内蒙古浑善达克沙地 97 种植物的光合生理特征

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摘要 报告了内蒙古浑善达克沙地不同生境下 97 种不同科、属植物的光合速率、蒸腾速率和水分利用效率特征。结果表明:猪毛菜(*Salsola collina*)、沙米(*Agriophyllum pungens*)、黑沙蒿(*Artemisia ordosica*)、狗尾草(*Setaria viridis*)、柠条(*Caragana microphylla*)等具有 C_4 光合碳同化途径或具固氮能力的植物种具有较高的光合能力,其净光合速率大于 $30 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$,而大部分具 C_3 途径和无固氮能力的植物种的净光合速率较低,为 $1.29 \sim 10 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$,71% 的植物种蒸腾速率集中在 $2 \sim 10 \text{ mmol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ 。所选出的高光效植物种在当地植被恢复与重建过程中应有很高利用价值。 C_4 植物种占所测植物种的 1/5 左右,主要分布于固定沙丘上,且随着生境土壤湿度的增大其与 C_3 植物种的光合速率差异逐渐缩小。在 3 种生境条件下,灌木和草本植物的光合速率和蒸腾速率顺序为:低湿地 > 滩地 > 固定沙丘 ($p < 0.01$),而乔木为固定沙丘 > 滩地 ($p < 0.01$)。不同功能型植物的气体交换特征随生境的不同而异,在固定沙丘上,草本的蒸腾速率最高,乔木的水分利用率最高,三者光合速率相差不大。

关键词 光合作用 生境 C_4 途径 灌木 草本植物 浑善达克沙地

COMPARISON OF GAS EXCHANGE TRAITS OF DIFFERENT PLANT SPECIES IN HUNSHANDAK SAND AREA

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Abstract Net photosynthetic rates (P_n), transpiration rates (E) and water use efficiencies (WUE) of 97 species among different habitats of Hunshandak Sand Area in Inner Mongolia were investigated. The results showed that some species such as *Salsola collina*, *Setaria viridis*, *Agriophyllum pungens*, *Artemisia ordosica*, *Caragana microphylla* and some other species which possess the C_4 photosynthetic pathway or with nitrogen fixation ability had higher net photosynthesis rates ($> 30 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), while most of the species which possess the C_3 photosynthetic pathway or lacked nitrogen fixation ability had lower photosynthesis rates ($1.29 \sim 10 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$). Species with transpiration rates between $2 \sim 10 \text{ mmol H}_2\text{O} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ comprised 71% of the species studied. The selected species which have high photosynthetic capability should be preferentially used in rehabilitating degraded grassland. Of the plants measured, C_4 species are mainly distributed on fixed sand dunes. The differences between C_4 and C_3 species decreased gradually with increasing soil moisture. Of the habitats studied, the values of both P_n and E of grasses and shrubs were found to be in the order of wetland > lowland > fixed dunes, whereas those of trees were in the order of fixed dune > lowland. The order of WUE was opposite to those of P_n and E . Gas exchange traits of three growth forms growing in different habitats were widely different. In fixed dunes, P_n of three growth forms were not greatly different, while the highest E and WUE were found in grasses and trees, respectively.

Key words Photosynthesis, Habitat, C_4 pathway, Shrub, Grass, Hunshandak Sand Area

In natural ecosystems, different plant species have different physiological strategy to adapt to the habitat. For example, the plants growing in an arid habitat can adapt to the habitat by some changes in ecophysiological traits, such as higher water use efficiency (WUE) and midday closing of stoma (Sala & Tenhunen, 1994; Jiang & Zhu, 2001). Photosynthesis and transpiration are the most im-

portant ecophysiological traits embodying plant's adaptive strategy. Some ecological factors such as light, water, temperature, CO_2 concentration and mineral nutrient supply on which plants depend may influence most of the physiological process such as the photosynthesis and transpiration (Lawlor, 1995; Valladaves & Allen, 1997). As such, the study of changes in photosynthesis and tran-

spiration in response to changes in environmental habitat is one of the cores of ecophysiological studies. Recently , the studies on photosynthesis of different species have attracted more and more attention from the ecophysiolgists (Bassow & Bazzaz , 1997 ; Prado & De Moraes , 1997 ; Jiang & Dong , 2000). In order to fully understand the importance of species in constituting an ecosystem and the response of species to variable environment , the ecophysiological traits especially the photosynthetic rate need to be intensively studied.

Hunshandak Sand Area , with a width of 50-300 km and a total area of 52 000 km² , is one of the five most important sandy areas in China , located within 200 km on the north of Beijing. It is considered as one of the major sources of sandy storm in Beijing , and the active sand dune is moving 1.8 km per year toward the capital of China. The restoration of degraded ecosystem in Hunshandak is now the most important task to protect the environment surrounding Beijing and Tianjin , as well as to favor the 2008 Olympic games. A careful comparative study of photosynthetic rate , transpiration rate and water use efficiency of its vegetation could provide the ecophysiological basis of the choice of species we need to regenerate the degraded land there. Although some researchers have done such kinds of study in other areas(Jiang & He , 1999 ; Xiao & Zhou , 2001) , no such study had been done in this sandy area.

The aims of this study are : 1) to compare the photosynthesis , transpiration and water use efficiency of a large number of arid sand plant species distributed in the various habitats of Hunshandak Sand Area and in order to reveal the significance of plant diversity as a natural resource , and then to provide some useful guides to vegetation recovery ; 2) to study the distribution of C₄ plant among three habitats and their photosynthetic traits ; 3) to compare the photosynthetic rate , transpiration rate and water use efficiency of different functional types of plants living in different habitats , and then to exploit their adaptations for increasing productivity in unfavorable habitats , i. e. , arid areas.

1 Materials and methods

1.1 Study area

The study was carried out in Hunshandak Sand Area , located in the south part of Xilingele plateau of Inner Mongolia Autonomous Region (about 42°23' N and 112°23' E). The climate is temperate semiarid with an annual mean temperature of 1.7 °C , annual precipitation of 250-400 mm and annual potential evaporation of 2 000-2 700 mm. Because of the extensive coverage by sand and remarkable landscape heterogeneity , the substrates here are highly diversified , creating the highly varied micro-

habitats : i. e. , fixed sand dune , lowland and wetland. The soil water content in different habitats is shown in Fig. 1 (A). Three functional types , including trees , shrubs and grasses , have developed in these habitats , with shrubs and grasses being the predominant ones. All the species tested in our experiment except *Zea mays* , *Salix matsudana* , and *Lycium chinensis* are naturally growing ones. The names of species distributed in the three habitats are listed in Table 1. The identification of C₄ plants were based on the studies of other people (Li , 1993 ; Tang *et al.* , 1999).

Fig.1 Soil water potential(A), distribution of C₄ plants (B) and their corresponding photosynthetic rates (C) among three habitats.

1.2 Gas exchange measurement

Net photosynthesis rates and transpiration rates were measured simultaneously by using an open infrared gas analysis system (LCA-4 Analytical Development Company Limited , ADC , Hoddesdon , England). Measurements

were performed from 8:00 – 10:00 am on clear days in August ($PAR > 1\,200\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). About twenty species were measured everyday. Most of the measurements were made on shrubs and grasses. The leaves measured of shrubs and grasses were about 8 cm below the tops of plants , while those of trees were on the tip of lower branches. Three leaves of each species were measured and each leaf was repeated three times. The leaf chamber of LCA-4 was placed directly under sunlight.

1.3 Data analysis

All data were entered into a portable computer with the LCA-4 program. Values of WUE were calculated by Pn/E . The ultimate date was the average of three leaves dates. The analysis of original Pn , E and WUE data of different species was performed using the EXCELL program in Office 2000. Significant differences between growth forms in different habitats were reported , if not otherwise indicated. The figures were drawn by Sigmaplot 4.0 software.

2 Results

2.1 Physiological traits of different species

Net photosynthetic rates , transpiration rates and water use efficiency were quite different between different species(Table 1). The highest Pn was recorded in *Sal-sola collina* in fixed sand dunes with a value of $36.2\ \mu\text{mol}\ \text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, while the lowest one appeared in *Orostachys malacophyllus* , also in fixed sand dunes.

Some species of *Chenopodiaceae* , *Leguminosae* , *Gramineae* , such as *Agriophyllum pungens* , *Salsola collina* , *Corispermum heptapotamicum* , *Setaria viridis* , *Caragana microphylla* , *Melilotoides suaveolens* , etc. which possess C_4 photosynthesis pathway or with nitrogen fixation capability had high photosynthetic rates , while most of the *Compositae* and *Gramineae* species which have the C_3 photosynthesis pathway had relatively low photosynthesis rates. 50% of all the species had photosynthesis rates of $10\text{--}20\ \mu\text{mol}\ \text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 22% of less $10\ \mu\text{mol}\ \text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, 21% of $20\text{--}30\ \mu\text{mol}\ \text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ and 6% above $30\ \mu\text{mol}\ \text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fig. 2). Transpiration rate varied from $1.55\ \text{mmol}\ \text{H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (*Cynanchum thesioides* in fixed sand dune) to $23.19\ \text{mmol}\ \text{H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (*Kobresia bellardii* in wetland)(Table1). A large percentage of species (75%) had rates of transpiration between $1.55\text{--}10\ \text{mmol}\ \text{H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ (Fig. 2). Water use efficiency also differed greatly from species to species in a range from $0.323\ \mu\text{mol}\ \text{CO}_2\cdot\text{mmol}^{-1}\text{H}_2\text{O}$ (*Allium tenuissimum* in fixed sand dune) to $8.894\ \mu\text{mol}\ \text{CO}_2\cdot\text{mmol}^{-1}\text{H}_2\text{O}$ (*Amaranthus retroflexus* in lowland)(Table 1). 88% of species had WUE from 0.32 to $4\ \mu\text{mol}\ \text{CO}_2\cdot\text{mmol}^{-1}\text{H}_2\text{O}$, while 29% from 3 to $6\ \mu\text{mol}\ \text{CO}_2\cdot\text{mmol}^{-1}\text{H}_2\text{O}$. Only two species , i. e. , *Amaranthus retroflexus* , *Chenopodium aristatum* had WUE above $6\ \mu\text{mol}\ \text{CO}_2\cdot\text{mmol}^{-1}\text{H}_2\text{O}$.

Table 1 Net photosynthetic rates (Pn) , transpiration rates (E) and water use efficiency (WUE) of different plant species with different growth forms on the fixed sand dunes , lowland and wetland in the Hunshandak Sand Area

Habitats	Families	Species	Growth form	Photosyn thesis pathway	Pn ($\mu\text{mol}\ \text{CO}_2\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	E ($\text{mmol}\ \text{H}_2\text{O}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$)	WUE ($\mu\text{mol}\ \text{CO}_2\cdot\text{mmol}^{-1}\text{H}_2\text{O}$)
Fixed dune	Ulmaceae	<i>Ulmus pumila</i>	T		17.26 ± 2.10	4.24 ± 0.79	4.07 ± 0.5
		<i>Malus baccata</i>	T		12.61 ± 1.45	2.52 ± 0.45	4.99 ± 0.56
	Salicaceae	<i>Salix gordejewii</i>	S		14.03 ± 2.09	2.4 ± 0.41	5.85 ± 1.40
		<i>Salix psammophila</i>	S		17.42 ± 4.43	4.62 ± 0.80	3.77 ± 0.84
	Leguminosae	<i>Caragana microphylla</i>	S		32.03 ± 6.25	9.62 ± 0.68	3.33 ± 0.59
		<i>Astragalus efoliolatus</i>	G		14.12 ± 1.18	19.3 ± 0.29	0.73 ± 0.28
		<i>Thermopsis lanceolate</i>	G		7.15 ± 1.77	2.71 ± 0.81	2.62 ± 0.29
	Liliaceae	<i>Allium tenuissimum</i>	G		1.46 ± 1.30	4.51 ± 0.16	0.32 ± 0.70
	Crassulaceae	<i>Orostachys malacophyllus</i>	G		1.29 ± 1.28	3.02 ± 2.31	0.50 ± 0.58
	Chenopodiaceae	<i>Chenopodium glaucum</i>	G	C_4	29.04 ± 3.01	22.02 ± 5.36	1.32 ± 0.40
		<i>Bassia dasyphylla</i>	G	C_4	18.01 ± 0.42	7.48 ± 0.73	2.41 ± 0.21
		<i>Agriophyllum pungens</i>	G	C_4	30.73 ± 3.38	9.42 ± 1.33	3.26 ± 0.53
		<i>Corispermum heptapotamicum</i>	G	C_4	22.34 ± 8.07	6.84 ± 1.76	3.26 ± 2.03
		<i>Salsola collina</i>	G	C_4	36.22 ± 7.32	6.44 ± 1.23	5.63 ± 0.84
		<i>Penniselum centrasialicum</i>	G	C_4	28.61 ± 1.50	10.2 ± 0.48	2.81 ± 0.58
		<i>Carex duriuscula</i>	G		11.72 ± 3.84	3.97 ± 1.50	2.94 ± 1.65
	Gramineae	<i>Calamagrostis epigejos</i>	G		5.72 ± 1.42	2.51 ± 0.54	2.29 ± 0.19
		<i>Setaria viridis</i>	G	C_4	32.44 ± 1.06	20.8 ± 0.35	1.55 ± 0.42
		<i>Leymus chinensis</i>	G		2.09 ± 2.79	3.02 ± 1.68	0.69 ± 1.56
		<i>Heteropappus hispidus</i>	G		9.41 ± 1.75	2.04 ± 0.91	4.61 ± 3.77
Compositae		<i>Sonchus oleraceus</i>	G		13.21 ± 1.68	4.69 ± 0.64	2.81 ± 0.47
		<i>Artemisia ordosica</i>	G	C_4	36.14 ± 5.92	16.06 ± 3.42	2.28 ± 0.76

		<i>Artemisia argyi</i>	G		10.31 ± 3.47	4.53 ± 0.91	2.28 ± 0.35
		<i>Echinops gmelini</i>	G		17.62 ± 2.62	5.97 ± 0.34	2.94 ± 0.46
	Caryophyllaceae	<i>Dianthus chinensis</i>	G	C ₄	25.92 ± 1.86	11.4 ± 1.10	2.26 ± 0.32
		<i>Silene repens</i> var. <i>latifolia</i>	G		11.63 ± 1.20	5.62 ± 0.87	2.07 ± 0.22
	Ranunculaceae	<i>Thalictrum squarrosom</i>	G		14.02 ± 1.19	3.96 ± 0.65	3.53 ± 0.81
		<i>Clematis aethusifolia</i>	G		12.17 ± 0.82	3.73 ± 0.51	3.24 ± 0.57
	Caprifoliaceae	<i>Lonicera chrysantha</i>	S	C ₄	24.12 ± 2.36	4.28 ± 0.40	5.61 ± 1.51
	Asclepiadaceae	<i>Cynanchum thesioides</i>	G		5.74 ± 1.59	1.55 ± 0.46	3.67 ± 0.53
	Saxifragaceae	<i>Ribes pulchellum</i>	S		19.63 ± 2.18	5.92 ± 1.22	3.32 ± 0.58
	Polygonaceae	<i>Polygonum divaricatum</i>	G		12.42 ± 2.41	4.52 ± 0.77	2.74 ± 0.29
	Umbelliferae	<i>Ferula bungeana</i>	G		15.61 ± 1.94	3.11 ± 0.25	5.02 ± 0.72
Lowland	Betulaceae	<i>Betula fruticosa</i>	S		12.74 ± 2.27	3.32 ± 0.29	3.81 ± 0.57
	Gramineae	<i>Agropyron cristatum</i>	G	C ₄	29.33 ± 3.04	10.3 ± 0.84	2.86 ± 0.21
		<i>Cleistogenes squarrosa</i>	G	C ₄	27.72 ± 2.20	11.03 ± 1.16	2.53 ± 0.20
		<i>Achnatherum splendens</i>	G		11.95 ± 2.50	5.99 ± 0.99	1.99 ± 0.19
		<i>Panicum miliaceum</i>	G	C ₄	20.32 ± 2.21	5.32 ± 1.05	3.81 ± 0.16
		<i>Zea mays</i>	G	C ₄	27.51 ± 0.85	9.91 ± 0.24	2.77 ± 0.69
		<i>Setaria italica</i>	G	C ₄	26.18 ± 0.59	8.20 ± 0.23	3.18 ± 0.87
	Compositae	<i>Artemisia dracunculus</i>	G	C ₄	26.31 ± 1.85	12.80 ± 2.19	2.06 ± 0.34
		<i>Artemisia annua</i>	G		12.44 ± 1.06	7.46 ± 0.55	1.66 ± 0.22
		<i>Inula britanica</i>	G		14.72 ± 1.79	2.82 ± 0.59	5.21 ± 0.69
		<i>Cirsium esculentum</i>	G		6.18 ± 1.92	2.64 ± 0.64	2.34 ± 1.33
		<i>Aster tataricus</i>	G		13.31 ± 1.83	7.02 ± 0.43	1.89 ± 0.98
		<i>Artemisia dracunculus</i>	G	C ₄	28.10 ± 2.19	18.44 ± 0.34	1.53 ± 0.81
		<i>Saussurea japonica</i>	G		7.19 ± 7.31	3.73 ± 4.54	1.95 ± 0.19
		<i>Artemisia demissa</i>	G		15.06 ± 7.76	8.35 ± 5.19	1.80 ± 0.22
		<i>Heteropappus altaicum</i>	G		17.41 ± 1.86	8.55 ± 0.51	2.03 ± 1.21
		<i>Leontopodium leontopodioides</i>	G		5.97 ± 1.06	9.11 ± 0.39	0.66 ± 0.49
		<i>Cirsium japonicum</i>	G		14.43 ± 7.18	7.47 ± 3.14	1.93 ± 0.11
	Leguminosae	<i>Sphaerophysa salsula</i>	G		14.31 ± 3.06	7.93 ± 1.62	1.8 ± 0.32
		<i>Melilotus suaveolens</i>	G		23.90 ± 1.83	13.2 ± 0.26	1.81 ± 0.68
		<i>Melilotoides ruthenica</i>	G		18.75 ± 2.81	5.28 ± 1.02	3.55 ± 0.33
		<i>Pisum sativum</i>	G		7.33 ± 5.70	7.82 ± 2.74	0.93 ± 0.35
		<i>Medicago falcata</i>	G		15.91 ± 1.14	18.2 ± 0.37	0.88 ± 0.43
		<i>Amorpha fruticosa</i>	S		27.14 ± 2.37	8.14 ± 0.68	3.33 ± 0.28
		<i>Gueldenstaedtia multiflora</i>	G		13.74 ± 7.21	10.2 ± 5.42	1.34 ± 0.26
		<i>Hedysarum scoparium</i>	G		28.53 ± 1.50	7.04 ± 0.84	4.05 ± 0.35
		<i>Oxytropis glabra</i>	G		20.06 ± 4.95	11.04 ± 4.31	1.81 ± 0.23
	Rosaceae	<i>Sanguisorba officinalis</i>	G		5.04 ± 0.99	5.83 ± 0.28	0.86 ± 0.44
		<i>Agrimonia pilosa</i>	G		13.06 ± 6.92	7.54 ± 4.70	1.72 ± 0.18
		<i>Potentilla strigosa</i>	G		21.62 ± 1.91	9.69 ± 0.45	2.23 ± 0.54
	Ranunculaceae	<i>Anemone silvestris</i>	G		14.03 ± 6.38	12.3 ± 3.09	1.14 ± 0.34
		<i>Nymphoides peltata</i>	G		12.94 ± 5.08	5.92 ± 2.39	2.18 ± 0.20
	Chenopodiaceae	<i>Suaeda glauca</i>	G		16.13 ± 1.06	9.59 ± 1.76	1.67 ± 0.17
		<i>Chenopodium aristatum</i>	G	C ₄	22.72 ± 2.35	3.75 ± 0.39	6.06 ± 1.18
	Amaranthaceae	<i>Amaranthus retroflexus</i>	G	C ₄	22.04 ± 2.00	2.47 ± 0.53	8.89 ± 1.52
	Liliaceae	<i>Allium condensatum</i>	G		9.07 ± 6.61	5.22 ± 5.59	1.74 ± 0.45
		<i>Asenescens</i>	G		3.81 ± 6.36	2.36 ± 3.18	1.61 ± 0.29
	Umbelliferae	<i>Bupleurum sibiricum</i>	G		9.11 ± 5.21	8.06 ± 2.84	1.13 ± 0.17
		<i>Cnidium monnieri</i>	G		9.04 ± 0.91	5.11 ± 0.16	1.77 ± 0.67
	Campanulaceae	<i>Campanula rutundifolia</i>	G		14.14 ± 1.00	15.7 ± 0.40	0.90 ± 0.47
	Loganiaceae	<i>Buddleja alternifolia</i>	G		12.62 ± 6.35	17.90 ± 3.27	0.70 ± 0.36
	Salicaceae	<i>Salix matsudana</i>	T		6.98 ± 5.64	2.51 ± 2.69	2.78 ± 0.17
	Solanaceae	<i>Lycium chinensis</i>	S		26.46 ± 1.41	6.77 ± 0.45	3.90 ± 0.53
	Equisetaceae	<i>Equisetum ramosissimum</i>	G		14.13 ± 2.16	13.80 ± 1.01	1.02 ± 0.19
	Iridaceae	<i>Iris lactea</i> var. <i>chinensis</i>	G		12.17 ± 1.48	6.32 ± 0.23	1.91 ± 0.20
	Urticaceae	<i>Urtica cannabina</i>	G		18.61 ± 2.63	3.28 ± 0.36	5.67 ± 0.96

Wetland	Cruciferae	<i>Thellungiella salsuginea</i>	G		5.98 ± 2.11	1.56 ± 0.35	3.83 ± 1.32
	Gramineae	<i>Phragmites australis</i>	G		6.54 ± 2.19	3.09 ± 0.58	2.12 ± 1.50
		<i>Echinochloa crusgalli</i>	G	C ₄	17.64 ± 2.61	10.71 ± 2.05	1.64 ± 0.18
		<i>Eragrostis pilosa</i>	G	C ₄	17.15 ± 1.88	13.73 ± 0.51	1.25 ± 0.65
Cyperaceae		<i>Scirpus yagara</i>	G		18.81 ± 1.06	10.10 ± 0.40	1.87 ± 0.52
		<i>Kobresia bellardii</i>	G		26.64 ± 5.14	23.20 ± 6.90	1.15 ± 0.64
Compositae		<i>Taraxacum dissectum</i>	G		29.16 ± 3.18	10.8 ± 0.32	2.69 ± 2.28
		<i>Saussurea runcinata</i>	G		17.82 ± 3.19	9.77 ± 0.32	1.82 ± 2.25
		<i>Xanthium sibiricum</i>	G		17.53 ± 1.07	4.77 ± 0.37	3.67 ± 0.43
Plantaginaceae		<i>Plantago major</i>	G		10.37 ± 2.17	2.48 ± 0.57	4.15 ± 0.44
Crassulaceae		<i>Rhodiola rosea</i>	G		15.54 ± 3.12	8.41 ± 0.33	1.84 ± 2.25
Juncaceae		<i>Juncus gracillimus</i>	G		34.91 ± 2.85	9.11 ± 0.68	3.84 ± 0.24
Gentianaceae		<i>Nymphoides peltata</i>	G		9.37 ± 2.82	4.76 ± 0.35	1.97 ± 2.22
Polygonaceae		<i>Polygonum hydropiper</i>	G		10.45 ± 2.43	5.36 ± 0.37	1.95 ± 2.11
Scrophulariaceae		<i>Linaria vulgaris</i>	G		10.72 ± 2.42	3.90 ± 0.55	2.75 ± 2.16
Myrtaeear		<i>Rhodomyrtus</i>	G		16.91 ± 2.90	5.51 ± 0.36	3.07 ± 2.37
Ranunculaceae		<i>Halerpests ruthenica</i>	G	C ₄	28.63 ± 1.59	13.40 ± 0.43	2.14 ± 0.53
Rosaceae		<i>Potentilla flagellaris</i>	G		9.79 ± 2.01	5.26 ± 0.31	1.86 ± 0.38

G. Grasses S. Shrubs T. Trees

Fig.2 The relationship of transpiration rate (E), net photosynthetic rate (Pn) and water utilization efficiency (WUE) in different habitats of the Hunshandak Sand Area

2.2 The distribution of C₄ plants in different habitats and their net photosynthetic rates

The percentages of numbers of C₄ plant species differed in different habitats (Fig. 1B), which were 30 % , 19.2 % and 11.8 % in fixed sand dune , lowland and wetland respectively. Among the three habitats , the order of soil water potential was fixed sand dune < lowland < wetland (Fig. 1A), that is to say where water potential was higher , the C₄ percentage was lower. In the same habitats , Pn of C₄ plant was higher than that of C₃ plant. But the differences between them decreased with the increasing soil water content until they were about equal in wetland. The order of Pn in C₄ plants was fixed sand dune > lowland > wetland , whereas the reverse trend was found in C₃ plant (Fig. 1C).

2.3 Differences among habitats

Differences in Pn , E and WUE among plants living in different habitats in Hunshandak Sand Area were shown in Fig. 3. Because the species composition differed among different habitats , we only grouped the figures of species

according to their growth forms , i. e. , trees , shrubs and grasses. Different trends of Pn and E appeared for different growth forms among the three habitats : the orders of those for both shrubs and grasses were wetland > lowland > fixed dunes (p < 0. 01) , while those of trees were fixed dune > lowland (p < 0. 01). The order of WUE for the three growth forms was just opposite to that of Pn and E. Among the three growth forms in the same habitat , the order differed in different habitats. In both lowland and fixed dune , the orders of Pn were shrubs > grasses > trees , while those of E were grasses > shrubs > trees. Different orders of WUE were found in fixed sand dune and lowland , which in the former was trees > shrubs > grasses while that in the latter was shrubs > trees > grasses.

3 Discussion

3.1 Interspecific differences in Pn、E and WUE

A number of authors have found significant interspecific differences in rates of Pn , E and WUE , even for species living in very similar habitats (Smith & Griffus , 1998). These differences are the result of natural selection. Our measurements made on the 97 species distributed in Hunshandak Sand Area showed that species with higher Pn such as *Agriophyllum pungeus* , *Corispermum heptapotamicum* , *Salsola collina* , *Setaria viridis* , *Caragana microphylla* and etc. belong chiefly to Gramineae , Chenopodiaceae and Leguminosae in both lowland and fixed sand dune. Species in Chenopodiceae owe their high Pn to the C₄ pathway ; while some species in Leguminosae , including *Hedysarum scoparium* , *Melilotus suaveolens* , *Caragana microphylla* owe their high Pn to nitrogen fixation ability (Tan *et al.* , 1996). In degraded ecosystems , nutrients especially N is absence. Plants of Leguminosae can compensate N through its nitrogen fixation ability , therefore they had higher photosynthetic rate

(Zanetti & Hartwig, 1997). Such kind of result has also been reported by others (Li *et al.*, 2001). The patterns of P_n , E and WUE in Hunshandak were to some extent in agreement with other authors. Jiang and He (1999) had also found that species from Chenopodiaceae and Leguminosae in Maowusu Sand Area had higher P_n . But its physiological mechanism is not made clear, thus the corresponding research needs further be studied.

Fig.3 Comparison of net photosynthetic rates (P_n)(A), transpiration rates (E)(B), and water utilization efficienc (WUE) (C) of trees, shrubs and grasses in different habitats of the Hunshandak Sand Area

One species (*Orostachys malacophyllus*) with the CAM photosynthetic pathway was observed in this study which was found in lowland. This is the strongest evidence of the dryness and hotness of the habitats.

Agriophyllum pungens and *Salsola collina* were found frequently in fixed sand dune. High P_n and WUE ensured their high efficiency of utilization of light and wa-

ter in arid environment. Therefore, they can survive in shifting sand dune and become the pioneer species of fixed sand dune. Such traits should be fully used by human. People can use abundant seeds of *Agriophyllum pungens* or *Salsola collina* at the transitory period of adequate rainwater to accelerate the fixation of sand dune. Other species such as *Juncus gracillimus*, *Artemisia ordosica* and *Caragana microphylla* which with their high P_n and WUE can efficiently utilize resources to get high productivity and to adapt to Hunshandak environment much better than others should be preferentially used in reconstructing the degraded grass land, especially *Lonicera chrysantha* and *Caragana microphylla*, which could be used either to decelerate wind or to fix sand.

3.2 The distribution of C_4 plants

The ecological significance of C_4 has been studied in detail. The common view that C_4 plants are mainly distributed in dry and hot area has been confirmed by researchers (Smith, 1997). Our results also showed that C_4 plants in Hunshandak Sand Area primarily occupy the environment where the temperature and light are abundant but water is scarce that C_3 plants can not grow well. Such traits may be simply a correlated characteristic of their origin in tropical environments. Ludlow (1980) also pointed out that the higher water use efficiency of C_4 plants was related to a greater drought tolerance or ability to withstand low water potential. This may be a proof that C_4 plants are more advanced in evolution than C_3 plants (Edwards & Furbank, 2001).

The high photosynthetic rate of C_4 plants is not absolute. It can only be displayed in an environment where it is well adapted, otherwise the competitive advantages will not be brought to effect. Percy *et al.* (1981) had drawn a conclusion after comparing C_4 and C_3 plants under natural understorey environment that the photosynthetic behaviors of these two species were remarkably similar in spite of the differences in photosynthetic pathway. Similar results are shown in our study that P_n of C_4 plants in wetland were not higher than that of C_3 plants (Fig.1C). In addition, the photosynthetic pathway is not fixed. For example, CAM route can be stopped and replaced by C_4 route in humid seasons but back to CAM route again if another dry season comes (Ehleringer, 1979). The percentage and P_n of different photosynthetic types is just the physiological response to environment. It is such flexible physiological response which enables plants to make full use of natural resource in a variable environment.

3.3 The differences in gas exchange traits among plants from living in different habitats and in different growth forms

The characteristics of gas exchange discussed above were also strongly habitat-dependent. From Fig. 3, we can see that shrubs and grasses had similar adaptive strategies to environment. In their own habitats, where the environment was drier, shrubs and grasses have lower

P_n and E but higher WUE . This showed that drought may be the limiting factor to the P_n of grasses and shrubs in Hunshandak Sand Area. But species can overcome limitations through physiological changes. In order to use water more efficiently in dry environment, shrubs and grasses lowered their transpiration rates though at the expense of P_n . Similar results had also been reported by other authors (Terwilliger & Zeroni, 1994; Filella *et al.*, 1998). The WUE difference of three growth forms among habitats indicated that species are forced to survive in dry habitats rather than they prefer to live in such water-short conditions.

Only three species of trees live in this area. *Ulmus pumila* and *Malus baccata* are indigenous while *Salix matsudana* is introduced. The indigenous trees could keep moderate P_n through the long history of adaptation and natural selection but the introduced one had very low rates. Though the trees had low E , they waste large amounts of water because of the big surface. So planted trees may not survive in Hunshandak Sand Area where water is scarce as evidenced by lots of dead *Salix matsudana* there after one year's planting. From the above analysis, it can be seen that the selection of growth forms is important in reconstructing the degraded grassland. Shrubs and grasses especially the species with C_4 photosynthetic pathway or with the nitrogen fixation ability should be preferentially used.

Although in this study a large number of species were studied, not all of the species in the sand area were examined. However, this study does provide a useful guide for more comparative and experimental studies.

References

Bassow, S. L. & F. A. Bazzaz. 1997. Intra- and inter-species variation in canopy photosynthesis in a mixed deciduous forest. *Oecologia*, **109**: 507 ~ 515.

Edwards, G. E. & R. T. Furbank. 2001. What does it take to be C_4 ? Lessons from the evolution of C_4 photosynthesis. *Plant Physiology*, **125**: 46 ~ 49.

Ehleringer, J. R. 1979. General known to possess the crassulacean acid metabolism (CAM) pathway. *HortScience*, **14**: 217 ~ 222.

Filella, I., J. Llusia, J. Piol & J. Peuekas. 1998. Leaf gas exchange and the fluorescence of *Phyllirea latifolia*, *Pistacia lentiscus* and *Quercus ilex* samplings in severe drought and high temperature conditions. *Environmental and Experimental Botany*, **39**: 213 ~ 220.

Jiang, G. M. (蒋高明) & W. M. He (何维明). 1999. Study on eco-physiological traits of different plant species in the Maowusu Sandy Land. *Acta Botanica Sinica (植物学报)*, **41**: 1114 ~ 1124. (in Chinese with English abstract)

Jiang, G. M. (蒋高明) & M. Dong (董鸣). 2000. A comparative study on photosynthesis and water use efficiency between clonal and non-clonal plant species along the northeast China transect. *Acta Botanica Sinica (植物学报)*, **42**: 855 ~ 863. (in Chinese

with English abstract)

Jiang, G. M. (蒋高明) & G. J. Zhu (朱桂杰). 2001. Effects of natural high temperature and irrigation on photosynthesis and related parameters in three arid sandy shrub species. *Acta Phytocologica Sinica (植物生态学报)*, **24**: 554 ~ 559. (in Chinese with English abstract)

Lawlor, D. W. 1995. Photosynthesis, productivity and environment. *Journal of Experimental Botany*, **46**: 1449 ~ 1461.

Li, M. Y. (李美英). 1993. A list of C_4 -photosynthesis plants dicotyledon. *Plant Physiology Communications (植物生理学通讯)*, **29**: 221 ~ 240. (in Chinese)

Li, W. H. (李卫华), Q. T. Lu (卢庆陶), N. B. Hao (郝乃斌), Q. Y. Ge (戈巧英), Q. D. Zhang (张其德), W. G. Du (杜维广) & T. Y. Kuang (匡廷云). 2001. C_4 pathway enzymes in soybean leaves. *Acta Botanica Sinica (植物学报)*, **43**: 805 ~ 808. (in Chinese with English abstract)

Ludlow, M. M. 1980. Stress physiology of tropical pasture plants. *Tropical Grasslands*, **14**: 136 ~ 145.

Pearcy, R. W., N. Tumosa & K. Williams. 1981. Relationships between growth, photosynthesis and competitive interactions for a C_4 and C_3 plant. *Oecologia*, **48**: 371 ~ 376.

Prado, C. H. B. A. & J. A. P. V. De Moraes. 1997. Photosynthetic capacity and specific leaf mass in twenty woody species of Cerrado vegetation under field conditions. *Photosynthetica*, **34**: 103 ~ 112.

Sala, A. & J. D. Tenhunen. 1994. Site-specific water relations and stomatal response of *Quercus ilex* L. in a Mediterranean watershed. *Tree Physiology*, **14**: 601 ~ 617.

Smith, B. N. 1997. The origin and evolution of C_4 photosynthesis. *Handbook of photosynthesis*. New York: Marcel Dekker. 977 ~ 986.

Smith, E. C. & H. Griffiths. 1998. Intraspecific variation in photosynthetic responses of trebouxoid lichens with reference to the activity of a carbon concentrating mechanism. *Oecologia*, **113**: 360 ~ 439.

Tan, Z. Y. (谭志远), M. E. Zhu (朱铭莪), X. L. He (贺学礼) & Y. Li (李颖). 1996. Investigation of rhizobium of Leguminous plants in Shanxi province and some areas of Gansu province and Ningxia autonomous region. *Acta Botanica Boreali-Occidentalia Sinica (西北植物学报)*, **15**: 189 ~ 196. (in Chinese with English abstract)

Tang, H. P. (唐海萍), S. R. Liu (刘书润) & X. S. Zhang (张新时). 1999. The C_4 plants in Inner Mongolia and their eco-geography traits. *Acta Botanica Sinica (植物学报)*, **41**: 420 ~ 424. (in Chinese with English abstract)

Terwilliger, J. & M. Zeroni. 1994. Gas exchange of a desert shrub under different soil moisture regimes during summer drought. *Vegetatio*, **115**: 133 ~ 144.

Valladaves, F. & M. T. Allen. 1997. Photosynthetic response to dynamic light under field conditions in six tropical rain forest shrubs occurring along a light gradient. *Oecologia*, **111**: 505 ~ 514.

Xiao, C. W. (肖春旺) & G. S. Zhou (周广胜). 2001. The effect of irrigation on the gas exchange and photochemistry efficiency of *Salix psammophila* in Maowusu Sandy Area. *Acta Phytocologica Sinica (植物生态学报)*, **25**: 444 ~ 450. (in Chinese with English abstract)

Zanetti, S. & U. A. Hartwig. 1997. Does nitrogen restrict the CO_2 response of fertile grassland lacking legumes. *Oecologia*, **112**: 19 ~ 25.