplex halimus*, and *Limonium delicatulum*, growing in saline habitats are lower than individuals growing in other habitats (Khan and Aziz 1998; Walter 1964). In contrast, we found that leaf ψ_s increased with elevating soil salt content in different habitats (Fig. 4). Sufficient soil water availability in the top 0–40 cm soil layer (Table 3) of wetland might contribute to it, since ψ_s is closely related to the water supply (Munns 2002; Batanouny 1980). Another reason may be that plants were adapted to avoid the effects of salt (Bao 1994).

In conclusion, the leaf osmotic potentials of 104 species in Hunshandak Sandland were strongly species-specific. However, there were great differences that were closely related to different PFTs and habitats. Deep rooting plants, perennial woody plants and C_4 plants had lower values of leaf ψ_s, with the series: deep rooting<shallow rooting, shrubs<trees<grasses and C_4<C_3<CAM. In different habitats, leaf ψ_s decreased with increasing wetness, with the order being fixed sand dune<lowland<wetland.

Table 3 Soil matric potentials measured at 20 cm, 40 cm, 60 cm and 100 cm depth on shifting sand dunes, fixed sand dunes, lowland and wetland where leaf osmotic potentials were measured in the Hunshandak Sandland. The values shown are the average of three measurements

Habitats	Depth of soil profiles (cm)			
	0–20	20–40	40–60	60–100
Shifting sand dunes	–0.13	–0.07	–0.11	–0.03
Fixed sand dunes	–10.56	–1.2	–0.07	–0.06
Lowland	–0.92	–0.59	–0.06	–0.02
Wetland	–0.05	–0.17	–0.2	–0.1

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