Traits of chlorophyll fluorescence in 99 plant species from the sparse-elm grassland in Hunshandak Sandland

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Abstract

Sparse-elm grassland is the remarkable landscape of Hunshandak Sandland in Inner Mongolia Autonomic Region of China. Maximum quantum efficiency (F_v/F_m) of 99 native plant species (85 grasses, 11 shrubs, and 3 trees) of different plant functional types (PFTs) distributed in fixed sand dune, lowland, and wetland was investigated. Deep-rooted plant species (tree, shrub, and perennial grass) had higher F_v/F_m values than the shallow-rooted species (annual grasses), suggesting that soil drought is the major environmental stress. Annual C_4 grasses had higher F_v/F_m values than annual C_3 or CAM ones, indicating that C_4 photosynthesis is more ecologically adaptive than CAM and C_3 grasses. According to the habitats with annual C_3 grass distribution, F_v/F_m values were in the order of fixed dune>lowland>wetland, suggesting that salt and pH value may enhance irradiance or heat stress for those distributed in pickled and watery habitats. Based on such characteristics, *Ulmus pumila*, *Salix gordejevii*, *Caragana microphylla*, *Agriophyllum pungens,* and *Agropyron cristatum* are recommended as ideal species for ecological restoration in degraded sand-land ecosystems.

Additional key words: environmental stress; habitat; plant functional type; quantum efficiency; root system; semi-arid sandland; sparse-elm grassland.

Introduction

Plants respond to their habitats with different ecological strategies in resource utilization, reflected by different patterns in eco-physiological characteristics, even though they are distributed in adjacent and similar geographical habitats (De Lillis and Fontanella 1992, Prado and De Moraes 1997, Jiang and Dong 2000, Hamerlynck 2001). Maximum quantum efficiency (F_v/F_m) is always close to 0.80, independent of the species studied (Genty *et al.* 1989, Schreiber and Bilger 1993, Govindjee 1995). An F_v/F_m value lower than 0.80 indicates occurrence of the inactive or damaged photosystem 2 (PS2) reaction centres in significant proportion. Photoinhibition is often observed in plants under stress conditions (van Kooten and Snel 1990). F_v/F_m decreases with stress level (Krause and Weis 1991), such as drought stress (Karavatas and Manetas 1999, Yordanov *et al.* 2000, Winkel *et al.* 2002), temperature stress (Briantais *et al.* 1996, Yu and Ong 2002, Wang *et al.* 2003), salt stress (Lima *et al.* 1999), and high irradiance stress (Jiang and Zhu 2001, Peng and Gilmore 2003). Species living in different conditions differ greatly in photosynthetic features such as gas exchange (Park and Furukawa 1999) and chlorophyll (Chl) fluorescence kinetics (Bassow and Bazzaz 1997, Miszalski *et al.* 2000). Although the lower F_v/F_m may involve the inactivation of part of PS2 units as a protective device, the studies of F_v/F_m are widely recognized as an indicator in understanding the responses of plants under environmental stress (Roháček 2002). A plant with lower F_v/F_m under long-time environmental stress can not grow better than those with higher values (Nieva *et al.* 1999, Sayed 2003).

Plant functional types (PFTs) have been studied intensively (Smith *et al.* 1997, Williams *et al.* 1998, Oleson and Bonan 2000). Different PFTs have different adaptive mechanisms in nature, which might be reflected by their F_v/F_m signals occurring at particular time of a day. However, such comparisons need an exact, quick, steady, and portable apparatus that is suitable for the field works. The portable plant efficiency analyzer (PEA) can meet such requirements.

Hunshandak Sandland, only 200 km away from north Beijing, is one of the four largest sandy lands in China

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with ecological heterogeneity and various PFTs that enable us to investigate the different mechanisms of plant adaptation to their habitats. Besides, it is the source of sand dust storms occurring in North China, especially around Beijing Area (State Environmental Protection Administration 2001). In order to solve such problems before 2008, when the Olympic Games will take place in China, the government has invested a great deal of fund to treat sand dust storms, usually by planting trees (*Populus* sp.). Nevertheless, such selection was not based on ecological understanding of species distributed here. Most PFTs here, *e.g.* trees, shrubs, and grasses, are native and often suffer drought and high irradiance stresses, but their physiological characteristics have not been previously reported. Therefore, we chose the different PFTs in Hunshandak Sandland for this research. The aims of this study were: (*1*) to compare the differences in PS2 efficiency (F_v/F_m) of a large number of semi-arid sand plant species, (*2*) to reveal the different responses of PS2 of different PFTs under environmental stress, and (*3*) to find out the most suitable plant species for the ecological restoration.

Materials and methods

Study area: The study was conducted in the centre of Hunshandak Sandland in Inner Mongolia Autonomous Region of China (42º23′N, 116º23′E). The prevailing climate is of temperate semi-arid type, with an annual mean temperature of 1.7 °C, January average temperature of –11.1 °C, July average temperature of 25.1 °C, and an annual precipitation of 365 mm. Landscapes here are characterised by micro-habitats of shifting sandy dunes, fixed sand dunes, lowland, and wetland as the main ones. Wetland appears where underground water level is high, forming some small swamps. Soil moisture is in the order of wetland>lowland>fixed sandy dune>shifting sandy dune. Other soil characteristics are listed in Table 1. The special sandy habitats in Hunshandak Sandland are suitable for the survival of different PFTs, yielding the characteristic landscapes of sparse-elm grassland. Trees, grasses, and shrubs are of great ecological and economic importance, because they can survive in this region and stop the disposal of sand by wind. All the 99 plant species tested (Table 2) in our experiments are native and distributed in their typical habitats. C_4 plant species were determined according to Yin and Li (1997) and Tang and Liu (2001).

Measurements: F_0, F_m, F_v, and F_v/F_m were measured or calculated with a portable *FMS-2* Plant Efficiency Analyzer (PEA; *Hansatech*, King's Lynn, UK). Before measurements, the samples were dark-adapted for 30 min with clips. To make a record, the PEA sensor unit was held over the clip and the shutter opened. The single push button activates the high irradiance LED array within the sensor head providing a maximum irradiance of 3 000 µmol m^{-2} s^{-1}, sufficient for F_m to be reached in all species. Data acquisition triggered at 100 kHz (10 µs intervals) with a 12-bit resolution. All data was transported into a portable computer where customary 32-bit *Windows*® software permitted re-scaling. Measurements were performed when photosynthetic photon flux density (PPFD) >2 000 µmol m^{-2} s^{-1} and leaf surface temperature was >35 °C during a drought period (10 d after 15 mm rainfall, August 9–11), when the peak period of growth for almost all sand plant species occurred. The typical functional leaves of plants in this region were measured for all trees and shrubs plus 60 % of grass species in this region. Five replications were made for each species.

Data analysis: The large data set of F_v/F_m was entered into an *EXCEL* spread sheet in *Office XP*. Analysis of variance of leaf traits was carried out on each measurement. The least significant differences (LSD) between the means were estimated at 95 % confidence level. Calculation and linear regression were performed using a *Sigma-Plot 8.0* program. Significant differences among different plant species were reported at $p<0.05$ if not indicated otherwise.

Results

Differences between PFTs: Average F_v/F_m values of 99 plant species ranged from 0.57 (*Polygonum hydropiper*) to 0.79 (*Ulmus pumila*). F_v/F_m of *U. pumila*, *Salix gordejevii*, *Caragana microphylla*, *Agriophyllum pungens*, and *Agropyron cristatum*, *etc.* were higher than 0.76, which suggested that they are not as sensitive to environmental stress as other species (Table 2). Deeper-rooted plant species such as *U. pumila* can utilize deeper water in soil, being less sensitive to rainfall than the shallow-rooted species.

Average F_v/F_m in trees (0.78), shrubs (0.77), and perennial grasses (0.74) was higher than in annual grasses (0.72–0.73), and as concerns annual grasses, C_4 grasses (0.73)>CAM grasses (0.72)>C_3 grasses (0.72) (Fig. 1). Correlation analysis between root depth and F_v/F_m of grass species indicated that F_v/F_m was significantly correlated with root depth for the grasses (Fig. 2).

Differences among habitats: Fixed dune, lowland, and wetland are the major habitats in Hunshandak Sandland. Among the 52 annual C_3 grass species investigated, 20 species were found in fixed dune, 16 species in lowland, and 16 species in wetland. Although the species composition may differ with habitat, F_v/F_m was found in the order of fixed dune (0.74) and lowland (0.72)>wetland (0.69) (Fig. 3; p>0.01).

Discussion

Water is not only one of the limiting factors for plant growth and distribution, but also determines the eco-physiological characteristics of the plant species in semiarid regions. A number of investigators have observed changes in Chl fluorescence parameters along the environmental or ecological gradients, such as temperature and precipitation (Miszalski *et al.* 2000), and there were many F_v/F_m investigations made to compare the different plant species or cultivars (Nieva *et al.* 1999).

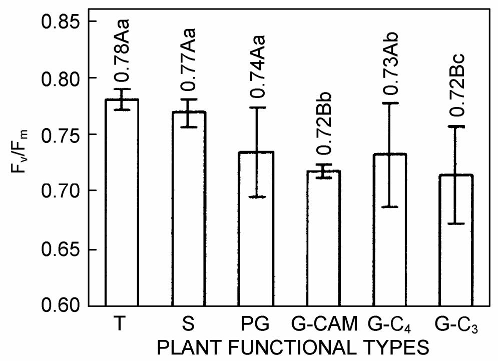

Fig. 1. Average F_v/F_m values of different plant functional types (PFTs) invested in Hunshandak Sandland. T, S, PG, G-CAM, G-C_4, and G-C_3 represent trees, shrubs, perennial grasses, annual CAM grass, annual C_4 and annual C_3 grasses, respectively. *Columns that share the same letters* had no significant difference at $p_{0.05}$ or $p_{0.01}$ (t-test).

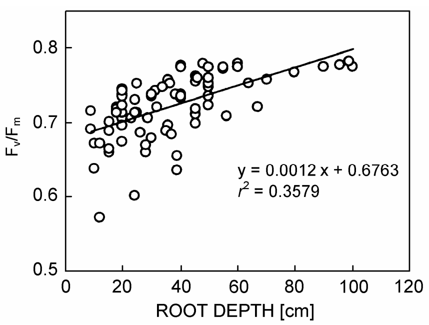

Fig. 2. Relationship between root depth and F_v/F_m values of grass species.

However, only a few investigations have been done on various plant species of different PFTs under their natural conditions. Our investigation on 99 native plant species under high irradiance, high temperature, and drought indicated that water is the major stress for different PFTs, especially for the shallow rooted species (Table 2 and Fig. 1). However, deep-rooted species did not show significant decreases in F_v/F_m (Table 2 and Fig. 2). The 99 native species have different strategies in utilizing water resource. For example, *U. pumila*, *C. microphylla,* and *S. gordejevii* have deep root systems to utilize underground soil waters. According to F_v/F_m, they are more ecologically suitable for short period drought than the short-lived grass species (Table 1 and Fig. 2). On the other hand, some shallow rooted and short-lived grass species, such as *A. squarrosum, C. declinatum, C. aristatum,* and *S. collina*, could accomplish their life cycles in the rainy season, even though their F_v/F_m values were relatively low.

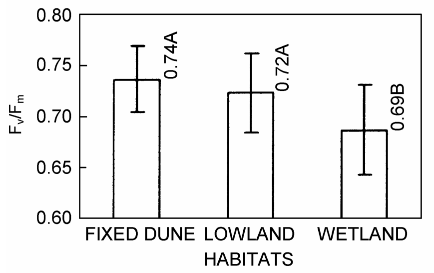

Fig. 3. Average F_v/F_m values of annual C_3 grasses distributed in different habitats of Hunshandak Sandland. *Columns that share the same letters* had no significant difference at $p_{0.05}$ or $p_{0.01}$ (t-test).

Table 1. Soil characteristics of different habitats in Hunshandake Sandland.

Habitat	Shifting dunes	Fixed dune	Lowland	Wetland
Organism [g kg^{-1}]	0.30	1.89	5.40	13.20
Total N [g kg^{-1}]	0.03	0.26	0.47	1.18
Total P [g kg^{-1}]	0.09	0.29	0.34	0.46
Total K [g kg^{-1}]	15.00	18.00	18.10	21.40
Total salt content [g kg^{-1}]	0.23	0.44	0.78	0.86
pH	6.6	7.8	8.5	8.6

C_3 and C_4 plants have different gas exchange and Chl fluorescence characteristics. Salt marsh C_3 and C_4 species have different strategies of PS2, *e.g.* F_v/F_m values of C_4 species were always higher than those of the C_3 species (Krall and Edwards 1990, Nieva *et al.* 1999). There were 13 annual C_4 grass species, 12 of them distributed in the

Table 2. Photochemical efficiency (mean±SD) of 99 plant species with different life types ("a" for annual and "p" for perennial), photosynthetic pathway (C_3, C_4, and CAM), life forms ("G" for grasses, "S" for shrubs, and "T" for trees), and habitat ("L" for lowland, "W" for wetland, and "F" for fixed dune) in a sparse-elm grassland of Hunshandak Sandland. Species with "√" had F_v/F_m values higher than 0.76 which might represent ecological adaptation to their habitats.

Family	Species	Life type	Photosynthetic pathway	Life form	Habitat	Root depth [cm]	F_v/F_m
Amaranthaceae	*Amaranthus retroflexus* √	a	C_4	G	L	40	0.775±0.001
	A. viridis √	a	C_4	G	F	40	0.776±0.003
Asclepiadaceae	*Cynanchum thesioides*	a	C_3	G	L	20	0.736±0.003
Betulaceae	*Betula fruticosa* √	p	C_3	S	L	120	0.769±0.005
Caprifoliaceae	*Lonicera chrysantha* √	p	C_3	S	F	100	0.765±0.018
Caryophyllaceae	*Dianthus chinensis*	a	C_3	G	F	45	0.710±0.014
	Silene repens √	a	C_3	G	F	50	0.773±0.032
Chenopodiaceae	*Agriophyllum pungens*	a	C_4	G	F	90	0.774±0.018
	Bassia dasyphylla	a	C_4	G	F	30	0.736±0.018
	Chenopodium aristatum	a	C_3	G	F	45	0.699±0.023
	C. glaucum	a	C_4	G	F	20	0.713±0.006
	Corispermum heptapotamicum	a	C_4	G	F	20	0.675±0.006
	Salsola collina √	a	C_4	G	F	55	0.771±0.007
	Suaeda glauca	a	C_4	G	L	10	0.672±0.013
Compositae	*Aster tataricus*	p	C_3	G	W	20	0.742±0.006
	Artemisia annua	p	C_3	G	F	28	0.670±0.001
	A. argyi √	p	C_3	G	L	60	0.773±0.009
	A. frigida √	p	C_3	S	F	100	0.770±0.001
	A. gmelinii √	p	C_3	S	F	100	0.782±0.014
	A. ordosica √	p	C_3	S	F	70	0.776±0.003
	Cirsium esculentum	a	C_3	G	W	36	0.697±0.009
	C. japonicum	a	C_3	G	W	35	0.689±0.006
	Echinops gmelini	a	C_3	G	F	18	0.720±0.007
	Heteropappus altaicus	p	C_3	G	F	30	0.738±0.009
	Inula britanica	a	C_3	G	W	12	0.672±0.003
	Leontopodium leontopodioides	a	C_3	G	W	18	0.714±0.020
	Saussurea japonica	a	C_3	G	L	32	0.720±0.007
	S. runcinata	a	C_3	G	L	39	0.634±0.021
	Stemmacantha uniflora	p	C_3	G	L	34	0.748±0.010
	Taraxacum dissectum	a	C_3	G	W	15	0.663±0.013
	T. mongolicum	a	C_3	G	W	40	0.684±0.008
	Xanthium sibiricum	a	C_3	G	W	26	0.687±0.020
Crasulaceae	*Orostachys malacophyllus*	a	CAM	G	L	9	0.675±0.013
	Sedum sarmentosum	a	CAM	G	L	20	0.742±0.007
Cruciferae	*Thellungiella salsuginea*	a	C_3	G	F	64	0.753±0.017
Cyperaceae	*Carex duriuscula*	a	C_3	G	W	20	0.697±0.012
	Scirpus triqueter	a	C_3	G	W	20	0.722±0.009
Equisetaceae	*Equisetum hiemale*	a	C_3	G	L	39	0.653±0.010
Geraniaceae	*Geranium erioetemon*	a	C_3	G	F	40	0.738±0.018
Gramineae	*Achnatherum splendens* √	a	C_4	G	L	100	0.781±0.004
	Agropyron cristatum	a	C_3	G	F	25	0.753±0.010
	Calamagrostis epigeios	a	C_3	G	F	15	0.744±0.006
	Cleistogenes squarrosa	p	C4	G	L	60	0.731±0.013
	Eragrostis minor	a	C4	G	W	9	0.692±0.012
	Leymus chinensis	p	C3	G	F	10	0.637±0.005
	Phragmites australis	p	C3	G	W	50	0.727±0.008
	Psammochloa villosa √	p	C3	G	F	100	0.777±0.009
	Setaria glauca	a	C4	G	L	15	0.689±0.001
	S. viridis	a	C4	G	F	15	0.660±0.003
	Solanum septemlobum	a	C3	G	L	18	0.718±0.007

Table 1 (continued)

Family	Species	Life type	Photosynthetic pathway	Life form	Habitat	Root depth [cm]	F_v/F_m
Iridaceae	*Iris ensaca* √	a	C_3	G	L	80	0.767±0.018
Labiatae	*Thymus serpyllum*	p	C_3	S	F	30	0.745±0.006
Leguminoseae	*Astragalus melilotoides* √	a	C_3	G	F	100	0.773±0.009
	A. mongholicus	p	C_3	G	F	50	0.751±0.023
	Caragana microphylla √	p	C_3	S	F	150	0.783±0.014
	Gueldenstaedtia verna	a	C_3	G	L	50	0.734±0.015
	Hedysarum fruticosum	p	C_3	S	F	24	0.730±0.012
	Medicago falcata √	a	C_3	G	F	100	0.778±0.004
	Melilotus suaveolens	a	C_3	G	L	70	0.756±0.009
	Oxytropis glabra	a	C_3	G	L	45	0.719±0.018
	Swainsonia sahsula	p	C_3	G	L	40	0.734±0.011
	Thermopsis lanceolata √	p	C_3	G	L	50	0.759±0.029
	Vicia amoena	a	C_3	G	W	28	0.660±0.010
Liliaceae	*Allium senescens*	a	C_3	G	F	20	0.737±0.025
	A. tenuissimum	a	C_3	G	L	20	0.742±0.006
	Asparagus schoberioides	a	C_3	G	F	56	0.708±0.025
	Hemerocallis minor	a	C_3	G	L	35	0.753±0.002
Malvaceae	*Malva verticillata*	a	C_3	G	L	45	0.755±0.017
Moraceae	*Cannabis ruderalis*	a	C_3	G	F	36	0.758±0.009
Plantaginaceae	*Plantago depressa*	a	C_3	G	W	29	0.743±0.030
	P. maritima	a	C_3	G	W	29	0.706±0.008
Polygonaceae	*Polygonum divaricatum* √	a	C_3	G	F	42	0.779±0.015
	P. hydropiper	a	C_3	G	W	16	0.570±0.008
	P. manshurica	a	C_3	G	L	23	0.705±0.016
	P. sibiricum	a	C_3	G	F	50	0.746±0.010
Ranunculaceae	*Anemone silvestris*	p	C_3	G	W	8	0.723±0.013
	Clematis aethusifolia	a	C_3	G	F	90	0.720±0.006
	Halerpestes ruthenica	a	C_3	G	W	24	0.712±0.014
	Ranunculus pulchillus	a	C_3	G	L	15	0.700±0.013
	Thalictrum petaloideum	a	C_3	G	L	50	0.722±0.013
	T. squarrosum √	a	C_4	G	F	50	0.773±0.014
Rosaceae	*Chamaerhodos erecta* √	p	C_3	G	F	45	0.761±0.006
	Malus baccata √	p	C_3	T	F	100	0.775±0.005
	Potentilla anserina	a	C_4	G	L	25	0.714±0.011
	P. chinensis	a	C3	G	F	20	0.705±0.010
	P. flagellaris	a	C_3	G	W	24	0.600±0.016
	P. strigosa	a	C_3	G	F	20	0.706±0.010
	Prunus padus √	p	C_3	T	F	160	0.778±0.006
	Sanguisorba officinalis √	p	C_3	G	L	30	0.764±0.006
	Spiraea trilobata	a	C_3	G	W	40	0.732±0.013
Salicaceae	*Salix gordejevii* √	p	C_3	S	F	90	0.766±0.013
	S. microstachya √	p	C_3	S	L	120	0.781±0.002
Saxifragaceae	*Ribes pulchellum*	p	C_3	S	F	60	0.752±0.011
Solanaceae	*Solanum septemlobum* √	p	C_3	G	F	60	0.779±0.007
Ulmaceae	*Ulmus pumila* √	p	C_3	T	F	200	0.792±0.005
Umbelliferae	*Bupleurum scorzonerifolium* √	a	C_3	G	L	55	0.775±0.001
	Cnidium monnieri	a	C_3	G	F	38	0.738±0.011
	Ferula bungeana	p	C_3	G	F	30	0.679±0.013
Urticaceae	*Urtica cannabina* √	p	C_3	G	F	46	0.760±0.001

fixed dune and lowland (Table 1). F_v/F_m of the C_4 species was higher than those of the CAM and C_3 species (Fig. 3), indicating that the C_4 species were more effective in resource utilization under environmental stresses.

Under high pH or high salt concentration, photosynthetic rate would decrease sharply (Akira 1996, Kao *et al.*

2001). In our investigation, wetland is more watery and pickled than lowland and fixed dune (Table 2). Hence C_3 species growing in wetland had lower maximum quantum efficiency than those in fixed dune and lowland (Fig. 3). This phenomenon implied that high irradiance and high temperature are limiting factors that influence photosynthetic characteristics for the species distributed in watery and pickled wetland, even though there is more nutrient matter in soil.

Because the severe wind dust storms have been threatening the ecological safety of North China, a lot of exotic species such as *Populus* spp. had been planted in Hunshandak Sandland as an ecological barrier. However, only few *Populus* trees could survive there, not only because *Populus* species could not adapt to the climate, but also the annual rainfall in this region was less than 400 mm and inadequate for forest distribution. Ecologically, sparse-elm grassland shapes up the characteristic landscape in Hunshandak Sandland, and elms (*U. pumila*) are more ecological and economic tree species in this region (Li *et al.* 2003). In the practices of vegetation restoration of Hunshandak Sandland, most of the native species with relatively high F_v/F_m (Table 2), such as *U. pumila*, *S. gordejevii*, *C. microphylla*, *A. squarrosum,* and *A. cristatum* should be preferentially chosen.

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