

Photosynthetic and morphological functional types for native species from mixed prairie in Southern Saskatchewan, Canada

R.Z. WANG, X.Q. LIU, and Y. BAI*

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

Department of Plant Sciences, University of Saskatchewan, 51 Campus Drive, Saskatoon, Sask. S7N 5A8, Canada*

Abstract

Photosynthetic pathways (*e.g.* C₃, C₄) and morphological functional types (*e.g.* trees, shrubs, high perennial grasses, perennial forbs) were identified for the native species from the Saskatchewan mixed prairie, using the data from references published between 1950 and 2003. Of the total 219 identified species in 145 genera and 45 families, 208 species in 137 genera and 44 families were found with C₃ photosynthesis, and most of these species are dominants (*e.g.* *Agropyron dasystachyum* Hook. and *Stipa spartea* var. *curtiseta* Hitchc.). 11 species in 10 genera and 3 families were identified with C₄ photosynthesis (*e.g.* *Atriplex argentea* Nutt., *Andropogon scoparius* Michx., *Boutelou gracilis* Lag., *Calamovilfa longifolia* Hook.). The amount of total identified C₄ species in the region is much less than that from the South Dakota mixed prairie (27 species). *Gramineae* is the leading family with C₄ photosynthesis (8 species), *Chenopodiaceae* ranks the second (2 species). Relatively less forb types [50 % perennial forbs (PEF) and 12 % annual forbs (ANF)] and more graminoid types (25 %) composition suggested that the rangelands in the region are relatively stable. Lacking of the knowledge on the optimal traits for PFTs classification in the region, further studies (*e.g.* C₃ and C₄ plant identification and optimal trait selection) are needed to explore the relationships between PFTs and vegetation variations, as well as land-use and climate changes.

Additional key words: C₃ and C₄ species; habitats.

Introduction

The classification of plant species into functional types has received much attention since the introduction of the concept of plant functional types (PFTs), because PFTs provide a logical links between physiological and life-history strategies at plant level, as well as ecological process at ecosystem and global levels (Paruelo and Lauenroth 1996, Wang 2003). PFTs are referred to groups or types of plant species that share morphological and physiological attributes and play a similar role in ecosystems (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). The common use of PFTs classifications has been proposed to describe biological attributes of vegetation in relation to climate changes (Teeri and Stowe 1976, Teeri *et al.* 1980, Box 1996,

Ehleringer *et al.* 1997, Collatz *et al.* 1998), geographical distribution (Collins and Jones 1985, Takeda and Hakoyama 1985, Keeley 1998, Pyankov *et al.* 2000, Wang 2002), disturbance regime and land use history (Williams and Markley 1973, Hattersley 1992, Liu *et al.* 2004). Some studies clearly document the importance of PFTs (*e.g.* photosynthetic pathways and morphological functional types) in predicting vegetation dynamics in grasslands (Williams and Markley 1973, Wang 2002, 2003). These works provide strong evidence that the abundance of PFTs correlated with vegetation differences, land use, and climatic change in local, regional, and global scales.

The mixed prairie is characterized by Clements as a region, the potential climax vegetation of which includes both mid-grasses and short-grasses. It lies entirely within the Great Plain, with a latitudinal range of about

Received 14 April 2005, accepted 11 July 2005.

Fax: 01186-10-82591781, e-mail: wangrenzh@sohu.com

Acknowledgements: We are grateful for the funding provided by Key Laboratory of Vegetation Ecology (Northeast Normal University), Ministry of Education, P.R. China and in part by Key Projects of Knowledge Innovation of Chinese Academy of Sciences (KSCX1-08-03).

2 600 km (29–52°), encompassing 3 Canadian provinces and 8 American states (Coupland 1992). The mixed prairie in the southern Saskatchewan, located at the northern end of the mixed prairie, covers large continuous area. Land use in the region is shared between crop production and rangeland grazing, and the proportion of the area allocated to each activity varies according to aridity of climate and the character of the soil. Studies on the rangelands, *e.g.* community classification, plant biomass, and grazing effects, have been well conducted

Materials and methods

The mixed prairie, widely distributed in southern Saskatchewan, lies near the northern edge of the mixed prairie association of Clements, and the zonal vegetation in the region was classified into five major community types (*e.g.* *Stipa–Agropyron*, *Stippa–Bouteloua*, *Bouteloua–Agropyron*, *Stippa–Bouteloua–Agropyron*, and *Agropyron–Koeleria*) (Coupland 1992). Floristic composition varies throughout the region in response to regional climate, soil texture, and physiographic position, and the rangeland is mainly dominated by xerophytes, *e.g.* *Agropyron dasystachyum* Hook. and *Stipa spartea* Trin. Most of the region has dark brown, brown, and sandy loam soils. Average soil pH for the region is about 8.0, rising from 7.2 to 8.3 (Jong and Stewart 1973, Coupland 1992). The climate of the region is generally dry-sub-humid to semi-arid, with some years ranging from humid to arid. Dry years tend to be grouped and periods of severe drought occur. Mean annual air temperature is about 4 °C, varying from –14 °C in January to 20 °C in July. Annual precipitation is about 400 mm, 70 % of

(Coupland 1961, 1992, Coupland *et al.* 1973), but the patterns of plant functional types and its relation with local climate remain unclear. The information could be important for predicting climate changes, vegetation dynamics, and land use at both local and global scales. We investigated the composition of photosynthetic pathways and morphological functional types in the region and the results may be useful for the interpretation of relationships between the changes of plant functional types and land use and climate changes.

which is falling mainly during the growing season. Winds are strong and frequent, particularly in spring.

Complete species' lists for the mixed prairie were obtained from local floras, published from 1950 to 1996 (Coupland 1950, 1961, 1992, Saskatchewan Agriculture and Food 1996). Photosynthetic pathway types for native species were determined by stable carbon isotope ratio ($\delta^{13}\text{C}$) and from the references published between 1985 and 2002 (*e.g.* Downton 1975, Raghavendra and Das 1978, Ode *et al.* 1980, Takeda and Hakoyama 1985, Li 1993, Redmann *et al.* 1995, Pyankov *et al.* 2000, Wang 2002, Rusch *et al.* 2003, Liu *et al.* 2004). Plants identified in the region were classified into both photosynthetic pathway types by physiological attributes ($\delta^{13}\text{C}$) and morphological functional types, *i.e.* trees (TRE), shrubs (SHR), high perennial grasses (HPG), short perennial graminaceous plants (grasses and sedge) (SPG), annual grasses (ANG), annual forbs (ANF), and perennial forbs (PEF), by morphological attributes (Table 1).

Table 1. Photosynthetic pathway (C_3 or C_4) and morphological functional types in mixed prairie in Southern Saskatchewan, Canada. Nomenclature follows Kitagawa (1979). Plant functional types: TRE = trees, SHR = shrubs and vines, 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: LT = level terrain, GS = grassy slopes, HW = hillwash, EE = eroding escarpments, CB = coulee bottoms, MC = miscellaneous (*e.g.* saline meadows, sand-gravel, disturbed lands).

	Species	C_3/C_4	PTFs	Habitat
<i>Pteridophyta</i>				
<i>Selaginellaceae</i>	<i>Selaginella densa</i> Rydb. var. <i>densa</i>	C_3	PEF	GS
<i>Angiospermae</i>				
<i>Pinaceae</i>	<i>Juniperus communis</i> L.	C_3	SHR	CB
	<i>J. horizontalis</i> Moench.	C_3	SHR	HW EE
<i>Dicotyledoneae</i>				
<i>Aceraceae</i>	<i>Acer negundo</i> var. <i>interius</i> (Britt.) Sarg.	C_3	TRE	HW
<i>Anacardiaceae</i>	<i>Rhus aromatica</i> var. <i>trilobata</i> Nutt.	C_3	SHR	HW EE
	<i>R. radicans</i> var. <i>rydbergia</i> (Small) Rehder	C_3	SHR	CB MC
<i>Apocynaceae</i>	<i>Apocynum cannabinum</i> L.	C_3	PEF	MC
<i>Betulaceae</i>	<i>Betula fontinalis</i> Sarg.	C_3	TRE	CB
<i>Boraginaceae</i>	<i>Cryptantha macounii</i> (Eastw.) Pays	C_3	ANF	HW EE
	<i>Lappula echinata</i> Gilib.	C_3	ANF	MC

Table 1 (continued)

	Species	C ₃ /C ₄	PTF type	Habitat
<i>Boraginaceae</i> (cont.)	<i>Lithospermum incisum</i> Lehm.	C ₃	PEF	MC
	<i>Plagiobothrys scopulorum</i> I. M. Johnston	C ₃	PEF	MC
<i>Cactaceae</i>	<i>Opuntia polyacantha</i> Haw.	C ₃	PEF	HW EE
	<i>O. fragilis</i> (Nutt.) Haw.	C ₃	PEF	MC
<i>Campanulaceae</i>	<i>Campanula rotundifolia</i> L.	C ₃	PEF	GS MC
<i>Caprifoliaceae</i>	<i>Lonicera dioica</i> var. <i>glaucescens</i> (Rydb.) Butters	C ₃	SHR	CB
	<i>Symphoricarpos occidentalis</i> Hook.	C ₃	SHR	GS CB MC
<i>Caryophyllaceae</i>	<i>Arenaria lateriflora</i> L.	C ₃	PEF	MC
	<i>Cerastium arvense</i> L.	C ₃	PEF	LT GS HW
	<i>Paronychia sessiliflora</i> Nutt.	C ₃	PEF	HW
<i>Chenopodiaceae</i>	<i>Atriplex argentea</i> Nutt.	C ₄	ANF	HW
	<i>A. nuttallii</i> S. Wats.	C ₃	SHR	LT GS MC
	<i>Chenopodium berlandier</i> Moq.	C ₃	ANF	MC
	<i>Ch. fremontii</i> S. Wats.	C ₃	ANF	MC
	<i>Ch. leptophyllum</i> Nutt.	C ₃	ANF	MC
	<i>Endolepis suckleyi</i> Torr.	C ₃	ANF	MC
	<i>Eurotia lanata</i> (Pursh) Moq.	C ₃	SHR	LT GS HW
	<i>Salsola kali</i> var. <i>tenuifolia</i> Tausch.	C ₄	ANF	MC
	<i>Suaeda maritime</i> var. <i>americana</i> (Pers.) Boivin	C ₃	ANF	MC
<i>Compositae</i>	<i>Achillea millefolium</i> var. <i>occidentalis</i> DC.	C ₃	PEF	LT GS CB MC
	<i>Agoseris glauca</i> (Pursh) Raf.	C ₃	PEF	CB MC
	<i>Antennaria parvifolia</i> Nutt.	C ₃	PEF	LT GS
	<i>Artemisia biennis</i> Willd.	C ₃	ANF	MC
	<i>A. caudata</i> var. <i>calvens</i> Lunell Cronq.	C ₃	PEF SHR	MC
	<i>A. druncunculus</i> L.	C ₃	PEF	HW EE
	<i>A. frigida</i> Willd.	C ₃	SHR	LT GS HW CB
	<i>A. longifolia</i> Nutt.	C ₃	PEF	EE
	<i>A. ludoviciana</i> var. <i>pabularis</i> (Nels.) Fern.	C ₃	SHR	MC
	<i>Aster falcatus</i> Lindl.	C ₃	PEF	LT GS MC
	<i>A. laevis</i> L.	C ₃	PEF	GS MC
	<i>Cirsium flodmanii</i> (Rydb.) Arthur	C ₃	PEF	MC
	<i>Crepis intermedia</i> Gray	C ₃	PEF	MC
	<i>Erigeron caespitosus</i> Nutt.	C ₃	PEF	GS HW MC
	<i>E. glabellus</i> var. <i>pubescens</i> Hook.	C ₃	PEF	MC
	<i>Gaillardia aristata</i> Pursh	C ₃	PEF	GS MC
	<i>Grindelia squarrosa</i> (Pursh) Dunal	C ₃	ANF	GS MC
	<i>Gutierrezia sarothrae</i> Britt. et Rusby	C ₃	ANF	LT GS HW
	<i>Haplopappus armeriodes</i> Nutt.	C ₃	ANF	HW MC
	<i>H. nuttallii</i> T. et G.	C ₃	PEF	MC
	<i>H. spinulosus</i> (Pursh) DC.	C ₃	PEF	HW MC
	<i>Helianthus annuus</i> L.	C ₃	ANF	HW MC
	<i>Heterotheca villosa</i> (Pursh) Shinnery	C ₃	PEF	HW
	<i>Hieracium umbellatum</i> L.	C ₃	PEF	CB
	<i>Hymenoxys richardsonii</i> Cocherell	C ₃	PEF	GS HW
	<i>Iva axillaris</i> Pursh	C ₃	PEF	HW MC
	<i>Lactuca pulchella</i> (Pursh) DC.	C ₃	PEF	HW MC
	<i>Liatris punctata</i> Hook.	C ₃	PEF	MC
	<i>Ratibida columnifera</i> Wooton et Standl.	C ₃	PEF	LT GS HW
	<i>Senecio canus</i> Hook.	C ₃	PEF	GS HW MC
	<i>Solidago canadensis</i> var. <i>gilvocanescens</i> Rydb.	C ₃	PEF	MC
	<i>S. missouriensis</i> Nutt.	C ₃	PEF	GS HW MC
	<i>S. rigida</i> L.	C ₃	PEF	GS MC
	<i>S. spathulata</i> var. <i>neomexicana</i> Cronq.	C ₃	PEF	MC
	<i>Stephanomeria runcinata</i> Nutt.	C ₃	PEF	HW MC
	<i>Taraxacum officinale</i> Weber	C ₃	PEF	MC
	<i>Townsendia exscapa</i> (Rich.) Porter	C ₃	PEF	HW MC

Table 1 (continued)

	Species	C ₃ /C ₄	PTF type	Habitat
<i>Compositae</i> (cont.)	<i>Tragopogon dubius</i> Scop.	C ₃	ANF	LT GS CB MC
<i>Cornaceae</i>	<i>Cornus stolonifera</i> Michx.	C ₃	SHR	MC
<i>Convolvulaceae</i>	<i>Convolvulus sepium</i> L.	C ₃	PEF	MC
<i>Cruciferae</i>	<i>Arabis hirsuta</i> Scop.	C ₃	ANF	LT GS
	<i>A. holboellii</i> var. <i>retrofracta</i> (Graham) Rydb.	C ₃	PEF	HW
	<i>Descurainia pinnata</i> var. <i>brachycarpa</i> Fern.	C ₃	ANF	LT MC
	<i>D. sophia</i> (L.) Webb.	C ₃	ANF	MC
	<i>Erysimum cheiranthoides</i> L.	C ₃	ANF	CB
	<i>E. inconspicuum</i> (S. Wats.) Macm.	C ₃	PEF	CB
	<i>Lepidium densiflorum</i> Schrad.	C ₃	ANF	HW EE
	<i>Lesquerella arenosa</i> (Richards.) Rydb.	C ₃	ANF	HW MC
	<i>Rorippa sinuata</i> (Nutt.) Hitchc.	C ₃	PEF	MC
<i>Elaeagnaceae</i>	<i>Elaeagnus commutata</i> Bernh.	C ₃	SHR	MC
	<i>Shepherdia argentea</i> Nutt.	C ₃	SHR	CB
<i>Euphorbiaceae</i>	<i>Euphorbia serpyllifolia</i> Pers.	C ₄	ANF	MC
<i>Fabaceae</i>	<i>Astragalus bisulcatus</i> (Hook.) A. Gray	C ₃	PEF	CB MC
	<i>A. danicus</i> Retz.	C ₃	PEF	LT GS MC
	<i>A. gilviflorus</i> Sheldon	C ₃	PEF	HW MC
	<i>A. lotiflorus</i> Hook.	C ₃	PEF	MC
	<i>A. missouriensis</i> Nutt.	C ₃	PEF	HW
	<i>A. striatus</i> Nutt.	C ₃	PEF	HW MC
	<i>A. tenellus</i> Pursh	C ₃	PEF	HW MC
	<i>Glycyrrhiza lepidota</i> (Nutt.) Pursh	C ₃	PEF	HW
	<i>Hedysarum boreale</i> var. <i>cinerascens</i> Rollins	C ₃	PEF	HW MC
	<i>Oxytropis sericea</i> var. <i>spicata</i> (Hook.) Barneby	C ₃	PEF	LT GS HW
	<i>Petalostemon candidum</i> (Willd.) Michx.	C ₃	PEF	HW
	<i>P. purpureum</i> (Vent.) Rydb.	C ₃	PEF	HW MC
	<i>Psoralea argophylla</i> Pursh	C ₃	PEF	MC
	<i>P. esculenta</i> Pursh	C ₃	PEF	HW MC
	<i>Thermopsis rhombifolia</i> (Nutt.) Richards	C ₃	PEF	HW
	<i>Vicia americana</i> Muhl.	C ₃	PEF	LT GS
<i>Haloragidaceae</i>	<i>Myriophyllum exalbescens</i> Fern.	C ₃	PEF	MC
<i>Labiatae</i>	<i>Moldavica parviflora</i> (Nutt.) Britt.	C ₃	PEF	CB
	<i>Monarda fistulosa</i> var. <i>menthaefolia</i> (Grah.) Fern.	C ₃	PEF	MC
<i>Linaceae</i>	<i>Linum perenne</i> var. <i>lewisii</i> (Pursh) Eat et Wright	C ₃	PEF	LT GS
	<i>L. rigidum</i> Pursh	C ₃	ANF/ PEF	HW
<i>Malvaceae</i>	<i>Sphaeralcea coccinea</i> (Pursh) Rydb.	C ₃	SHR	HW
<i>Onagraceae</i>	<i>Gaura coccinea</i> Pursh	C ₃	PEF	HW EE
	<i>Oenothera caespitosa</i> Nutt.	C ₃	SHR	MC
<i>Plantaginaceae</i>	<i>Plantago major</i> L.	C ₃	PEF	CB MC
<i>Polemoniaceae</i>	<i>Collomia linearis</i> Nutt.	C ₃	ANF	CB
	<i>Phlox hoodii</i> Richards	C ₃	PEF	HW EE
<i>Polygonaceae</i>	<i>Eriogonum flavum</i> Nutt.	C ₃	PEF	HW EE
	<i>Rumex salicifolius</i> var. <i>mexicanus</i> C.L. Hitchc.	C ₃	PEF	MC
<i>Primulaceae</i>	<i>Androsace occidentalis</i> Pursh	C ₃	ANF	CB
	<i>A. septentrionalis</i> var. <i>puberulenta</i> (Rydb.) Knuth.	C ₃	ANF	LT GS
	<i>Glaux maritime</i> L.	C ₃	ANF	MC
	<i>Sterionema ciliatum</i> (L.) Raf.	C ₃	PEF	MC
<i>Ranunculaceae</i>	<i>Anemone canadensis</i> L.	C ₃	PEF	CB
	<i>A. patens</i> var. <i>wolfgangiana</i> (Bess.) Koch	C ₃	PEF	GS HW
	<i>Clematis ligusticifolia</i> Nutt.	C ₃	PEF	CB
	<i>Ranunculus abortivus</i> L.	C ₃	PEF	CB
	<i>R. aquatilis</i> var. <i>capillaceus</i> (Thuill.) D.C.	C ₃	PEF	MC

Table 1 (continued)

	Species	C ₃ /C ₄	PTF type	Habitat
<i>Ranunculaceae</i> (cont.)	<i>R. cymbalaria</i> Pursh	C ₃	PEF	MC
	<i>Thalictrum venulosum</i> Trel.	C ₃	PEF	CB
<i>Rosaceae</i>	<i>Amelanchier alnifolia</i> Nutt.	C ₃	SHR	HW CB
	<i>Crataegus rotundifolia</i> Moench	C ₃	TRE	CB MC
	<i>Fragaria vesca</i> var. <i>americana</i> Porter	C ₃	PEF	GS
	<i>Geum perincisum</i> Rydb	C ₃	PEF	CB
	<i>G. triflorum</i> Pursh.	C ₃	PEF	LT GS
	<i>Potentilla anserina</i> L.	C ₃	PEF	MC
	<i>P. argentea</i> L.	C ₃	PEF	MC
	<i>P. concinna</i> Rich.	C ₃	PEF	HW
	<i>P. gracilis</i> Dougl.	C ₃	PEF	CB
	<i>P. pensylvanica</i> L.	C ₃	PEF	LT GS
	<i>Prunus pensylvanica</i> L.	C ₃	SHR	HW CB
	<i>P. virginiana</i> L.	C ₃	SHR	HW CB
	<i>Rosa alcea</i> Greene	C ₃	SHR	HW MC
	<i>R. arkansana</i> Porter	C ₃	SHR	MC
<i>Rubiaceae</i>	<i>Galium boreale</i> L.	C ₃	SHR	GS CB
<i>Salicaceae</i>	<i>Populus deltoids</i> Marsh. var. <i>occidentalis</i> Rybd.	C ₃	TRE	CB
	<i>P. tremuloides</i> Michx.	C ₃	TRE	CB
	<i>Salix bebbiana</i> Sarg	C ₃	TRE/SHR	CB
	<i>S. interior</i> Rowiee	C ₃	SHR	CB
	<i>S. lutea</i> Nutt.	C ₃	TRE/SHR	CB
<i>Saxifragaceae</i>	<i>Heuchera richardsonii</i> R. Br.	C ₃	PEF	GS MC
	<i>Ribes oxycanthoides</i> L.	C ₃	PEF	CB
<i>Scrophulariaceae</i>	<i>Orthocarpus luteus</i> Nutt.	C ₃	ANF	HW MC
	<i>Penstemon albidus</i> Nutt.	C ₃	PEF	HW EE
	<i>P. nitidus</i> Dougl.	C ₃	PEF	HW EE
<i>Umbelliferae</i>	<i>Cymopterus acaulis</i> (Pursh) Raf.	C ₃	PEF	HW EE
	<i>Heracleum lanatum</i> Michx.	C ₃	PEF	CB MC
	<i>Lomatium foeniculaceum</i> Nutt.	C ₃	PEF	LT GS CB MC
	<i>Musineon divaricatum</i> Nutt.	C ₃	PEF	HW EE
	<i>Zizia aptera</i> Fern.	C ₃	PEF	MC
<i>Urticaceae</i>	<i>Urtica dioica</i> var. <i>procera</i> (Muhl.) Wedd.	C ₃	PEF	CB
<i>Violaceae</i>	<i>Viola adunca</i> J.E. Smith	C ₃	PEF	CB
	<i>V. nuttallii</i> Pursh	C ₃	PEF	HW MC
	<i>V. rugulosa</i> Greene	C ₃	PEF	CB
<i>Monocotyledoneae</i>				
<i>Alismaceae</i>	<i>Alisma triviale</i> Pursh	C ₃	PEF	MC
	<i>Sagittaria cuneata</i> Sheldon	C ₃	PEF	MC
<i>Cyperaceae</i>	<i>Carex atherodes</i> Spreng.	C ₃	SPG	MC
	<i>C. brevior</i> (Dewey) Mack.	C ₃	SPG	HW
	<i>C. eleocharis</i> Bailey	C ₃	SPG	HW EE
	<i>C. filifolia</i> Nutt.	C ₃	SPG	MC
	<i>C. praegracilis</i> W. Boott	C ₃	SPG	MC
	<i>C. rossii</i> Boott	C ₃	SPG	HW
	<i>Eleocharis palustris</i> (L.) R. et S.	C ₃	SPG	MC
	<i>Scirpus americanus</i> Pers.	C ₃	HPG	MC
	<i>Agropyron albicans</i> Scribn. et Smith	C ₃	HPG	LT GS
<i>Gramineae</i>	<i>A. albicans</i> var. <i>griffithsii</i> Scribn. et Smith	C ₃	HPG	LT GS
	<i>A. dasystachyum</i> Hook.	C ₃	HPG	LT GS HW
	<i>A. dasystachyum</i> var. <i>riparium</i> Bowden	C ₃	HPG	LT GS HW
	<i>A. smithii</i> Rydb.	C ₃	HPG	LT GS HW CB
	<i>A. trachycaulum</i> Link	C ₃	HPG	CB MC
	<i>Alopecurus aequalis</i> Sobol.	C ₃	HPG	MC
	<i>Andropogon scoparius</i> Michx.	C ₄	HPG	MC

Table 1 (continued)

	Species	C ₃ /C ₄	PTF type	Habitat
<i>Gramineae</i> (cont.)	<i>Beckmannia syzigachne</i> Fern.	C ₃	ANG	MC
	<i>Bouteloua gracilis</i> Lag.	C ₄	SPG	GS
	<i>Bromus anoma</i> Rupr.	C ₃	HPG	CB
	<i>Calamagrostis canadensis</i> (Michx.) Beauv.	C ₃	HPG	MC
	<i>C. inexpansa</i> A. Gray	C ₃	HPG	GS
	<i>C. montanensis</i> Scribn.	C ₃	HPG	GS
	<i>Calamovilfa longifolia</i> (Hook.) Scribn.	C ₄	HPG	GS
	<i>Danthonia intermedia</i> Vasey	C ₃	SPG	MC
	<i>Deschampsia caespitosa</i> (L.) Beauv.	C ₃	HPG	MC
	<i>Distichlis stricta</i> (Torr.) Rydb.	C ₄	SPG	MC
	<i>Elymus canadensis</i> L.	C ₃	HPG	CB
	<i>E. glaucus</i> Buckl.	C ₃	HPG	MC
	<i>E. glaucus</i> var. <i>glaucus</i> Buckl	C ₃	HPG	CB
	<i>Festuca altaica</i> Trin.	C ₃	HPG	GS MC
	<i>Helictotrichon hookerii</i> (Scribn.) Henr.	C ₃	HPG	CB
	<i>Hierochloa odorata</i> (L.) Beauv.	C ₃	HPG	CB
	<i>Hordeum jubatum</i> L.	C ₃	HPG	MC
	<i>H. jubatum</i> var. <i>caespitosum</i> A.S. Hitchc.	C ₃	HPG	CB MC
	<i>Koeleria cristata</i> Pers.	C ₃	HPG	LT GS HW
	<i>Muhlenbergia cuspidata</i> (Torr.) Rydb.	C ₄	HPG	HW EE
	<i>M. richardsonis</i> (Trin.) Rydb.	C ₄	HPG	MC
	<i>Oryzopsis hymenoides</i> (Roem et Schult.) Ricker	C ₃	HPG	MC
	<i>Poa canbyi</i> (Scribn.) Piper	C ₃	SPG	MC
	<i>P. compressa</i> L.	C ₃	SPG	MC
	<i>P. cusickii</i> Vasey	C ₃	SPG	LT GS
	<i>P. glaucifolia</i> Scribn. et Williams	C ₃	SPG	MC
	<i>P. interior</i> Rydb.	C ₃	SPG	MC
	<i>P. juncifolia</i> Scribn.	C ₃	SPG	MC
	<i>P. palustris</i> L.	C ₃	SPG	HW CB
	<i>P. pratensis</i> L.	C ₃	SPG	CB MC
	<i>P. sandbergii</i> Vasey	C ₃	SPG	LT GS HW
	<i>P. secunda</i> Pressl.	C ₃	SPG	LT GS HW
	<i>Puccinellia nuttalliana</i> (Schult.) Hitch.	C ₃	HPG	MC
	<i>Schizachyrium scoparium</i> (Michx.) Nash	C ₄	SPG	MC
	<i>Spartina gracilis</i> Trin.	C ₃	HPG	MC
	<i>Sporobolus cryptandrus</i> A. Gray	C ₄	HPG	MC
	<i>Stipa comata</i> Trin. et Rupr.	C	HPG	GS HW
	<i>S. spartea</i> var. <i>curtiseta</i> Hitchc.	C ₃	HPG	GS HW MC
	<i>S. viridula</i> Trin.	C ₃	HPG	LT GS HW
<i>Iridaceae</i>	<i>Sisyrinchium montanum</i> Greene	C ₃	PEF	LT
<i>Juncaceae</i>	<i>Juncus balticus</i> Will.	C ₃	PEF	MC
<i>Juncaginaceae</i>	<i>Triglochin maritima</i> L.	C ₃	PEF	MC
<i>Liliaceae</i>	<i>Allium textile</i> Nels. et Macbr.	C ₃	PEF	HW
	<i>Disporum trachycarpum</i> (Wats.) B. et H.	C ₃	PEF	CB MC
	<i>Smilacina stellata</i> (L.) Desf.	C ₃	PEF	CB MC
<i>Potamogetonaceae</i>	<i>Potamogeton richardsonii</i> (Benn.) Rydb.	C ₃	PEF	MC

Results

Floristic composition of photosynthetic pathway types: 219 vascular plant species, in 45 families and 145 genera, were identified with C₃ and C₄ photosynthesis (Table 1). Of these species, 1 species was in *Pteridophyta* and 218 species in *Angiospermae*. About 71 % (154 of 219) was found in *Dicotyledoneae*, e.g. *Compositae* (38

species), *Chenopodiaceae* (9 species), *Cruciferae* (9 species), *Fabaceae* (16 species), *Rosaceae* (14 species), and *Ranunculaceae* (7 species). 29 % were in *Monocotyledoneae*, e.g. *Gramineae* (47 species), *Liliaceae* (3 species), *Cyperaceae* (8 species), and *Iridaceae* (1 species). As for photosynthetic pathway

types, 208 species (95 % of the identified species in Table 1) in 137 genera and 44 families were found with C_3 photosynthesis, 11 species in 10 genera and 3 families with C_4 photosynthesis. 5 % (11 of 219) of the identified species in Table 1 was found with C_4 photosynthesis, e.g. *Gramineae* (8 species), *Chenopodiaceae* (2 species), and *Euphorbiaceae* (1 species). The occurrence of C_4 species was not common in *Gramineae* (17 %) and *Chenopodiaceae* (22 %). Number of C_4 species in the Saskatchewan mixed prairie was much less than those from the mixed prairie of South Dakota (27 species) and Mongolian steppe (25 species).

The occurrence of C_4 species was related with habitats in the mixed prairie in the region (Table 1). 7 species can be found in the miscellaneous habitats (e.g. saline meadows, sand-gravel, disturbed lands), 2 in grassy slopes, 2 in hillwash, and 1 in eroding. *Bouteloua gracilis* Lag. and *Calamovilfa longifolia* Scribn. can be dominant species in the driest part of the Saskatchewan mixed prairie, in which underling shale deposits have imposed a solonchic character to the soils.

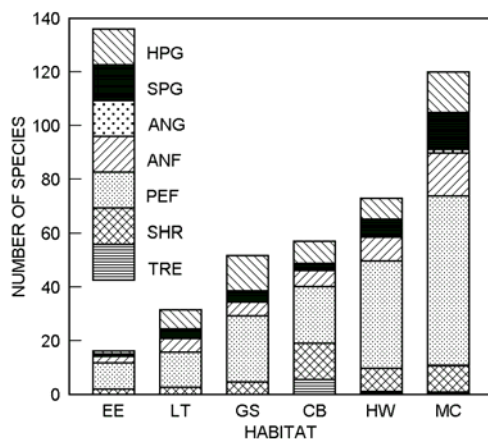


Fig. 1. Plant functional type compositions in habitats in the Saskatchewan mixed prairie.

Discussion

The PFTs framework constitutes a useful tool for studying the logical links between physiological and life-history strategies at plant level and ecological process at ecosystem and global level, as well as for predicting the vegetation and biodiversity changes as consequences of environmental and disturbance changes and land use shifts at regional and global level (Chapin 1993, Paruelo and Lauenroth 1996, Wang 2003). But one of the crucial problems is how to define the optimal and comparable PFTs for the regional vegetation types (Pillar 1999, Wang 2003). This requires the screening and synthesis of traits from a large number of species across broad environmental and disturbance gradients (Rusch *et al.* 2003, Wang 2004). The studies on coarse traits (photosynthetic pathways) of PFTs in American mixed prairie have been

Morphological functional types: According to plant morphological attributes, growth form, and life-span, the identified plant species were classified into 7 functional types, e.g. TRE, SHR, ANF, PEF, HPG, SPG, and ANG (Table 1). Of the total 219 species, 50 % was PEF functional type and 12 % species was ANF, while these two types make up only 1–12 % of the total forage production in the region. 11 and 3 % of these total species were in SHR and TRE types, respectively. Graminoids (grasses and sedge) formed about 25 %, e.g. HPG (15 %), ANG (0.5 %), and SPG (10 %), and graminoid types about 83–98 % of forage production in the region. Many grasses are the dominant species, e.g. *Agropyron dasystachyum* Hook., *A. smithii* Rydb., *Stipa spartea* var. *curtiseta* Hitchc., *Bouteloua gracilis* Lag., and *Calamovilfa longifolia* Scribn. This indicated that HPG and SPG functional types are the dominant PFTs, even though their species abundances were less than fords (ANF and PEF).

The responses of morphological functional type compositions to habitats were remarkable in the Saskatchewan mixed prairie (Fig. 1). Five PFTs were found in EE, LT, and GS, and the species numbers were 16, 31, and 51, respectively. Six PEFs and relative more species (56 and 72) were identified in HW and CB. All the 7 PFTs (119 species) were in MC, and 52 % of these species was in PEF type. This indicated that complex habitat comprises lead to relative high PFTs abundances.

Like that in the South Dakota mixed prairie, dicotyledonous C_4 species were mainly annual forbs, e.g. *Atriplex argentea* Nutt., *Salsola kali* var. *tenuifolia* Tausch., and *Euphorbia serpyllifolia* Pers., while most of the C_4 species were HPG and SPG grasses, e.g. *Andropogon scoparius* Michx., *Bouteloua gracilis* Lag., *Calamovilfa longifolia* (Hook.) Scribn., *Muhlenbergia cuspidata* (Torr.) Rydb., and *M. richardsonis* (Trin.) Rydb. This suggests that C_4 species occurred mainly in few PFTs in the region.

conducted (Teeri and Stowe 1976, Teeri *et al.* 1980, Rusch *et al.* 2003), but PFTs compositions of Canadian mixed prairie remain unclear. The floristic composition of the Saskatchewan mixed prairie is similar in terms of C_3 and C_4 representatives to that predicted by the coarse floristic analysis of Teeri and Stowe (1976). They found that the distribution of C_4 grasses in North America was significantly correlated with mean July consequence minimum temperatures. Their regression model predicts that Saskatchewan mixed prairie should have a grass flora composed 12 % C_4 grass species. Eight of 47 grass species examined in this study, or 17 %, are in fact C_4 species. This is relatively more than in coarse model prediction. The dicotyledonous C_4 species were about 2 % (or 3 of 154), and this supported Teeri and Stowe's

model which predicts that about 2 % of native dicotyledonous flora should be C_4 species. The total number of C_4 species (11 species) in the Saskatchewan mixed prairie was less than a half of those from the South Dakota mixed prairie (27 species) and Mongolian steppe (25 species). This consists with conclusion of Ehleringer *et al.* (1997) that the C_4 species favoured the higher temperature and lower CO_2 concentration regions. A cold semi-desert climate dominates the Saskatchewan mixed prairie, leading relatively less C_4 species occurrence, even though some C_4 plants can be dominants species in the driest part of the mixed prairie (*Boutelou gracilis* Lag. and *Calamovilfa longifolia* Scribn.). Relative stability of the Saskatchewan mixed prairie may also lead to less C_4 species occurrence, for stable ecosystems may reduce the introduction of weeds and forbs [*e.g.* *Portulaca oleracea* L., *Salsola iberica* Senner *ex* Pau, *Echinochloa crus galli* L., and *Setaria glauca* (L.) Beauv. in the South Dakota mixed prairie]. Within the Saskatchewan mixed prairie, the distribution of C_4 species appears to fall within two categories: miscellaneous habitats (*e.g.* saline meadows, sand-gravel, disturbed lands) and the driest lands (grassy slopes and hillwash); this suggests that C_4 plants are more tolerant to environmental stresses (*e.g.* salinity, dryness, and high temperature).

Plant photosynthetic pathways or photosynthetic functional types are relative coarse in describing the PFTs in regional and local scales, while morphological functional types may more fit for depicting the PFTs differences among the habitats, land-use, and community types (Wang 2004), and for reflecting their seasonal

dynamics. Only about 50 and 12 % of the identified species fall within two categories PEF and ANF types, respectively, while those for Mongolian steppe are about 60 and 15 %. Graminoid types (*e.g.* HPG, SPG and ANG) in the region form about 25 % of the total species in local flora, but that in Mongolian steppe is 18 %. Relatively more graminoid types and less forb functional types suggest that most of the Saskatchewan mixed prairie is in a relatively fair condition.

Morphological functional types reflect vegetation spatial changes in rangeland ecosystems (Fig. 1). In general, species numbers of PEF, ANF, SHR, and graminoid types increased from EE to MC, indicating that PFTs abundances varied significantly with the habitat changes. There were less PFTs in the early succession stages (*e.g.* eroding escarpments and sand-gravel), while complex habitat lead to relative high PFTs abundances in MC. Most of the stable communities in the habitats (*e.g.* LT, GS, HW, and CB) have relatively less PFTs composition in the Saskatchewan mixed prairie. This is also supported by previous observations (Wang 2003, 2004). This and early study (Teeri and Stowe 1976, Ode *et al.* 1980) document the importance of plant function types (*e.g.* photosynthetic pathways and morphological functional types) in predicting vegetation and habitat changes, land-use, and climate changes in the mixed prairie. To select optimal traits for PFTs classification in the region by the present knowledge, further studies (*e.g.* C_3 and C_4 plant identification, optimal traits' selection) are needed exploring the relationships between PFTs and vegetation variations, as well as land-use and climate changes.

References

- Box, E.O.: Plant functional types and climate at the global scale. – *J. Veget. Sci.* **7**: 309-320, 1996.
- Chapin, P.S.: Functional role of growth forms in ecosystem and global processes. – In: Ehleringer, J.R., Field, C.B. (ed.): *Scaling Physiological Processes: Leaf to Globe*. Pp. 287-312. Academic Press, San Diego 1993.
- Collatz, G.J., Berry, J.A., Clark, J.S.: Effects of climate and atmospheric CO_2 partial pressure on the global distribution of C_4 grasses: present, past, and future. – *Oecologia* **114**: 441-454, 1998.
- Collins, R.P., Jones, M.B.: The influence of climatic factors on the distribution of C_4 species in Europe. – *Vegetatio* **64**: 121-129, 1985.
- Coupland, R.T.: Ecology of mixed prairie in Canada. – *Ecol. Monogr.* **20**: 271-315, 1950.
- Coupland, R.T.: A reconsideration of grassland classification in the northern Great Plain of North America. – *J. Ecol.* **49**: 135-167, 1961.
- Coupland, R.T.: Mixed prairie. – In: Coupland, R.T. (ed.): *Ecosystems of the World*. Vol. 8A. Pp. 151-182. Elsevier, Amsterdam 1992.
- Coupland, R.T., Ripley, E.A., Robins, P.C.: Floristic composition and canopy architecture of the vegetation cover. – Univ. Saskatchewan, Saskatoon 1973.
- Downton, W.J.S.: The occurrence of C_4 photosynthesis among plants. – *Photosynthetica* **9**: 96-105, 1975.
- Ehleringer, J.R., Cerling, T.E., Helliker, B.R.: C_4 photosynthesis, atmospheric CO_2 , and climate. – *Oecologia* **112**: 285-299, 1997.
- Hattersley, P.W.: C_4 photosynthetic pathway variation in grasses (Poaceae): its significance for arid and semi-arid lands. – In: *Desertified Grasslands: Their Biology and Management*. Pp. 181-212. Linnean Society, London 1992.
- Jong, E.D., Stewart, J.W.: *Soil Characterization*. – Univ. Saskatchewan, Saskatoon 1973.
- Keeley, J.E.: C_4 photosynthetic modifications in the evolutionary transition from land to water in aquatic grasses. – *Oecologia* **116**: 85-97, 1998.
- Kitagawa, M.: *Neo-lineamenta Floreae Manshuricae*. – J. Cramer, Vaduz 1979.
- Li, M.: [List of plants with C_4 photosynthesis.] – *Plant Physiol. Commun.* **29**: 148-159, 221-240, 1993. [In Chin.].
- Liu, X.Q., Wang, R.Z., Li, Y.Z.: Photosynthetic pathway types in rangeland plant species from Inner Mongolia, North China. – *Photosynthetica* **42**: 339-344, 2004.
- Ode, D.J., Tieszen, L.L., Lerman, J.C. The seasonal contribution of C_3 and C_4 species to primary production in a mixed prairie. – *Ecology* **61**: 1304-1311, 1980.
- Paruelo, J.M., Lauenroth, W.K.: Relative abundance of plant functional types in grassland and shrublands of North

- America. – *Ecol. Applic.* **6**: 1212-1224, 1996.
- Pillar, V.D.: On the identification of optimal plant functional types. – *J. Veget. Sci.* **10**: 631-640, 1999.
- Pyankov, V.I., Gunin, P.D., Tsoog, S., Black, C.C.: C_4 plants in the vegetation of Mongolia: their natural occurrence and geographical distribution in relation to climate. – *Oecologia* **123**: 15-31, 2000.
- Raghavendra, A.S., Das, V.S.R.: The occurrence of C_4 -photosynthesis: A supplementary list of C_4 plants reported during late 1974-mid 1977. – *Photosynthetica* **12**: 200-208, 1978.
- Redmann, R.E., Yin, L., Wang, P.: Photosynthetic pathway types in grassland plant species from Northeast China. – *Photosynthetica* **31**: 251-255, 1995.
- Rusch, G.M., Pausas, J.G., Lepš, J.: Plant functional types in relation to disturbance and land use: introduction. – *J. Veget. Sci.* **14**: 307-310, 2003.
- Saskatchewan Agriculture and Food: Managing Saskatchewan Rangeland. – Saskatchewan Agriculture and Food, Saskatchewan 1996.
- Takeda, T., Hakoyama, S.: Studies on the ecology and geographical distribution of C_3 and C_4 grasses. 2. Geographical distribution of C_3 and C_4 grasses in far east and south east Asia. – *Jap. J. Crop Sci.* **54**: 65-71, 1985.
- Teeri, J.A., Stowe, L.G.: Climatic patterns and the distribution of C_4 grasses in North America. – *Oecologia (Berlin)* **23**: 1-12, 1976.
- Teeri, J.A., Stowe, L.G., Livingstone, D.A.: The distribution of C_4 species of the *Cyperaceae* in North America in relation to climate. – *Oecologia* **47**: 307-310, 1980.
- Wang, R.Z.: The C_4 photosynthetic pathway and life forms in grassland species from North China. – *Photosynthetica* **40**: 97-102, 2002.
- Wang, R.Z.: Photosynthetic pathway and morphological functional types in the steppe vegetation from Inner Mongolia, North China. – *Photosynthetica* **41**: 143-150, 2003.
- Wang, R.Z.: C_4 species and their response to large-scale longitudinal climate changes along Northeast China Transect (NECT). – *Photosynthetica* **42**: 71-79, 2004.
- Williams, G.J., III, Markley, J.L.: The photosynthetic pathway type of North American shortgrass prairie species and some ecological implications. – *Photosynthetica* **7**: 262-270, 1973.