Plant functional types and their ecological responses to salinization in saline grasslands, Northeastern China

R.Z. WANG

Laboratory of Quantitative Vegetation Ecology, Institute of Botany, the Chinese Academy of Sciences, No. 20 Nanxincun, Xiangshan, Beijing, 100093, China

Abstract

Photosynthetic pathways (C_3, C_4,, and CAM) and morphological functional types (*e.g.* shrubs, high perennial grasses, short perennial graminaceous plants, annual grasses, annual forbs, perennial forbs, halophytes, and hydrophytes) were identified for the species from salinity grasslands in Northeastern China, using the data from both stable carbon isotope ratios ($\delta^{13}C$) and from the references published between 1993 and 2002. 150 species, in 99 genera and 37 families, were found with C_3 photosynthesis, and most of these species are dominants [*e.g.* *Leymus chinensis* (Trin.) Tzvel., *Calamagrostis epigeios* (L.), *Suaeda corniculata* (C.A. Mey.) Bunge]. 40 species in 25 genera and 8 families were identified with C_4 photosynthesis [*e.g.* *Chloris virgata* Sw., *Aeluropus littoralis* (Gouan) Parlat] and 1 species with CAM photosynthesis. *Gramineae* is the leading family with C_4 photosynthesis (27 species), *Chenopodiaceae* ranks the second (5 species). The significant increase of C_4 proportions with intense salinity suggested this type plant is remarkable response to the grassland salinization in the region. 191 species were classified into eight morphological functional types and the changes of most of these types (*e.g.* PEF, HAL, and HPG) were consistent with habitats and vegetation dynamics in the saline grassland. My findings suggest that the photosynthetic pathways, combined with morphological functional types, are efficient means for studying the linkage between species and ecosystems in this type of saline grassland in Northeastern China.

Additional key words: C_3, C_4, CAM species; ecological responses; morphological functional types; saline grasslands.

Introduction

Photosynthetic pathways (C_3, C_4, and CAM) and morphological types are the main composition of plant functional types (PFTs), and the popular means for studying the logical links between physiological and life-history strategies at plant level, as well as ecological process at ecosystem and global levels (Chapin 1993, Paruelo and Lauenroth 1996, Wang 2003). PFTs are defined based on the relevant traits, *e.g.* plant morphology, physiology, life history, and bio-climatic tolerance, depending on the intentions and studying scales (Wang 2003). Some studies proved that grassland management decisions must take into account photosynthetic and morphological functional types, because they are closely related to seasonal development patterns (warm season *versus* cool season) (Williams and Markley 1973) and grazing succession (Wang 2002a).

Saline grasslands, one of main vegetation types, cover an area of about 17 000 km^2 in the central part of Northeastern China. The usual growing conditions of the grasslands produce herbage superior both in quality and in quantity, so that this type of grassland is one of the best suited for the rangeland industry in Northeastern China (Wang 2002a). There has, however, been deterioration and salinization of the grasslands since the 1960's, because of the increasing demand for agricultural land and need for more livestock. The substantial reduction in canopy cover throughout much of the grasslands, combined with soil salinization, has led to considerable changes in vegetation, *e.g.* plant composition, distribution, and plant functional types. Studies on the grasslands, *e.g.* community classification, plant biomass, and grazing effects, have been conducted in the region (Zheng and Li 1993, Wang 2002a), but the patterns of photosynthetic and morphological functional types remain unclear. Present study investigated the composition of photosynthetic pathways and morphological functional types and their ecological roles in the saline grasslands. The results could be important for the interpretation of relationships between the changes of plant functional types and grassland use.

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Fax: 0086-01-82591781, e-mail: wangrenzh@sohu.com
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Materials and methods

This study was conducted in the Songnen grasslands (43°30'~48°40'N, 121°30'~127°00'E), typical saline grasslands in Northeastern China. The grasslands are widely distributed at the eastern end of the Eurasian steppe zone, on average 141 m above sea level, varying from 137.8 to 144.9 m. Most of the region has meadow chernozem soil, with 3.5 to 6.0 % organic matter in the surface layer. Average soil pH for this soil type is about 8.7, rising as high as 10.0 in the spring (Wang and Ripley 1997). For at least 20 years prior to 2003, the grasslands were grazed and mowed, and transient floods may occur in autumn. In winter, the climate of the area is dominated by the Mongolian anticyclone, which produces a westerly flow of cold, dry air and little snowfall. As the anticyclone breaks down in spring, the region comes increasingly under the influence of moist Pacific air masses, reaching a climax in the summer monsoon, which lasts 2–3 months. The mean annual air temperature is about 5 °C, varying from –18 °C in January to 23 °C in July. Annual precipitation varies from 300 to 600 mm, falling mainly during the summer monsoon. Precipitation is not distributed evenly over growing season, of which 70 % falls between June and August in this region.

Floristic species were obtained from the sampling data conducted from 1986 to 2003 and from references published from 1993 to 2002 (Zheng and Li 1993, Wang 2002a). Photosynthetic pathway types for the forage species were determined by stable carbon isotope ratio ($\delta^{13}C$) and from the references published between 1985 and 2002 (*e.g.* Takeda and Hakoyama 1985, Li 1993, Redmann *et al*. 1995, Yin and Li 1997, Pyankov *et al.* 2000, Wang 2002c,d). Plants with $\delta^{13}C$ values above –19 ‰ were considered to have the C_4 photosynthesis, and $\delta^{13}C$ values lower than –21 ‰ to have C_3 photosynthesis (Redmann *et al*. 1995). Plants identified in the region were classified into both photosynthetic pathway types by physiological attributes ($\delta^{13}C$) and morphological functional types, *e.g.* shrubs (SHR), high perennial grasses (HPG), short perennial graminaceous plants (grasses and sedge) (SPG), annual grasses (ANG), annual forbs (ANF), perennial forbs (PEF), halophytes (HAL), and hydrophytes (HYD) by morphological attributes (Table 1).

Table 1. Photosynthetic pathway (C_3 or C_4) and morphological functional types in saline grasslands, Northeastern China. Nomenclature follows Kitagawa (1979). Plant functional types: SHR = shrubs, HPG = high perennial grasses, SPG = short perennial graminaceous plants (grasses and sedge), ANG = annual grasses, ANF = annual forbs, PEF = perennial forbs, HAL = halophytes, HYD = hydrophytes. Habitat types: DB = disturbed and cultivated land, DU = dune, LS = light salinity, MS = moderate salinity, HS = heavy salinity, SM = saline marsh.

	Species	C_3 / C_4	PTF type	Habitat
Gymnospermae				
Ephedraceae	*Ephedra sinica* Staph.	C_3	SHR	DU
Angiospermae				
Dicotyledoneae				
Amaranthaceae	*Amaranthus ascendens* Lois.	C_4	ANF	DB
	A. blitoides S. Watson	C_4	ANF	DB
	A. retroflexus L.	C_4	ANF	DB
Apocynaceae	*Apocynum lancifolium* Russan.	C_3	HAL	MS HS
Asclepiadaceae	*Cynanchum amplexicaule* Hemsl.	C_3	PEF	LS
	C. chinensis R. Br.	C_3	PEF	DU
	Pycnostelma paniculatum K. Schum.	C_3	PEF	DU
Bignoniaceae	*Incarvillea sinensis* Lamark.	C_3	ANF	LS DU
Boraginaceae	*Cynoglossum divaricatum* Steph.	C_3	PEF	DU
	Lappula echinata Gillb.	C_3	PEF	DU LS
	L. intermedia (Ledeb.) M. Pop.	C_3	PEF	DU
Campanulaceae	*Adenophora stenophylla* Hemsley	C_3	PEF	DU LS
	Platycodon grandiflorum D.C.	C_3	PEF	DU
Caryophyllaceae	*Dianthus amurensis* Jacq.	C_4	PEF	DU LS
	Silene repens Pall.	C_3	PEF	DU
Chenopodiaceae	*Agriophyllum arenarium* Bieb.	C_4	ANF	DU
	Axyris amaranthoides L.	C_3	ANF	DB
	Bassia dasyphylla O. Kuntze	C_4	ANF	DU
	Chenopodium acuminatum Willd.	C_3	ANF	DB

Table 1 (continued)

	Species	C_3 / C_4	PTF type	Habitat
Chenopodiaceae (cont.)	*Chenopodium album* L.	C_3	ANF	DB
	Ch. glaucum L.	C_3	HAL	DB HS
	Kochia prostrata Schrad.	C_4	SHR	DB
	K. scoparia (L.) Schrad.	C_4	ANF	DB
	K. sieversiana (Pall.) C.A. Mey.	C_4	HAL	MS SM
	Salsola collina Pall.	C_4	ANF	DB DU
	S. foliosa (L.) Schrad.	C_4	ANF	DB
	Suaeda corniculata (C.A. Mey.) Bunge	C_3	HAL	HS SM
	S. glauca Bunge	C_3	HAL	HS SM
	S. heteroptera Kitag.	C_3	HAL	HS SM
Compositae	*Artemisia anethoides* Mattf.	C_3	ANF	DB LS
	A. anethifolia Weber	C_3	HAL	HS
	A, annua L.	C_3	ANF	DU LS
	A. argyi Levl. *et* Vant.	C_3	PEF	DU LS
	A. desertorum Spreng.	C_3	PEF	DU
	A. frigida Willd.	C_3	SHR	LS MS
	A. integrifolia L.	C_3	PEF	LS
	A. japonica Thunb. var. *manshurica* Kom.	C_3	PEF	DU LS
	A. laciniata Willd.	C_3	PEF	LS
	A. mongolica Fisch.	C_3	PEF	LS MS
	A. scoparia Waldst. *et* Kit.	C_3	HAL	DB LS MS
	A. sieversiana Willd.	C_3	PEF	DB
	Filifolium sibiricum Kitam.	C_3	PEF	DU
	Heteropappus altaicus (Willd.) Novopokr.	C_3	HAL	LS MS DU
	Hypochaeris grandiflora Ledeb.	C_3	PEF	LS
	Inula britanica L.	C_3	PEF	LS DB
	I. japonica Thunb.	C_3	PEF	LS
	Ixeris chinensis Nakai subsp. *graminifolia* Kitag.	C_3	PEF	DB
	I. chinensis Nalai var. *intermedia* Kitag.	C_3	PEF	DB
	I. sonchifolia Hance	C_3	PEF	DB
	Lactuca indica L.	C_3	PEF	LS
	Leontopodium leontopodioides Beauv.	C_3	PEF	DU LS
	Ligularia mongolica (Turcz.) DC.	C_3	PEF	MS LS
	Neopallasia pectinata (Pall.) Polijak	C_3	ANF	LS DU
	Picris japonica Thunb.	C_3	PEF	LS DB
	Saussurea glomerata Poir.	C_3	HAL	MS HS
	S. runcinata D.C.	C_3	HAL	MS HS
	Scorzonera glabra Rupr.	C_3	PEF	LS
	Senecio ambracens Turcz.	C_3	PEF	LS MS
	S. integrifolius Claiville.	C_3	PEF	LS
	Serratula yamatsutana Kitag.	C_3	PEF	DU LS MS
	Taraxacum mongolicum Hand.	C_3	HAL	MS HS
	T. ohwianum Kitam.	C_3	HAL	MS HS
	Xanthium strumarium L.	C_3	ANF	DB LS
Convolvulaceae	*Calystegia pellita* Ledeb.	C_3	PEF	LS
Crassulaceae	*Sedum aizoon* L.	CAM	PEF	DU
Cruciferae	*Dontostemon micranthus* C.A. M.	C_3	ANF	DU LS
	Lepidium apetalum Willd.	C_3	ANF	DB LS
	Ptilotrichum elongatum C.A. May	C_3	SHR	DU
Dipsacaceae	*Scabiosa comosa* L.	C_3	PEF	DU
Euphorbiaceae	*Euphorbia esula* L.	C_3	PEF	DU
	E. humifusa Willd.	C_4	ANF	DB
Fabaceae	*Astragalus melilotoides* Pall.	C_3	PEF	DU
	Gueldensfaedtia stenophylla Bunge	C_3	PEF	LS
	Kummerowia stipulacea (Maxim.) Makino	C_3	ANF	DB
	K. striata (Thunb.) Schindler	C_3	ANF	DB

Table 1 (continued)

	Species	C_3 / C_4	PTF type	Habitat
Fabaceae (cont.)	*Lespedeza davurica* Schindler	C_3	SHR	DU
	Melilotus suaveolens Ledeb.	C_3	ANF	DB
	Oxytropis hirta Bunge	C_3	PEF	DU
	O. myriophylla D.C.	C_3	PEF	DU
	Thermopsis lanceolata R. Br.	C_3	PEF	LS
Geraniaceae	*Erodium stephanianum* Willd.	C_3	ANF	DU
Labiatae	*Phlomis tuberosa* L.	C_3	PEF	LS MS
	Schizonepeta multifida (L.) Briq.	C_3	ANF	DU LS MS
	Scutellaria baicalensis Georgi	C_3	PEF	LS
	S. ikonnikovii Juz.	C_3	PEF	LS
	S. scordifolia Fisch.	C_3	PEF	LS
	Thymus serphyllum L.	C_3	SHR	DU
Linaceae	*Linum stelleroides* Planchon	C_3	ANF	DU
Orobanchaceae	*Orobanche caerulescens* Stephan	C_3	ANF	DU
Plantaginaceae	*Plantago asiatica* L.	C_3	PEF	MS LS
	P. depressa Willd.	C_3	PEF	MS LS
Plumbaginaceae	*Limonium bicolor* O. Kuntze	C_3	HAL	HS SM
Polygalaceae	*Polygala tenuifolia* Willd.	C_3	PEF	LS
Polygonaceae	*Polygonum aviculare* L.	C_3	ANF	DB
	P. divaricatum L.	C_3	PEF	DB DU
	P. sibiricum Laxm.	C_3	HAL	HS SM
Portulacaceae	*Portulaca oleracea* L.	C_4	ANF	DB
Primulaceae	*Glaux maritima* L.	C_3	HAL	LS HS
Ranunculaceae	*Clematis hexapetala* Pall.	C_3	PEF	DU LS
	Pulsatilla chinensis (Bunge) Rgl.	C_3	PEF	DU LS
	Ranunculus japonicus Thumb.	C_3	PEF	LS
	Thalictrum petaloedeum L. *var. supr.* (Nakai) Kitag.	C_3	PEF	LS DU
	Th. simplex L.	C_3	PEF	LS
	Th. squarrosum Steph.	C_3	PEF	LS
Rosaceae	*Potentilla anserina* L.	C_3	HAL	LS HS
	P. betonicaefolia Poiret	C_3	PEF	DU
	P. chinensis Seringe	C_3	HAL	LS MS
	P. discolor Bunge	C_3	PEF	LS
	P. filipendula Willd.	C_3	PEF	LS MS
	P. flagellaris Willd.	C_3	PEF	LS MS
	P. verticillaris Steph.	C_3	PEF	DU LS
	Sanguisorba officinalis L.	C_3	PEF	LS
	S. tenuifolia Fisch	C_3	PEF	LS
Rubiaceae	*Galium verum* L.	C_3	PEF	LS
Rutaceae	*Haphophyllum dauricum* Juss	C_3	PEF	DU
Scrophulariaceae	*Cymbaria dahurica* L.	C_3	PEF	DU LS
	Veronica linearifolia Pall.	C_3	PEF	LS
Solanaceae	*Solanum nigrum* L.	C_3	ANF	DB
Thymelaeaceae	*Diarthron linifolium* Turcz.	C_3	ANF	DU
	Stellera chamaijasme L.	C_3	PEF	DU
Umbelliferae	*Bupleurum scorzonerifolium* Willd.	C_3	PEF	LS
	Sphallerocarpus gracilis (Bess.) K.	C_3	PEF	DB
	Siler divaricatum Benth. *et* Hook	C_3	PEF	LS
Violaceae	*Viola dissecta* Ledeb.	C_3	PEF	DU
Zygophyllaceae	*Tribulus terrestris* L.	C_4	ANF	LS

Table 1 (continued)

	Species	C_3 / C_4	PTF type	Habitat
Monocotyledoneae				
Commelinaceae	*Commelina communis* L.	C_4	PEF	DB
Cyperaceae	*Bolboschoenus compactus* Heffm.	C_3	HYD	SM
	B. maritimus (L.) Pall.	C_3	HYD	SM
	Carex duriuscula C.A.M.	C_3	HAL	HS MS
	C. pediformis C.A.M.B.	C_3	SPG	LS DU
	Heleocharis intersita Zinesrl.	C_3	HYD	SM
	Scirpus tabernaemontani Gmel.	C_3	HYD	SM
Gramineae	*Achnatherum avinoides* (Honda) Chang	C_4	HPG	LS MS
	A. sibiricum (L.) Keng	C_4	HAL	HS SM
	Aeluropus littoralis (Gouan) Parlat	C_4	HAL	HS SM
	Agropyron cristatum (L.) Gaertner	C_3	HPG	DU LS
	Arthraxon hispidus (Thunb.) Makino	C_4	HPG	DB
	Arundinella hirta (Thunb.) Tanaka	C_4	HPG	LS
	Avena fatua L.	C_3	HPG	DB
	Calamagrostis epigeios (L.) Roth	C_3	HPG	LS SM
	Chloris virgata Sw.	C_4	HAL	HS MS SM
	Cleistogenes chinensis (Maxim.) Keng	C_4	SPG	LS
	C. squarrosa (Trin.) Keng	C_4	SPG	LS
	Clinelymus sibiricus (L.) Nevski	C_3	HPG	LS MS
	Digitaria ciliaris (Rotz.) Koel	C_4	ANG	DB
	D. ischaemum (Schreb.) Schreb. *ex* Muhl.	C_4	ANG	DB
	D. lineis (Krock.) Crep	C_4	ANG	DB
	D. sanguinalis (L.) Scop.	C_4	ANG	DB
	Echinochloa caudata Roshev.	C_4	ANG	SM HS
	E. crus galli (L.) Beauv.	C_4	ANG	SM HS
	Eragrostis cilianensis (All.) Link.	C_4	HPG	DB
	E. filiformis Link.	C_4	HPG	DB
	E. pilosa (L.) P. B.	C_4	HPG	DB
	E. poaeoides Beauv.	C_4	HPG	DB LS
	Eriochloa villosa (Thunb.) Kunth L.	C_4	HPG	DU LS
	Festuca ovina L.	C_3	HPG	LS
	Hemarthria sibirica (Gand.) Ohwi	C_4	HYD	SM
	Hierochloe glabra Trin.	C_3	HPG	LS DB
	Hordeum brevisubulatum (Trin.) Link	C_3	HAL	HS SM
	H. brevisubulatum var. *hirtellum* Cheng *ex* Skv.	C_3	HPG	HS SM
	Imperata cylindrica (L.) P.B.	C_4	HPG	DU
	Koeleria cristata (L.) Pers.	C_3	HPG	LS
	Leymus chinensis (Trin.) Tzvel.	C_3	HPG	LS MS
	Miscanthus sacchariflorus (Maxim.) Hack.	C_4	HPG	LS
	Panicum ruderale (Kitag.) Cheng	C_4	SPG	DB
	Pennisetum flaecidum Griseb.	C_4	HPG	DU
	Phragmites communis Trin.	C_3	HYD	HS SM
	Poa pratensis L.	C_3	SPG	LS
	Puccinellia chinampoensis Ohwi.	C_3	HAL	HS SM
	P. jeholensis Kitag.	C_3	HAL	HS SM
	P. tenuiflora (Turcz.) Scrib. *et* Merr.	C_3	HAL	HS SM
	Setaria lutescens (Weigel) F. T. Hubb.	C_4	ANG	DB
	S. viridis (L.) Beauv.	C_4	ANG	DB
	Spodiopogon sibiricus Trin.	C_4	HPG	DU
	Stipa baicalensis Roshev.	C_3	HPG	DU LS
	S. grandis P. Smirn.	C_3	HPG	LS
Liliaceae	*Allium condensatum* Turcz.	C_3	PEF	DU
	A. macrostemon Bunge	C_3	PEF	DB LS
	A. polyrrhizum Turcz.	C_3	HAL	HS
	A. senescens L.	C_3	PEF	MS HS
	A. tenuissimum L.	C_3	PEF	DU

Table 1 (continued)

	Species	C_3 / C_4	PTF type	Habitat
Liliaceae (cont.)	*Anemarrhena asphodeloides* Bunge.	C_3	PEF	DU
	Asparagus davurica Fisch.	C_3	PEF	DU LS
	Lilium tenuifolium Fisch.	C_3	PEF	LS
	Scilla thunbergii Miyabe *et* Kudo	C_3	PEF	LS
Iridaceae	*Iris dichotoma* Pall.	C_3	PEF	DU LS
	I. pallasii Fisch.	C_3	HAL	HS MS
	I. ruthenica Ker-Gawl.	C_3	PEF	DU
	I. tenuifolia Pall.	C_3	PEF	HS MS
	I. ventricosa Pall.	C_3	PEF	MS LS
Typhaceae	*Typha minima* Funk	C_3	HYD	SM

Results

Floristic composition of photosynthetic pathway types: 191 vascular plant species (about 25 % of the total species in the Songnen grasslands), in 42 families and 124 genera, were identified with C_3, C_4, and CAM photosynthesis (Table 1). Of these species, 1 species was in *Gymnospermae*, 190 in *Angiospermae*. 65 % (124 of 191) was found in *Dicotyledoneae*, *e.g. Compositae* (34 species), *Chenopodiaceae* (14 species), *Fabaceae* (9 species), *Rosaceae* (8 species), and *Ranunculaceae* (6 species). 35 % were in *Monocotyledoneae*, *e.g. Gramineae* (44 species), *Liliaceae* (9 species), *Cyperaceae* (6 species), and *Iridaceae* (5 species). As for photosynthetic pathway types, 150 species (79 % of the identified species in Table 1) in 99 genera and 37 families were found with C_3 photosynthesis, 40 species in 25 genera and 8 families with C_4 photosynthesis, and 1 species with CAM photosynthesis. 21 % (40 of 191) of the identified species in Table 1, or about 6 % of identified species in local flora, was found with C_4 photosynthesis, *e.g. Gramineae* (27 species), *Chenopodiaceae* (5 species), *Amaranthaceae* (3 species), 1 species each in *Caryophyllaceae*, *Euphorbiaceae*, *Portulacaceae*, *Zygophyllaceae*, and *Commelinaceae*. The occurrence of C_4 species was common in *Gramineae* (68 %) and *Chenopodiaceae* (36 %), and all the species in *Amaranthaceae*, *Portulacaceae*, *Zygophyllaceae*, and *Commelinceae* were found with C_4 photosynthesis in the region.

The occurrence of C_4 species and C_4 proportion (C_4/total species) were significant response to habitats in the saline grasslands in the region (Fig. 1*A*). Disturbed and cultivated land (DB) had the highest number of C_4 species (22 species) and C_4 proportion (47.8 %), followed by saline marsh (7 species and 29.2 %). C_4 proportions increased significantly from light salinity (LS) to saline marsh (SM) or with the salinization. Some C_4 species, *e.g. K. sieversiana* (Pall.) C.A. Mey., *Chloris virgata* Sw., *Aeluropus littoralis* (Gouan) Parlat, and *Achnatherum avinoides* (Honda) Chang., can form large patch of consociations. This suggested that the occurrence of C_4 species was related with grassland salinity in the region.

Morphological functional types: According to plant morphological attributes and life-span, the identified plant species were classified into 8 functional types, *e.g.* SHR, HPG, SPG, ANG, ANF, PEF, HAL, and HYD (Table 1 and Fig. 1*B*). Of the total 191 species identified in Table 1, 44 % was PEF type, while this type makes up less than 10 % of the total forage production in the region. 16 % species was ANF type, followed by HAL (15 %), HPG (12 %), ANG (5 %), HYD (4 %), SHR (3 %), and SPG (3 %). The total amount of grass species, including HPG, ANG, SPG, and some species in HAL and HYD types, was about 23 %, and these grass types make up about 90 % forage production in this type of grassland. Most grasses are the dominant species, *e.g. Leymus chinensis* (Trin.) Tzvel., *Calamagrostis epigeios* (L.) Roth., *Chloris virgata* Sw., and *Cleistogenes squarrosa* (Trin.) Keng. 15 % of the total species in this type of grassland was halophytes (HAL), *e.g. Suaeda corniculata* (C.A. Mey.) Bunge, *S. glauca* Bunge, *Aeluropus littoralis* (Gouan) Parlat, *Chloris virgata* Sw., and most of these species were also dominant species in heavy salinity area, *e.g.* water supply, camp near the centre of the grassland, and in the vicinity of gates to grazed areas. There were few SHR functional type species in the grasslands, *e.g. Ephedra sinica* Staph., *Kochia prostrata* Schrad., *Artemisia frigida* Willd., and *Ptilotrichum elongatum* C.A. May. SHR type species were only about 3 % of the total identified in the Table 1.

The responses of morphological functional type compositions to grassland salinity were remarkable in the saline grasslands (Fig. 2). Species numbers of PEF, HPG,and ANF decreased with the saline intensity or from light salinity to saline marsh, while those for HAL, HYD, and ANG increased considerably. Relative more abundance for HAL and ANG indicated that the saline stress was higher in these habitats.

Photosynthetic pathway compositions varied considerably in these morphological functional types (Fig. 1*B*). C_4 proportion (C_4/total species) was relatively higher in the grass functional types, *e.g.* HPG (52 %), ANG

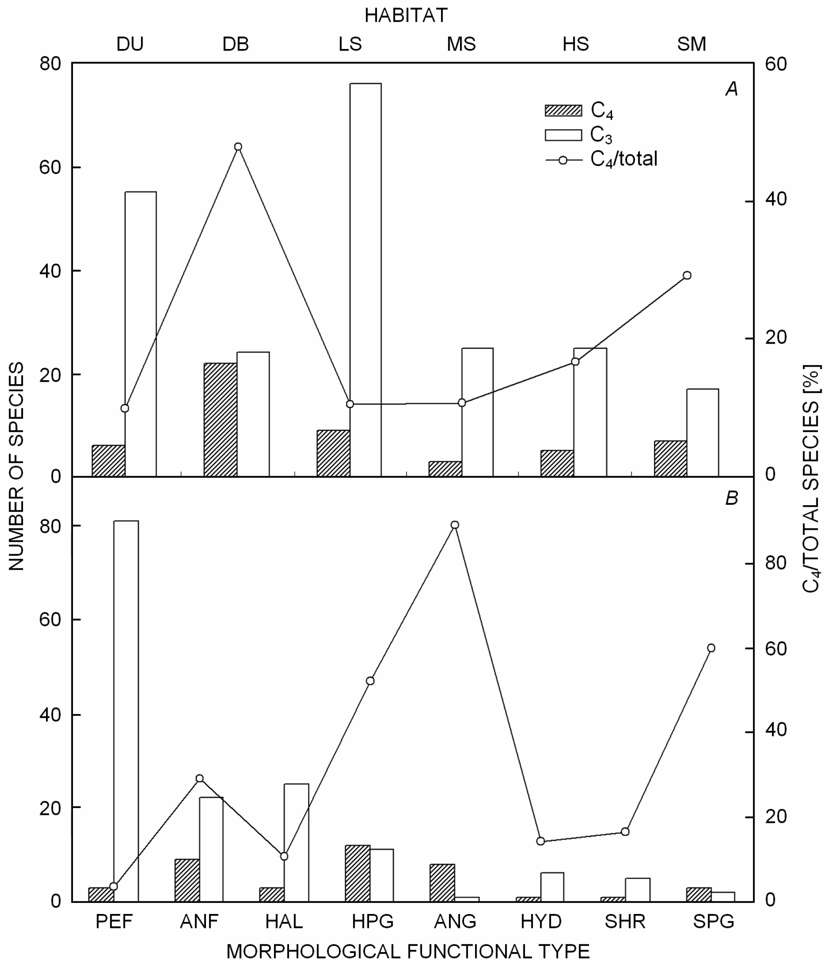

Fig. 1. The numbers of photosynthetic pathway types (C_3, C_4, and CAM) in different habitats (*A*) and photosynthetic pathway compositions in morphological functional types (*B*) in the saline grasslands, Northeastern China. Habitats: DB = disturbed and cultivated land, DU = dune, LS = light salinity, MS = moderate salinity, HS = heavy salinity, SM = saline marsh.

(89 %), SPG (60 %), and annual forbs (ANF) type (29 %), but much lower in PEF (4 %), HAL (11 %), HYD (14 %), and SHR (17 %). Larger C_4 proportion in ANG and ANF was related with vegetation dynamics, because most annual C_4 species are the pioneer species in grassland succession.

Discussion

Plant functional types, including photosynthetic pathways and morphological functional types, bring more details for studying the logical linkage between species and ecosystems at both species and global levels (Collins and Jones 1985, Chapin 1993, Cramer 1997, Leemans 1997, Duckworth 2000). The occurrence of C_4 species was not only related with large-scale climate variations, but also affected by local soil and community differences. Both the number of C_4 species and C_4 proportion in the saline grasslands were higher than in the other grassland types in Northeastern China, likely due to complex geo-relief, landscape, and soils (Wang 2002a). 40 C_4 species were identified in this type grassland, which was about 48 % and 74 % greater than those from steppe and desert border on the western part of this saline grassland. This may be mainly due to the intense salinity soil with pH average about 8.7, rising as high as 10.0 in the spring, and sufficient precipitation (450 mm per year) in the region. The occurrence of halophyte and hydrophyte C_4 species, *e.g. K. sieversiana* (Pall.) C.A. Mey., *Chloris virgata* Sw., *Aeluropus littoralis* (Gouan) Parlat, *Achnatherum avinoides* (Honda) Chang., and *Echinochloa caudata* Roshev., was very common (Table 1), because these C_4 species had relative higher saline tolerance and water use efficiency (Redmann *et al.* 1995, Yin and Li 1997, Wang 2002c). Relatively more annual precipitation resulted in the higher abundance of C_4 grasses (27 species), which is the leading family with C_4 photosynthesis. This finding is much different from the work by Pyankov *et al.* (2000): they found that *Chenopodiaceae* was the leading C_4

family, while the *Gramineae* ranks the second in desert and steppe in Mongolia (Pyankov *et al*. 2000). The other previous studies (Wang 2002a,b,c) also proved that the abundance of C_4 *Chenopodiaceae* species was relatively higher in the steppe and desert, which is much drier than the saline grasslands.

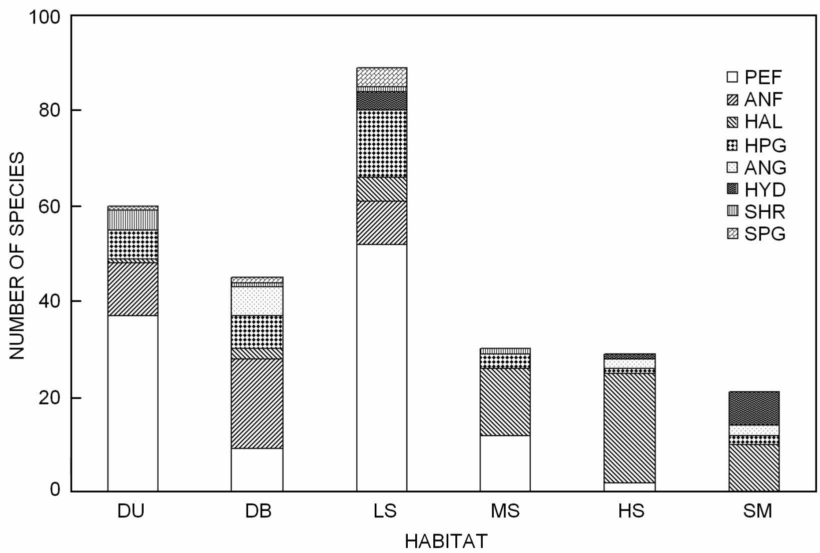

Fig. 2. The morphological functional type compositions in different habitats in the saline grasslands, Northeastern China. Habitats: DB = disturbed and cultivated land, DU = dune, LS = light salinity, MS = moderate salinity, HS = heavy salinity SM = saline marsh.

The occurrence of C_4 species is consistent with grassland conditions, *e.g*. salinity, deterioration, and grazing intensities in the region (Wang 2002a,c). This is supported by the observations that C_4 species number and C_4 proportion increased significantly with the saline intensity or from light salinity to saline marsh (Fig. 1*A*). Some C_4 species, *Chloris virgata* Sw., *Aeluropus littoralis* (Gouan) Parlat, and *Achnatherum avinoides* (Honda) Chang have higher salt tolerance to survive intense salinity condition and become the pioneer species in the restoration succession of salinized grassland, and can form large patch of consociations in the region. The earlier study (Wang 2002a) also proved that the C_4 species had greater capacity to tolerate environment stresses (saline and drought) caused by animal grazing.

The use of morphological functional types, combined with photosynthetic pathways, has become essential to study and predict consequences of environment changes on vegetation and ecosystem processes. Morphological functional types clearly reflect spatial and temporal changes in saline grassland ecosystems in local and region scales (Fig. 1*B*). Comparing with the adjacent steppe, the saline grassland had more perennial forbs and hydrophyte species, but less shrubs, short perennial graminaceous plants (grasses and sedge), and no succulents, indicating this type of grassland was more moist than steppe (Table 1, Fig. 1*B*; Wang 2003). Morphological functional type components varied significantly with the habitat types in the saline grasslands (Fig. 2). The number of PEF type decreased with grassland deterioration and salinity or from LS to DB, MS, HS, and SM, while that for HAL increased significantly (Fig. 2). This suggested the responses of these two functional types to the grassland salinity were different and can be used for predicting consequences of vegetation dynamics and grassland deterioration in local scale. Relatively more C_4 species found in ANF, HPG, ANG, and SPG types indicate that these functional types are more fit for the saline and moist grassland in the region. This and an earlier study (Wang 2002a) clearly document the importance of plant function types (*e.g*. photosynthetic pathways and morphological functional types) in predicting vegetation dynamics in the saline grassland and the occurrence of C_4 species and halophytes can be indicator plants for both diagnosis of grassland conditions and management decisions in the region.

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