Climatic ultra-continentality and the abrupt boreal-nemoral forest boundary in northern Manchuria

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Interior northeastern Eurasia has the world's most continental non-polar climate, with annual temperature amplitude so wide that large areas can have moderately warm summers and yet mean annual temperature below 0 ℃, which results in permafrost soils. The vegetation on the consequently very shallow soils of these boreal permafrost areas is mostly *Larix* woods. Northern Manchuria represents the southeastern part of this ultra-continental region. Here, even in the lower parts of the Da Hinggan Ling mountains, summers can be warm enough for deciduous *Quercus mongolica* forest, which appears as soon as one comes off the underlying permafrost. This direct abutment of permafrost (boreal) and temperate (nemoral) regions, without an intervening sub-boreal transition, is unique in the world. A third intersecting vegetation region in the Da Hinggan Ling area is the Mongolian steppe to the west. The composition and structure of the following natural vegetation types in northern Manchuria are described by full-floristic stand samples (Braun-Blanquet relevés) : forests of *Quercus mongolica* and *Larix gmelinii* a relict stand of *Pinus sylvestris* var. *mongolica*, Mongolian steppe, a mountain wet meadow, and aquatic vegetation at a large *Phragmites* marsh complex. If global warming reduces the extreme annual temperature range in this region, the direct permafrost-temperate boundary may eventually disappear and an intervening mixed-forest zone develop.

Key words : larch forest, Mongolian steppe, nemoral forest, permafrost, *Phragmites*, *Quercus mongolica*, ultra-continental climate, vegetation boundary, vegetation response to warming, wet meadow.

INTRODUCTION

Manchuria (see Fig. 1) is the region northeast of Beijing and historical Han China, up to and along the Heilong (=Amur) River, which separates the People's Republic of China from eastern Siberia (Russia). The Da (=Greater) Hinggan (=Xingan) Ling, a range of moderate mountains, separates Manchuria into a larger east side, including the fertile Manchurian Plain, and a west side which belongs already to Neimenggu (Inner Mongolia). The whole region has moderate summers and severely cold winters. Manchuria was also the original homeland of the Manchu people, who began to reject Chinese overlordship around 1610, captured Beijing in 1644, and controlled all of China by 1690, deposing the Ming Dynasty and establishing an expanded Chinese empire that eventually included Mongolia, Dzhungaria, eastern Turkestan, Tibet, and parts of Southeast Asia (Rand McNally 1995). Although Russian expansion into eastern Asia crossed the Amur River only in Primorye (to Vladivostok by 1860), most of Manchuria was under strong Russian influence by the end of the 1800s, an influence which is still visible today in the architecture of many larger buildings. In the 20th Century, Manchukuo was a

separate state under Japanese rule but reverted to China in 1946. Manchuria now has large cities such as Harbin (=Haerbin) as well as modern, highly productive agricultural landscapes which feed much of China. Politically, Manchuria includes the provinces of Heilongjiang, Jilin and Liaoning plus the northeastern part of Inner Mongolia. Within the People's Republic of China, however, the region is now known more commonly simply as Dongbei, meaning the Northeast.

Manchuria is important biologically, as are all regions, because it contains species and ecological systems which do not occur elsewhere. It is also, however, parf of the only area in the world where boreal and temperate-deciduous forest regions occur contiguously without a transitional mixed-forest zone, as occurs in Europe, western Siberia, and North America. Due to the enormous size of Eurasia, the ultra-continental climate becomes warm enough in summer for nemoral (typical temperate deciduous broad-leaved) tree species. Mean annual temperature, however, is still below 0℃ in northern Manchuria, especially in the mountains, so permafrost is widespread and delimits the northward extent of the nemoral forest. Southern Manchuria (Liaoning, Jilin, southern Heilongjiang) has cool-temperate deciduous forests similar to those of northern Japan and eastern North America, with tree taxa such as *Tilia, Fraxinus, Acer, Betula,* and a five-needle pine, *Pinus koraiensis.* In northern Manchuria the simpler forest involves mainly *Betula* and *Populus,* sometimes *Acer mono,* and begins to include *Larix,* which comes to dominance on permafrost as the nemoral species drop out. *Quercus mongolica* is especially interesting since it occurs throughout most of lowland Manchuria and adjacent areas, even appearing occasionally in scattered stands at lower elevations on the west side of the Da Hinggan Ling. Northern Manchuria (including the Amurland) is one of few places in the world where *Quercus* and *Larix* occur very close to each other, sometimes intermixed in the same stand (near the southern permafrost boundary). In the east-west direction there is a climatic wetness gradient, and the forest grades into grassland to the west. This transition is truncated on the north by the permafrost, more than by the shorter boreal growing season and longer winter. Wetlands of various kinds occur throughout the region, from countless saline depressions in the flat grasslands to marsh complexes along rivers flowing out onto the Dongbei Plain.

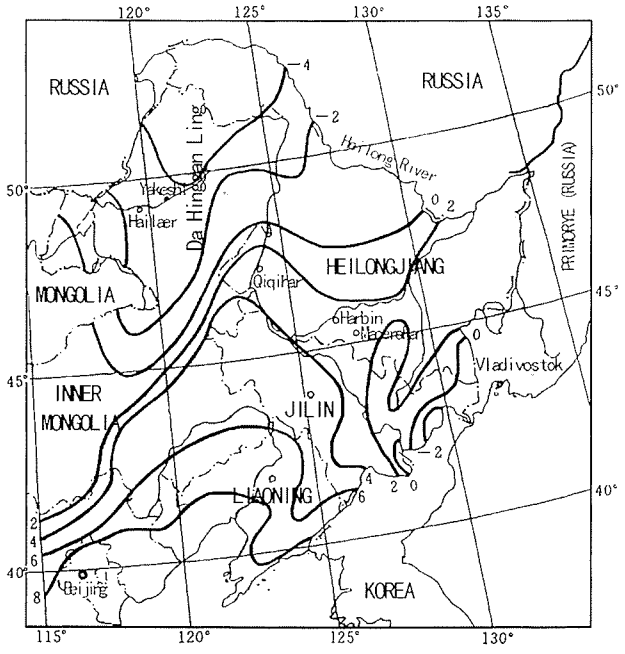

Fig. 1. Chinese Manchuria (Dongbei) and surrounding areas, with isotherms of mean annual temperature. Dongbei includes Liaoning, Jilin, Heilongjiang, and northeastern Inner Mongolia. The study area in northern Manchuria involves Heilongjiang (except eastern) and the Da Hinggan Ling mountains and foothills in northern Inner Mongolia (centered especially on Yakeshi). Note that the big cities of Heilongjiang, Haerbin and Qiqihar, lie south of the 0℃ isotherm and thus do not have permafrost. Essentially all of the Da Hinggan Ling area, however, including the transition to the Mongolian steppe, is underlain by at least discontinuous if not continuous permafrost. The temperature gradient is especially steep in the southern Da Hinggan Ling west and southwest of Qiqihar. Map by YHM, based on Zhou (1997).

We were able to visit northern Manchuria in June 2000, partly in connection with doctoral fieldwork by the second author (You 2001). Our work was hosted by the Northeast Forestry University, at Harbin in southern Heilongjiang. The purpose of this paper is to describe the climatic control of vegetation patterns, to present some initial field data on vegetation composition in the region, and to attempt a bioclimatic synthesis.

Table 1 : Climatic data for locations in Manchuria and adjacent areas.

Location	Lat	Elev	Tyr	Tmax	Tmin	Tabmin	Precip	MI
Neimenggu (northeastern)								
Yitulihe	50.4	950m	-4.0	16.5	-27.6		455	1.06
Manzhouli	49.6	710m	-1.5	20.2	-25.4		295	0.60
Hailaer	49.2	650m	-2.0	20.2	-27.3	-49.3	341	0.69
Mianduhe	49.1	705m	-3.1	19.5	-27.7	-50.1	356	0.77
"Hingan"	48.8	982m	-3.2	17.3	-27.1		609	1.40
Bugt	48.8	695m	-1.0	18.1	-21.5	-39.1	469	1.00
Arxan	47.2	770m	-2.6	16.4	-24.8		466	1.08
Heilongjiang								
Huma	51.7	150m	-1.3	20.3	-25.9	-46.3w	466	0.90
Nenjiang	49.2	222m	-0.4	20.7	-25.3	-47.3	485	0.91
Qiqihar	47.4	150m	3.4	23.3	-19.6	-35.3w	424	0.71
Anda	46.4	147m	2.5	23.8	-22.1	-44.3k	427	0.72
Haerbin	45.7	151m	3.5	23.1	-19.6	-41.4k	550	0.92
Mudanjiang	44.6	241m	3.3	22.2	-19.1	-45.2k	532	0.93
Southern Dongbei and Beijing								
Changchun	43.9	216m	4.8	23.2	-16.6	-36.5w	615	1.02
Changbai-Shan	42.0	2624m	-7.3	8.4	-24.0	-44.0	1340	4.68
Shenyang	41.8	45m	7.7	24.7	-12.3	-33.1m	715	1.09
Dalian	38.9	97m	10.3	24.2	-5.0	-21.1w	616	0.92
Beijing	39.9	52m	11.8	26.1	-4.5	-27.4w	630	0.83

Column abbreviations:

Lat = latitude (°N, decimal digit)
Elev = elevation (meters)
Tyr = mean annual temperature (°C)
Tmax = mean temperature of warmest month
Tmin = mean temperature of coldest month
Tabmin = absolute minimum temperature
Precip = average annual precipitation (mm)
MI = Precip/potential evapotranspiration

The single letters following the Tabmin value indicate the source of the value:

k = *Klimadiagramm-Weltatlas* (Walter & Lieth 1960-67)
w = *Zhongguo Zhibei* (Wu 1980)
m = Müller (1982)

STUDY AREA AND METHOD

The study area included southern and western Heilongjiang and the Da Hinggan Ling area of northeastern Inner Mongolia. Elevation throughout Heilongjiang and the Dongbei Plain is mostly below 250m, while average elevation at the western base of the Da Hinggan Ling is 600-750m. The passes crossing the Da Hinggan Ling are at around 1,000m. Climatic data for locations in the region, plus latitude and elevation, are shown in Table 1. Beijing and the alpine research station in the Changbai-Shan (along the Korean border) are also shown, for comparison.

The region has a strongly continental climate

throughout. In southern Heilongjiang (cf Haerbin), July mean temperatures generally exceed 20℃ while winter temperatures approach boreal levels of -20℃ or below. Recorded absolute minimum temperatures are generally below -40℃, except where measurement periods are too short. Precipitation is typically 400-550mm, concentrated in the summer. Both precipitation and annual moisture balance increase somewhat with elevation and decrease to the west toward Mongolia. As one moves northwest from Harbin, mean annual temperature falls rapidly, from 2-4℃ in southern and central Heilongjiang to well below 0℃ in the Da Hinggan mountains and western foothills (see Fig. 1). As a result, permafrost appears in most of this area. Near the 0℃ isotherm for mean annual temperature, the occurrence of permafrost may be patchy and often depends strongly on local topography and the effect of vegetation cover on the annual energy balance.

The main vegetation types in northern Dongbei are nemoral forest to the south and east, grassland in the drier west, and *Larix* forest to the north and in the mountains, where permafrost occurs. There is enough summer warmth for nemoral *Quercus mongolica* forest (and some simpler northern variants) where at least four months have mean temperature above about 10℃, i. e. throughout most of the region. There is a broad transition as it becomes drier to the west, from forest on the western slopes and foothills of the Da Hinggan Ling to the Mongolian steppe. The change northward and upward, however, from nemoral forest to boreal larch (*Larix*) forest, is abrupt and occurs as soon as permafrost appears.

The plant communities of the Da Hinggan Ling were first described about 50 years ago (Chang 1955 ; cf Küchler 1948). Broad treatments of Chinese vegetation types and regions have appeared more recently (e. g. Hou 1960, 1979, 1983; Wu 1980, 1995; Institute of Botany 1982; China Natural Geography Committee 1983 ; Song 1983). The "Vegetation of Inner Mongolia" appeared in the 1980s (Editorial Group for Veg. of Neimenggu 1986). Most recently, descriptions have appeared of the vegetation of the Da Hinggan Ling (Zhou 1991) and of vegetation geography in Dongbei in general (Zhou & Zu 1997; cf Xu 1983,1986).

Our fieldwork involved full-floristic documentation of relatively mature stands of representative vegetation by means of Braun-Blanquet relevés (cf Fujiwara 1987). Stand samples were made at Maoershan (about 45° N, southeast of Harbin), at the Zhalong Lake wetland complex near Qiqihar (47° N), in the western foothills and slopes of the Da Hinggan Ling northeast of Yakeshi (about 49.3° N, 700m, in northern Inner Mongolia), and in the grassland transition west of Yakeshi. Botanical terminology follows the Chinese floristic manuals, mainly the woody flora of Heilongjiang (Zhou 1986), a more complete flora of Heilongjiang (Zhou et al., 1992-ongoing), and the "Flora of China" (Institute of Botany 1972-85).

RESULTS

Quercus mongolica forests and outliers

A main character tree of most of Manchuria, occurring also in north China, Korea, and the Amurland, is *Quercus mongolica* (You et al., in press). This important species (*sensu lato*) even extends into Japan as *Qu. mongolica* var. *grosseserrata,* a main species of forests in Hokkaido and Tohuku. One goal of our field reconnaissance was to document the composition of *Qu. mongolica* stands near the limits of its range, to the north and west. Relevé data are presented for a typical Manchurian *Qu. mongolica* forest, at Maoershan in southern Heilongjiang, and for two stands northeast of Yakeshi, in the Da Hinggan Ling foothills, where *Qu. mongolica* was mixed with *Larix gmelinii.*

At Maoershan, relevés were made at 330m (mid-slope) and 370m (upper slope) in a relatively natural *Qu. mongolica* forest behind the Field Station of the Northeast Forestry University. These are shown in Table 2. *Qu. mongolica* is the overwhelming canopy dominant, with *Tilia amurensis* and *Betula dahurica* also in the canopy at mid to lower positions on the slope. This may be due to shallower soil and less available soil water toward the top. *Acer mono* was prominent in the tree understorey, with *Spiraea canescens* and *Corylus heterophylla* important in the shrub layer. Regeneration by the main tree species can be seen in both stands but was more at mid-slope. The mid-slope plot has a much richer herb layer than

the upslope plot, but the two plots have remarkably similar layer structure and cover degrees.

Further north, in northern Heilongjiang and in the Da Hinggan Ling, the forests are mainly classified as *Larix* forest (see Zhou 1997). *Quercus mongolica* is generally not considered to be a major component of such forests, although *Qu. mongolica-Pinus koraiensis* mixed forest does occur in the mountains of eastern Dongbei (Zhou 1997, p. 113). Nevertheless, in the lower Da Hinggan mountains, clusters of short *Qu. mongolica* do occur in some *Larix* forests. Relevés from two such stands, near Wenkutu and Xiriteqi (western slopes of the Da Hinggan Ling, northeast of Yakeshi), are shown in Table 3. These may be typical of the last outposts of *Qu. mongolica* toward the continental interior.

Near Wenkutu, *Qu. mongolica* occurred in the quite open (55%) canopy of a short (13m) forest on a slight south-facing slope above the road (515m). The canopy also contained both local *Betula* species, *Populus davidiana,* and less *Larix gmelinii.* Fire scars were clearly visible on some trees, and some *Quercus* trees had been cut, but *Quercus* appeared to be regenerating in the shrub and herb layers more

Table 2 : Samples of *Quercus mongolica* forest near Harbin, northern Manchuria

	T1	16 m	75 %		T1	17 m	75 %
	T2	12 m	15 %		T2	10 m	15 %
	S	4 m	80 %		S	3 m	80 %
	H	0.4 m	35 %		H	0.4 m	30 %
T1:	4.4	*Quercus mongolica*		4.4	*Quercus mongolica*		
	2.3	*Tilia amurensis*		+	*Acer mono*		
	1.2	*Betula dahurica*					
T2:	2.2	*Acer mono*		2.2	*Acer mono*		
	1.1	*Quercus mongolica*		2.3	*Tilia mandschurica*		
	+	*Tilia amurensis*					
S:	3.4	*Spiraea canescens*		3.3	*Spiraea canescens*		
	2.3	*Acer mono*		3.3	*Corylus heterophylla*		
	2.3	*Corylus heterophylla*		1.2	*Tilia mandschurica*		
	1.1	*Quercus mongolica*		1.2	*Tilia amurensis*		
	1.1	*Tilia amurensis*		+.2	*Euonymus alatus*		
	1.2	*Euonymus alatus*		+	*Ulmus macrocarpa*		
	1.2	*Rhamnus davurica*		2.3	*Lonicera chrysantha*		
	1.1	*Schisandra chinensis*		2.3	*Deutzia grandiflora*		
	+.2	*Ulmus macrocarpa*		1.2	*Acanthopanax sessiliflorus*		
	+.2	*Viburnum sargenti*		+	*Fraxinus mandschurica*		
	+.2	*Lonicera chrysantha*					
	+	*Deutzia grandiflora*					
H:	2.2	*Paris verticillata*		+.2	*Paris verticillata*		
	2.2	*Carex callitrichos*		+.2	*Carex callitrichos*		
	1.2	*Acer mono*		1.1	*Acer mono*		
	1.2	*Angelica viridiflora*		1.1	*Angelica viridiflora*		
	1.1	*Eriophorum gracile*		+.2	*Carex siderosticta*		
	1.1	*Melandrium brachypetalum*		+	*Quercus mongolica*		
	+.2	*Asparagus cochinensis*		1.1	*Fraxinus mandschurica*		
	+.2	*Cacalia hastata*		+.2	*Tilia amurensis*		
	+.2	*Carex pilosa*		+.2	*Tilia mandschurica*		
	+.2	*Carex siderosticta*		+.2	*Actaea asiatica*		
	+.2	*Stellaria dichotoma*		+	*Artemisia stolonifera*		
	+	*Quercus mongolica*		+.2	*Brachybotrys pavidiformis*		
	+	*Fraxinus mandschurica*		1.1	*Carex ciliata-marginata*		
	+	*Populus davidiana*		+	*Dioscorea nipponica*		
	+	*Tilia amurensis*		2.2	*Euonymus alatus*		
	+	*Actaea asiatica*		1.2	*Lonicera chrysantha*		
	+	*Ampelopsis brevipedunculata*		+	*Polygonatum humile*		
	+	*Artemisia stolonifera*		+.2	*Lespedeza bicolor*		
	+	*Aster ageratoides*		+.2	*Spiraea canescens*		
	+	*Brachybotrys pavidiformis*		+	*Cypripedium macranthum*		
	+	*Carex ciliata-marginata*		+	*Heracleum moellendorfii*		
	+	*Convallaria keiskei*		+	*Paeonia lactiflora*		
	+	*Dioscorea nipponica*					
	+	*Euonymus alatus*					
	+	*Galium tokyoense*					
	+	*Lonicera chrysantha*					
	+	*Osmorhiza aristata*					
	+	*Polygonatum humile*					
	+	*Rubia cordifolia*					
	+	*Saussurea subtriangulata*?					
	+	*Schisandra chinensis*					
	+	*Schizachyrium* sp.?					
	Total number of species: 39			Total number of species: 26			

The relevés were made at mid-slope (330m, left) and upper slope (370m, right) behind the Maoershan Field Station, near Harbin (Heilongjiang), in northeastern China. Both relevés were 20 x 15 m, on 20-25° slope to the SW. Relevé personnel: EB, YHM, Chen Li-xin, Deng Zhen-qang, and Wang Xiao-hua.

Table 3. Some stands with *Quercus mongolica* near its distributional limit.

	Wenkutu	Xiriteqi	
	DB-11	DB-12	DB-13
	515m	700m	700m
	5° S	15°SW	18° W
	30x15m	20x25m	20x25m
T1:	- - -	18m	20m
		50%	50%
Larix gmelinii		2.2	3.4
Betula dahurica		1.1	1.1
Populus davidiana		2.3	
T2:	13m	10m	10m
	55%	40%	40%
Quercus mongolica	2.2	3.3	3.3
Larix gmelinii	1.1	1.2	2.2
Betula dahurica	2.3		1.2
Betula platyphylla	2.4		
Populus davidiana	2.2	+	
S:	5m	3m	4m
	25%	30%	30%
Quercus mongolica	3.3	1.2	2.3
Betula dahurica	1.1	+	1.1
Larix gmelinii			1.1
Lespedeza bicolor		3.3	2.3
Corylus heterophylla	1.1		
H:	70cm	50cm	60cm
	65%	40%	40%
Quercus mongolica	1.2	1.1	1.2
Lespedeza bicolor	3.3	1.1	3.4
Populus davidiana	+	1.2	
Betula dahurica		+	
Corylus heterophylla	3.3		
Rubus arcaicus	+.2		
Rosa davurica	+		
Adenophora gmelinii	1.2	+	+
Artemisia jap. var. *manshurica*	1.2	+	1.2
Chrysanthemum carinatum	1.2	+.2	+.2
Euphorbia fischeriana	+	+.2	+.2
Paeonia lactiflora	1.1	1.2	1.1
Polygonum odoratum	+.2	1.1	+
Sanguisorba officinalis	+	1.1	+.2
Synurus deltoides	+	+.2	+
Thalictrum baicalense	1.2	1.1	+.2
Valeriana officinalis	+	+	+
Convallaria keiskei	3.3	1.2	
Carex lanceolata	3.3		2.3
Aconitum ambiguum	1.2		
Adenophora tetraphylla	+.2		
Dictamnus albus var. *dasycarpus*	+		
Doellingeria scaber	+		
Galium bungei	+		
Geranium eriostemon	+.2		
Iris kobayashii	+.2		
Lilium concolor var. *pulchellum*	+		
Patrinia heterophylla	+.2		
Scutellaria scordifolia	+		
Saussurea recurvata	+		
Spiraea elegans	+		
Vicia pseudorobus	+.2		
Campanula punctata	(+.2)		
Saussurea ussuriensis?	(1.1)		
decussate-forb pink-rubioid	+.2		
Sedum aizoon?	1.1	+	
Hemerocallis minor	+	+	
Potentilla rupestris?	1.1		+.2
Trifolium lupinaster	+		+.2
Carex globularis		3.3	3.3
Adenophora divaricata		+.2	+
Artemisia blepharolepis		+.2	+
Artemisia mongolica		+.2	1.2
Iris uniflora		1.2	1.2
Saussurea maximowiczii		+.2	+.2
Saussurea salicifolia?		+	+
Sedum middendorfianum		1.2	+.2
Vicia multicaulis		+.2	+.2
Viola variegata		+.2	+.2
Eragrostis curvula		+	
Saussurea parviflora		1.1	
Saussurea sinuata		+	
Serratula marginafolia		+	
Seseli seseloides		+	
Vicia ramuliflora		+.2	
Aconitum barbatum			+
Cleistogenes chinensis			1.2
Cimicifuga dahurica			+.2
Daucus carota?			+
Geranium sibiricum			+
Polygonatum humile			+.2
Polygonum ajanense			+
Potentilla fragarioides			+.2
Polygonum alpinum			(+.2)
Total number of species:	41	34	36

The three relevés were from two sites on the lower western slopes of the Da Hinggan Ling mountains, east-northeast of Orqohan (=Wuerqihan), northeast of Yakeshi (northeastern Inner Mongolia). Both sites were on a slope above a forest road, where *Quercus mongolica* could easily be seen, either forming a distinct understorey (at Xiriteqi) or mixed in the short canopy (at Wenkutu). At DB-12, a probably planted stand of *Populus davidiana* delimited the *Quercus mongolica* area on one side. Relevé DB-13 was adjacent to DB-12, away from the *Populus* stand. (Relevé personnel: EB, YHM, LDL)

Table 4. *Larix gmelinii* natural forest and forestry plantation, in the Da Hinggan mountains of northeastern Inner Mongolia.

	Natural forest: 1000m (5° to E, 20 x 20m)			Plantation: 700m (2° to S, 30 x 40m)	
T1	27 m	65 %	T1	20 m	80%
T2	13 m	5 %	T2	12 m	2%
S	6 m	60 %	S	1.2 m	2%
H	0.8 m	95 %	H	0.3 m	50%
T1:	4.4 *Larix gmelinii*		T1:	5.4 *Larix gmelinii*	
				1.1 *Populus davidiana*	
				1.1 *Betula dahurica*	
T2:	1.1 *Larix gmelinii*		T2:	+ *Larix gmelinii*	
				1.1 *Populus davidiana*	
S:	3.4 *Betula platyphylla*		S:	1.1 *Populus davidiana*	
	2.2 *Larix gmelinii*			1.1 *Picea koraiensis*	
	+.2 *Rhododendron dahuricum*			+ *Prunus padus*	
				+ *Rhamnus dahurica*	
				+ *Rosa davurica*	
				+ *Spiraea flexuosa*	
H:	3.4 *Vaccinium vitis-idaea*		H:	+ *Potentilla rupestris*	
	3.3 *Maianthemum biflorum*			+ *Vicia*? sp.	
	3.4 *Melica nutans*			4.4 *Equisetum arvense*	
	2.3 *Dryopteris expansa*			+ *Rubus arcticus*	
	2.3 *Epilobium angustifolium*			1.1 *Galium bungei*	
	2.3 *Filipendula palmata*			+.3 *Pyrola incarnata*	
	2.2 *Sorbaria sorbifolia*			+ *Betula dahurica*	
	2.2 *Viola brachyceras*			+ *Saussurea amurensis*	
	1.2 *Clematis sibirica*			+.2 *Viola collina*	
	1.2 *Geranium eriostemon*			1.2 *Carex globularis*	
	1.2 *Potentilla fragarioides*			1.2 *Iris kobayashii*	
	1.2 *Vicia ramulitiflora*			1.1 *Thalictrum baicalense*	
	1.2 *Equisetum sylvaticum*			+.2 *Athyrium multidentatum*	
	1.1 *Saussurea parviflora*			+.2 *Ligularia fischeri*	
	1.1 *Elymus dahuricus*?			+.2 *Synurus deltoides*	
	1.1 *Linnaea borealis*			+.2 *Valeriana stubendorfianum*	
	+.2 *Rosa davurica*			+.2 *Lespedeza* sp.	
	+.2 Rubus arcticus			+.2 *Polygonatum* sp.	
	+.2 *Adenophora gmelinii*			+.2 Gramineae sp.	
	+.2 *Adenophora tetraphylla*			+ *Populus davidiana*	
	+.2 *Cacalia hastata*			+ *Quercus mongolica*	
	+.2 *Galium boreale*			+ *Artemisia mong.* v. *genuina*	
	+.2 *Pyrola incarnata*			+ *Convallaria keiskei*	
	+ *Larix gmelinii*			+ *Dendranthema oreastrum*	
	+ *Betula platyphylla*			+ *Ixeris chinensis*	
	+ *Sausurrea umbrosa*			+ *Paeonia lactiflora*	
	+ *Cerastium arvense* var. *angustifolium*			+ *Pulsatilla dahurica*	
	+ *Fimbristylis verrucifera*			+ *Sanguisorba officinalis*	
	+ *Viola collina*			+ *Saposhnikovia divarcata*	
	+ *Carex* sp.			+ *Sedum aizoon*?	
Total number of species: 31			Total number of species: 36		

The natural *Larix* forest was on permafrost, at about 1000m elevation, northeast of Yakeshi and generally east of Orqohan (Wuerqihan), in northeastern Inner Mongolia. The *Larix* plantation was in the same region but at lower elevation (about 700m), near an area with mixed *Quercus-Larix* secondary forests. Relevé personnel: EB, YHM, LDL, and Zhang Yu-zhen.

than the other canopy species. More common in the Da Hinggan Ling area, however, seemed to be the occurrence of *Qu. mongolica* as clumps of short trees or arborescents in forest understoreys, especially at even only slightly higher elevation. The two relevés near Xiriteqi were in adjacent areas of a rather open *Larix-Populus* forest (50% canopy cover) on a 15° west-southwest-facing slope (700m), also above a forest road. This forest also showed evidence of fire and other disturbance, and an adjacent area of *Populus davidiana* may have been planted. *Qu. mongolica* formed the understorey tree layer (40% cover), with smaller understorey amounts of *Larix* and *Betula dahurica*. *Lespedeza bicolor* was the most prominent shrub species. The herbaceous layer was relatively rich in all three relevés (both locations), with different *Carex* species prominent.

Larix forest

Four species of *Larix* occur in Manchuria: *L. gmelinii* (the Hinggan larch), mainly in the Da Hinggan Ling and northern Heilongjiang; *L. olgensis* var. *heilongensis*, also in Heilongjiang; *L. olgensis* var. *changpaiensis* in the Changbai-Shan along the Korean border; and *L. principis-rupprechtii* in a small area of southeastern Inner Mongolia (Zhou 1997, 1988). The Hinggan larch is especially interesting since it is a true boreal larch, able to occur elsewhere but coming to dominance on permafrost, which precludes the root development of most broad-leaved tree species. Permafrost occurs where mean annual temperature is below 0℃, i. e. throughout most of the Da Hinggan Ling area and over much of northern Heilongjiang (see Fig. 1).

The mechanisms by which permafrost fosters *Larix* forest are not completely clear but are certainly related to the shallowness of the active layer of permafrost soil. The shallow soil has a low water-holding capacity and is also relatively cold. These colder conditions may even maintain some degree of "fossil" permafrost, which in turn keeps wet soils even colder. In Siberia, *Larix* still occurs where reported annual precipitation falls to somewhat below one half of the (climatically estimated) annual potential evapotranspiration (Box 1981, 1995c). The ability of *Larix* to grow in such apparently dry conditions has been explained in terms of its deciduousness (low water use during early summer, while the soil is thawing) and the "rationing" of the available water across the growing season by the slow thawing of the active layer (Walter 1968). On the other hand, earlier weather-station data from Siberia show distinctly lower precipitation levels than are reported more

Table 5. A Natural *Pinus sylvestris* Forest Outlier near the eastern end of the Mongolian steppe.

T1	14 m	50 %		Elevation: 710 m
T2	8 m	15 %		Aspect: 5° slope to N
S	2.5 m	20 %		
H	0.5 m	60 %		30 x 40 m
T1:	4.3 *Pinus sylvestris* var. *mongolica* (to 42cm DBH)			
T2:	2.2 *Pinus sylvestris* var. *mongolica*			
S:	2.4 *Rosa davurica*		1.2 *Pinus sylv. v. mongolica*	
	1.1 *Prunus sibirica*		1.3 *Spiraea aquilegifolia*	
	+ *Spiraea sericea*			
H:	3.4 *Carex callitrichos*		2.3 *Pinus sylv. v. mongolica*	
	2.2 *Euphorbia fischeriana*		2.3 *Iris kobayashii*	
	1.2 *Ixeris chinensis*		1.1 *Polygonum ajanense*	
	1.2 *Potentilla longifolia*		1.1 *Scutellaria scordifolia*	
	1.2 *Taraxacum mongolicum*		1.1 *Thalictrum baicalense*	
	1.1 *Veratrum maackii*		+.2 *Agrimonia pilose*	
	+.2 *Chrysanthemum carinatum*		+.2 *Galium verum*	
	+.2 *Prunus sibirica*		+.2 *Pyrola incarnata*	
	+.2 *Rosa davurica*		+.2 *Sanguisorba officinalis*	
	+.2 *Saussurea maximowiczii*		+.2 *Veratrum nigrum*	
	+.2 *Vicia cracca*		+.2 *Viola variegata*	
	+ *Aconitum barbatum*		+ *Artemisia finita*	
	+ *Clematis hexapetala*		+ *Dendranthema zawadskii* var. *latiloba*	
	+ *Fragaria orientalis*			
	+ *Hylotelephium pallescens*		+ *Paeonia lactiflora*	
	+ *Polygonatum humile*		+ *Saussurea runcinata*	
	+ *Sedum aizoon*		+ *Vicia pseudorobus*	
		Total number of species: 35		

The site was on a hill above grassland, at Bai-Yun Chagan, southwest of Yakeshi along the road to Hailaer. (Relevé personnel: EB, YHM, LDL)

recently (by 20-30%), and climatic methods may overestimate potential evapotranspiration since they may not adequately consider the energy which goes into thawing the soil in early summer rather than evaporating water or heating the air.

Larix gmelinii and *Pinus sylvestris* are the only conifers occurring widely in the Da Hinggan Ling area. *P. sylvestris* regenerates better but is fire-sensitive. *Larix* is fire-tolerant and is thus more abundant. It germinates when it contacts mineral soil and can grow under its own canopy (An et al. 1997). There are thus no other pioneer tree species, and there are no successional stages in the *Larix* forests, only *Larix* stands of different age structure. The density and height vary, perhaps reflecting history as well as topography, forming varyingly open, pleasantly patchy landscapes.

A relatively mature, natural *Larix* forest remnant was studied near Orqohan, east-northeast of Yakeshi, at an elevation of about 1000m on the western side of the Da Hinggan Ling. A relevé was made on an east-facing slope of about 5° (thus moderately well drained) and is shown on the left side of Table 4. The relatively tall (27m), somewhat open canopy (65% cover) and very sparse understorey tree layer (5%) were both composed entirely of *Larix gmelinii,* which also occurred significantly in the shrub layer and sporadically in the herb layer. The only other tree species in the stand was *Betula platyphylla,* which was however the most abundant species in the 6 m shrub layer. In contrast to this relative poverty, the herb layer had 30 species, including *Vaccinium vitis-idaea* but mostly herbaceous species from both typical boreal genera (e. g. *Maianthemum, Linnaea*) and more widespread northern-Eurosiberian genera (e. g. *Adenophora, Epilobium, Filipendula*). Not included in the relevé but also abundant in the area was *Ledum palustre* var. *angustum,* which formed dense colonies 5-10m across and provided a strong turpentine-like smell.

Larix gmelinii is also widely used in forestry plantations, an example of which (from 700m elevation near Xiriteqi) is shown on the right side of Table 4. Compared with the natural *Larix* forest, the plantation stand is younger, has a shorter (20m) but denser (80%) canopy containing occasional *Betula* and *Populus* individuals, and has almost no shrub layer (perhaps cleared artificially). The relevé herb layer had about 30 species, as in the mature forest, but there were very few herbaceous species in common, and even common genera usually were represented by different species. Only *Equisetum arvense* was abundant in the plantation herb layer, as opposed to more equitable sharing of abundance by eight species in the natural forest.

Table 6. A sample of Mongolian steppe, near its eastern end and in a dry year.

(S 3 m 1 %)		Elevation: 630 m
H 0.5 m 75 %		Aspect: 2° slope to WSW
		40 x 40 m
S:	(1.3) *Prunus sibirica*	(+.2) *Rosa davurica*
H:	4.3 *Stipa baicalensis*	3.4 *Galium verum*
	2.3 *Artemisia frigida*	2.2 *Carex duriuscula?*
	2.2 soft, suffrut. rosmarinoid; lvs lin-lanc, whitish-pubesc.	1.3 *Aneurolepidium chinense*
	1.2 *Euphorbia fischeriana*	1.2 *Leontopodium conglobatum*
	1.1 *Potentilla conferta*	1.2 *Saposhnikovia divaricata*
	1.2 *Saussurea ussuriensis*	1.2 *Thymus serpylum* var. *asiaticus*
	1.2 *Veronica incana*	1.1 *Filifolium sibiricum*
	+.2 *Alyssum lenense*	+.2 *Artemisia acaulis*
	+.2 *Bupleurum sibiricum*	+.2 *Iris kaempferi*
	+.2 *Orostachys fimbriatus*	+.2 *Paeonia lactiflora*
	+.2 *Poa argunensis?*	+.2 *Sanguisorba officinalis*
	+.2 *Thalictrum petaloideum*	+ *Artemisia finita*
	+ *Festuca ovina*	+ *Hemerocallis minor*
	+ *Lespedeza hedysaroides*	+ *Lespedeza tomentosa*
	+ *Cleistogenes squarrosa*	+ *Stellera chamaejasme*
	+ *Hordeum brevisubulatum*	+ *Senecio flammeus*
	+ *Geranium maximowiczii*	+ *Helictotrichon schellianum*
		Total number of species: 33

The site was at Bai-Yun Chagan, southwest of Yakeshi along the road to Hailaer (all in northern Inner Mongolia). Relevé personnel: EB, YHM, LDL.

Table 7. Aquatic vegetation at one edge of the Zhalong lake sanctuary.

		DB-3 2x2m	DB-4 2x2m	DB-5 3x2m
H1:		70cm 20%	60cm 35%	1.3m 15%
	Sparganium stenophyllum	2.3	3.4	
	Sparganium simplex	1.1	2.3	
	Typha angustifolia	1.1	+.2	2.2
	Sagittaria trifolia	+.2	2.3	
	Hippuris vulgaris		1.2	
	Potamogeton pectinatus		+.2	
	Scirpus triangulatus		+.2	
	Phragmites communis			1.2
	Glyceria triflora			1.2
H2:		20cm 80%	20cm 60%	30cm 50%
	Myriophyllum spicatum	2.4	3.4	
	Potamogeton pectinatus	2.3	2.3	
	Nymphaea tetragona	2.3	2.3	
	Sagittaria latifolia	2.3	2.3	2.3
	Hippuris vulgaris	+.2		1.1
	Potamogeton lucens			2.3
	Myriophyllum verticillatum			2.2
	Utricularia vulgaris			1.1
	Sagittaria trifolia			+.2
	Najas minor			+
	Total number of species:	9	10	10

The vast expanse of Zhalong Lake, near Qiqihar, is mostly a monodominant stand of *Phragmites communis*, about 2-3m high and with around 90% cover. More species occur near the edges. The relevés were by a dirt road through the marsh, where water depth varied from about 8 to 26 cm. An artificial pond near a tourist area had some of these same species, including *Nymphaea tetragona*, dense *Myriophyllum* (85% cover), *Potamogeton maackianus*, and patchy *Phragmites* around the margin. Relevé personnel: EB, YHM. Most species were identified subsequently by YHM, from collected material.

Table 8. Composition of a dense, moist meadow in a flat mountain valley.

H	1 m 90 %	Elevation: 550 m 15 x 15m	
H:	5.5 *Festuca rubra*	2.3 *Eriophorum polystachion*	
	2.2 *Carex schmidtii*	1.1 *Sanguisorba tenuifolia*	
	1.2 *Stellaria palustris*	1.1 *Scirpus tabernaemontani*	
	1.1 *Salix kochiana*	+.2 *Equisetum arvense*	
	+.2 *Scutellaria scordifolia*	+.2 *Rumex patientia*	
	+ *Cicuta virosa* v. *angustifolia*	+ *Astragalus uliginosus*	
	+ *Trollius lebedourii*	+ *Caltha palustris*	
	+ *Lathyrus palustris*	+ *Valeriana amurensis*	

Total number of species: 16.

The site was in the Da Hinggan Ling mountains north of Yakeshi, along the road to Wenkutu, in the Orqohan area (northeastern Inner Mongolia). At the time of sampling, there was about 10cm of standing water in the wetland. (Relevé personnel: EB, YHM, LDL)

Table 9. Composition of short, sparse *Salix* scrub along a small stream, in the Da Hinggan Ling mountains of northeastern Inner Mongolia.

	S 2 m 20 %	Elevation: 550 m	
	H 0.6 m 15 %	Aspect: flat, riparian strip 2 x 10m	
S:	2.2 *Salix viminalis*	2.2 *Salix xerophilia*	
	2.2 *Salix siuzvii*	2.2 *Astragalus uliginosus*	
	1.1 *Salix rorida*		
H:	2.3 *Carex vesicaria*	1.2 *Betula platyphylla*	
	1.1 *Sanguisorba tenuifolia*	+.2 *Artemisia japonica* var. *manshurica*	
	+.2 *Astragalus uliginosus*	+.2 *Eriophorum polystachion*	
	+.2 *Clematis sibirica*	+.2 *Luzula rufescens*	
	+.2 *Equisetum arvense*	+ *Festuca rubra*	
	+.2 *Vicia multicaulis*	+ *Potentilla rupestris*	
	+ *Potentilla fragarioides*	+ *Sedum aizoon*	
	+ *Rumex patientia*	+ *Geum aleppicum*	
	+ *Stellaria palustris*		

Total number of species: 21

The relevé site was across the road from the moist meadow in Table 8, along a very small stream with little streambed. (Relevé personnel: EB, YHM, LDL)

A *Pinus sylvestris* forest outlier and the Mongolian steppe

The other conifer in the Da Hinggan Ling area is *Pinus sylvestris* var. *mongolica,* which occurs where fire is infrequent and permafrost less restrictive or absent altogether. A relict natural stand of *P. sylvestris* var. *mongolica* occurs on hilltops at Baiyun Chagan, in the drier steppe landscape that spreads south-southwest of Yakeshi into Mongolia. It was explained to us that, in this area, it is drier and warmer in summer and that summer is 15-20 days longer than at similar elevation (700m) near the mountains to the east. Macroclimatic extrapolation from nearby weather stations suggested that the mean annual temperature should be below freezing in this area too, but this may be modified by various factors. For one, drier conditions may translate into somewhat warmer summer conditions, since more sunlight may reach the surface (less reflected by clouds) and less energy is lost to melting snow and to evaporating water. Also, the somewhat flatter, more open terrain may be less subject to cold-air drainage in winter, such that its winter temperatures are higher than at similar elevation in the foothills and mountains.

A 30m x 40m sample of the pine forest, on a 5° north-facing slope at 710m, is shown in Table 5. The forest is not tall (14m) or closed (50% canopy cover), but the trees are relatively large and stately, the largest reaching 42cm in diameter (breast height). In the relevé area, only *Pinus sylvestris* var. *mongolica* occurred above the shrub layer. It also showed good regeneration in the shrub and herb layers. The ground cover was dominated by *Carex callitrichos,* with *Euphorbia fischeriana, Iris kobayashii,* and about 30 other, mainly herbaceous species. The shrub layer (20%) contained scattered but dense patches of *Rosa davurica,* along with more individually scattered *Prunus sibirica* and two *Spiraea* species.

Below the pine forest, the Mongolian steppe extends in all directions. Embedded within it, however, were islands of thicket composed mainly of *Prunus sibirica* and *Rosa davurica* (both also in the pine forest). The presence of such woody shrubs indicates that the grassland, at least at this eastern margin, is derived

Table 10. Climatic subdivisions for northeast Asia.

Climate Type	Tmean	N[T>10]	Tmax	Tmin	Tmmin	Tabmin
VIII Boreal	< 0°	<= 3	< 20°	< -20°		<< -20°
VIII-VI	< 0°	4-5	< 22°	< -20°		<< -20°
VI-VIII	> 0°	4-5	> 20°	< -18°		<< -18°
VI Typical Temperate	> 0°	>= 5	> 20°	< 0°	< 0°	<< -15°
VI-Ve			> 22°	> 0°	< 0°	< -15°
Ve-VI			> 23°	> 2°	> 0°	~ -15°
Ve Warm-Temperate			> 23°	> 5°	>>0°	> -15°

The main climate types of northeastern Asia are the boreal (VIII), typical temperate (VI) and warm-temperate (Ve). The fundamental breaks between these climate types (bold lines) occur between the reciprocally-numbered transitional types:

- between VIII-VI and VI-VIII, separated by the presence or absence of permafrost; and
- between VI-Ve and Ve-VI, separated less clearly but generally by Tmmin above or below freezing and by Tabmin not significantly below -15°C.

The core area of typical temperate (VI) climate is separated from its boreal transition (VI-VIII) by having less severe winter, Tmin significantly above -18°, and by definitely having 5 months with mean temperature above 10°C. The climate types are based on Walter (1968, 1970, 1974; Ve = east-side warm-temperate).

Abbreviations (all temperatures °C):

Tmean	= mean annual temperature
N[T>10]	= number of months with mean temperature above 10°C
Tmax	= mean temperature of warmest month
Tmin	= mean temperature of coldest month
Tmmin	= mean minimum of coldest month
Tabmin	= absolute minimum temperature (lowest ever measured)

and maintained, probably by fire as well as by grazing. A sample of the steppe, from an area that appeared to be less grazed and more semi-natural, is shown in Table 6. Most abundant were very leafy, distinct but sterile grass clumps (< 50 cm high) tentatively identified as *Stipa baicalensis;* and *Galium verum,* an erect forb with yellow flowers and filiform stem leaves in small whorls. Perhaps more interesting, however, were the smaller, xeromorphic life forms in this rather open steppe, including:

- whitish artemisioids (e. g. *Artemisia frigida*) and green *A. finita*
- a sedum-like rosette forb, *Orostachys fimbriatus*
- *Thymus serpyllum* var. *asiaticus*
- a steppe sedge, *Carex duriuscula*
- a small, white-pubescent lupinoid spike with blue flowers, *Veronica incana*
- a suffrutescent semi-shrub *Artemisia acaulis*
- *Leontopodium conglobatum,* and
- a fairly abundant, slightly whitish-pubescent, rosmarinoid suffrutescent which may also be a species of *Leontopodium.*

Aside from the leafy, bright green grass clumps, the smaller plant types were very reminiscent of the western end of the Eurasian steppe, which the first author had seen the previous year in the Crimea and eastern Transcaucasus.

Wetland vegetation

As in most cool regions, wetlands are common also in Manchuria, especially along the rivers flowing through the Dongbei plain but also on the Songnen Plain to the south, the dry flats to the west, and in the often flat-bottomed mountain valleys of the Da Hinggan Ling. Especially prominent is the Zhalong Lake along the Wuwei and Wuyuer Rivers where they come out into the Songnen Plain south of Qiqihar (see Figure 1). In this area the Zhalong Nature Reserve covers 210,000 hectares of mostly *Phragmites* marshland, with scattered areas of deeper water. It is especially important for cranes (*Grus* spp.) and other waterfowl that it supports.

When we were at Zhalong (late June) there was no standing water over wide areas, and the fine, grayish brown soil presented a cracked, claypan appearance, dry on the surface but mesic underneath. There was no litter layer visible. The vegetation over enormous areas appeared to be composed of just the one species, *Phragmites communis,* about 2m high and with a cover of about 90%. Around the edge, in areas where there was standing water (often the result of digging), there were more species, both rooted and floating. Some of this vegetation, from water up to 25cm deep, is described in Table 7, based on a local species list (466 spp) and the "Flora of China" (Institute of Botany 1972-85). Prominent taller emergents included *Sparganium* spp., *Sagittaria trifolia* (with very slender leaves), *Typha angustifolia,* and *Scirpus triangulatus* (to 76cm high). Floating-leaved *Nymphaea,* several *Potamogeton* species, and *Sagittaria latifolia* were also abundant, as well as submerged *Myriophyllum* spp. Juncaceae and other Cyperaceae, however, did not appear to be abundant in this edge vegetation or in the marsh interior.

Smaller wetlands are scattered especially throughout the Songnen Plain, still on the east side of the Da Hinggan range but further south, especially in Jilin. From the air (flightline Beijing to Harbin), the vast flat Songnen grassland was visible stretching to the west, dotted with countless saline depressions. Some of the wetland communities to be found in these depressions include *Suaeda corniculata* saline marshes (e. g. Wang et al. 1996) and *Puccinellia chinamopensis* meadows (Wang et al. 1998).

On the west side of the mountains, north of Yakeshi, a grassy, dense wet meadow (cover about 90%) was found in a wide, flat-bottomed mountain valley at about 550m. This meadow was dominated by *Festuca rubra,* growing about 1 m high in about 10cm of standing water, even near its edge (see Table 8). Also significant were graminoids *Carex schmidtii, Eriophorum polystachion,* and *Scirpus tabernaemontani,* along with forbs such as *Sanguisorba tenuifolia, Stellaria palustris, Scutellaria scordifolia,* and *Rumex patientia.* Across the road was a small stream in a very shallow, gravelly floodplain a few meters wide, about 2m below terraces with trees growing to about 5m. The composition of the very narrow, sparse riparian strip on the gravel along the stream is represented in Table 9. It included four *Salix* species, a *Betula platyphylla* sapling, plus *Astragalus uliginosus, Carex vesicaria,* and several other species that also occurred in the wet meadow.

SYNTHESIS

Northern Manchuria represents the convergence of three contrasting climatic influences and their corresponding landscape types : longer growing seasons and more precipitation from the east and southeast, and thus nemoral forests ; drier, more continental conditions from the west, and thus grassland ; and longer, more severe winters from the north, with permafrost and *Larix* forest where mean annual temperature is below 0℃. In most parts of the Northern Hemisphere, the transition between nemoral and boreal forest is determined by the length of the growing season and others aspects of summer warmth. In the ultra-continental climates of northern Manchuria and southern Siberia, on the other hand, the transition is more abrupt and is related mainly to the presence or absence of permafrost. Thus, even though summer may be warm, mean annual temperature and modification of the annual energy balance by local topography, producing or precluding permafrost, seem to be the main controls on the vegetation.

Unlike temperature minima and total warmth, mean annual temperature normally does not correlate with vegetation boundaries and rarely appears in quantitative global models of vegetation (cf Box 1981, 1995a). In Manchuria, however, the role of permafrost suggests a different basis for separating the basic bioclimatic zones. This is attempted in Table 10, using the zonal climate types of Heinrich Walter (1970, 1974; Walter & Box 1976) as an overall framework.

Between the two core climate zones, i. e. the boreal (Ⅷ) and nemoral (or typical temperate, VI), two transition areas can be identified, denoted by the two permutations of the adjacent core zones, i.e. transition Ⅷ-VI (presumably more boreal-like) and transition VI-Ⅷ (more nemoral). The true "break" between adjacent zones comes between the two transition areas. The most striking difference between the nemoral and boreal climatic regions in Manchuria is the change from deciduous broad-leaved forest to larch forest, which occurs near the permafrost boundary. So a value of 0℃ for mean annual temperature can be used as the boundary between Ⅷ-VI and VI-Ⅷ (across which boundary there is not such a large difference in the other climatic variables). Further south, a similar double transition can be recognized between the nemoral zone of deciduous forests (VI) and warm-temperate zone (Ve) in which evergreen broad-leaved woody plants appear, such as evergreen *Quercus* and other Fagaceae, *Ilex*, Lauraceae, and Theaceae. This appears to be related to the occasional occurrence of temperatures below about -15℃ (Walter 1970, Larcher 1976, Woodward 1987, Box 1988, 1995b). This value can be used to separate VI-Ve (with very few evergreens, only in the understorey) and Ve-VI (distinctly semi-evergreen, though with evergreens still mainly in the understorey). The prevalence of nighttime temperature minima above 0℃, even in the coldest month, may also permit more evergreen broad-leaved forms to occur. This quantitative scheme for zonal climatic subdivisions may or may not hold outside East Asia.

Finally we should consider the sensitivity of the Manchurian vegetation zonation to persisting changes in climatic conditions, as may occur under global warming. Permanent warming of the climate in East Asia will affect the occurrence of permafrost, even though permafrost does much to maintain its own colder local climate by diverting summer energy inputs into thawing rather than into heating the air. If the large land areas of the Northern high latitudes warm the most, as is usually suggested (e.g. IPCC 1996, cf Schlesinger & Mitchell 1987), then the climate of Manchuria would become less continental. A warmed region may appear, toward the north, in which summers are warm enough for some typical "northern hardwood" broad-leaved deciduous trees (e.g. *Fraxinus, Acer, Tilia,* nemoral *Betula*), plus temperate pines and perhaps eventually *Quercus* spp., and in which there is no longer any permafrost. In this case the distributions of these taxa would not be stopped so far south by permafrost, and a zone of transitional mixed forest could appear, as occurs in eastern North America and eastern Europe. Such a mixed forest may involve nemoral deciduous trees, some typical boreal conifers such as *Picea* and perhaps *Larix,* hard-needled boreal *Pinus* spp., and perhaps temperate conifers such as *Pinus koraiensis.* Wetlands may not be affected as much by reduced

continentality in the temperature regime *per se* but could be greatly affected if warming involves net drying.

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Appendix: Species Identified in the Manchurian Relevés

Part 1 : Woody Vegetation

Pteridophyta

Dryopteridaceae

Athyrium multidentatum
Dryopteris expansa

Equisetaceae

Equisetum arvense
Equisetum sylvaticum

Gymnospermae

Pinaceae

Larix gmelinii
Picea koraiensis
Pinus sylvestris var. *mongolica*

Monocotyledonae

Cyperaceae

Carex callitrichos
Carex ciliata-marginata
Carex globularis
Carex lanceolata
Carex pilosa
Carex siderosticta
Carex sp.
Carex vesicaria
Eriophorum gracile
Eriophorum polystachion
Fimbristylis verrucifera

Gramineae

Cleistogenes chinensis
Elymus dahuricus
Eragrostis curvula
Festuca rubra
Gramineae sp.
Melica nutans
Schizachyrium sp.

Iridaceae

Iris kobayashii
Iris uniflora

Juncaceae

Luzula rufescens

Liliaceae

Asparagus cochinensis
Convallaria keiskei
Hemerocallis minor
Lilium concolor var. *pulchellum*
Maianthemum biflorum
Paris verticillata
Polygonatum humile
Polygonatum odoratum
Polygonatum sp.
Veratrum maackii
Veratrum nigrum

Orchidaceae

Cypripedium macranthum

Dicotyledonae

Aceraceae

Acer mono

Araliaceae

Acanthopanax sessiliflorus

Betulaceae

Betula dahurica
Betula platyphylla
Corylus heterophylla

Boraginaceae

Brachybotrys pavidiformis

Campanulaceae

Adenophora divaricata
Adenophora gmelinii
Adenophora tetraphylla
Campanula punctata

Caprifoliaceae

Linnea borealis
Lonicera chrysantha
Viburnum sargenti

Caryophyllaceae

Cerastium arvense var. *angustifolium*
Melandrium brachypetalum

Stellaria dichotoma
Stellaria palustris

Celastraceae

Euonymus alatus

Compositae

Artemisia blepharolepis
Artemisia finita
Artemisia japonica var. *mandshurica*
Artemisia mongolica and *A. mongolica* var. *genuina*
Artemisia stolonifera
Aster ageratoides
Cacalia hastata
Chrysanthemum carinatum
Dendranthema oreastrum
Dendranthema zawadskii var. *latiloba*
Doellingeria scaber
Ixeris chinensis
Ligularia fischeri
Saussurea amurensis
Saussurea maximowiczii
Saussurea parviflora
Saussurea recurvata
Saussurea runcinata
Saussurea salicifolia
Saussurea sinuata
Saussurea subtriangulata
Saussurea ussuriensis
Sausurrea umbrosa
Serratula marginafolia
Synurus deltoides
Taraxacum mongolicum

Crassulaceae

Hylotelephium pallescens
Sedum aizoon
Sedum middendorfianum

Dioscoreaceae

Dioscorea nipponica

Ericaceae

Pyrola incarnata
Rhododendron dahuricum
Vaccinium vitis-idaea

Euphorbiaceae

Euphorbia fischeriana

Fagaceae

Quercus mongolica

Geraniaceae

Geranium eriostemon
Geranium sibiricum

Hydrangeaceae

Deutzia grandiflora

Labiatae

Scutellaria scordifolia

Leguminosae

Lespedeza bicolor
Lespedeza sp.
Trifolium lupinaster
Vicia cracca
Vicia multicaulis
Vicia pseudorobus
Vicia ramuliflora
Vicia sp.

Oleaceae

Fraxinus mandschurica

Onagraceae

Epilobium angustifolium

Paeoniaceae

Paeonia lactiflora

Polygonaceae

Polygonum ajanense
Polygonum alpinum
Polygonum odoratum
Rumex patientia

Ranunculaceae

Aconitum ambiguum
Aconitum barbatum
Actaea asiatica
Cimicifuga dahurica
Clematis hexapetala
Clematis sibirica
Pulsatilla dahurica
Ranunculus chinensis
Thalictrum baicalense
Trollius lebedourii

Rhamnaceae

Rhamnus davuricus

Rosaceae

Agrimonia pilose
Filipendula palmata
Fragaria orientalis
Geum aleppicum
Potentilla fragarioides
Potentilla longifolia
Potentilla rupestris
Prunus padus
Prunus sibirica
Rosa davurica
Rubus arcticus
Sanguisorba officinalis
Sanguisorba tenuifolia
Sorbaria sorbifolia
Spiraea aquilegifolia
Spiraea canescens
Spiraea elegans
Spiraea flexuosa
Spiraea sericea

Rubiaceae

Galium boreale
Galium bungei
Galium tokyoense
Galium verum
Rubia cordifolia

Rutaceae

Dictamnus albus var. *dasycarpus*

Salicaceae

Populus davidiana
Salix kochiana
Salix rorida
Salix siuzvii
Salix viminalis
Salix xerophilia

Schisandraceae

Schisandra chinensis

Tiliaceae

Tilia amurensis
Tilia mandschurica

Ulmaceae

Ulmus macrocarpa

Umbelliferae

Angelica viridiflora
Daucus carota
Heracleum moellendorfii
Osmorhiza aristata
Saposhnikovia divaricata
Seseli seseloides

Valerianaceae

Patrinia heterophylla
Valeriana officinalis
Valeriana stubendorfii

Violaceae

Viola brachyceras
Viola collina
Viola variegata

Vitaceae

Ampelopsis brevipedunculata

Part 2 : Grassland Relevé (DB-16)

Monocotyledonae

Gramineae

Aneurolepidium chinense
Cleistogenes squarrosa
Festuca ovina
Helictotrichon schellianum
Hordeum brevisubulatum
Poa argunensis
Stipa baicalensis

Other monocot families

Carex duriuscula (Cyperaceae)
Iris kaempferi (Iridaceae)

Dicotyledonae

Alyssum lenense (Cruciferae)
Artemisia acaulis (Compositae)
Artemisia frigida (Compositae)
Bupleurum sibiricum (Umbelliferae)
Filifolium sibiricum (Compositae)
Galium verum (Rubiaceae)
Geranium maximowiczii (Geraniaceae)
Leontopodium conglobatum (Compositae)
Lespedeza hedysaroides (Leguminosae)
Lespedeza tomentosa (Leguminosae)
Messerschmidtia sibirica var. *angustior* (Boraginaceae)
Orostachys fimbriatus (Crassulaceae)
Potentilla conferta (Rosaceae)
Pulsatilla dahurica (Ranunculaceae)
Senecio flammeus (Compositae)
Stellera chamaejasme (Thymelaeaceae)
Thalictrum petaloideum (Ranunculaceae)
Thymus serpylum var. *asiaticus* (Labiatae)
Veronica incana (Scrophulariaceae)

Unknown

"soft rosmarinoid (suffrutescent, woody base), 10-15cm; leaves 1.5-2cm linear-lanceolate, slightly whitish pubescent (esp. undersides) " é *Leontopodium?*

Part 3 : Wetland Relevés (DB3-7 and DB-9)

Monocotyledonae

Allium anisopodium (Liliaceae)
*Carex schmidt*ii (Cyperaceae)
Glyceria triflora (Gramineae)
Najas minor (Najadaceae)
Phragmites communis (Gramineae)
Potamogeton lucens (Potamogetonaceae)
Potamogeton maackianus (Potamogetonaceae)
Potamogeton pectinatus (Potamogetonaceae)
Potamogeton perfoliatus (Potamogetonaceae)
Sagittaria latifolia (Alismataceae)
Sagittaria trifolia (Alismataceae)
Scirpus tabernaemontani (Cyperaceae)
Scirpus triangulatus (Cyperaceae)
Sparganium simplex (Sparganiaceae)
Sparganium stenophyllum (Sparganiaceae)
Typha angustifolia (Typhaceae)

Dicotyledonae

Astragalus uliginosus (Leguminosae)
Caltha palustris (Ranunculaceae)
Cicuta virosa var. *angustifolia* (Umbelliferae)
Hippuris vulgaris (Hippuridceae)
Lathyrus palustris (Leguminosae)
Myriophyllum spicatum (Haloragidaceae)
Myriophyllum verticillatum (Haloragidaceae)
Nymphaea tetragona (Nymphaeaceae)
Utricularia vulgaris (Lentibulariaceae)
Valeriana amurensis (Valerianaceae)

REFERENCES

An Sh. -Q., Zhang Ji-Shu, & Li H. 1997. Research on natural regeneration of Dahurian larch under the canopy of trees. J. Neimenggu Forestry College, 19 (1) : 1-8 (in Chinese).

Box, E. O. 1981. Macroclimate and Plant Forms : An Introduction to Predictive Modeling in Phytogeography. Tasks for Vegetation Science, Vol. 1. Dr. W. Junk bv, Publishers, den Haag (The Hague).

Box, E. O. 1988. Some similarities in the climates

and vegetations of central Honshu and central eastern North America. Veröff. Geobot. Inst. ETH, Stiftung Rübel (Zürich), 98: 141-168.

Box, E. O. 1995a. Factors determining distributions of tree species and plant functional types. Vegetatio, 121: 101-116.

Box, E. O. 1995b. Climatic Relations of the Forests of East and Southeast Asia. In: Vegetation Science in Forestry (E. O. Box et al., eds.), Handbook of Vegetation Science, vol. 12/1, pp. 23-55. Kluwer, Dordrecht.

Box, E. O. 1995c. Global Potential Natural Vegetation: Dynamic Benchmark in the Era of Disruption. In: Toward Global Planning of Sustainable Use of the Earth -- Development of Global Eco-engineering (Sh. Murai, ed.), pp. 77-95. Elsevier, Amsterdam.

Chang Y.-L. 1955. The Plant Communities of the Greater Khingan Mountains. Contributions to Plant Ecology and Geobotany, No. 1. Science Press, Beijing. (In Chinese).

Chen Da-Ke & Zhu Ning 1989. Forest Types and Floral Elements in Northeast China. In: Northern Forest Silviculture and Management, pp. I4-I5. Summary of IUFRO Symposium 1989. Northeast Forestry University Press Harbin.

China Natural Geography Editorial Committee (eds.) 1983. (China Natural Geography: Plant Geography.) Academia Sinica. Science Press, Beijing. (in Chinese).

China Natural Geography Editorial Commission (eds.) 1984. (China Natural Geography: Climate.) Academia Sinica. Science Press, Beijing. (in Chinese).

Editorial Group for Vegetation of Nei Mongol 1986. (Vegetation of Nei Mongol). Science Press, Beijing. (in Chinese).

Fujiwara, K. 1987. Aims and methods of phytosociology or "vegetation science." In: Papers on Plant Ecology and Taxonomy to the Memory of Dr. Satoshi Nakanishi, pp. 607-628. Kobe Geobotanical Society.

Hou X.-Yu 1960. Vegetation of China. Education Press, Beijing. (In Chinese).

Hou X.-Yu 1983. Vegetation of China with reference to its geographical distribution. *Ann.* Missouri Bot. Garden, 70: 509-548.

Hou X.-Yu (ed. /author-in-chief) 1979. Vegetation Map of China. Institute of Botany, Academia Sinica. Map Press, Beijing. Map (1: 4,000,000, in Chinese) + separate legend manual (Chinese and English versions).

Institute of Botany 1972-85. Iconographia Cormophytorum Sinicorum. Academia Sinica. Science Press, Beijing. 5 vols. +2 supplements, (in Chinese, with Latin indices).

Institute of Botany 1982. Vegetation Map of China. 2nd ed. Academia Sinica. Cartographic Publishing House, Beijing. (In Chinese, with legend in Chinese and English).

IPCC (Intergovernmental Panel on Climate Change) 1996. Climate Change 1995: The Science of Climate Change (J. T. Houghton et al., eds.). Cambridge University Press.

Küchler, A. W. 1948. A new vegetation map of Manchuria. Ecology, 29: 513-516.

Larcher, W. 1976. Ökologie der Pflanzen. Verlag Eugen Ulmer, Stuttgart.

Müller, M. J. 1982. Selected Climatic Data for a Global Set of Standard Stations for Vegetation Science. Dr. W. Junk bv, Publishers, den Haag (The Hague).

Rand McNally 1995. Atlas of World History. Revised Edition (originally 1981). Rand McNally Co.

Schlesinger, M. E., & J. F. B. Mitchell 1987. Model Projections of the Equilibrium Climatic Response to Increased Carbon Dioxide. In: Projecting the Climatic Effects of Increasing Carbon Dioxide (M. C. MacCracken and F. M. Luther, eds.), pp. 81-147. Report no. DOE/ER-0237. Department of Energy, Washington.

Song Y.-Ch. 1983. Die räumliche Ordnung der Vegetation Chinas. Tuexenia, 3: 131-157.

Walter, H. 1968. Die Vegetation der Erde in ökophysiologischer Betrachtung. Vol. 2 : Die gemässigten und arktischen Zonen. Gustav-Fischer-Verlag, Stuttgart.

Walter, H. 1970. Vegetation und Klimazonen. Verlag Eugen Ulmer, Stuttgart.

Walter, H. 1974. Die Vegetation Osteuropas, Nord- und Zentralasiens. Vegetation der einzelnen Grossräume. Gustav-Fischer-Verlag, Stuttgart.

Walter, H., & E. O. Box 1976. Global classification of natural terrestrial ecosystems. Vegetatio, 32 (2): 75-81.

Walter, H., & H. Lieth 1960-67. Klimadiagramm-Weltatlas. Gustav-Fischer-Verlag, Stuttgart.

Wang Chi-Wu 1961. The Forests of China, with a Survey of Grassland and Desert Vegetation. Maria Moors Cabot Foundation Publ. no. 5. Harvard University, Cambridge (Mass.).

Wang R.-Zh., Li J.-D., & Gao Q. 1996. Study on water ecology of the *Suaeda corniculata* saline community in the Songnen Plain. Acta Phytoecologica Sinica, 20 : 472-477. (in Chinese).

Wang R. -Zh., Gao Q., & Li J. -D. 1998. Comparative study on water ecology of two *Puccinellia* communities in the Songnen grassland. Acta Ecologica Sinica, 18 : 107-112. (in Chinese).

Wang Yeh-chu 1989. Characteristics and Regeneration of Northern Forests in Northeast China. In : Northern Forest Silviculture and Management, pp. 11-13. Summary of IUFRO Symposium 1989. Northeast Forestry University Press.

Woodward, I. 1987. Climate and Plant Distribution. Cambridge University Press.

Wu Zheng-Yi & Committee (eds.) 1980. Vegetation of China. Science Press, Beijing. (in Chinese, with Latin-Chinese species lists ; no page index). (New edition 1995)

Xu W.-D. 1983. Correlations between distribution of the edificators of the zonal forest and water-temperature condition in northern China. Research on Forest Ecosystems, 3 : 73-81 (in Chinese).

Xu W.-D. 1986. The relation between the zonal distribution of types in northeast China. Acta Phytoecologica et Geobotanica Sinica, 10 (4) : 254-263.

You Hai-Mei 2001. A vegetation-ecological study of *Quercus mongolica* forests in China. Doctoral Thesis, Yokohama National University. (In Japanese)

You Hai-Mei, K. Fujiwara, Wu Su-J. & Wan X.-L. 2001. (in press). A preliminary vegetation-ecological study of *Quercus mongolica* forests in China. J. Phytogeogr. and Taxonomy (Japan), 49 (1).

Zhou Yi-L. (ed.) 1986. Ligneous Flora of Heilongjiang. Heilongjiang Science Press, Haerbin. (in Chinese).

Zhou Yi-L. 1988. Summergreen coniferous forests. Biology Reports (China), 5 : 6-10 (in Chinese).

Zhou Yi-L. (ed.) 1991. Vegetation of the Da Hinggan Ling in China. Science Press, Beijing. (in Chinese).

Zhou Yi-L. & Zu Y.-G. (eds.) 1997. Geography of the Vegetation In Northeast China. Science Press, Beijing. (in Chinese).

Zhou Yi-L. & Collaborators 1992-ongoing. Flora Heilongjiangensis. 11 vols. (vols. 2, 11 in print). Northeast Forestry University Press, Haerbin. (in Chinese).