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Vegetative zonation patterns in depression and riparian wetlands of the Sanjiang Plain, Northeastern China

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The vegetation of depressional and riparian wetlands in the Sanjiang Plain of Northeastern China was studied to describe their vegetation composition and to quantify community differences. Reciprocal transplants were performed to test the importance of biotic factors in governing zonation. One hundred and seventy-two (172) sampling plots in depression and riparian wetland was used. Samples were classified in 9 groups at the fourth level using two-way indicator species analysis (TWINSPAN): Four marsh communities, one meadow marsh community, one wet meadow community, two swamp communities and one island forest community. The TWINSPAN groups could be recognized in the detrended correspondence analysis (DCA) graph. DCA ordination indicated a wetness gradient associated with altitude. The species turnover between communities were rather high (similarity index less than 0.40), and this indicated that the corresponding habitats heterogeneity increased gradually. Three transplanted species showed different effects of biomass production among vegetation zones. The greatest transplant effect occurred for *Carex lasiocarpa*, followed by *Calamagrostis angustifolia*, with the least effect for *Carex appendiculata*. This study provides evidence that hydrologic gradients and biotic factors commonly determine the spatial pattern of wetland plant communities. This should therefore be considered in future management and protection under the circumstance of climate change and human activities.

Key words: Vegetation classification, ordination, community similarity, depression and riparian wetlands, Sanjiang Plain.

INTRODUCTION

Zonal patterns of wetland vegetation in depressional and riparian wetlands occur frequently, and vegetation type, species composition and its environmental controlling variables of this pattern have been explored in Northern Europe, Japan, and North America (Wheeler and Proctor, 2000; Zoltai and Vitt, 1995; Rydin and Jeglum, 2006; Whitehouse and Bayley, 2005; Asada, 2002; Kazuyuki and Kazyo, 1997; Hudon, 2004; Timoney, 2008; Steven and Toner, 2004. Nevertheless, vegetation patterns in wetlands in Northern China have not been well described. Moreover, wetland habitats are one of the most threatened in China, and detailed knowledge of relationships between wetland vegetation and environmental conditions is very important for nature conservation. Therefore, it is essential to understand the structure and composition of natural plant communities along environmental gradients and its underlying ecological determinants in this part of the world.

According to studies in the northern hemisphere, the zonal series, community type and floristic composition are very different from one continent to another, while the vegetation distribution patterns in zonal wetlands is usually controlled by the gradients in hydrology, salinity, nutrient concentrations in soil, as well as disturbance, competition and traits of the plant species themselves

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Abbreviations: TWINSPAN, Two-way indicator species analysis; **DCA,** detrended correspondence analysis.

(Brotherson, 1987; Sanderson et al., 2008; Blom et al., 1990; Dwire, 2004; Wilson and Keddy, 1985; Vanderijt et al., 1996; Shipley et al., 1991; Sanderson et al., 2008; Johnson et al., 1987; Dwire, 2004; Luo et al., 2008). Moreover, Community differences and species turn-over in zonal wetlands are usually high.

The Sanjiang Plain in Northeastern China once had vast wetland areas, which are still important for main-taining global and regional biodiversity (Liu and Ma 2002). Depressional wetlands and riparian wetlands are the main wetland types in this region, and most of these wetlands may have been degraded severely or lost entirely through agri- cultural uses. Therefore, we selected these two wetland types as our subject. Our objectives were to: (1) describe the plant species assemblages within these wetlands and compare them with other parts of the world; (2) to discern underlying environmental variables that controlled veget- ation patterns; and (3) to quantify species turnover within and among these vegetation types.

MATERIALS AND METHODS

Study area

The Sanjiang Plain in Northeastern China is an extensive alluvial plain formed by the Amur, Ussuri, and Songhua Rivers (Figure 1). The region has a low and flat topographically, and has a slope grade of less than 1: 10,000, which is favorable for wetland formation. A sub-humid climate with mean annual temperature of 3.8°C (with an average annual maximum of 21 to 22°C in July, and an average annual minimum of -18°C in January) and precipitation of 500 to 650 mm (80% of rainfall occurs between May and September). The water and soil in these marshes are completely frozen from late October to April and begin to thaw in late April, with the highest daily temperatures in July. Intensive agricultural development since the 1950s has significantly diminished the natural wetlands from 5.3×10^6 ha in 1949 to 0.96×106 ha in 2005 (Song et al., 2008).

There are numerous isolated depressional wetlands and riparian wetlands in the Sanjiang Plain. These wetlands have varied morphology and geologic origins, but function in similar ways ecologically. Some of these wetlands are small and dish-shaped, while others have irregular shapes. Their hydrologic regimes are mainly driven by rain-fall, flooding water and surface run-off. They are influenced by natural disturbances such as occasional drought. Historically, most of these wetlands may have been degraded severely or lost entirely through agricultural uses. The study was conducted in Honghe National Natural Reserve (47°42′18″~ 47°52′07″N, 133°34′38″~133°46′29″E, including Nongjiang river's tributary riparian wetland and one depression wetland), and the experimental site of wetland in Sanjiang Plain National Station (47°35′N, 133°31′E, including two depressions), Bielahong River and Naoli River riparian wetland (Figure 1).

Sampling of vegetation

All vegetation sampling was carried out in July and August from 2002 to 2006. By using a line-intercept method similar to transect-based point sampling, in each wetland, two lines transect was laid from low marsh (depression center or near water sites of riparian wetland) to upland forest (Figure 1), transect lengths ranged from 50 to 500 m. We set three replicates of quadrats (island forest could be less than three plots because of its small area) at each community type along each transect. The size of plots for herb, shrub and forest was 1×1 m², 2 × 2 m² and 10×10 m², respectively. In total, 172 plots of ten transects were investigated. The species and visual estimates of cover for each species were noted. Nomenclature for vascular species follows Fu (1995) and for bryophytes species, Gao (1994).

Reciprocal transplant experiment

To explore if the physiological responses of each dominant species along the water depth zone (*Carex lasiocarpa*, *Carex appendiculata*, *Calamagrostis angustifolia*) is the same, reciprocal transplant were executed in the Sanjiang marsh field station. Transplants were done among three herb zones. To avoid the difficulty of digging frozen soil in early spring, 9 blocks of substrate (50 × 50 cm, 30 cm deep) containing live rhizomes for each dominant species were dug from originate zone, three of which were lifted from ground, rotated 90°C, and placed back in the same location, and then the remaining block were placed into other two zones in September, 2004. In total, 27 plots in the experiment site were divided into 3 species × 3 zones of 3 transplants each. At the same time, for each dominant species, three control plots were marked in its original zone. Dominant species cover in the block was similar to mean values in vegetation zone sampling plots. In late August 2005, all above-ground vegetation in each plot was harvested and dried to a constant mass at 80°C and weighed. In comparison to unmanipulated control stands of each species, the transplanting operation reduced above-ground biomass production by 30 to 40%. Although, transplantation experiment was only examined for one season, the consistency of our results among species and between rhizomes suggest that it accurately assessed relative plant success in vegetation zones.
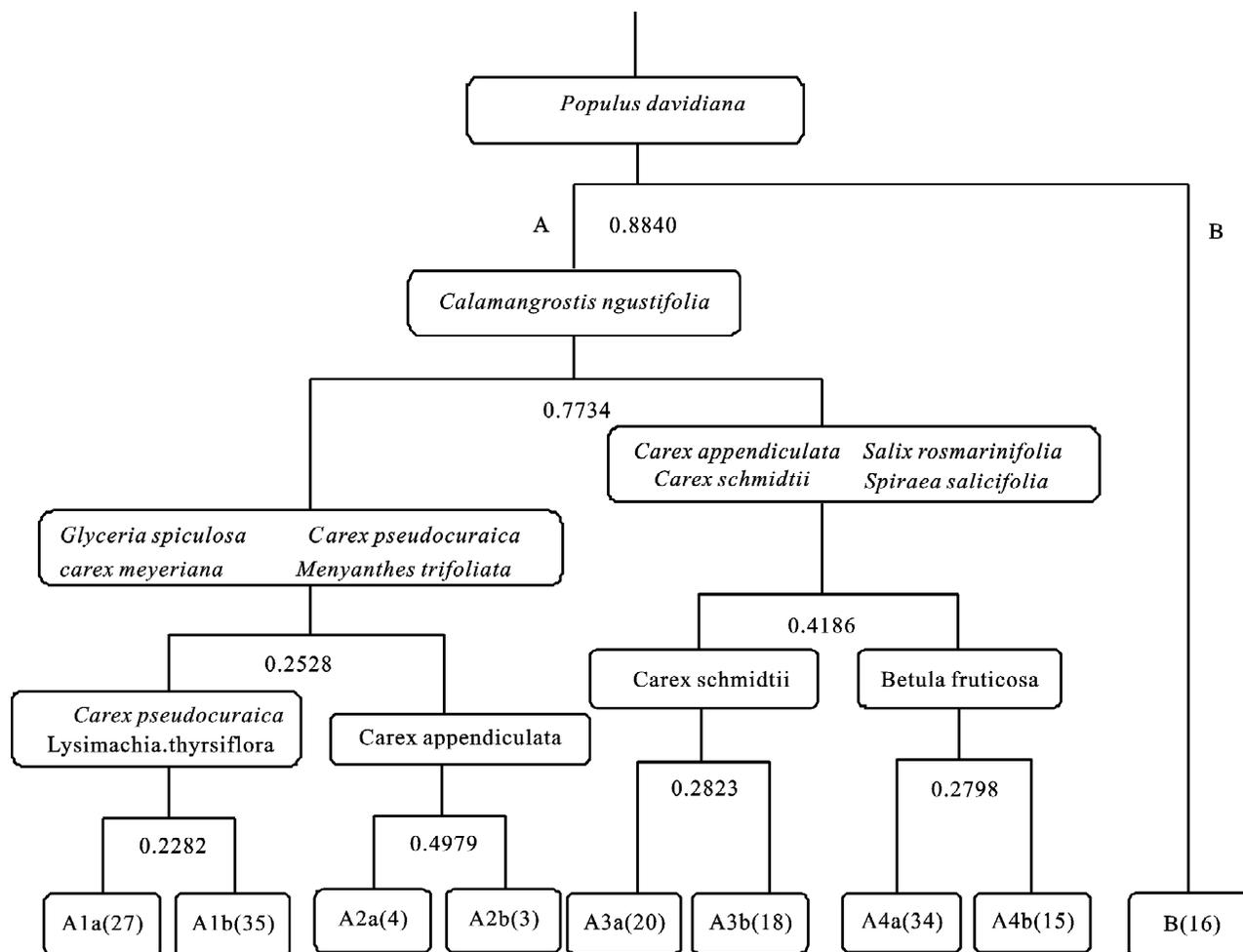
Data analysis

Vegetation data were analyzed using classification and ordination techniques. In 172 sampling plots, 213 species were registered. However, only cover percentage of the species over 5% was included in data analysis in a total 33 species. Sampling plots (based on species cover) were classified by two-way indicator species analysis (TWINSPAN; Hill, 1979). The cut levels elected were 0, 2, 5, 10 and 20. Detrended correspondence analysis (DCA) (Hill and Gauch, 1980) ordinations were conducted on vegetation data matrices using the program PC-ORD (McCune and Mefford, 1999) and CANOCO 4.0 package (Ter Braak and Smilauer, 2002). For the survey of community similarity, Sorenson index was chosen (Whittaker, 1972). SPSS software was used for one way analysis of variance (ANOVA) and the construction of scatter plots.

RESULTS

Vegetation classification

In the first division, TWINSPAN separated the herb and shrub wetland (group A) vs. Island forest wetland (group B) and this was characterized by the abundance of *Populus davidiana* (Figure 2). The second division separated marsh from marsh meadow and swamp and the third division separated emergent marsh, tussock meadow marsh, marsh meadow, shrub swamp. Eight end   groups

Figure 1. Location of the study site and field sampling design in the Sanjiang Plain, northeastern China.

were distinguished at the forth level of division (A1a, A1b, A2a, A2b, A3a, A3b, A4a and A4b) within group A (Figure 2). All these rather well-delimited vegetation types can be regarded as communities. Four of them represented the marsh vegetation, while the other four groups belonged to the marsh meadow and shrub swamp vegetation. The species frequency of these groups is shown in Table 1, which lists only the most abundant ones. TWINSPAN did find several subgroups in Group B, but these subgroups were not analyzed further because the herb and shrub wetland were of greater interest here. Nine groups were described as follows:

Group A1a: *Carex pseudocuraica* marsh is one of the primary marsh types and occupies small area. It is "flat" and situated in the center of the depression and near water of the riparian wetland. Water depth over surface in its habitats varied from 20 to 30 cm. Besides the dominant species *C. pseudocuraica,* typical associated species included *Glyceria spiculosa*, *C. lasiocarpa*, *Menyanthes trifoliata* and *Equisetum fluviatile* f.*linnaeanum*, which have higher than 30% frequency.

GroupA1b: *C. lasiocarpa* marsh, a widespread marsh type. The habitat of this community is similar to *C. pseudocuraica* marsh, although the water depth is relatively shallow and varied from 5 to 20 cm. The primary associated species are *Lysimachia thyrsiflora, G. spiculosa, C. pseudocuraica, E. fluviatile* f.*linnaeanum, Comarum palustre, M. trifoliate, Iris laevigata, Salix myrtilloides.* The cover of moss layer is about 30%, primarily including *Campylium stellatum*, *Campylium somerfettii*, *Helodium paludosum*, *Drepauocladus aduncus* var. *kneiffii, Leptodictyum riparium*, *D. aduncus* f. *pseudofluitans and Sphagnum contortum*.

GroupA2a and GroupA2b: The Carex tussock marsh, which occupies a small area. It includes two community types- *C. appendiculata* community and *Carex meyeriana* community.

The most frequently occurring species were *C. angustifolia, Sanguisorba parviflora, G. spiculosa, C. lasiocarpa, Caltha palustris* and *C. pseudocuraica*. The cover of moss layer is about 20%, primary including *Sphagnum platyphyllum*, *Drepauocladus uncinatus* f.

Figure 2. TWINPAN dendrogram of samples with indicator species and Eigenvalues for each division for wetland types (or zones) in the Sanjiang Plain, northeastern China. The number of samples in each end group is indicated in parentheses.

plumulosum, Pohlia nutans, Bryum caespiticium and *Sphagnum inundatum.*

Group A3a: *C. appendiculata – C. angustifolia* marsh meadow, which is one of the most widespread marsh meadow occupies large area in Sanjiang Plain. This community was characterized by tussock *C. appendiculata* and wet meadow species *C. angustifolia.* The most consistent associates are *Sanguisorba parviflora, C. palustris, Pedicularis grandiflora, Lathyrus palustris* var. *pilosus* and *Stachys baicalensis.* The community structure is relatively complex and species composition is rich.

Group A3b: *C. angustifolia* wet meadow, which is also primary meadow vegetation occupies large area in Sanjiang Plain. *Calamagrostis angustifolia* is the constructive and dominant species, and is the most dominant species in the community. Tussocks of *C.*

appendiculata were scattered throughout this community, but always occurred at very low frequency. The common companion species are *S. parviflora, C. lasiocarpa, C. pseudocuraica, Lycopus lucidus, S. baicalensis, Scutellaria baicalensis, L. palustris* var. *pilosus,*

Group A4a: *Salix rosmarinifolia - Carex schmidtii – C. angustifolia* shrub swamp was characteristics of the shrub swamp. *S. rosmarinifolia* and *C. angustifolia* together dominate this community, but the habitat of this type is tussock dominated by *Carex schmidtii.* The primary associated species are *S. parviflora, Spiraea salicifolia, L. palustris* var. *pilosus, Lysimachia davurica, Anemone dichotoma.*

Group A4b: *Betula fruticosa* (or *Alnus sibirica*) – *C. schmidtii –C. angustifolia* shrub swamp, occupied a small area. It was characterized by developed shrub layers dominated by *B. fruticosa* (or *A. sibirica*), some other

Table 1. Frequency of occurrence (%) of species in the eight groups interpreted from TWINSPAN.

TWINSPAN group	A1a	A1b	A2a	A2b	A3a	A3b	A4a	A4b
Species / Number of plots	27	35	4	3	20	18	34	15
Carex pesudocuraica	100	48	75	33	15	28		
Carex lasiocarpa	76	100	100	100	31	39	38	
Glyceria spiculosa	56	56	75	100	24	6	13	
Menyanthes trifoliata	44	49						
Lysimachia thyrsiflora	36	56	50	33	31			
Equietum fluviatile f. *linnaeanum*	36	49	50	67	8	17		
Eriophorum gracile	28	17			23			
Comarum palustre	16	29			15			
Salix myrtilloides	12	40	25	33	15		25	
Iris laevigata	12	29		33	23			
Caltha palustris	12	29	50	67	23		38	7
Cicuta virosa	8	19		33				
Pedicularis grandiflora		3	25	33	8			
Stachys baicalensis		10	25	33	8	22	13	29
Stellaria longifolia		6	25		23		19	
Carex meyeriana			100					
Carex appendiculata				100	100			
Calamagrostis angustifolia	8	27			100	100	100	100
Scutellaria baicalensis			25		8	11	38	43
Sanguisorba parviflora					54	28	63	50
Carex schmidtii							25	71
Salix rosmarinifolia							75	86
Spiraea salicifolia							75	79
Lathyrus palustris Var. *pilosus*					31	44	38	36
Betula fruticosa								93
Alnus sibirica								36
Lycopus lucidus					23	17		36
Anemone dichotoma							13	36

species such as *S. rosmarinifolia* and *S. salicifolia* also occur with high frequency (92 and 77%, separately). The herb layer was dominated by *C. angustifolia*. The habitat was also tussock dominated by *C. schmidtii. S. parviflora* were present with nearly 80% of plots. In addition, *S. baicalensis, L. lucidus* and *A. dichotoma* were also common.

Group B: *Populus davidiana - Betula platyphylla* island forest, which is the wet secondary forest is represented on the relatively high island distributing outer of the depression. *P. davidiana* occupies 40 to 60% of the coverage, and *B. platyphylla* come next with about 20 to 30%.

The common companion species are *Quercus mongolica, Tilia mandshurica, Ulmus japonica, Acer ginnala*, and *Cacalia hastate* in the tree layer, *Vitis amurensis* and *Lespedeza bicolor* in the shrub layer, and *Convallaria keiskei, Paris verticillata, Anemone udensis* in the herb layer.

Ordination

Species and plots ordination in the space defined by the two first DCA axes is shown in Figures 3 and 4.The Eigen values obtained for these axes were 0.985 and 0.439, respectively (Table 2). Ter Braak (1987) considers the results not much greater than 0.3 as more normal in ecological studies. The first two axes of DCA collectively explained 24.2% of the variation in the species data. The length of the gradient was 11.380 and 2.481 for the first second axis, respectively; indicating that species turnover along the first axis is vastly greater than the second axis. Along the first axis, communities are arranged as a vegetation gradient from marsh through meadow marsh, wet meadow and shrub swamp to island forest, and it is moisture gradients controlled by the change of elevation. Along the second axis, the wet meadow community and shrub swamp communities were clearly separated from each other. It is moisture gradients controlled by micro-geomorphology. Clearly, the ordination diagram   of
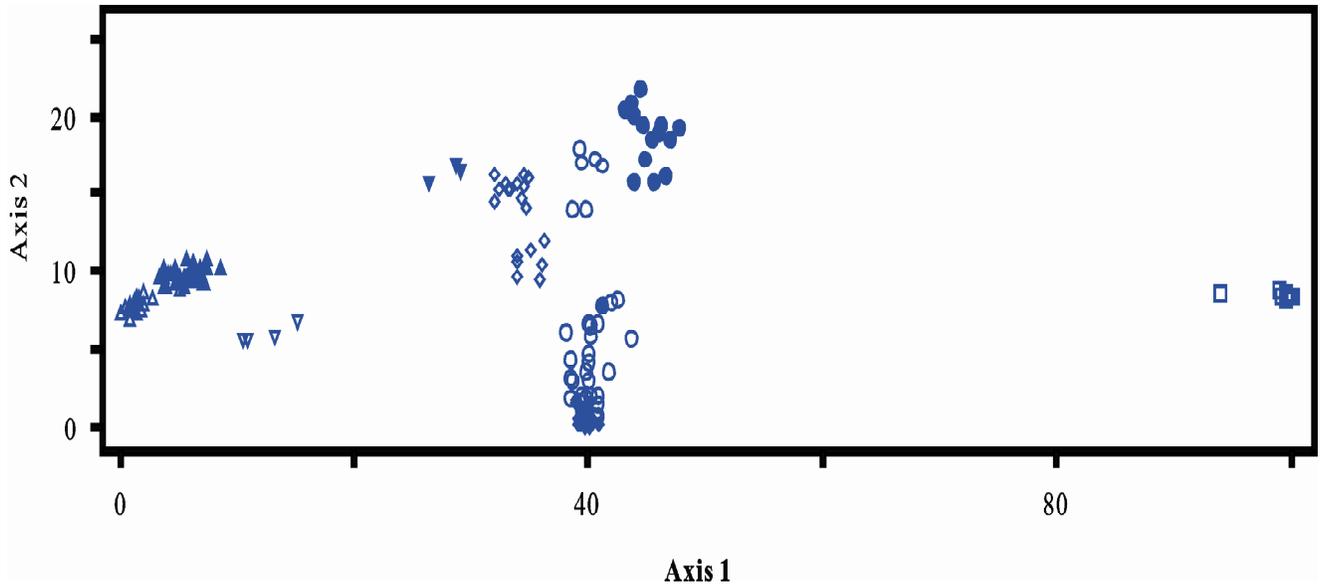
Figure 3. Detrended correspondence analysis ordination of 172 plots superimposed by TWINSPAN group. Δ, *Carex pseudocuraica* marsh; ▲, *Carex lasiocarpa* marsh; ▽ and ▼, *Carex* tussock marsh; ◊, *Carex appendiculata - Calamagrostis angustifolia* marsh meadow; ♦, *Calamagrostis angustifolia* wet meadow ○, *Salix rosmarinifolia - Carex schmidtii - Calamagrostis angustifolia* shrub swamp ●, *Betula fruticosa*(or *Alnus sibirica*)- *Carex schmidtii -Calamagrostis angustifolia* Shrub swamp.
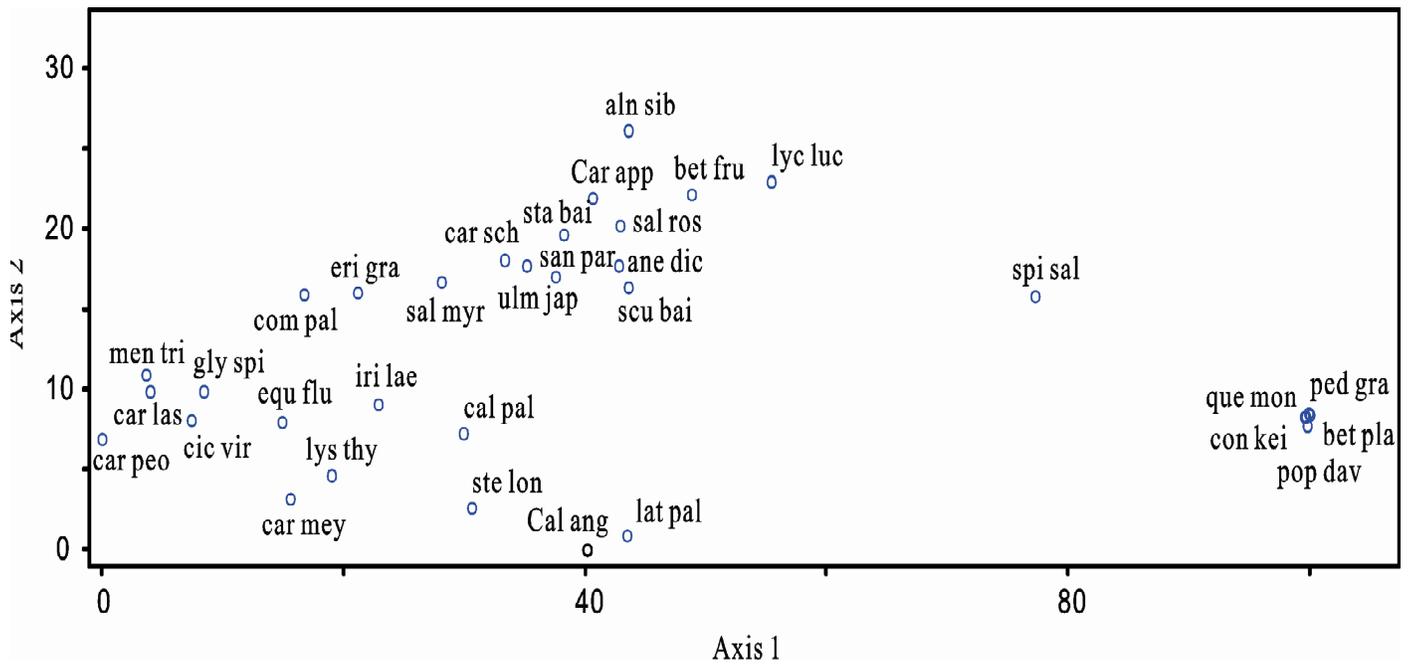
Figure 4. Detrended correspondence analysis ordination of the 33 species superimposed by TWINSPAN.

plots revealed that the groups defined by TWINSPAN classification constituted distinct clusters. So the ordination of the samples showed close agreement with the TWINSPAN classification.

The ordination of the species revealed essentially the same pattern, but formations were less distinctly recognized due to the presence of species that tolerated a wider range of habitat condition. Table 3 shows 17

Table 2. The calculation result of first four axis of DCA ordination for plots.

Axis	Eigenvalue	Length of gradient	Cumulative percentage variance of species data
Axis 1	0.985	11.380	16.7
Axis 2	0.439	2.481	24.2
Axis 3	0.249	2.594	28.4
Axis 4	0.182	2.235	31.5

Table 3. Species correlations with DCA ordinations in species space for wetland in Sanjiang Plain.

Species	Species code	Pearson's r	Axis of correlation
Carex pseudocuraica	Car pse	-0.506	1
Carex lasiocarpa	Car las	-0.604	1
Glyceria spiculosa	Gly spi	-0.436	1
Menyanthes trifoliata	Men tri	-0.377	1
Lysimachia thyrsiflora	Lys thy	-0.329	1
Equietum fluviatile f.*linnaeanum*	Equ flu	-0.343	1
Eriophorum gracile	Eri gra		
Comarum palustre	Com pal		
Salix myrtilloides	Sal myr		
Iris laevigata	Iri lae		
Caltha palustris	Cal pal		
Cicuta virosa	Cic Vir		
Pedicularis grandiflora	Ped gra		
Stachys baicalensis	Sta bai		
Stellaria longifolia	Ste lon		
Carex meyeriana	Car mey		
Carex appendiculata	Car app	0.344	2
Calamagrostis angustifolia	Cal ang	-0.625	2
Scutellaria baicalensis	Scu bai		
Sanguisorba parviflora	San par		
Carex schmidtii	Car scu	0.393	2
Salix rosmarinifolia	Sal ros	0.397	2
Spiraea salicifolia	Spi sal		
Lathyrus palustris var. *pilosus*	Lat pal		
Betula fruticosa	Bet fru	0.500	2
Alnus sibirica	Aln sib	0.389	2
Lycopus lucidus	Lyc luc	0.336	2
Anemone dichotoma	Ane dic		
Populus davidiana	Pop dav	0.763	1
Betula platyphylla	Bet pla	0.565	1
Quercus mongolica	Que mon	0.618	1
Anemone dichotoma	Ane dic		
Convallaria keiskei	Con kei	0.512	1

China (R^2>0.10 for all species shown).

species with strong correlations to the ordination structure. Ten species are correlated with Axis 1; this axis provides nearly most of the overall explanation for the ordination structure. The tree species, *P. davidiana, B. platyphylla, Q. mongolica*, etc, appeared towards the positive end of the first axis. The herbaceous species, such as *C. pseudocuraica, C. lasiocarpa, G. spiculosa*, etc, frequently present in habitats with several centimeters deep water, appeared towards the negative end of first axis. Most species correlated with Axis 2 are wet meadow and
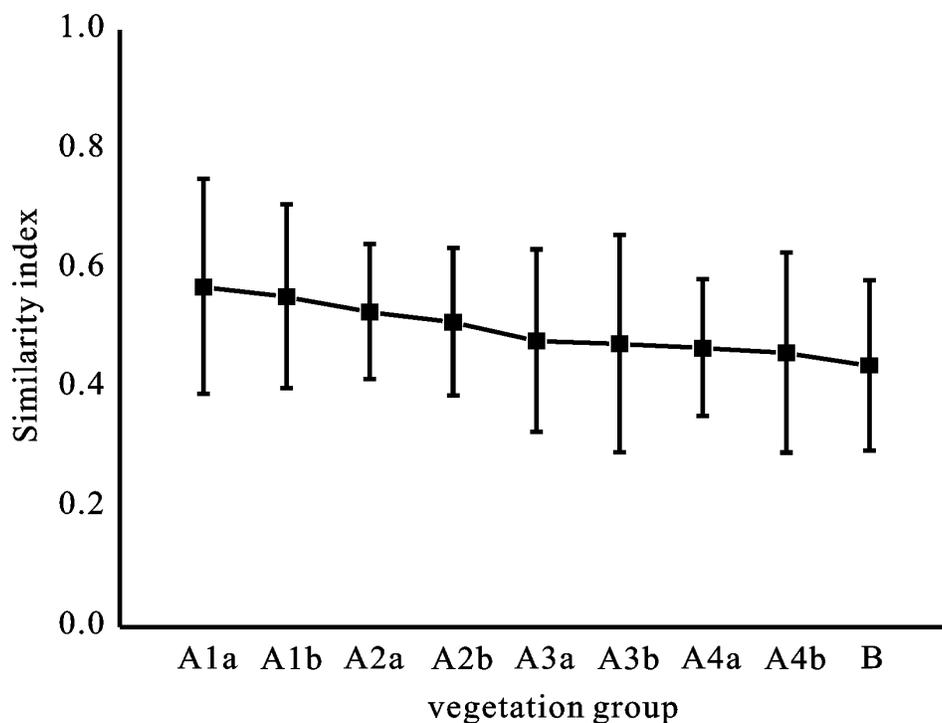
Figure 5. The community similarity of nine group classified by TWINSPAN (A1a: *Carex pseudocuraica* marsh, A1b: *Carex lasiocarpa* marsh, A2a and A2b: *Carex* tussock marsh, A3a: *Carex appendiculata - Calamagrostis angustifolia* marsh meadow, A3b: *C. angustifolia* wet meadow, A4a: *Salix rosmarinifolia - Carex schmidtii – C. angustifolia* shrub swamp, A4b: *Betula fruticosa* (or *Alnus sibirica)- C. schmidtii –C. angustifolia.* shrub swamp).

Table 4. Vegetation type similarity matrix for the nine vegetation types distinguished by TWINSPAN analysis, for wetland types in the Sanjiang Plain, northeastern China.

Group	A1b	A2a	A2b	A3a	A3b	A4a	A4b	B
A1a	0.40	0.32	0.31	0.16	0.15	0.08	0.08	0.01
A1b		0.36	0.34	0.27	0.24	0.12	0.12	0.01
A2a			0.39	0.32	0.30	0.16	0.15	0.02
A2b				0.37	0.34	0.27	0.25	0.02
A3a					0.38	0.31	0.29	0.06
A3b						0.35	0.33	0.08
A4a							0.36	0.12
A4b								0.14

swamp constructive and dominant species. For instance, *C. angustifolia,* with absolutely high cover in wet meadow, appeared towards the negative end of second axis, *Betula fruticosa,* with greater cover and only present in shrub swamp, appeared towards the positive end of second axis. This further indicated above-mentioned gradient pattern determined by plots.

Community similarity and species turn-over

Many species identified in this study had low frequency.

Of the 213 taxa identified across the 172 plots, 65 occurred in only one plot. Only less than half of the total species (87 taxa) occurred in at least five of the 172 plots. As expected, the lowest turnover was measured between the replicates at each community (Figure 5). Similarity indices between replicates ranged from 0.57 to 0.43, with both extremes occurring at community C. *pseudocuraica* and community *P. davidiana - B. platyphylla*. From group A1a to B, similarity gradually reduced; moreover, the difference among communities was significant (F=4.276, P<0.01). Looking at the different communities (Table 4),

Table 5. Above-ground biomass (0.25m^2 mean ± SD) following reciprocal transplants for *Carex lasiocarpa, C. appendicular* and *Calamagrostis angustifolia*.

Zone	Above-ground biomass		
	Carex lasiocarpa	*Carex appendiculata*	*Calamagrostis angustifolia*
Carex lasiocarpa	94.21 ± 16.05[a]	87.01 ± 10.09[a]	53.08 ± 16.28[a]
Carex appendiculata	66.07 ± 12.86[b]	83.29 ± 12.05[a]	158.50 ± 23.70[b]
Calamagrostis angustifolia	36.03 ± 7.79[c]	79.62 ± 9.59[a]	144.72 ± 31.19[b]

Letter denote significant differences of plant group at the p<0.05 level.

similarity in species composition is best reflected by geographical distance, that is, the communities that are more closer have higher similarity. The greatest species turnover was measured between community *C. pseudocuraica* and community *P. davidiana -B. platyphylla*, which shared hardly any same species. Given that only 5% of the total taxa (33) occurred in 10 or more replicate plots, the low percentage of shared species between each community must be the result of high species turnover between the communities.

Reciprocal transplant experiment

Reciprocal transplants of dominant species among zones showed that the effect on biomass production of transplantation to other vegetation zones for three dominant species is different (Table 5). The smallest effect of transplantation occurred for C. *appendiculata*; biomass production did not differ among treatments for transplantation *in situ* and to other two zones (P>0.05). Also, the greatest effect occurred for *C. lasiocarpa*; biomass production decreased significantly by 30 and 61% when transplanted to *C. appendiculata* and *C. angustifolia* zones, respectively. The effect on biomass production in *C. angustifolia* differs according to the zone of transplantation. When transplanted to the *C. appendiculata* zone, biomass production did not differ from its original zone (P>0.05), but biomass production reduced 63% when transplanted into the *C. lasiocarpa* zone.

DISCUSSION

Classification and ordination technique are often used to define plant communities and to identify the underlying environmental gradients (Kent and Ballard, 1988). In the present study, the types of wetland communities defined by both methods were similar. The wetland vegetation in Sanjiang plain of northeast China is classified into nine groups; this is a marsh- marsh meadow -wet meadow-swamp-upland forest gradient pattern. More concretely, for marsh, it also includes flat-lawn-hummock series; this is an emergent marsh-meadow marsh

gradient pattern. And for swamp, it includes *Salix* swamp and *Betula* (or *Alnus*) swamp; this is low shrub swamp- tall shrub swamp gradient pattern. These pattern was similar to that of wetland vegetation in Changbai Mountain of China (Mou, 1998), Hokkaido of Japan (Asada Taro, 2002), Alberta (Whitehouse and Bayley, 2005; Bayley and Mewhort, 2004) and Ontario (Rydin and Jeglum, 2005) of Canada. This is consistent with the hypothesis that vegetation patterns were determined by the climate in large scale, because the above-mentioned sites are in same latitude zone and have similar climate. However, for community and indicator species, Sanjiang Plain was not identical with aforementioned region. For example: *C. lasiocarpa* was distributed in Hokkaido and Alberta, but peat was not developed; for tussock marsh meadow, the dominant species were *C. appendiculata* and *C. angustifolia* in Sanjiang Plain, while *Carex caespitosa* and *Calamagrostis langsdorffii* in Hokkaido, *Carex stricta* and *Calamagrostis canadensis* in Ontario. Furthermore, as for the dominant species of swamp, *B. fruticosa, A. sibirica* and *S. rosmarinifolia* in Sanjiang Plain, while *A. japonica* in Hokkiado, *Alnus glutinosa* in Ontario, this could be related to region species pool, precipitation, water chemistry and regional micro-climate.

However, within a region, vegetation patterns are produced by multiple factors in small scale (Keddy, 2000). On one hand, our transplant experiments showed that the biomass response of three dominant species to different vegetation zone (wetness gradients) was different. This suggested that they have different tolerance for physical conditions to different wetness gradient. *C. appendiculata* has the widest tolerance for physical conditions across the zones, followed by *C. angustifolia, with C. lasiocarpa* the least tolerant of variation in physical conditions across the zones. This is also consistent with the opinion of many studies (Bertness and Ellison, 1987; Wilson and Keddy, 1985; Shipley et al., 1990; Blom et al., 1990) that differences among vegetation zones along water gradient are controlled by their abilities to cope with hydrology condition. On the other hand, as deduced from many studies (Gore, 1983; Tsuyuzaki, 1997), our result also supported that water depth was one of prime importance for the herbaceous vegetation pattern. Water depth was significantly related to species establishment in the of

studied wetland; *Carex* tend to grow in the habitats water depth and in contrast, tussock-forming sedges usually become established in the sites of dry-humid alternation, while the shrub *Alnus* and *Betula* grow in these habitats. In addition, several factors not addressed in this study could also influence the long-term distribution and composition of vegetation zones in these wetlands. For example, nutrient and mineral concentration is strongly influenced by hydrologic patterns.

Generally, the similarity of community species com-position is the simple measure of community habitats heterogeneity. In our study, from marsh to swamp to upland forest, the similarity gradually reduced, so it implied that habitats heterogeneity should be higher along above gradients. Besides, similar studies are few; hence the comparison cannot be executed. Nevertheless, of the 213 taxa identified across the 172 plots, 65 occurred in only one plot. Only 87 taxa had a frequency more than 5%, and 18 species had a frequency of twenty percent or greater. While these values do not represent actual similarity indices, they are indicative of the low similarity in species composition for this community type. High turnover resulted from environmental gradients in the wetland that produce overlapping ranges of optimal conditions for a wide variety of plant species (Deborah, 2004). In this study, there were significant differences in wetness conditions between the nine communities. Moreover, the nutrient gradient and other underlying environmental gradients could also exist because of the concept of marsh and swamp. Certain species may be responding to gradients in wetness and substrate nutrient conditions that are present across the community. The multiple combinations of these many environmental variables may have created several meaningful gradients across the study site that account for high species turnover.

In this study, our classification provides the first quantitative description of the vegetation in Sanjiang Plain. This would provide base root for future management and protect under the circumstance of climate change and human activities since; (1) it provides a base framework to identify wetland community based on floristic and (2) the indicator species provide us a direction in species choosing of wetland restoration and role allotment of wetland assessment. In addition, our study also revealed the different physiological response of three dominant species to hydrologic condition. This provides the foundation for forecasting the zonation shift in Sanjiang plain under the background of climate change and human activities. In recent years, climate change and human activities (ground water pumping resulting from agricultural production) have aggravated drought and reduced water levels in wetland (Luo et al., 2008), so that the zone of *C. angustifolia*, which is not adapted to flooding condition is widened, but the zone of *C. lasiocarpa* is narrower and as so much disappeared because of its low tolerance to non-standing water

habitats.

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