INFLUENCE OF SOIL-ECOLOGICAL CONDITIONS ON VEGETATION ZONATION IN A WESTERN MONGOLIAN LAKE SHORE-SEMI-DESERT ECOTONE

With 6 figures, 4 tables and 4 photos

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Vegetationsgeographie, Bodengeographie, Umweltforschung, Zentralasien, aride Räume

Zusammenfassung: Der Einfluss bodenökologischer Bedingungen auf die Vegetationszonierung in einem Seeufer-Halbwüsten-Ökoton der westlichen Mongolei

Das Becken der Großen Seen in der Westmongolei ist geprägt von ausgedehnten Wüsten-, Halbwüsten- und Steppenarealen sowie von Seen und umgebenden einzigartigen Feuchtgebieten. Diese Feuchtgebiete sind bedeutende Elemente der Landschaftsökosysteme semi-arider und arider Räume. Andererseits ist die Kenntnis selbst grundlegender Ökosystemkomponenten wie Vegetation und Böden noch sehr lückenhaft.

Das Ziel der vorliegenden landschaftsökologischen Studie entlang eines Seeufer-Halbwüsten-Ökotons war es, das kleinräumige Muster von Standortfaktoren entlang eines ausgeprägten Umweltgradienten sowie den Einfluss dieses Musters auf die Vegetationszonierung zu analysieren. Um die Veränderungen in dem Übergangsbereich zwischen aquatischen und terrestrischen Lebensräumen adäquat zu erfassen, wurden die Daten mit einem Transekt-Ansatz aufgenommen. Pflanzengesellschaften wurden nach der Braun-Blanquet-Methode klassifiziert. Die Vegetations- und Bodendaten wurden einer Detrended Correspondence Analysis und einer Canonical Correspondence Analysis unterzogen, um Veränderungen in der Artenzusammensetzung mit Veränderungen bodenökologischer Parameter entlang des Transektes korrelieren zu können.

Die Analyse der annähernd gürtelförmigen Vegetationszonierung ergab eine Abfolge von fünf verschiedenen Pflanzengesellschaften auf einer Länge von 250 m. Die Übergangsbereiche zwischen den Gesellschaften waren in der Regel nicht durch scharfe Grenzen, sondern durch mosaikartige Strukturen geprägt. Die Abfolge der Gesellschaften entspricht dem Wandel bodenökologischer Bedingungen; sie korreliert mit einem komplexen Bodenfeuchte- bzw. Bodentextur-Gradienten. In Richtung Halbwüste nehmen Bodenfeuchte und die Gehalte an Stickstoff und organischer Substanz ab, während pH-Werte und Lagerungsdichten zunehmen. Karbonat- und Salzgehalte zeigen keine einheitliche Tendenz. Der Bodenfeuchte muss die größte Bedeutung für die Vegetationsdifferenzierung beigemessen werden. Die Bodenfeuchte und eng korrelierte Parameter wie Humusgehalt, Lagerungsdichte und pH erklären den größten Anteil der Varianz im Vegetationsdatensatz. Unter mehr oder weniger gleichartigen Bodenfeuchtebedingungen üben Lagerungsdichte, pH, $CaCO_3$- und Humusgehalte wesentlichen Einfluss auf die Vegetationsdifferenzierung aus.

Innerhalb einer Pflanzengesellschaft zeigen einzelne Bodenparameter mitunter große Schwankungsbreiten, d.h. die Pflanzengesellschaften sind offensichtlich an eine gewisse Bandbreite an Konstellationen sich verändernder Standortsfaktoren angepasst. Da sich der Beweidungsdruck auf die See- und Flussauen mit ihrem günstigen Bodenwasserhaushalt und ihrer vergleichsweise hohen Produktivität konzentriert, sind alle Feuchtgebietgesellschaften in ihrer Artenzusammensetzung mehr oder weniger stark verändert worden. Die ursprüngliche Vegetation, die insbesondere in den Flussauen auch Wälder und Gebüsche umfasste, ist inzwischen weitgehend zerstört worden.

Summary: The Great Lakes Basin of W Mongolia encompasses vast stretches of deserts, semi-deserts, steppes as well as lakes and surrounding unique wetlands. These wetlands must be considered important elements of landscape ecosystems in semi-arid/arid environments. On the other hand, the knowledge of even basic ecosystem components like soils and vegetation is still very fragmentary.

We present a landscape-ecological study of vegetation and soil zonation along a western Mongolian lake shore-semi-desert ecotone. Our objective was to analyse fine-scale patterns of environmental variables along a marked environmental gradient and to find out their specific controls on the zonation of wetland plant communities. We followed the transect approach in order to document and understand patterns and changes in transitional areas between aquatic and upland habitats. We classified plant communities according to the Braun-Blanquet approach and subjected the vegetation and soil data sets to DCA and CCA (Detrended and Canonical Correspondence Analysis) in order to detect the main correlations between plant species turnover and changing site conditions along the transect.

Analysis of the more or less belt-like vegetation zonation at the southwestern shore of Khar Us Nuur showed that five plant communities replace each other at a distance of only 250 m. In transitional areas, wetland plant communities form a mosaic or patch structure with shifting species dominances rather than sharp boundaries. Community replacements correspond to changing soil-ecological conditions. Along the transect from lake shore to the semi-desert, soil moisture, nitrogen and organic matter contents decrease, whereas soil pH and bulk density values increase. Calcium carbonate contents and soil salinity do not show uniform trends. Plant communities of the lake shore-semi-desert ecotone are distributed along a complex soil moisture/soil texture gradient. Soil moisture is the most critical environmental variable for vegetation patterns. Differences in soil moisture and related parameters like organic matter content, bulk density, and soil pH explain maximum vegetation variation. Within areas of more or less homogeneous soil moisture conditions in the wetland part of the transect, vegetation differentiation must be mainly attributed to differences in bulk density, soil pH, $CaCO_3$ contents, and organic matter contents.

Single soil parameters may vary widely within one plant community along the transect. Plant communities are obviously associated with a certain constellation of varying edaphical factors and have to adapt to a wider range of environmental conditions.

Since grazing pressure concentrates on river and lake floodplains with its favourable soil water budget and productivity, all of the wetland communities are more or less changed in their species composition. Most of the original vegetation, including forests and shrublands, had already been destroyed.

1 *Introduction*

Thorough analyses of ecosystem structure and functioning is fundamental to understanding the sensitivity of ecosystems to global environmental change. The semi-arid and arid ecosystems of Central Asia tend to be very sensitive to climate change as expressed, e.g., in altering soil water availability and shifting biomass patterns (OJIMA et al. 1998; OPP a. KHAKIMOV 2003; CHRISTENSEN et al. 2004). In semi-arid steppe ecosystems in the Asian region, above-ground grass production was found to be more correlated to growing season rainfall than to annual precipitation amounts (XIAO et al. 1995). Seasonal shifts in rainfall patterns or increased evaporation due to increased temperatures could greatly affect semi-arid/arid ecosystem functions like net primary productivity and storage of soil carbon and nitrogen. It has been predicted that carbon and nitrogen in soil organic matter of Mongolian grasslands will decrease by 10 and 3% respectively given a temperature increase of 3 °C (DAGVADORJ et al. 2002). Actually, analyses of recorded annual temperatures showed an increase by about 1.8 °C in western Mongolia for the 1940 to 1995 period (DAGVADORJ a. MIJIDDORJ 1996). Unusual warming in the region, corroborated by other studies (OPP 1994, 1996; JACOBY et al. 1999; OBYAZOV 1999; KRÜGER 2001), is particularly reflected by rising autumn, winter, and spring temperatures. A slight increase in annual precipitation in recent decades also pertains mainly to winter precipitation whereas summer rainfall is characterized by extraordinarily high variability. In the Great Lakes Basin of W Mongolia, summer rainfall, averaging ca. 65% of the annual sum, may be as low as 35 mm in dry years, but may amount to 225 mm in wet years (cf. KRÜGER 2001). Here, a decline in water resources, which is expected in the long term, will have serious impacts on wetlands ecosystems and land use (BATIMA 2002).

Land use change is another major issue of global environmental change in Mongolia. The economy has been traditionally based on pastoral nomadism, and mobile livestock keeping is still the dominant strategy of the rural population for sustaining livelihoods (cf. JANZEN a. BAZARGUR 2003). Approximately 75% of the nation's territory is used for livestock grazing (Mongolia Ministry for Nature and the Environment et al. 1999). The centrally planned economy during the period of the People's Republic resulted in a decline in number of nomadic herders (MÜLLER 1999), but total numbers of livestock remained roughly the same from the 1940s until the collapse of communism in 1991 (GOMBOEV 1996). Fundamental changes in mobile pastoralism and in the rural environment in Mongolia have taken place since the process of transformation towards market economy and democracy ensued (MÜLLER 1997; JANZEN a. BAZARGUR 1999, 2003). The revival of Mongolian nomadism resulted in substantially increasing pressure on grazing lands. Socio-economic transition had led to a rapid increase in livestock numbers, from 24 million head in 1989 to ca. 33 million head in 1998 (MÜLLER 1999). In the meantime, three consecutive years of drought and harsh winters (1999–2002) again reduced the national herd (MEARNS 2004). The dismantling of herding collectives (*negdels*) rendered formal and informal institutions, which have regulated pastoral land use in former times, ineffective so that insecure pastoral tenures and unsustainable land use patterns can be observed (FERNANDEZ-GIMENEZ 1999, 2002; JANZEN a. BAZARGUR 2003). Increasing proportions of the country are now characterized by overstocking and overgrazing (BASTIAN 2000; BATKHISHIG a. LEHMKUHL 2003) potentially causing significant damage to biodiversity, ecosystem, and habitat. Consequences may include decline in vegetation cover, succession towards less edible or unpalatable plant species, increasing evaporation, loss of soil moisture, deflation of the humus soil layer, water erosion, and increasing expansion of deserts (GUNIN et al. 1999). Adverse ecological effects are to be expected in growing land areas, if careful herding practices and appropriate pasture conservation measures are not implemented (cf. MÜLLER a. BOLD 1996; OPP 2002; SCHICKHOFF a. ZEMMRICH 2003).

Predicting the effects of environmental changes in Mongolia on ecosystem structure and functioning is hampered by still very fragmentary knowledge of even basic ecosystem components like soils and vegetation. HILBIG (1995) in his benchmark publication stressed the need for more basic vegetation data and pointed out that detailed inventories of flora and vegetation are still lacking for major parts of Mongolia, even for nature reserves and national parks. Regions of deficient knowledge include the Great Lakes Basin of W Mongolia with its vast stretches of deserts, semi-deserts and steppes, as well as lakes and surrounding unique wetlands that contain some of the last remaining extensive reed beds in Central Asia (KIPPER et al. 1999). These wetlands must be considered important components of landscape ecosystems in semi-arid/arid environments. Their significance as breeding grounds and staging posts for migrating waterfowl and waders was documented by BRÄUNLICH (1995). As ecotones between aquatic and upland ecosystems, wetland meadows and pastures are among the most productive vegetation types due to the favourable soil water availability during the vegetation period. Transformed from original poplar and willow forests/shrublands by centuries of grazing and wood extraction (HILBIG 1995), wetland meadows are subjected to severe grazing pressure. Moreover, they are an essential winter pasture for nomadic herders, e.g., when reed islands become accessible due to freezing-up of the lakes. Extensive pasture use has caused severe degradation of about 80–90% of wetland areas within dry steppes and deserts of Mongolia (VOSTOKOVA et al. 1995). On the other hand, these wetlands are still strongly under-researched. HILBIG (1995) ascertained a particularly pressing need for more data on halophytic vegetation, marshlands, meadows, and sedge marshes.

To reduce prevailing research deficits regarding W Mongolian ecosystems is a prerequisite in order to derive strategies from a solid scientific basis for the sustainable management of grazing lands and for the conservation of biodiversity. As for the groundwater-dependent vegetation of floodplains and lake basins in the Great Lakes Basin, HILBIG (1995) gave a general overview based on own previous studies (HILBIG 1983, 1990a, b; HILBIG a. SCHAMSRAN 1976, 1977) as well as on other sources (e.g., YUNATOV 1950; LAVRENKO 1979; MIRKIN et al. 1988). Recent contributions to ecological knowledge of wetland vegetation are included in BUYAN-ORSHIKH (1992), RACHKOVSKAYA (1993), OYUNCHIMEG (1998), GUNIN et al. (1999), HILBIG et al. (1999), HILBIG (2000a, b), and OPP and HILBIG (2003). Some basic information on western Mongolian soils in general were provided by BESPALOV (1951), HAASE (1983), OPP (1994, 1998), DORZHGOTOV (1992), VOSTOKOVA et al. (1995), GRUNERT et al. (2000), BLANK and KRÜGER (2001), KNOTHE et al. (2001), and OPP and HILBIG (2003). However, wetland soils are very poorly studied so far. And, none of the above studies addresses relationships between wetland soil-ecological conditions and the differentiation of vegetation in greater detail. Studies of the vegetation zonation along sharp environmental gradients from aquatic to upland habitats in the Great Lakes Basin and of respective correlations with soil-ecological parameters are missing up to now.

In this paper we present a landscape-ecological study of vegetation and soil zonation along a western Mongolian lake shore-semi-desert gradient. The most common approach to studying ecological transition zones is to detect patterns and changes of environmental variables and species compositions/dominances across adjacent habitats along transects (WHITTAKER 1978; RISSER 1995). The transect approach allows analyzing maximum variation over the shortest distance in the minimum time (KENT a. COKER 2000). We followed this approach in order to document and understand patterns and changes in transitional areas between aquatic and upland habitats. Our objective was to analyse fine-scale patterns of environmental variables along a marked environmental gradient and to find out their specific controls on the zonation of wetland plant communities. Since soil water availability is the most important limiting factor in semi-arid/arid environments (NOY-MEIR 1973), we hypothesized that soil moisture is the most critical environmental variable and that other site parameters like soil reaction, nutrients etc. are of subordinate importance for the patch structure of plant communities in the lake shore-semi-desert ecotone. At the same time we expected that each plant community represents edaphically distinct habitats and that a transition from one plant community to another indicates changes in soil ecological conditions. We were also interested in analysing the causal factors of the mosaic of vegetation patches within small-scale areas of comparable soil water availability.

2 *Study area*

The study area, the southwestern lake shore of the Khar Us Nuur, is located in the Great Lakes Basin, a large intermountain depression surrounded by the Mongolian Altai (4,374 m) in the west, the Gobi Altai

(3,957 m) in the south, Khangai Mts. (3,905 m) in the east, and the Tannu Ola Mts. (3,351 m) in the north (Fig. 1). The Great Lakes Basin occupies an area of approx. 106,000 km^2 and can be divided into three endorheic sub-basins with a series of smaller and larger lakes, predominantly salt lakes including Uvs Nuur (largest Mongolian salt lake; 3,350 km^2) and Khargas Nuur (Murzaev 1954). All these lakes are considered remnants of an extensive Pleistocene freshwater basin (Murzaev 1954; Dulma 1979). Khar Us Nuur (Photo 1) and Khar Nuur, fed by the Khovd-gol and other Mongolian Altai rivers and streams with higher discharge (Barthel 1990), are the only large present freshwater lakes. The large lakes of the depression are surrounded by gently undulating plains, often interspersed with small lakes, salt pans, and low hilltops. At some distance from the lake shores, pronounced terraces are developed marking mid-Holocene high stands of lake levels that were 5–7 m higher than today (Walther et al. 2003). At Khar Us Nuur, this lake terrace covered by chee-grass stands (*Achnatherum splendens*) is situated about 4.5 m above the current lake level. The altitude of Khar Us Nuur and surrounding wetland areas, representing the core zone of the Khar Us Nuur National Park, is about 1,160 m a.s.l. The maximum length of the lake is 78 km, its maximum width is 26 km. The open water surface, extending southward into nearly 160 km^2 of swamp and reeds, decreased from 1,607 km^2 in 1992 to 1,523 km^2 in 1997 (Batnasan a. Batima 2000).

Desert and desert-steppe vegetation covers vast areas of the Great Lakes Basin indicating the markedly continental and arid/semi-arid climate (Lavrenko 1979; Karamysheva a. Khramtsov 1995). Here extratropical deserts and desert-steppes penetrate far north and exceed 50° N (about the same latitude as Prague in Central Europe). Mean annual precipitation on the leeward side of the Mongolian Altai rarely exceeds 100 mm. The climate diagram of the station Khovd (1,397 m; Fig. 2), about 50 km to the west of Khar Us Nuur, clearly shows pronounced continental and arid conditions with maximum precipitation in the short, warm summer (annual mean: 122 mm) and very low winter temperatures with an average of five months below 0 °C (Beresneva 1992). Low winter temperatures (mean January temperature: –24.3 °C), caused by the persistent Asian cold anticyclone absorbing cold polar

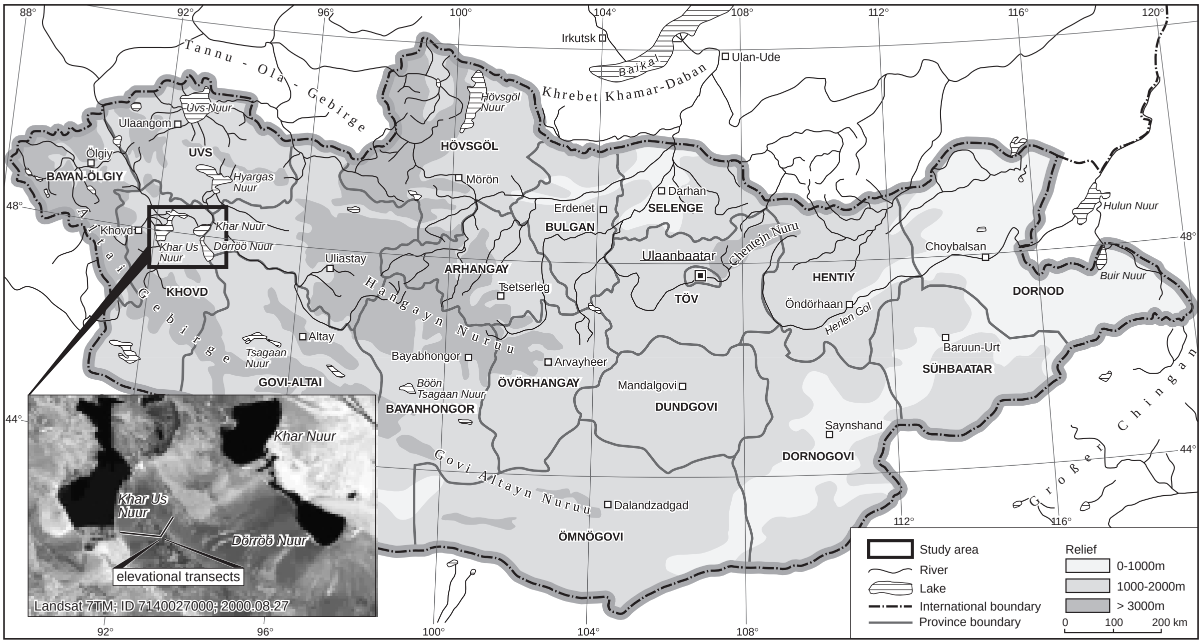

Fig. 1: Location of the study area in western Mongolia. Lake Khar Us Nuur with the transect site enlarged in the satellite picture

Lage des Arbeitsgebiets in der West-Mongolei. Der See Khar Us Nuur mit dem bearbeiteten Transekt ist im Satellitenbild vergrößert dargestellt air masses, contrast with relatively high temperatures in summer (mean July temperature: 18.9 °C) when cyclonic circulation predominates. Stable stratification of airflows in winter favours the development of high-reaching and long-lasting temperature inversions, resulting in thermal belts above cold air accumulations in depressions and valley floors. According to GRAVIS (1974), the Great Lakes Basin is an area of sporadic permafrost occurrence.

The vegetation of deserts/semi-deserts and desert steppes in the depressions of Hyargas Nuur and Khar Us Nuur is dominated by dwarf semi-shrubs (*Anabasis brevifolia)*, dwarf shrubs (*Reaumuria soongorica*), grasses (*Stipa glareosa*, *Stipa gobica*, *Cleistogenes squarrosa*) and forbs (*Convolvulus ammanii*, *Allium* spp.). Principal species of shrub steppes are larger shrubs like *Caragana leucophloea*, *Caragana bungei*, *Atraphaxis frutescens*, and several semi-shrubs of the genus *Artemisia*. Large areas of the wetlands surrounding the lakes are occupied by reed beds dominated by *Phragmites australis*. Other wetland vegetation types include tall marshlands of *Bolboschoenus planiculmis* and/or *Typha laxmannii*, saline meadows (*Halerpestes salsuginosa*, *Potentilla anserina*, *Glaux maritima*, *Triglochin palustre*), stands of annual halophytic species (*Salicornia europaea*, *Suaeda* spp., *Chenopodium* spp.) as well as chee-grass stands (*Achnatherum splendens;* syn. *Lasiagrostis splendens*), which mark the transition from groundwater-influenced vegetation to steppic and desertic vegetation (cf. HILBIG 1995).

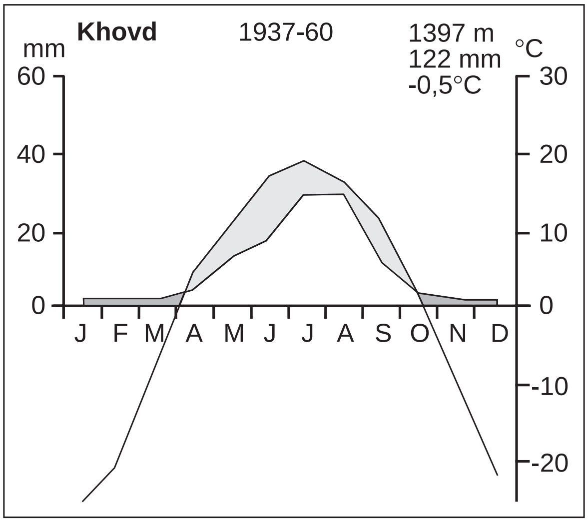

Fig. 2: Climate diagram of the station Khovd (Source: HILBIG 1995, modified), located immediately west of the study area

Klimadiagramm der unmittelbar westlich des Arbeitsgebietes gelegenen Station Khovd (Quelle: HILBIG 1995, verändert)

Most people in the study area follow a pastoral semi-nomadic lifestyle. The average population density in the Khar Us Nuur National Park is less than 1.2 persons/km^2 (KIPPER et al. 1999). Nevertheless, considerable semi-desert, steppe and wetland areas show signs of overgrazing like low floristic diversity, reduced vegetation height and cover, and high proportions of weeds and unpalatable species. The herders exploit the good grazing grounds at the lakeshores during spring, autumn and winter (BRÄUNLICH 1995; BATOCHIR 2002). Khar Us Nuur, having a maximum depth of 4.5 m, freezes over in October or November and thaws in April/May (DULMA 1979). During this period the thick ice cover (> 100 cm) provides access for livestock to the grazing grounds on numerous small lake islands at the southern lake margin.

3 Methods

3.1 Field sampling

The study was conducted along a E–W transect of 250 m length at the southwestern lake shore of Khar Us Nuur (47°50' N; 92°02' E) (Photo 1). Data were collected in the summer of 2002. The transect was laid out as a continuous belt transect perpendicular to the vegetation zonation in order to record the main ecological gradient. It crosses the entire wetland transition zone from the immediate lake shore to the border of the semi-desert on the upper lake terrace. Along the transect, a total of 25 vegetation and soil samples (0–30 cm) were analysed in 10 m intervals. This data set represents a sub-set of a larger data base of 264 relevés and 25 soil profiles from other wetland areas of Khar Us Nuur which was used for verification of plant communities. All sample sites were documented by GPS (Global Positioning System) measurements.

The relevés were completed according to the Braun-Blanquet approach (BRAUN-BLANQUET 1964; DIERSCHKE 1994). Determination of the size of the sample plots followed the minimal area method according to DIERSCHKE (1994). At each sample plot, all vascular plant species were recorded (bryophyte and lichen species were not found), and a voucher specimen of each species was collected for final identification in the herbaria of Khovd and/or Greifswald University. Species cover was estimated in nominal percentages ('+' and 'r' as in WILMANNS 1998) and according to the WILMANNS (1998) cover-abundance-scale. Vegetation height and cover of separate vegetation layers (shrub, field and litter layer) were measured or estimated. For the determination of vascular plants, GRUBOV (2001) and ROTHMALER (2002) were used. The nomenclature of vascular plant species follows GUBANOV (1996).

At each sample plot, a soil profile was described according to AG Boden (1994), and soil samples (3 x 100 cm^3 cylinder samples) were collected from the uppermost mineral soil horizon in each soil pit. Description of peat and gyttja types including the degree of decomposition followed SUCCOW and STEGMANN (2001), for field estimation of soil texture and bulk density SCHLICHTING et al. (1995) was used. Laboratory soil analyses in the Botanical Institute, University of Greifswald, comprised soil pH (in $CaCl_2$), C_{total}/N ratio, C_{org}/N ratio, N, P, C_{anorg}, C_{org}, organic matter, EC[1)] (electroconductivity), and percentage of gravel, sand, silt, and clay. Bulk density and water content of the soil samples were measured in the laboratory of Khovd University. Fresh field samples were oven-dried until weight constancy was reached. Soil classification was carried out both after HAASE (1983) and FAO (1988).

3.2 Data analysis

Vegetation was classified according to the Braun-Blanquet sorted table method, i.e. the relevés were arranged in a phytosociological table to differentiate and characterize the sampled vegetation units. Table work was carried out by means of a common table calculation program (Microsoft EXCEL). We tried to assign the differentiated plant communities to already described western Mongolian plant communities of HILBIG (1995, 2000b) using his diagnostic species or species combinations. However, our main intention was not classification of relevés. For that we would have needed a much larger data set. Instead, we wanted to analyse specific controls of site conditions on the zonation of wetland plant communities.

Therefore, we subjected the vegetation and soil data sets to DCA and CCA (Detrended and Canonical Correspondence Analysis) using PC-ORD 4.0 (MCCUNE a. MEFFORD 1999) in order to detect the main correlations between plant species turnover and changing site conditions along the transect. The direct ordination method CCA was applied for the entire transect because we wanted to test the hypothesis of soil moisture and moisture-dependent parameters being the most critical environmental variables for variation in the vegetation data. Moreover, we used the indirect ordination method DCA for the wetland part of the transect omitting drier upland sites and the transition to semi-desert in order to generate hypotheses about the relationships between site parameters and the patch structure of vegetation within areas of more or less homogeneous soil moisture conditions. For this purpose, DCA was considered a more appropriate technique than a constrained (direct) ordination like CCA, because the problematic dependency of constrained ordination axes on recorded environmental variables regarding an unbiased interpretation of all explanatory variables of complex gradients should be avoided (cf. ØKLAND 1996). In both cases, cover-abundance values of species were given in actual percentage cover in the main matrices. Only '+' was converted to a value of 0.5% (DIERSCHKE 1994), 'r' was not present in the data set. We included the measured environmental variables possibly influencing vegetation like electroconductivity, soil pH, bulk density, water content, $CaCO_3$ content, C_{org}, C_{org}/N ratio, N and P content as well as grazing marks in the second matrix.

A landscape-ecological profile showing vegetation and site characteristics along the lake shore-semi-desert ecotone was prepared to illustrate in summary the relationships between the alteration of site parameters and the change of vegetation types. In addition to the analysed belt transect, information about further nearby soil pits with extensive descriptions (down to 87–115 cm soil depth) from the larger data set were included.

4 Results

4.1 Vegetation zonation and soil-ecological conditions

As illustrated by both the landscape-ecological profile (Fig. 3) and the vegetation table (Tab. 1), the typical vegetation zonation at the southwestern shore of Khar Us Nuur reflects pronounced directional community replacements and changing community characteristics according to environmental alterations. At a distance of only 250 m, five plant communities replace each other, controlled by microscale soil ecological gradients. Along the lake shore-semi-desert transect, soil pH and bulk density values increase whereas soil moisture con-

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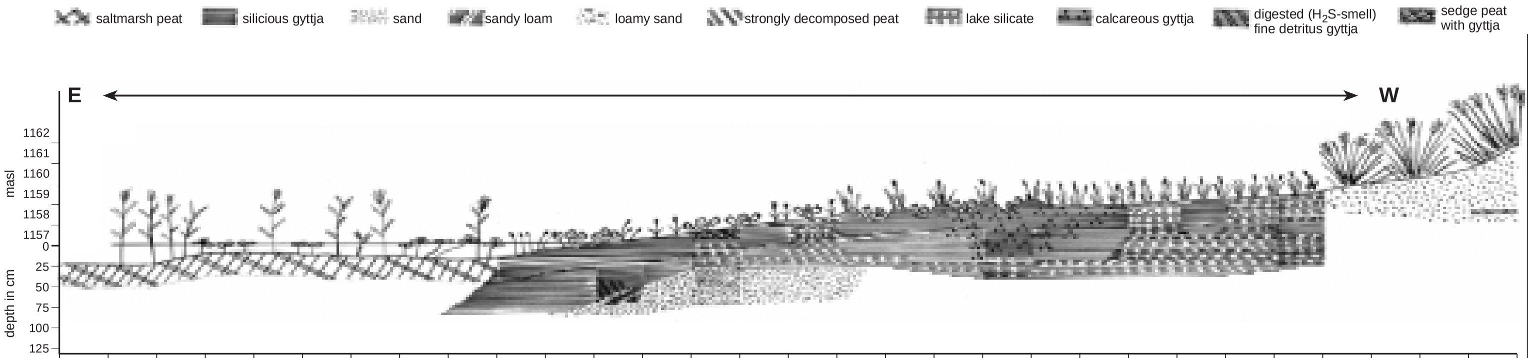
[1)] We used EC values as proxy for the salinity of soils. However, the estimation of water-soluble salts of the soil by measurement of EC once in summer can give only rough information due to the great seasonal variety of salt concentrations in the soil.



distance from open water in m	40		60		80		100		120		140			160			180		200			220		240		260			280	300
relevé/soil profile (SP) number	1	2	3	4	5	6	7	8	9	10	11	SP10	12	SP9	13	14	15	16	17	SP24	18	19	20	21	22	SP11	23	24	25	SP18
relief of the lake shore	slightly concave slope, 1 % E																1 % E, hummocks ± 15 cm caused by cryoturbation				slightly concave slope, 1 % E						lake shore terrace around the lake, lower part of the slope, 5 % E			
soil type according to HAASE (1983) (in German)	(Kryo-) Moorboden- Solontschak				(Kryo-) Gley	(Kryo-) Moorboden-Solontschak	(Kryo-) Gley-Solontschak																					mittlerer Parakastannosem		
soil type ISSU/ISRIC/FAO (1998)	(Gelic) Histosols									(Gelic) Histosols				Gleyic Solonchaks														Haplic Kastanozems		
classification of peat types, limnic sediments (according to SUCCOW & STEGMANN 2001) and texture	salt marsh peat (partly below 30 % organic matter)									silicious gyttja				fine sedge peat$^+$ silicates	silicious gyttja	lake silicates	silicious gyttja		calcareous gyttja				lake silicates	silicious gyttja	lake silicates	silicious gyttja		Ss		
soil moisture (AG Boden 1994)	feu6; water depth 10-25 cm										feu4					feu3-2					feu2						feu1			
plant community sensu HILBIG (1995; 2000 b)	*Nymphoidetum peltatae* (Allorge 1922) Bellot 1951, also characteristics of *Phragmitetum communis* (Gams 1927) Schmale1939, *Mentha arvensis subass.* Hilbig 1987, *Puccinellia tenuiflora var.* Hilbig 1995									*Phragmitetum communis* (Gams 1927) Schmale 1939, *Mentha arvensis subass.* after Hilbig 1987, *Puccinellia tenuiflora var.* Hilbig 1995			*Halerpesto-Hordeetum brevisubulati* Hilbig (1987) 1990, typical *subass.*, *Glaux maritima var.* after Hilbig 1987				*Halerpesto-Hordeetum brevisubulati* Hilbig (1987) 1990, typical *subass.*, *Glaux maritima var.* after Hilbig 1987 in hollows, *Leymus paboanus tussock* grassland Hilbig 2000 on hummocks				*Leymus paboanus tussock* grassland Hilbig 2000						*Glycyrrhizo uralensis-Achnatheretum splendentis* Hilbig (1987) 1990			
soil moisture in vol. %	78,2	78,2	77,9	75,7	--	78,6	76,2	100,0	100,0	76,2	51,4	--	58,6	--	52,0	29,9	47,1	44,4	10,4	--	5,0	17,0	26,0	14,3	7,0	--	6,2	0,9	0,3	--
pH	6,8	6,9	6,8	7,1	7,3	7,0	7,4	7,2	7,,2	7,2	7,3	7,0	7,4	8,2	7,6	8,0	7,7	7,8	7,8	7,8	7,9	7,8	8,5	7,9	7,5	9,0	7,9	7,5	7,3	7,3
Corg / N	10,2	10,2	11,1	10,7	10,2	10,7	10,1	10,0	11,0	10,3	10,1	9,6	10,4	10,3	10,7	8,3	8,6	8,7	9,7	8,3	9,8	9,2	9,0	11,7	9,5	8,8	9,6	7,5	11,3	10,2
N %	1,7	1,7	1,9	1,8	1,1	1,5	1,3	0,9	1,2	0,9	0,7	1,2	0,8	1,2	0,6	0,2	0,5	0,5	0,3	0,4	0,4	0,3	0,3	0,3	0,2	0,3	0,2	0,1	0,,1	0,1
EC in mS / cm	16,6	22,0	14,9	17,2	9,0	15,4	22,7	9,8	14,4	9,5	19,1	12,3	6,4	64,3	30,3	24,0	64,5	61,4	26,7	25,9	26,9	31,7	63,2	26,5	25,3	87,6	23,3	1,0	1,9	4,3
organic matter (Corg*2) %	33,7	34,9	41,7	39,3	23,1	32,2	26,6	17,7	27,0	18,7	14,8	23,7	15,9	23,8	13,7	2,7	9,1	7,8	6,4	6,8	7,3	5,6	4,8	5,9	2,8	5,0	4,0	0,9	1,3	1,7
CaCo$_3$ in %	7,5	8,3	1,9	6,33	10,0	9,3	12,4	11,4	12,9	13,9	13,3	15,6	16,9	21,0	20,8	11,9	28,0	27,4	31,9	25,6	30,8	30,4	15,6	8,7	13,6	14,9	1,8	1,4	0,4	1,8
Phosphorus % dry matter	0,4	0,4	0,2	0,3	0,3	0,2	0,1	0,1	0,1	0,1	0,1	--	0,1	0,2	0,1	0,2	0,1	0,1	0,1	0,1	0,1	0,1	0,2	0,3	0,2	0,4	0,4	0,2	0,1	0,4
Bulk density in g / cm^3	0,2	0,2	0,2	0,2	0,3	0,2	0,3	0,4	0,3	0,4	0,7	--	0,8	--	0,9	1,3	0,9	0,8	1,2	--	1,1	1,0	1,1	1,2	1,4	--	1,3	1,5	1,4	--

Fig. 3: Landscape-ecological profile at the southwestern shore of Khar Us Nuur
Landschaftsökologisches Profil am Südwestufer des Khar Us Nuur

Table 1: Plant community table of the transect

Tabelle der Pflanzengesellschaften des Transekts

Relevé-No.	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25
Relevé size in m^2	4m^2	4m^2	4m^2	4m^2	4m^2	4m^2	4m^2	4m^2	4m^2	4m^2	4m^2	8m^2	8m^2	8m^2	8m^2	8m^2	8m^2	8m^2	8m^2	8m^2	8m^2	8m^2	16m^2	16m^2	16m^2
Slope, aspect	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1%E	1%E	6%E	6%E	6%E
Number of vascular taxa	8	11	12	11	11	12	10	10	11	11	16	10	12	12	9	9	8	4	3	3	2	2	1	2	3
Cover of herb layer %	87,5	25%	55%	50%	60%	75%	90%	90%	40%	85%	85%	98%	97%	97%	60%	60%	50%	40%	55%	55%	55%	55%	65%	50%	40%
Cover of litter layer %	–	–	–	–	–	–	–	–	–	–	–	5%	60%	60%	8%	8–10%	4%	5%	5%	8%	8%	10%	15%	5%	2%
Height of herb layer in cm	172	50	35	30	35	40	40	25	25	80	45	35	20	20	67	67	80	60	50	36	40	38	100	100	70
Grazing marks %	8%	95%	95%	95%	90%	50%	30%	40%	29%	5%	65%	80%	50%	50%	40%	10%	30%	80%	80%	85%	80%	90%	20%	20%	50%
Diagnostic species of Nymphoidetum peltatae																									
Nymphoides peltata	5	1	1	.	.	1	.	2a	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Persicaria amphibia	2a	1	.	1	1	2a	2a	2a	2a	2b	1	+	.	+	.	.	.	.	.	.	.	.	.	.	.
Diagnostic species of Phragmitetum communis																									
Phragmites australis	2a	2b	2a	2a	2b	2b	2b	2a	1	.	1	+	1	2a	1	+	.	.	.	.	.	.	.	.	.
Beckmannia syzigachne	+	+	+	+	+	1	1	1	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Diagnostic species of Halerpesto-Hordeetum brevisubulati																									
Glaux maritima	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	+	.	.	.	.	.	.	.	.
Juncus gerardii	.	.	.	.	.	.	.	.	.	.	.	.	+	1	2a	1	1	.	.	.	.	.	.	.	.
Potentilla anserina	.	.	+	.	.	+	.	.	1	2a	1	2b	2a	1	.	.	.	.	.	.	.	.	.	.	.
Halerpestes salsuginosa	.	.	.	.	.	.	.	.	.	.	1	1	3	3	3	3	2b	.	.	.	.	.	.	.	.
Puccinellia tenuiflora	+	.	+	+	1	1	+	+	1	2b	2b	2b	2a	1	1	.	.	.	.	.	.	.	.	.	.
Triglochin palustre	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	+	1	.	.	.	.	.	.	.	.
Hordeum roshevitzii	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.	.
Diagnostic species of Leymus paboanus tussock grassland																									
Leymus paboanus	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2a	3	3	3	4	4	5	5	.	.	.
Diagnostic species of Glycyrrhizo uralensis-Achnatheretum splendentis																									
Achnatherum splendens	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	4	4	3
Companions:																									
Halerpestes sarmentosa	.	1	1	2a	1	1	1	+	2b	2a	2a	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Hippuris vulgaris	2a	1	2a	+	2b	2b	5	4	2a	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Scirpus hippoliti	2b	1	2a	2b	1	1	1	1	1	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Utricularia vulgaris agg.	.	1	+	+	+	1	1	2a	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Eleocharis mamillata	.	.	2b	2b	.	.	.	.	1	2a	2b	2a	2b	.	.	+	.	.	.	.	.	.	.	.	.
algae	.	4	5	.	5	4	4	4	2b	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Suaeda corniculata	.	.	.	.	.	.	.	.	.	.	.	.	.	2a	1	1	1	+	+	+	.	.	.	.	.
Saussurea salsa	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1	+	1	1	1	1	.	.	.
Ranunculus radicans	.	+	+	+	.	+	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa tibetica	.	.	.	.	.	.	.	.	.	.	+	1	1	1	1	1	.	.	.	.	.	.	.	.	.
Bidens tripartita	+	1	+	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Plantago major	.	.	.	.	.	.	.	.	.	+	+	2a	+	.	.	.	.	.	.	.	.	.	.	.	.
Atriplex laevis	.	.	.	.	.	.	.	.	.	+	+	.	+	.	.	.	.	.	.	.	.	.	.	.	.
Carex duriuscula	.	.	.	.	.	.	.	.	.	.	.	.	3	1	1	.	.	.	.	.	.	.	.	.	.
Poa spec.	.	.	.	.	.	.	.	.	.	.	.	.	.	2a	.	1	+	.	.	.	.	.	.	.	.
Potamogeton rostratus	.	.	.	+	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Taraxacum leucanthum	.	.	.	.	.	.	.	.	.	.	.	+	.	1	.	.	.	.	.	.	.	.	.	.	.
Knorringia sibirica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.
Micropeplis arachnoidea	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	2a
Chenopodium glaucum	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	1
Chenopodium album	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Poa pratensis	.	.	.	.	.	.	.	.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	.	.	.
Spergularia marina	.	.	.	.	.	.	.	.	.	.	+	.	.	.	.	.	.	.	.	.	.	.	.	.	.
Atriplex sibirica	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	.	+	.

siderably decreases, and nitrogen and organic matter contents decrease to a lesser extent (Fig. 4). EC values show mid-transect peaks. As for peat types and soil textures, salt marsh peats at the lake shore are followed by gyttja and sandy textures at the inland end of the transect. Expressed in soil types, Histosols are replaced by Solonchaks and further inland by Kastanozems.

The vegetation zonation starts with the *Nymphoidetum peltatae*[2)] at the lake end of the transect (cf. Tab. 1; Fig. 3). The floating community of the fringed water-lily (*Nymphoides peltata*) occupies shallow water areas at the lake shore (until 25 cm water depth) where it grows on salt marsh peats. Accordingly, the soils which have formed can be placed in the Histosol order. They are mainly characterized, apart from their high water content, by comparatively lowest soil pH, ranging from 6.8 to 7.4, highest organic matter content (between 17.7 and 41.7%) and lowest $CaCO_3$ content (mostly below 10%) and bulk density (0.25 g/cm^3 at average). Moreover, the soils are very rich in nutrients (N, P). The occurrence of the *Nymphoidetum peltatae* is obviously favoured by cattle grazing in reed stands (*Phragmites australis*) since it is widespread where reed stands are grazed down. The species composition includes some characteristic taxa of the *Phragmitetum communis*, another indication of the status of *Nymphoidetum* as a replacement community for the latter. Typical species like the floating-leaved *Nymphoides peltata* as well as *Persicaria amphibia* grow amidst some less vigorous *Phragmites australis* and other taxa of the reed community like *Puccinellia tenuiflora*, *Scirpus hippoliti*, *Hippuris vulgaris*, *Halerpestes sarmentosa*, and *Beckmannia syzigachne*.

At the immediate lake shore where the soil is no longer constantly covered by water but where the groundwater level is still very close to the surface, the *Nymphoidetum peltatae* gives way to the *Phragmitetum communis* (Tab. 1; Fig. 3). The reed community grows on a silicious gyttja type of sediment. The soil type can be classified as Gelic Histosol due to permafrost in the lower subsoil. Soil moisture drops to about 50–75 vol. %. Soil pH is in about the same range as with the *Nymphoidetum* (7.0–7.3). However, the organic matter content decreases considerably to c. 20%, whereas $CaCO_3$ content (around 15%) and bulk density (0.4–0.7 g/cm^3) strongly increase. The grazed reed community resembles a saltmarsh pasture with high species number and high vegetation cover (cf. Tab. 1). Principal species are *Phragmites australis* and *Beckmannia syzigachne* (*Poaceae*), further common taxa include *Halerpestes sarmentosa, Eleocharis mamillata, Hippuris vulgaris, Potentilla anserina*, and *Puccinellia tenuiflora*.

Proceeding inland, the reed community is followed by the *Halerpesto-Hordeetum brevisubulati* (Tab. 1; Fig. 3), which is a true pasture community in Mongolian river and lake floodplains. The summer groundwater level here is in approx. 15–40 cm depth. Soil moisture may already drop to 30–50 vol. %. Compared to the above communities, soil pH rises up to 8.2. Organic matter content further decreases and may drop below 10%. At the same time, $CaCO_3$ content and bulk density further increase. Within this community belt, soil types change from Gelic Histosols to Gleyic Solonchaks, both developed on silicious gyttjas, the latter also on fine sedge peat and lake silicates. Gyttjas are remnants of former lake soil, which is now covered by wetland vegetation. They indicate higher lake levels in the past and the former lake extent respectively. The *Halerpesto-Hordeetum brevisubulati* is a species-rich saltmarsh pasture community with dense vegetation cover. Diagnostic species include not only the name-giving *Halerpestes salsuginosa* (*Ranunculaceae*) and *Hordeum roshevitzii* (*Poaceae*) as well as widespread grazing-adapted taxa like *Potentilla anserina* and *Puccinellia tenuiflora*. Additionally, the occurrence of typical European (coastal) saltmarsh species like *Glaux maritima*, *Juncus gerardii*, and *Triglochin palustre* (cf. Tab. 1) characterizes this community.

With considerably decreasing soil moisture further inland, a transition zone follows with a microrelief that is characterized by frost mounds ('bugry' = small mound in Russian) formed by cryoturbation. The frost mounds, resembling the Icelandic thufurs in shape and size (HAASE 1983), are covered by *Leymus paboanus* tussock grassland whereas the *Halerpesto-Hordeetum brevisubulati* still occupies the hollows between bugrys. Where the frost mounds are levelled out by rising terrain, the *Leymus paboanus* grassland is prevalent in its typical appearance (Tab. 1; Fig. 3). Here, the groundwater level is at 60–110 cm depth, and soil moisture may drop to 5–7%. Soils, which have developed on calcareous and silicious gyttjas and lake silicates, can still be termed Gleyic Solonchaks. Soil pH is further increasing and ranges from 7.5 to 9.0, coinciding with very low available nitrogen and very low organic matter content (below 10%). On the other hand, $CaCO_3$ contents reach its maximum along the transect, especially on calcareous gyttjas. Vegetation cover and average species numbers are relatively low in this community (cf. Tab. 1), which is mainly formed by the dominant species *Leymus paboanus* (*Poaceae*), often accompanied by *Suaeda corniculata* (*Chenopodiaceae*). Both species are typical for saline lake coasts, subsaline depressions

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[2)] Synonyms and author names of plant communities are given in figure 3.

among sands, alkaline sandy-pebble river banks, and dry and moist Solonchaks.

The upland dry end of the transect is characterized by the chee-grass community *Glycyrrhizo uralensis-Achnatheretum splendentis* (Tab. 1; Fig. 3), which is common at somewhat saline sandy lake terraces and marks the transition zone to semi-desert and steppes. Accordingly, soil moisture is mostly below 1% and groundwater levels are below 130 cm depth. The soil types change from Gleyic Solonchaks to Haplic Kastanozems with sandy textures and very low nitrogen contents. Organic matter contents, $CaCO_3$ contents, and electroconductivity show lowest values along the entire transect. On the other hand, bulk density (1.3–1.5 g/cm^3) is highest. Soil pH is alkaline, ranging from 7.3 to 7.9. The tall tussock grass *Achnatherum splendens* clearly dominates this community, which is often developed as *Achnatherum* monostands. Between the tall tussocks very few other species were found (cf. Tab. 1).

4.2 Ordination

The CCA of the entire transect (Fig. 5) calculated a high total variance (inertia) of 4.99 (Tab. 2), pointing to a steep floristic gradient with high species turnover. The first axis has a high eigenvalue of 0.922, thus explaining a large proportion of the total variance. The CCA indicates that the studied environmental factors, which altogether explain 42% of vegetation variation, can be roughly divided into two groups. The first group refers to differences in soil moisture and related parameters like organic matter content and bulk density. These parameters show highest loadings on the first axis (Tab. 3), i.e. water content and organic matter show high positive correlations, whereas bulk density and soil pH show high negative correlations with this axis. Accordingly, the wetland communities are distributed along a complex soil moisture/soil texture gradient within the ordination space with floating-leaved and reed communities in the left part of the graph and alkaline/subsaline meadows and communities at drier sites in the right part (cf. Fig. 5). The second group refers to differences in calcium carbonate and nutrients, environmental variables which differentiate plant communities along the second axis and explain the great distance between the *Glycyrrhizo uralensis-Achnatheretum splendentis* and the *Halerpesto-Hordeetum brevisubulati* in the ordination space. Both complex gradients as expressed in Axis 1 and 2 contribute to the very isolated position of the chee-grass community (cf. Fig. 5), which is associated with driest sites and lowest trophic levels.

The outstanding importance of the soil moisture gradient gave rise to omit the relevés on drier sites when performing DCA. We subjected only the data set of the

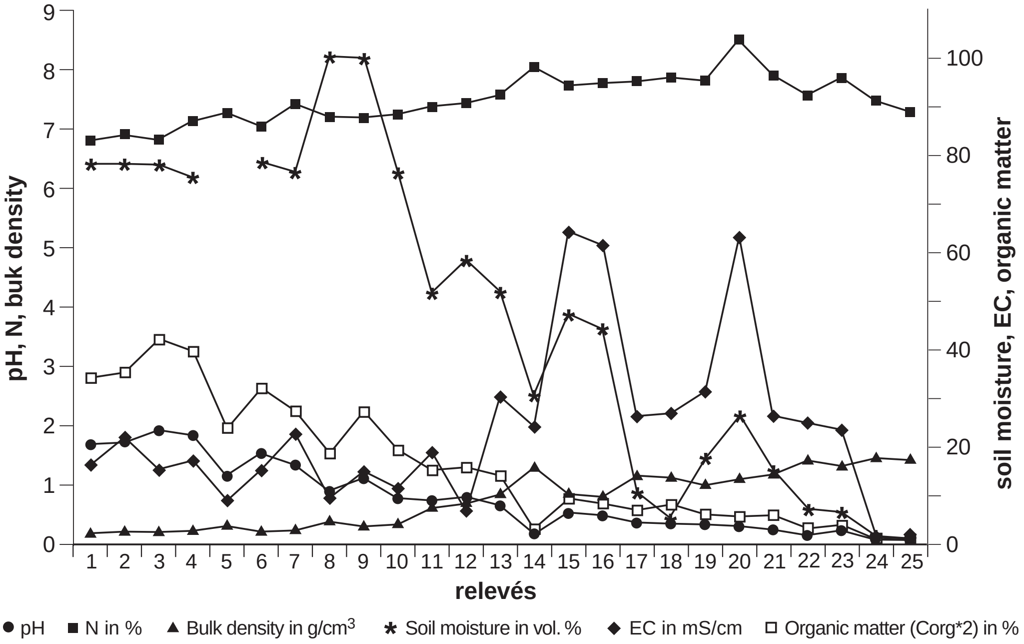

Fig. 4: Change of selected soil parameters along the transect from lake shore to semi-desert

Veränderungen ausgewählter Bodenparameter entlang des Transektes vom Seeufer zur Halbwüste

Photo 1: The transect was laid out at this location at the southwestern shore of Khar Us Nuur, crossing the entire wetland transition zone to the border of the semi-desert: a- open lake water with reed islands, b- *Nymphoidetum peltatae*, c- *Phragmitetum communis*, d- *Halerpesto-Hordeetum brevisubulati*, e- *Halerpesto-Hordeetum brevisubulati* in hollows and *Leymus paboanus* tussock grassland on hummocks, f- *Leymus paboanus* tussock grassland (Photo: U. SCHICKHOFF, 14.08.2003)

An dieser Stelle am SW-Ufer des Khar Us Nuur wurde das Transekt bearbeitet, das sich vom Flachwasserbereich über die gesamte Übergangszone bis zur Halbwüste erstreckt: a- offenes Wasser des Sees mit Schilfinseln, b- *Nymphoidetum peltatae*, c- *Phragmitetum communis*, d- *Halerpesto-Hordeetum brevisubulati*, e- *Halerpesto-Hordeetum brevisubulati* in Senken und *Leymus paboanus* tussock grassland auf Bulten, f- *Leymus paboanus* tussock grassland (Photo: U. SCHICKHOFF, 14.08.2003)

Photo 2: Chee grass (*Achnatherum splendens*) stands mark the transition zone from wetlands to semi-desert and steppes and indicate the presence of plant-available groundwater (Photo: A. STRAUSS, 27.08.2002)

Kamelgrasbestände markieren den Übergangsbereich von Feuchtgebieten zu Halbwüsten und Steppen und sind Indikatoren für pflanzenverfügbares Grundwasser

Photo 3: Grazing down of dense reed communities (*Phragmitetum communis*) leads to altered light conditions that favour the expansion of the *Nymphoidetum peltatae* (Photo: U. SCHICKHOFF, 02.09.2002)

Weidebedingte Erniedrigung der Schilfbestände (*Phragmitetum communis*) führt zu veränderten Lichtverhältnissen, was die Expansion des *Nymphoidetum peltatae* begünstigt

Photo 4: During dry summer periods desiccating soils at the lake shore may be covered by huge salt accumulations (Photo: U. SCHICKHOFF, 24.08.2002)

Während trockener Phasen im Sommer können die austrocknenden Böden am Seeufer von mächtigen Salzausblühungen bedeckt sein

Table 2: Axis summary statistics for the CCA ordination

Achsenstatistik der CCA-Ordination

Number of canonical axes: 3

Total variance ("inertia") in the species data: 4.9869

	Axis 1	Axis 2	Axis 3
Eigenvalue	0.922	0.682	0.492
% of variance in species data explained	18.5	13.7	9.9
Cumulative % of variance in species data explained	18.5	32.2	42.0
Pearson Correlation, Spp-Envt	0.988	0.879	0.819
Kendall (Rank) Corr., Spp-Envt	0.753	0.700	0.567

wetland part of the transect (relevés no. 1–16 with soil moisture between c. 50 and 100 vol. %) to DCA in order to avoid maximum differences in soil moisture obscuring relationships between species distributions and other environmental variables. DCA results (Fig. 6) still show a strong influence of soil moisture, however, soil water content itself is only ranked fifth in the loadings on Axis 1 (Tab. 4). Among the different variables, bulk density, soil pH, $CaCO_3$ contents, and organic matter contents play major roles in differentiating plant communities along more or less comparable soil moisture conditions. These variables are combined to a complex gradient that largely provides for the distant position of the *Nymphoidetum peltatae* (far left in the

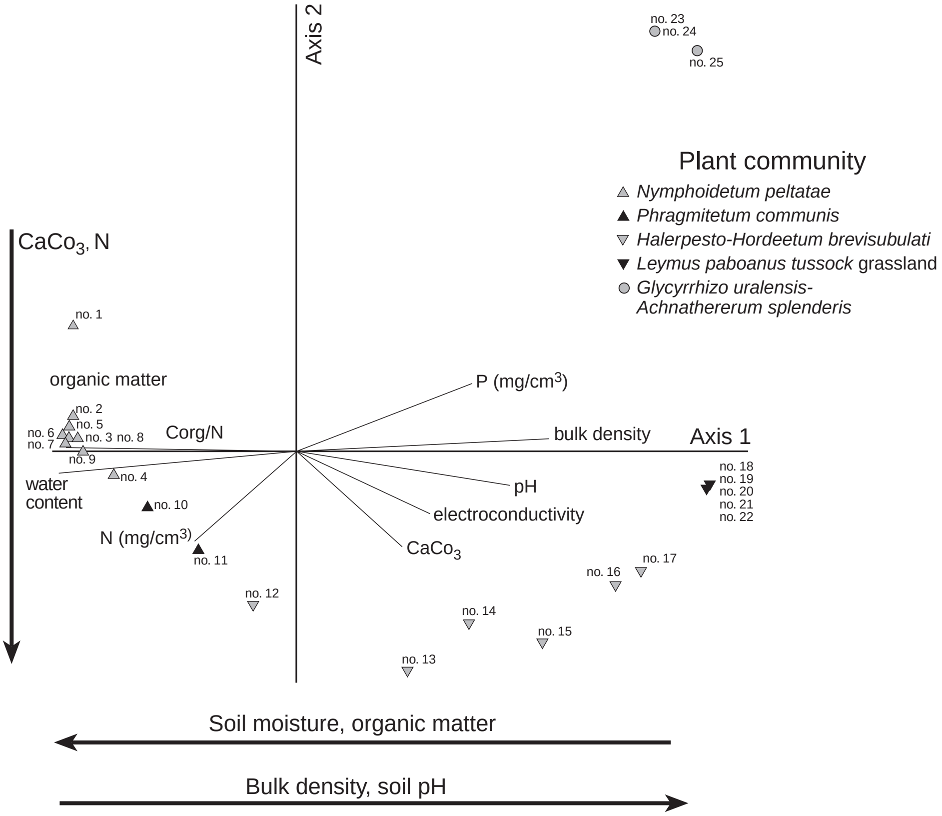

Fig. 5: CCA of the entire transect. The cutoff value (r^2) is 0.200

CCA des gesamten Transekts. Der Trennwert (r^2) liegt bei 0.200

Table 3: Inter-set correlations for the environmental variables used in the CCA ordination

Korrelationen der in der CCA-Ordination verwendeten Umweltvariablen mit den Hauptachsen

variables	correlations		
	Axis 1	Axis 2	Axis 3
bulk density	–0.940	0.080	0.189
water content	0.891	–0.163	–0.080
organic matter	0.861	0.021	–0.154
pH	–0.798	–0.237	0.025
P	–0.658	0.454	0.167
electroconductivity	–0.497	–0.436	0.225
C_{org}/N	0.420	–0.007	–0.156
$CaCO_3$	–0.394	–0.655	–0.165
N	0.377	–0.618	0.206
grazing marks	–0.154	–0.015	0.258

Table 4: Coefficients of determination (r^2) of environmental variables from the Pearson test derived by the DCA ordination

Bestimmtheitsmaße (r^2) der in der DCA-Ordination verwendeten Umweltvariablen (Pearson-Test)

variables	coefficients of determination r^2		
	Axis 1	Axis 2	Axis 3
bulk density	0.750	0.003	0.280
pH	0.683	0.011	0.337
$CaCO_3$	0.647	0.000	0.201
C_{org}	0.619	0.003	0.258
water content	0.508	0.015	0.226
electroconductivity	0.450	0.006	0.479
C_{org}/N	0.370	0.004	0.476
P	0.248	0.075	0.515
N	0.070	0.001	0.303
grazing marks	0.048	0.008	0.009

graph) and the *Halerpesto-Hordeetum brevisubulati* (far right; cf. Fig. 6). Figure 6 depicts a combination of Axis 1 and 3 since there are no significant correlations between any of the variables and Axis 2 (cf. Tab. 4). Axis 3 contributes an interesting gradient that is mainly caused by nutrient contents and salinity of the soils (cf. also Tab. 4). This gradient explains the distant position of single relevés of the *Halerpesto-Hordeetum brevisubulati* in the second dimension of the ordination space.

Summarizing the ordination results, it has to be stated that a complex gradient with bulk density and soil moisture conditions as the most important variables, closely followed by organic matter content and soil pH, causes the vegetation zonation along the lake shore-semi-desert ecotone. Within areas of more or less homogeneous soil moisture conditions in the wetland part of the transect, vegetation differentiation must be mainly attributed to differences in bulk density, soil pH, $CaCO_3$ contents, and organic matter contents.

5 *Discussion*

5.1 *Vegetation zonation*

Our study confirms the more or less belt-like zonation of different vegetation types in ecotones between river/lake floodplains and steppes/semi-deserts of the Great Lakes Basin that was described in previous studies (e.g. HILBIG a. SCHAMSRAN 1977; LAVRENKO 1979; BUYAN-ORSHIKH 1992; OYUNCHIMEG 1998; HILBIG et al. 1983, 1999; OPP a. HILBIG 2003). A very sharp boundary with complete species turnover exists between the *Leymus paboanus* grassland at the outer floodplain and the *Achnatherum splendens* community on the elevated lake terrace at the transition to the semi-desert. At the same time an abrupt change in soil physical and chemical conditions takes place. Vegetation zonation within the groundwater-influenced lake floodplain is, however, far from being regularly or schematically belt-like (cf. Fig. 3). As exemplified by the transitional zones between the *Nymphoidetum peltatae* and the *Phragmitetum communis* or between the *Halerpesto-Hordeetum brevisubulati* and the *Leymus paboanus* tussock grassland, the wetland plant communities form a mosaic or a patch structure with shifting species dominances rather than sharp boundaries in transitional areas. Patch structures may be caused by small-scale differences in natural environmental factors as in the case of 'bugry' formation due to cryogenetic processes (cf. VOSTOKOVA et al. 1995) in the transition zone between the *Halerpesto-Hordeetum brevisubulati* and the *Leymus paboanus* grassland. The occurrence of the former community in hollows and of the latter on frost mounds may serve as a classical example for patch structures.

On the other hand, such structures may also be caused or at least reinforced by anthropogenic interferences. Mosaic-like community patterns in shallow waters at the lake shore are likely to be strongly influenced by grazing down of dense reed communities. Altered light conditions favour the competitiveness of the *Nymphoidetum peltatae* that expands into former community areas of the *Phragmitetum communis* (Photo 3). Similar observations were made in W Mongolia by HILBIG and SCHAMSRAN (1977) and elsewhere in Eurasia, e.g., in the Danube floodplain of SE Europe by Horvat et al. (1974). Hilbig (1995) stressed that nearly all tall reed marsh and swamp communities are severely and continuously disturbed by cattle. High grazing pressure in our stands of the *Phragmitetum communis* is also indicated by the occurrence of *Beckmannia syzigachne* and *Puccinellia tenuiflora*. According to Hilbig (1995), these species are characteristic for heavily grazed reed beds.

In general, vegetation zonation at lake shores in the Great Lakes Basin has to be interpreted in the light of human intervention and change of lake floodplain ecosystems. All of the floodplain communities are more or less changed in their species composition by grazing and other uses that have been increasing in the last two to four millennia (cf. Gunin et al. 1999; Grunert et al. 2000; Schlütz 2000). Grazing pressure, that has been reinforced after 1990 (Nyamdavaa 1997; Janzen a. Bazargur 2003), concentrates on river and lake floodplains since these areas are islands of favourable soil water budget and productivity within a sea of parched steppes and semi-deserts. As already pointed out by Yunatov (1950), Kashapov et al. (1972), Hilbig and Schamsran (1977), Hilbig (1987), Titov et al. (1990a, b) and others, grazing use was directed to floodplains for many centuries, thereby also destroying most of the original poplar forests (*Populus* spp.) and shrubberies of willows (*Salix* spp.), sea-buckthorn (*Hippophae rhamnoides*) or other species. Wood was not only extracted to increase and improve grazing grounds but also to reduce the severe wood deficit in the Great Lakes Basin south of the larch forest belt. Hilbig (1995) pointed out that larger, continuous willow shrubberies, that are partially only secondary stands at sites of former poplar woods, are nowadays restricted to poorly accessible sites such as river islands or oxbows. At the south shore of Khar Us Nuur woods or shrubberies are not to be found anymore.

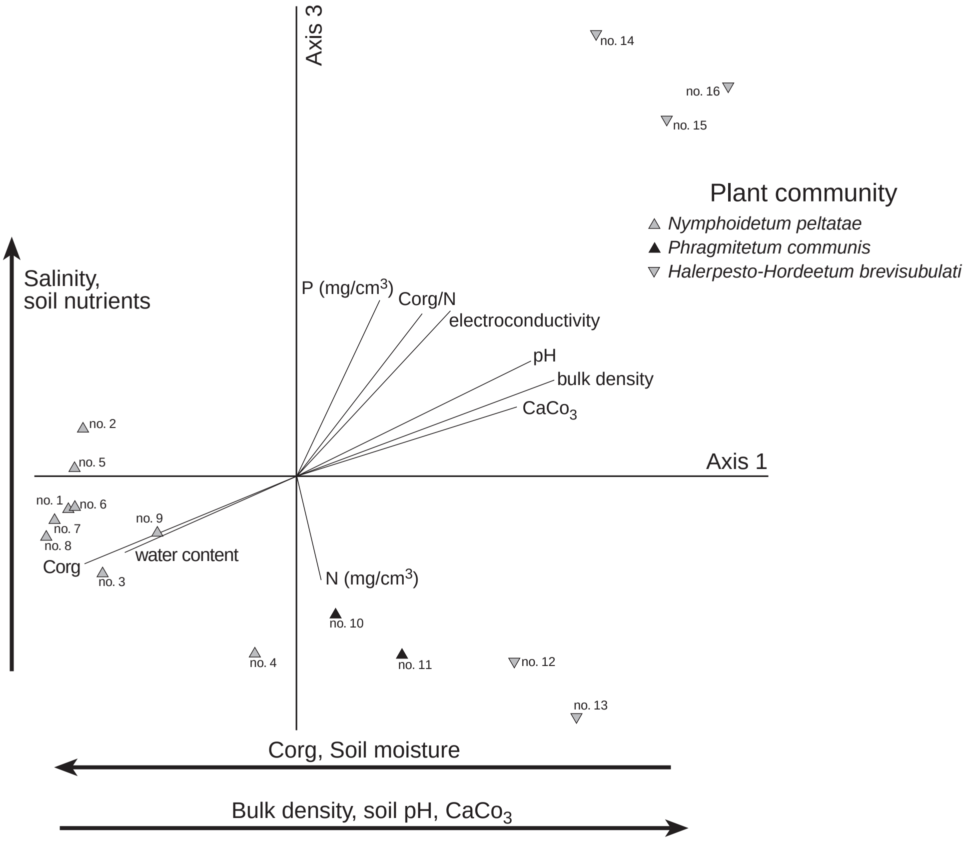

Fig. 6: DCA of the moistest section of the transect (without relevés of the *Glycyrrhizo uralensis-Achnatheretum splendentis*). The cutoff value (r^2) is 0.200

DCA des feuchten Transektabschnitts (ohne die Aufnahmen des *Glycyrrhizo uralensis-Achnatheretum splendentis*). Der Trennwert (r^2) liegt bei 0.200

Retrogressive successions at sites of original poplar and willow woods obviously lead to the development of the *Halerpesto-Hordeetum brevisubulati* as evident from floristic similarities of present-day pasture meadows and herb layers of remnant poplar and willow stands (Hilbig a. Schamsran 1977; Hilbig 1995). Based on our observations in Buyant and Khovd river floodplains we agree with this view contradicting that of Mirkin et al. (1980) that *Salix* shrublands are merely variants of meadow and reed marsh communities. Pasture communities being anthropogenic replacement communities that obviously belong to the *Halerpesto-Hordeetum brevisubulati* were also reported from other regions in Mongolia (cf. Yunatov 1950; Petrov 1963; Mirkin et al. 1980; Hilbig et al. 1983; Kowalkowski et al. 1983; Titov et al. 1990a, b; Hilbig 1995; Wallis de Vries et al. 1996). Where grazing pressure is most severe, a grazing facies dominated by the unpalatable *Iris lactea* and with high cover-abundance of *Carex duriuscula* is developed within the *Halerpesto-Hordeetum brevisubulati* (Hilbig 2000b; own observations). We did not observe *Iris lactea* along our transect and in the immediate surroundings, but we recorded *Carex duriuscula*, pointing to a high, but not excessive grazing pressure. Recorded grazing marks were integrated in our CCA and DCA as variables but did not show any significance for vegetation differentiation.

Vegetation zonation at the southwestern shore of Khar Us Nuur may also be influenced by further environmental factors not recorded in this study. Since lake shores are dynamic environments, natural disturbances such as water-level changes, wind, waves, ice scouring or floating and accumulating plant debris may play a certain role in shaping plant communities as well as the transition zones between them (cf. Minchinton a. Bertness 2003; Ostendorp et al. 2003 for reed communities). E.g., disturbances determine plant population dynamics and successional stages by creating open habitats for the establishments of plants or by facilitating dispersal of seeds and plant fragments (Pickett a. White 1985). In order to understand how disturbance processes influence vegetation patterns at the Khar Us Nuur lake shore, longer-term observations would be necessary. Respective research has not been conducted in the Great Lakes Basin so far. However, it is known that, due to the changing inflow of feeding rivers, wind, and evaporation, seasonal fluctuations of the lake level of about 100 cm occur, in extreme cases up to 200 cm (IUS 2000). As a consequence, groundwater depths in lake floodplains show considerable variations (cf. Blank a. Krüger 2001 for Uvs Nuur). Maximum lake level is reached in late summer since 90% of the annual volume of feeding rivers is discharged between July and October. These data suggest that along our lake shore-semi-desert transect the *Halerpesto-Hordeetum brevisubulati* is still in the range of periodical inundations whereas the *Leymus paboanus* grassland is only flooded during extraordinary events. The transitional zone between these communities is obviously an important vegetation-ecological boundary. This is supported by the species distributions along the entire transect showing maximum species turnover just in this transitional zone.

5.2 Vegetation and soil-ecological conditions

Although changes in vegetation patterns and in soil-ecological conditions along the lake shore-semi-desert transect are closely interrelated, the relationships of plant communities and soils are not as distinct as expected. Single soil parameters vary widely within the distributional range of a single plant community. As it is obvious from the ordination results, different soil parameters are connected to a complex gradient that causes both general patterns in vegetation zonation and small-scale, subtle changes in species compositions of communities. We could not clearly separate the influences of bulk density, soil moisture, organic matter content, and soil pH since these variables are covariated to a large extent. However, general patterns of vegetation zonation seem to be best explained by the variable soil moisture. The water content of the soil largely determines organic matter contents and exerts a great influence on bulk density and soil pH. A complete soil moisture gradient from 100 vol. % (shallow water) to 0.3 vol. % (dry sandy lake terrace) is developed along the transect. Even within the wetland section of the transect, soil moisture and its co-variated variables largely determine community patterns. And, maximum species turnover along the transect occurs where the decrease in soil moisture is most pronounced (transitional zone to *Leymus paboanus* grassland). Our results verify the hypothesis that soil moisture is the most critical environmental variable for vegetation patterns in the lake shore-semi-desert ecotone and that other site parameters are only of subordinate importance.

As stated above, single soil parameters may vary widely within a vegetation zone along the transect. Plant communities are obviously associated with a certain constellation of varying edaphic factors and have to adapt to a wider range of environmental conditions. This holds especially true for the *Phragmitetum communis* with regard to the water factor. Reed vegetation at Khar Us Nuur can be found both in shallow water and as terrestrial reed, pointing to the great ecological amplitude of *Phragmites australis* known from other regions (e.g. KRAUSCH 1965). Reed is recorded to grow well in Mongolian steppe lakes to a depth of about 100–140 cm, surviving till 170 cm (IUS 2000). On the other hand, VOSTOKOVA et al. (1962) found the species to occur up to groundwater depths of 3 m under terrestrial conditions. Due to great variations in soil moisture the *Phragmitetum communis* has to be adapted to considerably varying other soil parameters like soil pH, bulk density, organic matter content, and salinity.

Likewise, the *Halerpesto-Hordeetum brevisubulati* occupying the mid-transect vegetation zone on Solonchaks has to cope with greatly varying soil conditions. Contrasting nitrogen levels (cf. Fig. 6) that must be attributed to grazing influences necessitate adaptation to differing trophic conditions. But more important, seasonal fluctuations in groundwater depth and related soil parameters cause stress for the plant cover because it involves far-reaching changes in soil chemical conditions. During summer high evaporation and transpiration rates and an upward flux of soil water prevails. Accordingly, carbonates and soluble salts accumulate in the topsoil as assessed in other groundwater-influenced soils of the Great Lakes Basin (cf. KNOTHE et al. 2001) (Photo 4). Changing groundwater depths and heating of soils during summer may lead to precipitates of chlorides and sulphates even below the top-soil. KNOTHE et al. (2001) measured topsoil salt contents above 0.5% and soil pH between 7 and 8.5 in comparable Solonchaks in the Uvs Nuur Basin. Transport and solution processes are reflected in relatively high $CaCO_3$ and EC values in the Solonchaks below the *Halerpesto-Hordeetum brevisubulati* and, in particular, in the halophytic species composition of this pasture community. Its halophytic composition and its occurrence on halomorphic soils has been stressed by several authors before (cf. HILBIG a. SCHAMSRAN 1977; MIRKIN et al. 1980; HILBIG et al. 1983; HILBIG 1995), and gave rise to integrate it into the plant-sociological class *Asteretea tripolium* (GOLUB 1994). Interestingly, the species composition shows some parallels to those of semi-natural (grazed) salt grasslands at the Baltic coast in NE Germany. Both salt grassland types have several species in common (e.g. *Juncus gerardii*, *Glaux maritima*, *Triglochin maritimum*, *T. palustre*, and *Potentilla anserina*) – an expression of a similar selection and adaptation to severe grazing impact within the Northern hemispheric halophytic species pool.

Variability in soil-ecological conditions decreases towards the drier section of the transect as the influence of soil moisture is diminished. The *Leymus paboanus* community that occupies a similar ecotonal position in the Uvs Nuur Basin (cf. HILBIG 1995) still has to adapt to greater variations in soil chemical conditions ($CaCO_3$, salinity, organic matter) on Gleyic Solonchak. However, the *Glycyrrhizo uralensis-Achnatheretum splendentis* at the transition to semi-desert is associated with more or less homogeneous soil-ecological conditions of Haplic Kastanozems. Not being influenced by ordinary fluctuations of the lake level and by seasonal groundwater fluctuations in upper soil horizons, the chee-grass community is connected to a comparatively distinct habitat edaphically, being expressed in the isolated position in the CCA (cf. Fig. 5). Thus, *Achnatherum splendens* is a good indicator species for a certain, comparatively narrow range of soil-ecological conditions. VOSTOKOVA a. KAZANTSEVA (1995) reported similar results with regard to soil-chemical conditions under *Achnatherum splendens* stands. In contrast to the semi-desert and steppe vegetation adjacent further inland, *Achnatherum* tussocks (Photo 2) indicate the presence of plant-available groundwater, even if only at greater depth. Whereas the roots of the majority of steppe and desert species do not penetrate below 30–60 cm (BAITULIN 1993), *Achnatherum* develops a dense and far-reaching root system enabling the uptake of soil water from considerable depths. The dependence on groundwater influence was also observed by YUNATOV (1950), HANELT and DAVAZAMC (1965), KASHAPOV et al. (1972), and HILBIG and SCHAMSRAN (1977). Other soil conditions (in topsoil) for the Khar Us Nuur lake shore indicated by *Achnatherum* stands include sandy texture, low soil moisture, weak salinity and low levels of nutrients, organic matter, and carbonates.

6 Conclusions

In conclusion, the transect approach proved to be a fruitful and appropriate approach to detect vegetation-environment-relationships along lake shore-semi-desert ecotones in the Great Lakes Basin. However, further detailed vegetation ecological studies are strongly needed to improve our knowledge of how the zonation and composition of wetland plant communities in lake floodplains is governed by fine-scale patterns of environmental variables, in particular beyond the overriding influence of soil moisture. Likewise, further studies are needed in order to judge whether the assessed relationships between plant communities and soil-ecological conditions can be transferred to other regions in Central Asia. Such studies are of special importance in view of existing uncertainties regarding the effects of climate change. Since soil moisture is the most critical environmental variable in lake floodplain ecosystems, any change in precipitation, evaporation and soil moisture levels will inevitably have potentially significant implications for the respective biocoenoses and for ecosystem structure and function. Further consequences include potentially serious impacts on land use, animal husbandry, and rural development.

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