

# Vegetation at the taiga forest–steppe borderline in the western Khentey Mountains, northern Mongolia

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Vegetation of an area of 500 km<sup>2</sup> in the western Khentey Mountains, northern Mongolia is phytosociologically classified with the help of 254 relevés. Twenty-one main vegetation units are described. The study area is situated at the interface between the western Siberian dark taiga, the eastern Siberian light taiga and the Mongolian-Daurian forest steppe. A small-scale pattern of these three major vegetation types was found depending on site characteristics. Dark taiga forests of *Pinus sibirica*, *Abies sibirica*, *Picea obovata*, and *Larix sibirica* grow at the most humid sites. Light taiga forests dominated by *Larix sibirica* and *Betula platyphylla* occur on relatively dry northern slopes of the lower montane belt. Sun-exposed, southern slopes of the lower montane belt are covered by montane meadow and mountain steppe. DCA ordination suggests that the distribution of vegetation types depends on water supply and altitude.

Key words: dark taiga, light taiga, meadow steppe, mountain steppe, subtaiga

## Introduction

Zonal vegetation of northern and central Asia is characterized by a sequence of latitudinal vegetation belts of (from north to south) tundra, taiga, forest steppe, steppe, semi-desert and desert. Each of these vegetation types covers large areas of Eurasia and forms spacious vegetation units, which can be rather uniform over long distances (Lavrenko 1979, Walter & Breckle 1986). However, at the borderlines between different vegetation belts, vegetation can be more diverse consisting of small-scale patterns of different

vegetation units (Franz 1973). The taiga forests are limited by low temperature in the north and by drought in the south. The present study deals with the southern border of the huge Siberian taiga forests towards the likewise huge Eurasian steppe region.

The Khentey Mountains in northern Mongolia represent the only area where central Siberian taiga vegetation directly borders on the open steppe. This area is of special botanical interest, because central Siberia has a highly diverse relief (Rylkov 1996) and because the central Siberian taiga is more diverse in tree species



**Fig. 1.** Location of the Khenkhey Mountains, of Khonin Nuga Research Station, and of the weather stations Bugant and Eroo in Mongolia. Grey areas indicate mountain taiga and white areas steppe vegetation.

than taiga vegetation in other parts of Siberia (Walter & Breckle 1986, Treter 1993). The latter is because, in central Siberia, the western Siberian dark taiga forests with *Picea obovata*, *Abies sibirica*, *Pinus sibirica* and *Larix sibirica* (Knystautas 1987) meet the eastern Siberian light taiga forests made up by *Betula platyphylla* and related species as well as by *Larix* spp. and *Pinus sylvestris* (Ermakov et al. 2002). The genus *Larix* is represented by *L. sibirica* in the Khenkhey Mountains and in western Siberia, but is replaced by *L. gmelinii* in the ultracontinental regions east and northeast of Lake Baikal (Walter & Breckle 1986). The “double” borderline situation makes the Khenkhey Mountains a unique place for flora and vegetation. Here the transitional zone between western and eastern Siberian taiga forests passes into the Mongolian-Daurian forest steppe within another transitional zone. Hence, the Khenkhey Mountains harbor a particularly high plant diversity. Within the Khenkhey Mountains, the western part is most diverse, because the dark taiga species, including *Abies sibirica* and *Picea obovata*, thin out in the eastern Khenkhey (Korotkov 1976, Tsendendash 1995). This is why the western Khenkhey Mountains were selected for the present investigation.

## Materials and methods

### Study area

Flora and vegetation were studied in an area of about 500 km<sup>2</sup> around Khonin Nuga Research Station (49°04'48"N, 107°17'15"E), run by the Center of Nature Conservation of the University of Göttingen and by the National University of Mongolia, Ulaanbaatar (Mühlenberg et al. 2000). Khonin Nuga Research Station (Fig. 1) is located 250 km north of Ulaanbaatar in a valley, where the rivers Šarlan Gol and Khongiyin Gol unite and become the river Eroo. The latter flows into the Orkhon river, then into the Selenge river and finally into Lake Baikal. The Khenkhey Mountains stretch across 200 km from the Mongolian capital in a north-easterly direction to the Russian border. In Russia, they further continue over 150 km to the northeast, changing their name to Chikoyskiy Khrebet and Khrebet Stanovik, respectively. North of these mountains arises the Transbaikalian Mountain System, the main ridges of which run in a west-east direction. The Khenkhey Mountains are surrounded by the Mongolian-Daurian steppe in the west and in the south and by the Eastern Mongolian steppe in the east. A 50–80-km-wide strip of the Mongolian-Daurian steppe and the river Orkhon separates the Khenkhey from the Khangay Mountains in the southwest.

Elevation of the study area ranges from 900 m in the river valleys up to 1600 m on the mountain tops. The central parts of the Khenkhey Mountains, east and southeast of the study area, generally exceed an elevation of 1500 m with the highest peak, Mt. Asralt-Khayrkhan, achieving 2799 m. Geologically, the Khenkhey mainly consists of Proterozoic and Paleozoic rocks, especially of granite (Anon. 1973). A typical feature of the Khenkhey are golez terraces (i.e., cryoplanation terraces; Lehmkuhl & Lang 2001) in the upper elevations deriving from Pleistocene glaciation. At the margins of golez terraces, boulder fields have been formed due to wash-out of fine-grained material. Permafrost is a characteristic feature of the soils of the Khenkhey Mountains. It occurs in patches in the west of the study area and as, respectively, insular, discontinuous or continuous permafrost in the east with increas-

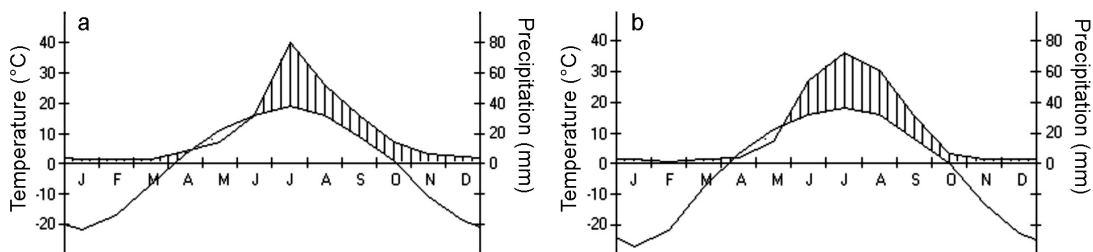


Fig. 2. Climate diagrams from the weather station (a) Bugant and (b) Eroo from the wider surroundings of the study area.

ing proximity to the central parts of the Khentey Mountains (Tsedendash 1995).

The climate of the Khentey Mountains is characterized by the Asiatic anticyclone in winter, which typically has its center southwest of Lake Baikal and causes dry and cold winters with mean January temperatures as low as  $-23$  to  $-28$  °C (Tsegmid 1969, Tsedendash 1995). Mean July temperatures published from the Khentey range from  $12$  to  $18$  °C. Frost occurs from the end of August to early June on 280–300 days per year. Most precipitation is received in July and August (Tsegmid 1969, Tsedendash 1995). Data from the closest permanent weather stations 42 or 87 km, respectively, from Khonin Nuga Research Station are shown in Fig. 2 (for geographical position cf. Fig. 1). At these weather stations, annual precipitation varies between 250 and 260 mm.

### Vegetation mapping

Eleven sites were selected for vegetation sampling. These sites should represent all habitat types of the study area and varied in height, exposition and geographical location within the area (Fig. 1); they were not randomly chosen. The small-scale pattern of vegetation units was investigated at six out of these eleven sites, where transects across river valleys were mapped. Two vegetation profiles from these transects are shown in Figs. 5 and 6. Relevés from a total of 254 homogenous plots of 100 m<sup>2</sup> are included in the present study. Cover of all vascular plant species and of dominant bryophyte species was estimated in percent stratified for tree, shrub, herb and bryophyte layers. Nomenclature of vascular plants refers to Gubanov (1996), that of bryophytes to Tsegmid (2001).

### Analysis of vegetation data

Vegetation data were sorted and classified according to Braun-Blanquet (1964). Cover values were grouped into seven classes:  $r$  cover  $< 1\%$ ;  $+$  =  $1\%$ ;  $1$  =  $5\%$ ;  $2$  =  $6\%$ – $25\%$ ;  $3$  =  $26\%$ – $50\%$ ;  $4$  =  $51\%$ – $75\%$ ;  $5$   $> 75\%$  (Dierschke 1994). These cover value data were used for classification and ordination of relevés, but are not directly presented here; they are published in Dulamsuren (2004). Constancy of species was classified as follows:  $r \leq 5\%$ ;  $+$  =  $6\%$ – $10\%$ ;  $I$  =  $11\%$ – $20\%$ ;  $II$  =  $21\%$ – $40\%$ ;  $III$  =  $41\%$ – $60\%$ ;  $IV$  =  $61\%$ – $80\%$ ;  $V$   $> 80\%$  (Dierschke 1994). Data processing for Braun-Blanquet classification was carried out with TAB 3.3 software (Peppler 1988). Though the Braun-Blanquet method was used to classify vegetation, associations were not named and formerly described after the respective nomenclature.

Detrended Correspondence Analysis (DCA) was applied for ordination analysis of vegetation data. It was calculated with PC-ORD 4.01 software (MjM Software, Gleneden Beach, Oregon, U.S.A.) with scalar-transformed Braun-Blanquet cover values. The ordination comprised all species of the herb layer. Rare species were down-weighted in analysis.

### Soil sampling and analysis

In the six transects across river valleys used for vegetation sampling, soil profiles were excavated to determine soil types (and chemical soil characteristics, which are not presented here). Depth, color (according to Munsell Soil Color Charts), mottling, humus content, graining, proportion of soil skeleton, texture, and root penetration were

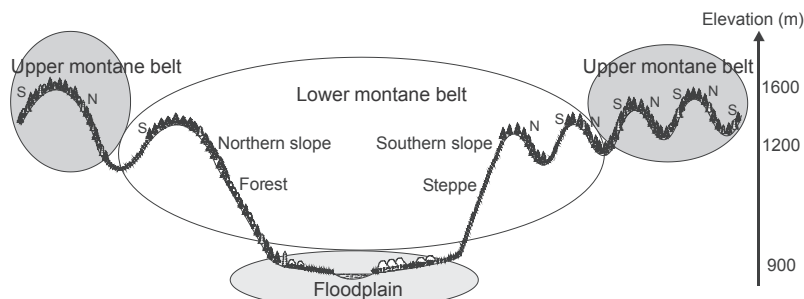


Fig. 3. Altitudinal belts of the study area.

separately recorded from each horizon. Nomenclature of soil types, which are given in Figs. 5 and 6, follows that of FAO (1988).

## Results

### Altitudinal and aspect-dependent variation of vegetation types

Vegetation of the Khentey Mountains strongly depends on altitude. Within the study area, the upper montane belt at 1200–1600 m is distinguishable from the lower montane belt at 900–1200 m as well as from the river valleys at an elevation of about 900 m (Hilbig & Knapp 1983). The upper montane belt is characterized by numerous small valleys due to tectonic depressions (Fig. 3). Subalpine and alpine vegetation occurs in higher elevations of the Khentey Mountains outside the study area.

Vegetation of the upper montane belt is dominated by dark taiga forests of *Pinus sibirica*, *Abies sibirica*, *Picea obovata*, and more rarely, *Larix sibirica* and *Betula platyphylla*. Furthermore, boulder fields have their main occurrence in the upper montane belt. Exposure has little impact on vegetation within the upper montane belt. In the eastern parts of the study area, which are closer to the (more highly elevated) central Khentey massif, the dark taiga forests descend to the northern slopes of the lower montane belt. However, *Pinus sibirica* is focussed on the upper montane belt. In the western parts of the study area, which belong to the more peripheral parts of the Khentey Mountains, the northern slopes of the lower montane belt are stocked with light forests dominated by *Betula platyphylla* and *Larix sibirica*. These light forests of the lower

montane forests in the forest–steppe transitional zone are often called subtaiga forests (Korotkov 1976, Savin *et al.* 1988, Tsedendash 1995). The southern slopes are covered with montane meadow or mountain steppe, or more rarely, with *Ulmus pumila* open woodland, regardless of the geographical position within the study area. The upper parts of southern slopes are often stocked with subtaiga forests of either *Pinus sylvestris*, *Pinus sylvestris* and *Betula platyphylla*, *Populus tremula*, or *Larix sibirica* and *Betula platyphylla*. Shrubland of *Betula fusca* can occur in contact with *Pinus sylvestris* and *Pinus sylvestris*–*Betula platyphylla* subtaiga forests.

Floodplain vegetation of the western parts of the study area is heterogeneous with various types of forest, shrub and meadow. Riverine forests are dominated by either *Betula platyphylla*, *Populus laurifolia* or different species of *Salix* including *S. miyabeana*, *S. rhamnifolia*, *S. rorida* and *S. schwerinii*. Shrubberies mainly consist of *Betula fusca* (rarely associated with *B. fruticosa*), *Padus asiatica* or *Salix rhamnifolia* and *S. schwerinii*. Floodplain meadows can be rich in herbs or *Carex* depending on moisture. In the eastern parts of the study area spatial heterogeneity of floodplain vegetation is lower primarily with forests of *Picea obovata* and shrubberies of *Betula fusca*.

### Vegetation classification

An outline of 21 main vegetation units is compiled in Table 1. Diagnostic species for those communities occurring in the upper and lower montane belt as well as in *Betula platyphylla* and *Picea obovata* riverine forests are given in Table 2. Other floodplain communities (nos.

**Table 1.** Main vegetation types of the study area.**1. *Picea obovata* dark taiga forest**

*Picea obovata*-dominated forest stands with occasionally associated *Betula platyphylla* (very rarely also *Abies sibirica*) occur in areas that are close to central parts of the Khentey Mountains (i.e., in the eastern parts of the study area) in the lower montane belt. They are characterized by a well developed bryophyte cover of, e.g., *Dicranum bonjeanii* and *Aulacomnium palustre*. *Picea obovata* forests stock in two different types of habitats, i.e., on humid northern slopes as well as near mountain streams, where they form riverine forests. Ground vegetation is similar in both habitats. Soils below *Picea obovata* forests are more acidic than below all other vegetation types of the study area.

**2. *Picea obovata*–*Abies sibirica* dark taiga forest**

*Picea obovata*–*Abies sibirica* dark taiga forests without significant participation of *Pinus sibirica* cover northern slopes of the lower montane belt in the eastern study area. Ground vegetation strongly differs from that of dark taiga forest in the upper montane layer with, e.g., *Ledum palustre*, *Pyrola incarnata* and *Schisachne callosa*.

**3. Mixed conifer–*Betula platyphylla* dark taiga forest**

Mixed dark taiga forests of *Picea obovata*, *Abies sibirica* and varying amounts of *Pinus sibirica* and *Betula platyphylla* occur in the lower montane belt of the eastern study area. The two latter species can be co-dominant or occur more rarely than *Picea obovata* and *Abies sibirica*. Because of the different tree layer, these forest stands were separated from the *Picea obovata*–*Abies sibirica* dark taiga, though ground vegetation does hardly differ. Mixed dark forests of the lower montane belt with *Cystopteris fragilis*, *Mitella nuda* and *Carex lanceolata* are named as *Cystopteris fragilis* variant.

**4. *Pinus sibirica*–*Picea obovata* dark taiga forest**

*Pinus sibirica* dominated forests are restricted to the upper montane belt. In these forests, *P. sibirica* is associated with other conifers. In lower elevations within the upper montane belt and in moist depressions, *Picea obovata* co-occurs with *Pinus sibirica*. Ground vegetation of these forests is characterized by *Rubus saxatilis*, *Iris ruthenica* and *Lathyrus humilis*. At dryer sites in more open forests, species that also occur in subtaiga forests, such as *Crepis sibirica*, *Ranunculus japonicus* and *Trifolium lupinaster*, form the *Crepis sibirica*–*Ranunculus japonicus* variant.

**5. *Pinus sibirica*–*Abies sibirica* dark taiga forest**

*Abies sibirica* is the prevalent tree species associated with *Pinus sibirica* in the study area. Ground vegetation of *Pinus sibirica*–*Abies sibirica* forests is markedly different from that of *Pinus sibirica*–*Picea obovata* forests with, e.g., *Rubus sachalinensis* and *Dryopteris expansa* as dominant species. The most humid sites with *Pinus sibirica*–*Abies sibirica* forest are inhabited by its *Cinna latifolia*–*Agrostis clavata* variant. *Picea obovata* can be part of the tree layer of *Pinus sibirica*–*Abies sibirica* forests and, more rarely, *Abies sibirica* can occur in *Pinus sibirica*–*Picea obovata* forests, but ground vegetation clearly separates these vegetation units.

**6. Mixed conifer–*Betula platyphylla* subtaiga forest**

Mixed subtaiga forests consist of *Betula platyphylla*, *Larix sibirica* and small amounts of *Pinus sibirica* and *Pinus sylvestris*. These forests inhabit northern slopes of the lower montane belt, but in contrast to mixed dark taiga forests (no. 3), this forest type grows in the more peripheral, western parts of the study area. Ground vegetation of the mixed conifer–*Betula platyphylla* subtaiga forest is similar to that of the *Saussurea recurvata* variant of *Larix sibirica*–*Betula platyphylla* forests (no. 7a).

**7. *Larix sibirica*–*Betula platyphylla* subtaiga forest**

This type of light subtaiga is the prevalent vegetation type on northern slopes of the lower montane belt in the western study area. The *Saussurea recurvata* variant (7a) with, e.g., *Artemisia sericea* and *Hieracium umbellatum* grows on dry mountain ridges and dry slopes. It also covers the upper parts of southern slopes, e.g., in the vicinity of montane meadow steppes. At such sites, it also occurs in the eastern study area. The *Cacalia hastata* variant inhabits more humid sites on gently inclined northern slopes as well as in small valleys and depressions. Here, e.g., *Festuca ovina* and *Rhododendron dauricum* occur. Steep, humid slopes are additionally characterized by *Gymnocarpium jessoense*, *Linnaea borealis* and *Viola biflora*.

**8. *Betula platyphylla* riverine forest**

Riverine forests of *Betula platyphylla* are the main forest type along rivers in the western parts of the study area. Corresponding to a loose tree layer of only 30%–40% cover, these forests have a rich shrub layer of *Crataegus sanguinea*, *Padus asiatica*, *Potentilla fruticosa*, *Ribes rubrum*, *Rosa acicularis*, and *Spiraea salicifolia*. Ground vegetation is a mixture of species of the *Larix sibirica*–*Betula platyphylla* subtaiga forests, such as *Cacalia hastata*, and of floodplain meadow species, such as *Carex arnellii*. A further typical species is *Vicia cracca*. At the most humid sites, *Picea obovata* and occasionally *Pinus sylvestris* occur in the *Betula platyphylla* riverine forest. These sites differ also in ground vegetation with *Carex schmidtii* and *Lysimachia dahurica*.

Continued



Table 1. Continued.

**9. *Populus tremula* subtaiga forest**

Stands of *Populus tremula* grow in upper parts of southern (more rarely western and eastern) slopes in the lower montane belt above dry montane meadow or mountain steppe on rocky substrate. *P. tremula* forests typically have a shrub layer of *Spiraea media*, *Cotoneaster melanocarpa* and *Rosa acicularis*. Ground vegetation is similar to that of the *Saussurea recurvata* variant of *Larix sibirica*–*Betula platyphylla* forests. Some additional species that prefer dry and open sites, e.g., *Vicia amoena*, distinguish ground vegetation of *Populus tremula* from *Larix sibirica*–*Betula platyphylla* subtaiga forests. In one case, *Populus tremula* was found to be associated with *Betula platyphylla*. This stand could be classified as *Betulo platyphyllae*–*Populetum tremulae* (Hilbig 1990).

**10. *Pinus sylvestris*–*Betula platyphylla* subtaiga forest**

This community occurs on moderately inclined southern, western and eastern slopes and on mountain ridges in the lower montane belt on moderately deep soil. Ground vegetation is characterized by the occurrence of, e.g., *Iris ruthenica*, *Anemone crinita* and *Pyrola incarnata*.

**11. *Pinus sylvestris* subtaiga forest**

At dryer sites, *Betula platyphylla* is omitted and two variants of *Pinus sylvestris* forest are found. The typical variant inhabits mountain ridges and gently inclined southern, eastern and rarely western slopes with moderately deep soil. The *Pulsatilla turczaninovii* variant grows on steep, dry slopes with thin soil layer. The latter type of *Pinus sylvestris* forest grows adjacent to mountain and montane meadow steppes and, thus, shares several species with them, e.g., *Bupleurum scorzoniferolium* and *Patrinia rupestris*.

**12. *Ulmus pumila* open woodland**

Open groves, where *Ulmus pumila* as the only tree species never exceeds cover values of 40%, occur on steep, stony southern slopes in the lower montane belt and are usually surrounded by mountain steppe. *Ulmus pumila* woodlands typically have a well-developed shrub layer of *Spiraea aquilegifolia*, *Ribes diacantha* and young growth of *Ulmus pumila*. The *Ulmus pumila* stands of the study area differ from the *Spiraea aquilegifoliae*–*Ulmum pumilae* of Hilbig (1990, 1995) by the occurrence of mountain steppe-inhabiting species, such as *Artemisia gmelinii*, *Carex pediformis*, *Potentilla acaulis*, *Pulsatilla turczaninovii* and *Youngia tenuicaulis*.

**13. *Festuca lenensis* montane meadow steppe**

This type of montane meadow steppe inhabits gently inclined southern slopes (up to 20–30°) with relatively good water supply in the lower montane belt. The *Festuca lenensis* meadow steppe often borders on *Larix sibirica*–*Betula platyphylla* subtaiga forests. Thus, these vegetation types have several species in common, e.g., *Artemisia sericea* and *Iris ruthenica*.

**14. *Pulsatilla ambigua* montane meadow steppe**

*Pulsatilla ambigua* montane meadow steppes grow on steeper (30–45°) and dryer southern slopes than the *Festuca lenensis* montane meadow steppe. Typical species are *Bupleurum bicaule*, *Papaver nudicaule* and *Poa botryoides*. Several species of the *Pulsatilla ambigua* montane meadow steppe also occur in mountain steppes, e.g., *Artemisia commutata*, *Carex korshinskyi*, *Potentilla acaulis*, and *Thymus gobicus*. The *Pulsatilla ambigua* montane meadow steppe often grows adjacent to *Pinus sylvestris* forests, especially, near stands of the *Pulsatilla turczaninovii* variant.

**15. *Artemisia frigida* mountain steppe**

The steepest southern slopes with thin soil layer and bad water supply are covered by *Artemisia frigida* mountain steppe. Total plant cover of this community is only 30%–60%. Many species typical for the mountain steppes of the study area have their main occurrence in the forest–steppe belt south of the study area, whereas mountain steppes of the forest–steppe belt harbor many species of the steppe belt, which are absent from the study area. Typical plant species of the *Artemisia frigida* mountain steppe are, e.g., *Artemisia frigida*, *Dontostemon integrifolius*, *Koeleria cristata* and *Goniolimon speciosum*.

**16. *Salix rhamnifolia*–*S. schwerinii* riverine forest**

In contrast to the *Betula platyphylla* riverine forest, the *Salix rhamnifolia*–*S. schwerinii* riverine forest has a dense tree layer (cover 80%), but a poorly developed shrub layer (< 5 %). Ground vegetation consists of species that also occur in *Betula platyphylla* riverine forests, riverine shrublands and floodplain meadows. Relatively high cover of *Ribes rubrum* both in the shrub and the herb layer is a typical feature of the *Salix rhamnifolia*–*S. schwerinii* riverine forest.

**17. *Salix rhamnifolia*–*S. schwerinii* riverine shrubland**

This community grows in regularly inundated floodplain areas. Typical herb species of these shrublands are *Achillea asiatica*, *Lactuca sibirica*, and *Tanacetum vulgare*. In addition reed species, such as *Carex dichroa* and *C. rostrata*, occur at more humid sites.

Continued

Table 1. Continued.

**18. *Betula fusca* shrubland**

*Betula fusca* shrubland occurs both in floodplain habitats and on southern slopes of the lower montane belt. When forming riverine shrubland, *B. fusca* inhabits less often inundated sites than *Salix* shrubbery on terraces of wide river valleys. Shrub species other than *B. fusca*, e.g., *Betula fruticosa*, *Potentilla fruticosa* and *Rosa acicularis*, regularly co-occur. In wet habitats, ground vegetation of riverine *Betula fusca* shrubland is dominated by *Carex caespitosa* and *C. rhynchophysa*, whereas *Anemone crinita* and *Carex amgunensis* prevail at sites of moderate moisture. *Carex pediformis*, *Artemisia tanacetifolia* and *Galium verum* are characteristic species of dry *Betula fusca* shrubland on southern slopes.

**19. *Iris sanguinea* floodplain meadow**

*Iris sanguinea* floodplain meadows occur in the river valleys in the western study area. Dominant species are meadow species, such as *Achillea asiatica* and *Pedicularis resupinata*, and species of light subtaiga forests, such as *Potentilla fragarioides* and *Vicia amoena*. The *Iris sanguinea* floodplain meadows are split in the *Anemone crinita*–*Polemonium racemosum* variant of moist sites and the *Phlomis tuberosa*–*Trifolium lupinaster* variant of dryer sites.

**20. *Carex dichroa* moist meadow**

This plant community grows at wet sites near rivers and ponds as well as in old river beds and depressions. It is, e.g., characterized by *Ligularia sibirica*, *Carex ensifolia* and *Poa palustris*.

**21. *Scirpus orientalis* reed**

The *Scirpus orientalis* reed inhabits river banks and shallow floodplain ponds. Prevalent species are, e.g., *Equisetum fluviatile*, *Glyceria triflora* and occasionally *Carex dichroa* and *C. rhynchophysa*.

16–21 in Table 1) were excluded from Table 2 to save printing space. This is justified, as these azonal vegetation units are of subordinate significance to describe the vegetation patterns that result from the forest–steppe transition in the study area. Rarer plant communities, where less than five relevés were available were excluded from Tables 1 and 2 (but not from Fig. 4). These vegetation units include riverine forests of *Populus laurifolia*, *Salix miyabeana* or *S. rorida*, riverine shrubberies of *Padus asiatica* or *Salix bebbiana* and *Betula fusca*, *Carex amgunensis* montane meadow steppes at forest edges, *Alopecurus arundinacea* floodplain meadow, *Carex rhynchophysa* moist meadow, as well as the vegetation of boulder fields, rocks and of dark taiga and light subtaiga forest clearings. A more detailed description of vegetation types is given in Dulamsuren (2004).

**DCA ordination**

DCA results for all vegetation units including 254 relevés are shown in Fig. 4. Axis 1 follows a humidity gradient with vegetation types of dry southern slopes in the lower montane belt on the right and vegetation units of northern slopes in the same belt in the center. Dark taiga

forests of the upper and lower montane belt are located on the left. Floodplain vegetation has an intermediate position on axis 1 between northern slope subtaiga forests and dark taiga habitats. Axis 2 represents an altitudinal gradient. It separates the relatively humid vegetation types of the dark taiga from floodplain habitats. The *Pinus sibirica*–*Picea obovata* forests form a link from the dark taiga to the light subtaiga forests. Their ground vegetation is closely related to that of northern slope subtaiga forests, though the former are limited to the upper montane belt and the latter to the lower montane belt. *Picea obovata* forests are in an intermediate position between dark taiga and floodplain vegetation, but are more closely related to the former. *Betula platyphylla* riverine forests as well as *Betula fusca* and *Padus asiatica* riverine shrubberies link floodplain vegetation with subtaiga and steppe vegetation of the lower montane belt.

**Vegetation profiles as examples for the spatial distribution of vegetation types**

Spatial distribution of vegetation units is shown in two vegetation profiles in Figs. 5 and 6. River valleys in the western parts of the study area are several kilometers wide (Fig. 5). They harbor

**Table 2.** Survey of diagnostic species of major vegetation units of the upper and lower montane belt<sup>a</sup>.

Community type <sup>b</sup>	1	2	3a	3b	4a	4b	5a	5b	6	7a	7b	8	9	10	11a	11b	12	13	14	15
Total of relevés	6	8	7	6	5	11	9	6	5	20	17	9	7	10	6	8	5	7	9	15
<b>Tree layer</b>																				
<i>Picea obovata</i>	V	V	V	V	V	V	III	III	II	I	I	II	I	–	–	–	–	–	–	–
<i>Abies sibirica</i>	I	IV	IV	V	I	I	V	V	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pinus sibirica</i>	–	II	V	V	IV	V	V	V	V	I	+	I	I	II	II	I	–	–	–	–
<i>Betula platyphylla</i>	V	III	V	V	V	II	III	–	V	V	V	V	III	V	IV	IV	–	–	–	–
<i>Larix sibirica</i>	–	I	II	–	II	IV	III	–	III	IV	IV	II	I	+	IV	III	–	–	–	–
<i>Populus tremula</i>	–	–	–	–	–	–	–	–	II	r	II	–	V	+	II	–	–	–	–	–
<i>Pinus sylvestris</i>	–	II	I	I	I	I	–	–	IV	I	II	II	–	V	V	V	–	–	–	–
<i>Ulmus pumila</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	III	–	–	–
<b>Shrub layer</b>																				
<i>Abies sibirica</i>	IV	II	V	III	II	II	V	V	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pinus sibirica</i>	III	–	V	V	II	III	IV	III	–	–	–	–	–	III	II	–	–	–	–	–
<i>Picea obovata</i>	I	I	III	II	I	IV	II	IV	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lonicera altaica</i>	–	–	I	I	–	I	III	V	–	–	–	–	–	–	–	–	–	–	–	–
<i>Rubus sachalinensis</i>	–	–	–	I	–	–	IV	III	–	–	–	–	–	–	IV	–	–	–	–	–
<i>Sorbus sibirica</i>	I	–	II	I	I	–	III	II	–	–	–	–	–	–	–	–	–	–	–	–
<i>Betula platyphylla</i>	V	–	V	IV	–	II	II	I	–	–	–	–	–	III	II	II	–	–	–	–
<i>Rosa acicularis</i>	II	III	III	III	II	II	III	–	III	II	II	V	IV	II	II	II	I	–	–	–
<i>Spiraea flexuosa</i>	I	II	I	V	I	II	I	II	–	I	II	–	–	IV	I	–	–	–	–	–
<i>Rhododendron dauricum</i>	–	III	IV	–	I	–	–	–	I	II	II	I	I	III	I	–	–	–	–	–
<i>Cotoneaster melanocarpus</i>	–	I	I	–	IV	II	–	–	III	II	I	I	III	IV	IV	II	III	–	–	–
<i>Spiraea media</i>	–	–	–	–	–	–	–	–	IV	II	+	I	V	+	III	IV	II	–	–	–
<i>Populus tremula</i>	–	–	–	–	–	–	–	–	–	I	I	–	III	–	III	II	–	–	–	–
<i>Crataegus sanguinea</i>	–	–	–	–	–	–	–	–	–	r	+	III	–	–	–	–	–	–	–	–
<i>Spiraea salicifolia</i>	–	–	–	–	–	–	–	–	–	–	–	–	IV	–	–	–	–	–	–	–
<i>Potentilla fruticosa</i>	–	–	–	–	–	–	–	–	–	r	–	II	–	–	–	–	I	–	–	–
<i>Ribes rubrum</i>	–	–	–	–	–	–	–	–	–	–	–	–	III	–	–	–	–	–	–	–
<i>Padus asiatica</i>	–	–	–	–	–	–	–	–	–	–	+	IV	I	II	–	I	I	–	–	–
<i>Spiraea aquilegifolia</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	V	–	–	–
<i>Ribes diacantha</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	IV	–	–	–
<i>Ulmus pumila</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	IV	–	–	–
<b>Herb layer</b>																				
<i>Dicranum bonjeanii</i>	V	I	–	III	I	+	II	III	–	–	–	–	–	–	–	–	–	–	–	–
<i>Aulacomnium palustre</i>	V	–	–	–	–	+	I	–	–	–	+	II	–	–	–	–	–	–	–	–
<i>Hypnum plicatulum</i>	III	II	–	–	–	–	I	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Carex arnellii</i>	IV	II	–	III	–	+	–	–	–	–	+	III	I	–	–	–	–	–	–	–
<i>Ledum palustre</i>	II	IV	V	III	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Pyrola incarnata</i>	I	V	V	V	II	II	–	–	–	–	–	–	–	IV	–	I	–	–	–	–
<i>Cystopteris fragilis</i>	–	–	–	V	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Mitella nuda</i>	I	III	–	V	–	+	III	V	–	–	–	–	–	–	–	–	–	–	–	–
<i>Iris ruthenica</i>	I	II	II	II	V	V	II	–	V	V	V	I	IV	V	I	II	–	–	–	–
<i>Rubus saxatilis</i>	–	III	–	I	V	V	II	–	V	V	V	II	III	V	III	IV	–	–	–	–
<i>Lathyrus humilis</i>	I	I	I	I	V	V	II	I	V	V	V	II	V	V	IV	III	–	–	–	–
<i>Crepis sibirica</i>	–	–	–	–	–	IV	II	I	–	–	–	–	–	–	–	–	–	–	–	–
<i>Ranunculus japonicus</i>	–	I	I	–	–	V	II	I	–	–	–	–	–	–	–	–	–	–	–	–
<i>Anemone crinita</i>	–	–	–	–	II	III	–	–	II	IV	III	II	IV	V	–	II	–	–	–	–
<i>Trifolium lupinaster</i>	–	–	–	–	–	IV	–	I	IV	IV	III	III	II	V	V	V	–	–	–	–
<i>Rubus sachalinensis</i>	–	–	–	II	–	–	V	V	–	–	–	–	–	–	–	–	–	–	–	–
<i>Dryopteris expansa</i>	–	–	–	–	–	–	IV	V	–	–	–	–	–	–	–	–	–	–	–	–
<i>Athyrium filix-femina</i>	–	–	–	–	I	I	IV	IV	–	r	II	–	–	–	–	–	–	–	–	–
<i>Geranium eriostemon</i>	–	–	III	–	I	I	IV	V	–	–	–	–	–	–	–	–	–	–	–	–

Continued



Table 2. Continued.

Community type <sup>b</sup>	1	2	3a	3b	4a	4b	5a	5b	6	7a	7b	8	9	10	11a	11b	12	13	14	15
Total of relevés	6	8	7	6	5	11	9	6	5	20	17	9	7	10	6	8	5	7	9	15
<i>Cerastium pauciflorum</i>	I	I	–	–	–	III	III	V	–	–	–	–	–	–	–	–	–	–	–	–
<i>Allium victorale</i>	–	I	–	–	–	II	III	V	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lycopodium annotinum</i>	–	–	–	–	–	–	II	I	–	–	–	–	–	–	–	–	–	–	–	–
<i>Cinna latifolia</i>	–	–	–	–	–	–	I	V	–	–	–	–	–	–	–	–	–	–	–	–
<i>Agrostis clavata</i>	–	–	–	–	–	–	–	V	–	–	–	–	–	–	–	–	–	–	–	–
<i>Rhytidium rugosum</i>	–	I	I	–	–	+	–	IV	–	–	–	–	–	–	–	–	–	–	–	–
<i>Diplazium sibiricum</i>	–	–	–	–	–	–	I	III	–	–	–	–	–	–	–	–	–	–	–	–
<i>Saxifraga punctata</i>	–	–	–	–	–	–	I	III	–	–	–	–	–	–	–	–	–	–	–	–
<i>Equisetum scirpoides</i>	–	–	–	–	–	–	I	III	–	–	–	–	–	–	–	–	–	–	–	–
<i>Saussurea recurvata</i>	–	–	–	–	I	II	–	–	IV	III	–	–	IV	III	IV	III	–	–	–	–
<i>Hieracium umbellatum</i>	–	–	–	–	–	–	–	–	II	III	I	–	I	–	–	–	–	–	–	–
<i>Artemisia sericea</i>	–	–	–	–	–	–	–	–	IV	III	+	–	V	III	III	IV	–	–	–	–
<i>Elymus confusus</i>	–	–	–	–	–	–	–	–	IV	II	I	–	III	III	I	II	I	–	–	–
<i>Cacalia hastata</i>	II	I	–	–	–	II	III	V	–	+	III	IV	–	–	–	–	–	–	–	–
<i>Festuca ovina</i>	–	–	–	–	–	–	–	–	–	+	III	III	–	–	–	–	–	–	–	–
<i>Viola biflora</i>	–	–	–	–	–	–	–	–	–	–	III	–	–	–	–	–	–	–	–	–
<i>Gymnocarpium jessoense</i>	–	–	–	–	–	–	–	–	–	–	III	I	–	–	–	–	–	–	–	–
<i>Rhododendron dauricum</i>	–	–	–	–	–	–	–	–	–	I	IV	–	–	II	I	–	–	–	–	–
<i>Vicia cracca</i>	–	–	–	–	–	–	–	–	–	r	II	IV	I	–	–	–	–	–	–	–
<i>Filipendula palmata</i>	–	–	–	–	–	–	–	–	–	r	I	V	–	–	–	–	–	–	–	–
<i>Equisetum arvense</i>	–	–	–	–	–	–	–	–	–	I	–	III	–	–	–	–	–	–	–	–
<i>Veronica longifolia</i>	–	–	–	–	–	–	–	–	–	–	–	III	–	–	–	–	–	–	–	–
<i>Potentilla fruticosa</i>	–	–	–	–	–	–	–	–	–	–	–	III	–	–	–	–	I	–	–	–
<i>Ranunculus monophyllus</i>	–	–	–	–	–	–	–	–	–	+	–	III	–	–	–	–	–	–	–	–
<i>Tanacetum vulgare</i>	–	–	–	–	–	–	–	–	–	–	–	III	–	–	–	–	–	–	–	–
<i>Lactuca sibirica</i>	–	–	–	–	–	–	–	–	–	r	–	III	I	–	–	–	–	–	–	–
<i>Carex pediformis</i>	–	–	–	–	–	–	–	–	–	I	–	–	I	II	V	V	V	V	V	III
<i>Polygonatum odoratum</i>	–	–	–	–	–	–	–	–	–	+	+	III	IV	+	IV	IV	–	–	–	–
<i>Vicia amoena</i>	–	–	–	–	–	–	–	–	I	I	I	V	I	–	I	IV	–	–	–	–
<i>Poa botryoides</i>	–	–	–	–	–	–	–	–	–	–	–	III	II	II	IV	IV	I	I	III	I
<i>Galium verum</i>	–	–	–	–	–	–	–	–	–	–	I	III	+	–	III	III	–	–	–	–
<i>Stipa sibirica</i>	–	–	–	–	–	–	–	–	–	I	+	I	III	–	–	–	III	V	II	II
<i>Phlomis tuberosa</i>	–	–	–	–	–	–	–	–	–	+	–	–	III	–	–	II	I	V	III	+
<i>Gentiana macrophylla</i>	–	–	–	–	–	–	–	–	I	I	–	III	–	–	–	–	–	–	–	–
<i>Artemisia laciniata</i>	–	–	–	–	–	–	–	–	II	+	–	I	III	–	–	–	–	–	–	–
<i>Galatella dahurica</i>	–	–	–	–	–	–	–	–	–	+	–	–	III	–	–	–	–	III	–	–
<i>Cotoneaster melanocarpus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	IV	I	IV	IV	–	–	–
<i>Potentilla fragarioides</i>	–	–	–	–	–	I	–	–	–	–	–	–	–	IV	IV	IV	–	–	–	–
<i>Viola brachyceras</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	IV	–	I	–	–	–	–
<i>Spiraea media</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	+	IV	IV	I	–	–	–
<i>Aster alpinus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	+	III	IV	II	–	–	–
<i>Veronica incana</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	III	I	–	III	II
<i>Bupleurum scorzoniferifolium</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	+	–	IV	II	V	IV	III
<i>Schizonepeta multifida</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	II	III	V	V	IV
<i>Patrinia rupestris</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I	III	–	IV	III	II
<i>Rhaponticum uniflorum</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	III	–	IV	IV	III
<i>Leontopodium leontopodioides</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	II	–	III	IV	III
<i>Hemerocallis minor</i>	–	–	–	–	–	–	–	–	–	–	–	–	II	–	–	III	–	–	–	–
<i>Scorzonera radiata</i>	–	–	–	–	–	–	–	–	I	II	+	–	–	II	–	IV	III	–	–	–
<i>Pulsatilla turczanovii</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	V	V	–	–	–
<i>Patrinia sibirica</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	V	I	I	II
<i>Lilium pumilum</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	IV	IV	II	III
<i>Thalictrum foetidum</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	IV	–	–	–

Continued

Table 2. Continued.

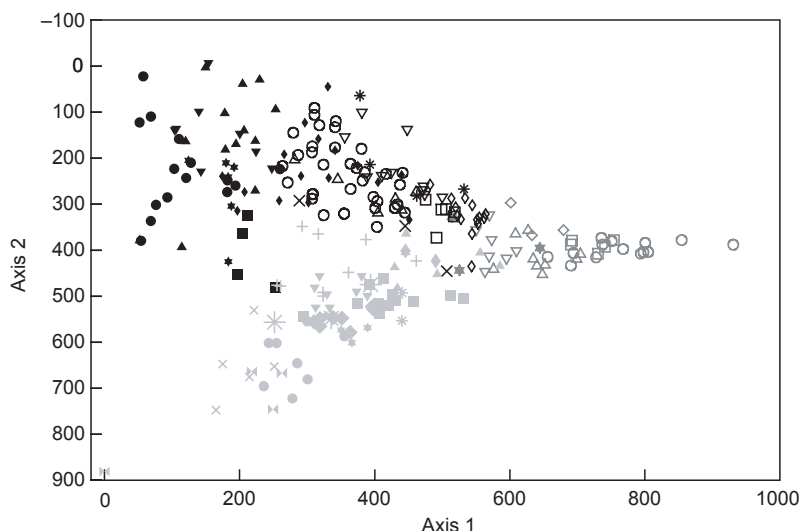
Community type <sup>b</sup>	1	2	3a	3b	4a	4b	5a	5b	6	7a	7b	8	9	10	11a	11b	12	13	14	15
Total of relevés	6	8	7	6	5	11	9	6	5	20	17	9	7	10	6	8	5	7	9	15
<i>Rheum undulatum</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	III	–	–	–
<i>Heteropappus biennis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	III	–	–	–
<i>Astragalus melilotoides</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	III	–	–	–
<i>Thymus gobicus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	IV	I	IV	V
<i>Potentilla acaulis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	IV	II	IV	V
<i>Artemisia commutata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	IV	II	V	V
<i>Aconogonum angustifolium</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	IV	III	III	IV
<i>Artemisia frigida</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	IV	–	II	V
<i>Spiraea aquilegifolia</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	IV	I	–	III
<i>Goniolimon speciosum</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	III	–	I	III
<i>Dontostemon integrifolius</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	II	–	I	III
<i>Koeleria cristata</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	III	I	II	IV
<i>Alyssum lenense</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	IV	I	I	III
<i>Chamaerhodos erecta</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I	II
<i>Thesium refractum</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	II
<i>Heteropappus altaicus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I
<i>Allium anisopodium</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I
<i>Eritrichium pauciflorum</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I
<i>Pulsatilla bungeana</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I
<i>Orostachys spinosa</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I
<i>Iris humilis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	III	II
<i>Carex korshinskyi</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	III	IV
<i>Veronica incana</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	III	II
<i>Thalictrum minus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	III	III	–
<i>Vicia unijuga</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	III	III	–
<i>Artemisia tanacetifolia</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	IV	III	–
<i>Phlomodoides tuberosa</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	V	III	–
<i>Senecio integrifolia</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	II	III	–
<i>Gentiana decumbens</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	II	III	+
<i>Linaria acutiloba</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	II	II	+
<i>Scutellaria scordiifolia</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	III	–	–
<i>Potentilla tanacetifolia</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	II	III	V	II	II
<i>Elymus gmelinii</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	III	–	–
<i>Festuca lenensis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	III	I	+
<i>Potentilla nivea</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	III	I	–
<i>Papaver nudicaule</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I	IV	I
<i>Pulsatilla ambigua</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	I	IV	I

<sup>a</sup> *Betula platyphylla* and *Picea obovata* riverine forests are included.

<sup>b</sup> 1 = *Picea obovata* dark taiga forest; 2 = *Picea obovata*–*Abies sibirica* dark taiga forest; 3 = Mixed conifer–*Betula platyphylla* dark taiga forest, a. Typical variant, b. *Cystopteris fragilis* variant; 4 = *Pinus sibirica*–*Picea obovata* dark taiga forest, a. Typical variant, b. *Crepis sibirica*–*Ranunculus japonicus* variant; 5 = *Pinus sibirica*–*Abies sibirica* dark taiga forest, a. Typical variant, b. *Cinna latifolia*–*Agrostis clavata* variant; 6 = Mixed conifer–*Betula platyphylla* subtaiga forest; 7 = *Larix sibirica*–*Betula platyphylla* subtaiga forest, a. *Saussurea recurvata* variant, b. *Cacalia hastata* variant; 8 = *Betula platyphylla* riverine forest; 9 = *Populus tremula* subtaiga forest; 10 = *Pinus sylvestris*–*Betula platyphylla* subtaiga forest; 11 = *Pinus sylvestris* subtaiga forest, a. Typical variant, b. *Pulsatilla turczanovii* variant; 12 = *Ulmus pumila* open woodland; 13 = *Festuca lenensis* montane meadow steppe; 14 = *Pulsatilla ambigua* montane meadow steppe; 15 = *Artemisia frigida* mountain steppe.

an irregular mosaic of several floodplain forest, shrubland and meadow vegetation types. Northern slopes are stocked with light subtaiga forests, mainly of *Larix sibirica* and *Betula platyphylla*.

In the eastern parts of the study area that are closer to the central Khentey Mountains, river valleys are only several hundred meters wide and mostly covered with *Betula fusca* or *Salix*



#### Dark taiga of the upper and lower montane belt

\* *Picea obovata* dark taiga forest; ▼ *Picea obovata*–*Abies sibirica* dark taiga forest; ▲ mixed conifer–*Betula platyphylla* dark taiga forest; ◆ *Pinus sibirica*–*Picea obovata* dark taiga forest; ● *Pinus sibirica*–*Abies sibirica* dark taiga forest; ■ dark taiga forest clearings.

**Boulder fields:** \* (upper and lower montane belt).

#### Lower montane belt, subtaiga forests

△ Mixed conifer–*Betula platyphylla* subtaiga forest; ○ *Larix sibirica*–*Betula platyphylla* subtaiga forest; ▽ *Pinus sylvestris*–*Betula platyphylla* subtaiga forest; ◇ *Pinus sylvestris* subtaiga forest; □ *Populus tremula* subtaiga forest; × subtaiga forest clearings.

#### Lower montane belt, southern slope vegetation (without subtaiga forests)

□ *Ulmus pumila* open woodland; ▽ *Festuca lenensis* montane meadow steppe; △ *Pulsatilla ambigua* montane meadow steppe; \* *Carex amgunensis* forest edge; ○ *Artemisia frigida* mountain steppe; ◇ rock vegetation.

#### Floodplains

+ *Betula platyphylla* riverine forest; ▼ *Salix rhamnifolia*–*S. schwerinii* riverine forest; \* *Populus laurifolia* riverine forest; ◆ *Salix rhamnifolia*–*S. schwerinii* riverine shrubland; ▲ *Betula fusca* shrubland; \* *Betula fusca*–*Salix bebbiana* riverine shrubland; ◆ *Padus asiatica* riverine shrubland; ■ *Iris sanguinea* floodplain meadow; \* *Alopecurus arundinacea* floodplain meadow; ▽ other floodplain meadows; ● *Carex dichroa* moist meadow; × *Scirpus orientalis* reed.

**Fig. 4.** DCA ordination of all vegetation units with 254 relevés and 496 vascular plant species of the herb layer. Total variance: 14.27. Eigenvalues, axis 1: 0.724, axis 2: 0.506. Length of gradient, axis 1: 5.122; axis 2: 5.620. 30 segments.

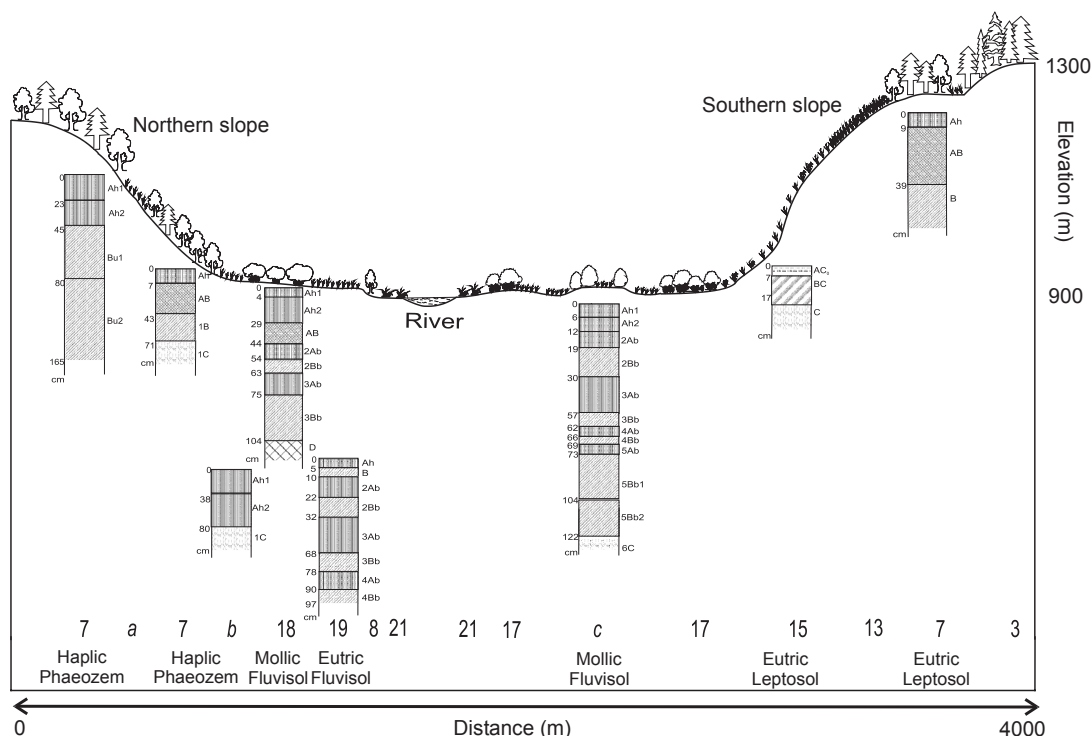
*schwerinii*–*S. rhamnifolia* shrubland and *Picea obovata* riverine forest. Fig. 6 shows an example from the valley of the river Ichlegiyn Gol, which is located 8 km east of Khonin Nuga Research Station.

## Discussion

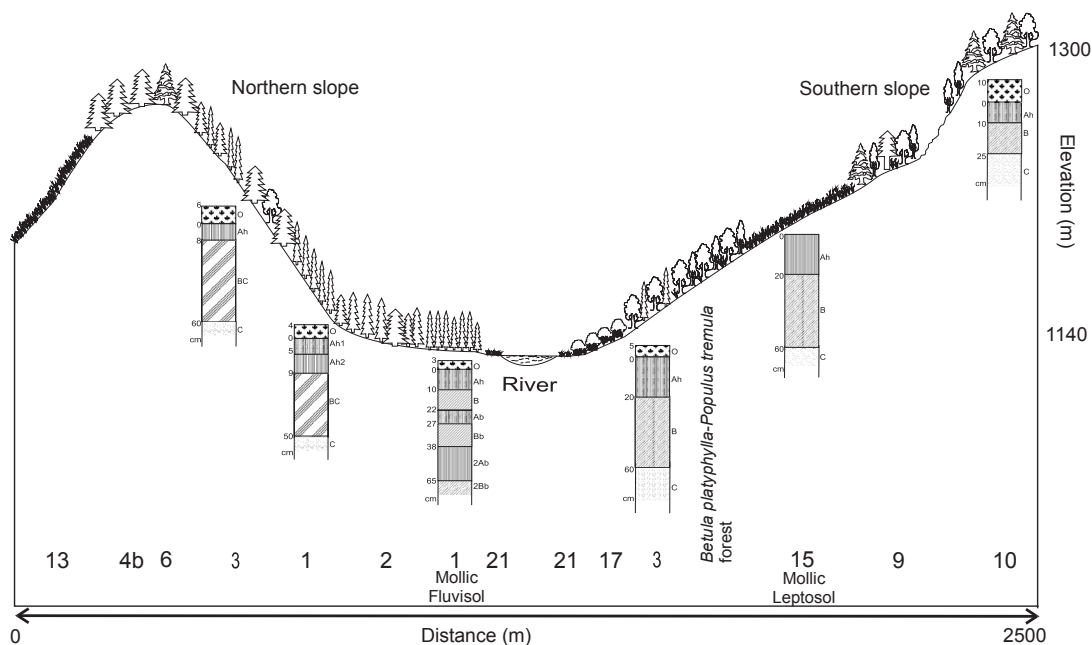
The Khentey Mountains are situated at the interface between three different major vegetation types, i.e., the western Siberian dark taiga forests, the eastern Siberian light (sub)taiga forests and the Mongolian forest steppe. The transition between taiga and forest steppe is a latitudinal

(zonal) one, that between dark and light taiga depends on an oceanity gradient. Because of its unique flora and vegetation, this transitional area including the Khentey Mountains has been separated from the circumboreal phytogeographical region as Central Siberian-Daurian phytogeographical region (Meusel *et al.* 1965, Hilbig & Knapp 1983). Within this area, the Khentey Mountains, together with the Transbaikalian Mountains and the Daurian forest steppe, belong to the Daurian phytogeographical province (Meusel *et al.* 1965).

The three major vegetation types that meet in the Daurian phytogeographical province occur in the western Khentey Mountains in different hab-



**Fig. 5.** Vegetation profile from the western study area in the valley of the Eroo near Khonin Nuga. Numbers refer to vegetation types in Table 1. Vegetation types not included there are: — a: subtaiga forest clearing; — b: *Carex amgunensis* forest edge; — c: *Padus asiatica* riverine shrubland.



**Fig. 6.** Vegetation profile from the eastern study area in the valley of the Ilchlegiyn Gol. Numbers refer to vegetation types in Table 1.

itats of the same geographical area. Dark taiga vegetation is found in the upper montane belt as well as on northern slopes of the lower montane belt and in river valleys. Light subtaiga vegetation of *Larix sibirica* and *Betula platyphylla* also grows on northern slopes of the lower montane belt and near rivers. Other light subtaiga forest communities, dominated by *Pinus sylvestris* or *Populus tremula*, occur on sun-exposed, southern slopes of the lower montane belt. However, grasslands are the most common vegetation type on southern slopes of the lower montane belt. These grasslands are formed of mountain steppe or different types of montane meadow steppe depending on inclination. Vegetation of east-exposed slopes is usually similar to that of northern slopes, whereas vegetation of western slopes often resembles that of south-exposed sites. Thus, the landscape of the western Khentey Mountains is a small-scale mosaic of dark and light taiga forests and of steppe vegetation.

Mountain steppes are characterized by a sparse vegetation of shortgrasses and short herbs that covers, in the study area, only 30%–60% of the ground. They are defined as azonal montane grasslands (Karamysheva & Khramtsov 1995). If the physiognomy and species composition of montane grasslands resembles that of steppes, which occur elsewhere (in a different vegetation zone) at lowland sites as zonal vegetation, these grasslands are taken as extrazonal types of the respective lowland vegetation type (Karamysheva & Khramtsov 1995). Therefore, grasslands with a ground cover between 60% and 95% and an up to 1 m high vegetation are named meadow steppes in the present study. In order to separate them from the zonal meadow steppes that formerly covered, e.g., extensive areas in the forest steppe of the plains of Russia, such extrazonal meadow steppes can be called montane or mountain meadow steppe (Bannikova 1983). In the present paper, the term “montane meadow steppe” is preferred to avoid confusion with the term “mountain steppe” used for the azonal grasslands. The demarcation of montane meadow steppe and mountain steppe is sometimes difficult. The driest type of montane meadow steppe described in the present paper, i.e., the *Pulsatilla ambigua* montane meadow steppe, has several species and physiognomic

features with the *Artemisia frigida* mountain steppe in common. However, we decided to call the *Pulsatilla ambigua* community montane meadow steppe, because, in our opinion, similarities to meadow steppe prevailed and to be consistent with Hilbig (1990), who described a similar community with relatively sparse and short vegetation on shallow soil as a subassociation of meadow steppe. Reshikov (1961), Lavrenko *et al.* (1991) and Dmitriev and Khramtsov (1995) used a different terminology calling the driest mountain grasslands of northern Mongolia and Transbaikalia petrophytic meadow steppe. The description of this vegetation type comes very close to our mountain steppes. The usage of the term mountain steppe agrees, e.g., with Kuminova (1982), who used the same term for similar communities in the southern central Siberian Sayan Mountains.

Within the study area, there is a gradient between the eastern parts, which are relatively close to the central Khentey Mountains, and the western, more peripheral parts, which are closer to the Mongolian-Daurian steppe. With decreasing distance to the central parts of the Khentey Mountains, precipitation increases, the valleys get narrower and permafrost is increasingly found even at the soil surface (Tsedendash 1995). These are good growth conditions for the dark taiga, because *Picea obovata* and even more *Abies sibirica* are more water-demanding than tree species of the light subtaiga (Zhukov *et al.* 1978, Gunin *et al.* 1999). *Pinus sibirica* needs even better water supply; therefore, its distribution is more focussed on the upper montane belt. Seed-producing and old trees of *P. sibirica* have never been observed during field work in the lower montane belt. *Pinus sibirica* requires relatively high precipitation, soil water content, air humidity, and high snow cover in winter time, but is undemanding in terms of nutrient availability (Vipper 1953). *Abies sibirica* needs soil with good water and nutrient supply and high air humidity (Zhukov *et al.* 1978). In the Khentey Mountains, *A. sibirica* is only capable of growing in company with *Pinus sibirica* or *Picea obovata*, as it requires shelter from drought by trees of other species (Zhukov *et al.* 1978). *Picea obovata* is more sensitive to late spring and summer frost and to rapid temperature changes



than *Abies sibirica* and *Pinus sibirica* (Zhukov et al. 1978). Therefore, *Picea obovata* is restricted to lower elevations of the upper montane belt and to the lower montane belt. The proximity to the subtaiga forests in the DCA ordination (Fig. 4) suggests that ground vegetation of *Pinus sibirica*–*Picea obovata* forests has apparently similar requirements as *P. obovata*. *Picea obovata* is less sensitive to water-logging than *Abies sibirica* and, thus, dominates the dark taiga riverine forests. Pure *Pinus sibirica* stands occur in the Khentey, but not in the study area (Tseden-dash 1995). They are only developed at sites with unfavorable growth conditions for spruce and fir, e.g., on nutrient-poor soil (Walter & Breckle 1986).

Sun-exposed slopes of the lower montane belt are too dry even for *Larix sibirica*–*Betula platyphylla* subtaiga forests. On the southern slopes, temperature increases and precipitation and air humidity decrease with increasing distance from the top (Vipper 1953). Therefore, the upper parts of most southern slopes are covered by *Larix sibirica*–*Betula platyphylla*, *Pinus sylvestris*–*Betula platyphylla* or *Pinus sylvestris* subtaiga. Below this forested area follow different types of montane meadow steppe depending on soil thickness and water supply. The steepest sunlit slopes are covered with mountain steppe. Because it is least water-demanding (Bannikova 2003), it often grows below a strip of montane meadow steppe.

Steppe vegetation occurs in the Khentey Mountains continuously since the middle Pleistocene (Krasheninnikov 1939). However, the borderline between steppe and forest vegetation is often influenced by human activities (Titlyanova & Kosykh 2000). The study area has not been subject to extensive human disturbances in the past. It was traditionally avoided by nomads because of high density of wolves and bears, which still today occasionally hunt horses from the research station. Furthermore, the dark taiga provides no good forage plants. If montane meadow and mountain steppes on the southern slopes of the lower mountain belt would derive from grazing by cattle they should be less frequent in the eastern parts of the study area, where steppe and subtaiga vegetation are surrounded by dark taiga forest both on northern slopes and

in valleys. This suggests that the general vegetation pattern of study area with montane meadow and mountain at the southern slopes of the lower montane belt may be natural. This assumption is supported by the lack of toxic and unwholesome plants, such as *Oxytropis pseudoglandulosa* and *Stellera chamaejasme*, that are avoided by the cattle and, thus, increase on pastured montane meadow steppes (Bannikova 2003). However, this does not rule out that human disturbances locally promoted the expansion of grasslands. Montane meadow steppe and subtaiga underlie a dynamic of frequent shifts of the steppe–forest borderline. In the eastern Khentey Mountain, montane meadow steppe can become wooded after some subsequent years with high precipitation within a few decades (Korotkov & Dorzhuren 1988). The inverse process from subtaiga to montane meadow steppe takes places even faster after dry years or disturbances, e.g., fire, timber harvest or grazing. On balance, the general occurrence of steppe vegetation in the study area can be assumed to be natural, because it already exists there since the Pleistocene. However, it is hard to decide for individual plots whether their grassland vegetation was anthropogenically promoted without detailed research, e.g., on soil characteristics. Under the montane meadow or mountain steppes, where soil analyses were carried out during the present study, no indication of a former subtaiga vegetation was found.

Both natural and anthropogenic forest fires as well as other disturbances, such as windfall, probably created the mixed conifer and mixed conifer–*Betula platyphylla* stands of the upper and lower montane belt. This is inferred from the absence of own characteristic species in the ground vegetation of these forest communities. Rather, ground vegetation in mixed forest of the upper montane belt is very similar to that of *Pinus sibirica*–*Picea obovata* or *Pinus sibirica*–*Abies sibirica* forests. Ground vegetation of mixed conifer–*Betula platyphylla* dark taiga forests of the lower montane belt resembles that of *Picea obovata*–*Abies sibirica* forests, that of mixed conifer–*Betula platyphylla* light subtaiga forests is similar to the *Larix sibirica*–*Betula platyphylla* community. In general, *Betula platyphylla* is apparently promoted by disturbances including wildfire and timber harvesting. This

observation parallels findings of Rylkov (1996) from the eastern Transbaikalian Mountains.

In conclusion, the transitional zone between the central Siberian taiga and the Mongolian-Daurian forest steppe in the western Khentey Mountains is characterized by a highly diverse vegetation pattern of dark taiga, light subtaiga and steppe vegetation. Each of these three major vegetation types colonizes different habitats in the study area, which provide, on a small-scale level, site characteristics that correspond to site conditions in western or eastern Siberia or in the Mongolian-Daurian forest steppe belt. The special vegetation mosaic found in the study area is limited to the western Khentey Mountains. *Abies sibirica*, for instance, has a very limited distribution in Mongolia. It covers less than 2000 ha in the entire country, i.e., 0.02% of the forested area (Zhukov *et al.* 1978). Forest communities, where *A. sibirica* is dominant, are restricted to the western Khentey. The prevalent tree species of the eastern and southeastern Khentey is *Larix sibirica*, which covers more than 80% of the forested area in Mongolia (Zhukov *et al.* 1978); *Pinus sibirica* can co-occur in *Larix sibirica* forests. *Picea obovata* is restricted to humid, shady sites (Vipper 1953, Tsedendash 1995). This lower tree diversity even in the neighboring, more continental parts of the Khentey Mountains, gives evidence of the uniqueness of the vegetation of the western Khentey Mountains and its high conservation value.

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