High-Mountain Vegetation

8

High-mountain vegetation (from the viewpoint of botany) comprises the area situated above the climatic limit of dense forests. They are characterized by specific environmental conditions: high solar radiation, high ratio of ultra-violet radiation, low temperature, intensive pressure of water vapour, etc. (Larcher 1980; Körner 2003). The mean temperature of the growth period is generally 6–8 °C (Körner et al. 2011; Pauli et al. 2011)

One of the most pronounced peculiarities of high-mountains is the diversity of habitats within even a very small area.

All the altitudinal belts characteristic of the Nemoral Zone of temperate climate are represented in the high-mountains of Georgia. The following altitudinal zones can be observed here: subalpine (from 1,800–1,900 up to 2,400–2,500 m), alpine (from 2,400–2,500 up to 2,960–3,000 m), subnival (from 2,900–3,000 up to 3,600–3,750 m) and nival (above 3,700 m a.s.l.).

The majority of Caucasian botanists regarded the high-mountain flora of the region to consist chiefly of the Boreal and Arcto-Alpine elements, which penetrated into this area during the Pleistocene; at the same time they presumed that only some high-mountain species were of autochthonous origin, genetically close to those of the low-mountain zones.

Later, it was stated that the most typical representatives of the Caucasian high-mountain flora are of autochthonous origin (Feodorov 1952; Kharadze 1960). According to these scholars, the high-mountain flora of today, being based on a Tertiary nucleus, developed during the Quaternary, in an autochthonous way.

According to Kharadze (1960), high-mountain landscapes of the Caucasus had been formed before the Pleistocene. The above-mentioned scholar does not share the opinion that the origin of high-mountain flora of the Caucasus is connected with the Late Quaternary. The high-mountain flora of the Caucasus is composed of ancient mesic and xeric elements.

In his analysis of the Caucasian endemism, Grossheim (1936) indicates that the area of the Greater Caucasus, where the "processing" of migrated boreal and Anterior Asian elements took place, is of special significance.

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Kharadze (1960) outlines the following species which have penetrated to the Central Caucasus from Daghestan: *Stipa daghestanica, Thymus daghestanicus, Heliotropium styligerum,* etc. The same scholar suggests that the limestone mountain massifs of the North Caucasus participated in the formation of the pre-Pleistocene xerophytic flora. The example of such mountains is the limestone Rocky Mountain Range. Autochthonous hemixerophytic elements are well represented in the areas of the Central Caucasus from the mid-mountain zone to high-mountains.

Among the distant relations of the Caucasian oreoxerophytic flora its connections with those of the Mediterranean and Anterior Asian should be mentioned. Ancient connections with the Mediterranean flora have been found in the following genera: *Astragalus, Nepeta, Scabiosa, Symphyandra, Edraianthus.* The Late Pliocene is the period of the most ancient migrations from Anterior Asia (= Asia Minor) to the Caucasus. Penetration of these elements into the Caucasus is attributed to the xeric periods of Pleistocene and also of Holocene (Grossheim 1936; Kharadze 1960; Janelidze and Margalitadze 1977).

Autochthonous oreoxerophytic species of the Caucasus reveal ancient connections with those of the Anterior Asian flora. Examples are *Salvia canescens, S. daghestanica, Betonica nivea,* species of *Silene, Astragalus, Scutellaria, Ziziphora,* etc.

Members of the autochthonous high-mountain flora of the Caucasus are regarded as xerophytic elements of the humid flora of the same region (Kharadze 1960).

According to Kharadze (1960), there have been two stages of formation of the Caucasian high-mountain elements. First, in the Miocene-Pliocene, more thermophilous elements had been formed, and after, in the Pliocene-Pleistocene the organisms fully changed in the direction of cryophytization. From the Upper Miocene to the Upper Pliocene, even the most elevated parts of the Greater Caucasus were populated by the representatives of thermophilous flora.

The most conservative palaeoendemics of the Caucasian high-mountains have remained in the mid-mountains and peripheries of the mountain glaciations. In the Alps and Carpathians, as well as in the Caucasus, the extreme mountain ranges served as refuges for the pre-glacial ancient endemic flora (Kharadze 1960). Both progressive and conservative palaeoendemics can be found in the Caucasian high-mountains. Conservative palaeoendemics are exemplified by *Sredinskya grandis, Campanula mirabilis, C. ossetica, Edraianthus owerinianus, Symphyandra lezgina.* Progressive palaeoendemics include such species, as *Charesia akinfievii, Petrocoma hoefftiana* and *Symphyandra pendula.*

Apart from the above-mentioned plants, high-mountains of the Caucasus are populated by the following species (Kharadze 1960):

1. Endemo-vicariants of the Miocene-Pliocene differentiation (*Gypsophila imbricata, Arabis sachokiana, Scabiosa gumbetica, Campanula kolenatiana*);
2. Endemo-vicariants with disjunctive distribution areas (*Ranunculus helenae, Hypericum nummularioides*);
3. Progressive palaeoendemics and highly specialized species of eucryophytic complexes (*Pseudovesicaria digitata, Trigonocaryum involucratum, Pseudobetckea caucasica*);

Table 8.1 Life forms (in a broad sense) of the high-mountain plants

Morphological types
1. *Woody plants*
Straight-trunk-trees: *Acer trautvetteri, Pinus kochiana, Quercus macranthera, Salix caprea*
Crook-stem forest trees: *Betula litwinowii, B. medwediewii, Quercus pontica*
Shrubs: *Rhododendron caucasicum, Rh. ponticum, Rh. ungernii, Rh. smirnowii, Juniperus communis, Rhamnus depressa, Rh. imeretina, Salix kazbekensis*
Dwarf subshrubs: *Daphne glomerata, Vaccinium myrtillus, V. vitis-idaea, Empetrum caucasicum, Dryas caucasica, Salix kazbekensis, Juniperus sabina*
Cushion-shaped shrubs: *Astragalus denudatus, A. microcephalus*
2. *Herbaceous plants*
Plants with upright shoots – *Centaurea cheiranthifolia, Aconitum nasutum, Gadellia lactiflora*
Rosette plants: *Taraxacum stevenii, Chamaesciadium acaule, Plantago caucasica*
Prostrate plants – *Veronica minuta, Minuartia aizoides, Astragalus captiosus, Trigonocaryum involucratum*
Megaphytes – *Heracleum sosnowskyi, Telekia speciosa, Gadellia lactiflora*
Cushion-shaped plants – *Minuartia inamoena, Saxifraga moschata, Draba bryoides*
Creeping plants – *Cuscuta epithymum, Convolvulus lineatus, Vicia grossheimii, V. alpestris*
Types based on relations of the perennating buds to the soil level
Phanerophytes
1. *Macrophanerophytes*: *Acer trautvetteri, Sorbus caucasigena, Betula litwinowii, Quercus macranthera, Salix caprea*
2. *Nanophanerophytes*: *Rhododendron caucasicum, Juniperus hemisphaerica, Rhamnus depressa*
Chamaephytes: *Vaccinium myrtillus, Daphne glomerata, Dryas caucasica*
Hemicryptophytes: *Bromopsis variegata, Festuca varia, Betonica macrantha*
Cryptophytes (e.g. geophytes, hydrophytes): *Fritillaria lutea, Lilium georgicum, Hippuris vulgaris*
Therophytes: All species of *Euphrasia spp, Rhinanthus spp., Gentianella caucasea, Lomatogonium carinthiacum*
Phenorhythmotypes
1. *Evergreen plants*
Continuously foliated plants: *Rhododendron caucasicum, Daphne glomerata, Saxifraga juniperifolia*
Summer-winter-green plants: *Festuca varia, Carex meinshauseniana, Alchemilla sericata*
2. *Vernal-summer-green plants*: *Rhododendron luteum, Betonica macrantha, Aconitum nasutum, Geranium ibericum*
3. *Plants with short vegetative period*: *Fritillaria lutea, Galanthus caucasicus, Gagea glacialis*

4. Endemo-vicariants of the Upper Pliocene differentiation (*Ranunculus lojkae, Cerastium undulatifolium, Cerastium kasbek, Senecio karjaginii*).

High-mountains of the Caucasus and Georgia in particular, display a great variety of life forms, which can be accounted for by their evolution under different climatic conditions, relief dissection, and also by the situation of the Caucasus at the junction of contrasting physico-geographical regions. Table 8.1 represents the classification of life forms.

8.1 Subalpine Vegetation

The subalpine belt involves the areas which are situated above the dense forests up to the lower limit of the prevailing alpine grassland. Thus, the vegetation of the subalpine belt includes not only shrubwoods but also thin crook-stem forests. The subalpine belt manifests remarkably high floristical and phytocoenotical diversity, stimulated by the following relatively optimal climatic conditions:

1. Low daily temperature variations;
2. High air humidity;
3. Rich soils;
4. Not so high (as in alpine and subnival belts) solar radiation.

Due to the climatic conditions, the lower boundary of the subalpine belt varies in altitude between 2,350 and 2,500 m. In eastern and partially in central parts of the Greater Caucasus the upper limit attains 2,450–2,500 m a.s.l.

Subalpine vegetation is well developed in the Caucasus, whereas in the Alps and Carpathians the typical subalpine meadows and tall herbs are comparatively poorly represented; at the same time elfin woodlands become substituted by low grass meadows.

Some botanists regard the subalpine belt as a part of the alpine zone. In the nineteenth and the beginning of the twentieth centuries, subalpine meadows were considered to be of secondary origin.

Later it was stated, that the above-mentioned meadows are examples of climax communities.

In treeless areas of South Georgian Upland, mountain steppes compete with alpine meadows. It is evident that the subalpine belt is not represented in these regions.

The following types of vegetation are well developed in the subalpine belt of the Caucasus and Georgia, in particular:

1. Crook-stem forests;
2. Elfin woodlands;
3. Subalpine tall herbaceous vegetation;
4. Subalpine meadows.

In several regions of Georgia, subalpine the belt is characterized by the occurrence of oreoxerophytic vegetation, as well as meadow steppes and steppes.

8.1.1 Subalpine Tall Herbaceous Vegetation

Unlike many other mountain systems (Alps, Rocky Mts, Himalaya, etc.), tall herbaceous vegetation is well represented in the subalpine belt of the Caucasus. Here it is confined to the lower part of the subalpine zone. Tall herbaceous vegetation is developed under the following favourable environmental conditions:

(a) Optimal air and soil temperature;
(b) Negligible daily fluctuations of temperature;
(c) High air humidity;
(d) Rich soils, etc.

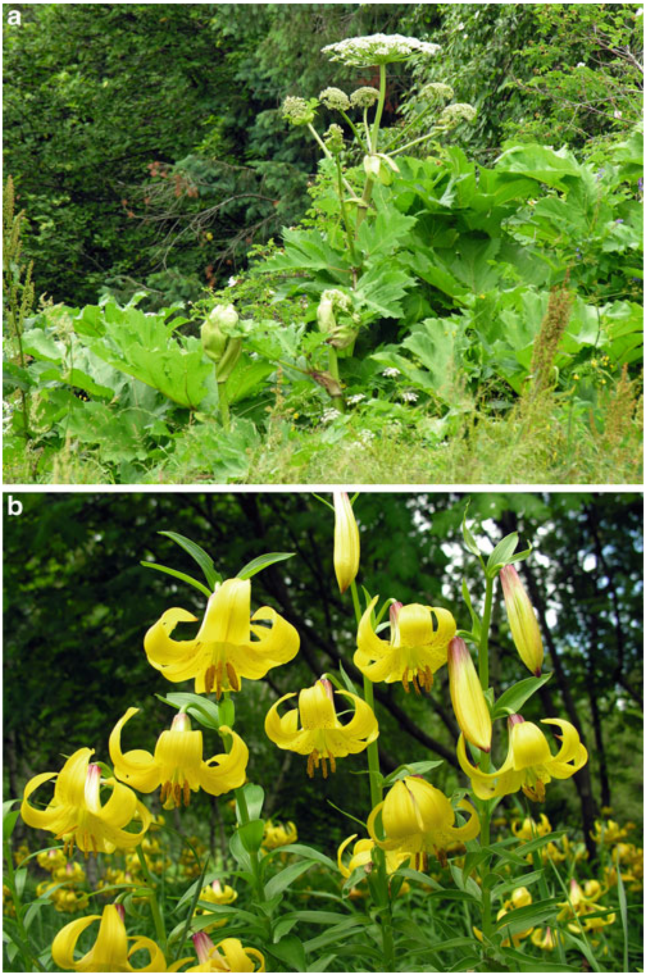


Fig. 8.1 (**a**) *Heracleum wilhelmsii*, Tskhratskaro Pass, Bakuriani region, Lesser Caucasus, (**b**) *Lilium georgicum*, Kazbegi, Central Caucasus (Photo O. Abdaladze)

Tall herbaceous vegetation is composed of tall (3–4 m) herbs, chiefly dicots (Figs. 8.1a, b and 8.2). They are characterized by rosetteless shoots, short top roots and rhizomes. Stratification is not pronounced within the tall herbaceous communities. According to Gagnidze (1974, 1977; Shetekauri and Gagnidze 2000), the total number of species occurring in subalpine tall herbaceous vegetation amounts to 90, while their floro-coenotic complex includes only 70 species (Table 8.2).

A turning point in the composition of the floral-coenotic complex of tall herbaceous vegetation has commenced as early as Middle Pliocene. During subsequent periods, areas with tall herbaceous vegetation underwent reduction and even lost some individual components. According to Gagnidze (1977), regularities of the

Fig. 8.2 *Gadellia lactiflora,* tall herbaceous vegetation, Bakuriani, Lesser Caucasus (Photo A. G. Dolukhanov)

present-day altitudinal distribution of the components of tall herbaceous vegetation of the Caucasus and the final formation of the corresponding floro-coenotical complex are related to the Pleistocene and Holocene.

Dolukhanov et al. (1946) indicate three groups of associations with the following leading species:

1. *Heracleum mantegazzianum, H. grossheimi, H. sosnowskyi,* etc.;
2. *Senecio platyphyllus, Inula grandiflora,* etc.;
3. *Rumex alpinus, Senecio othonnae,* etc.

According to Panjutin (1939), the following associations (plant community) are known from the north-western Colchis (Abkhazeti):

1. Inuletum *(Inula magnifica),*
2. Telekietum *(Telekia speciosa),*
3. Aconitetum *(Aconitum orientale),*
4. Cicerbitetum *(Cicerbita bourgaei, C. cacaliaefolia),*
5. Symphytetum *(Symphytum asperum),*
6. Heracleetum mantegazziani.

The same author attributes Anthriscietum and Campanuletum to intermediate associations (plant community). Weedy tall herbaceous vegetation should be divided into the following seven associations, such as:

1. Delphinietum pyramidati,
2. Senecietum platyphylli,
3. Senecietum chlorocomos,
4. Cirsietum obvallati,
5. Anthriscietum nemorosi,
6. Heracleetum asperi,
7. Pteridietum tauricumi.

We distinguish six formations of tall herbaceous vegetation, as well as several groups and association classes, characteristic of the subalpine belt of Lagodekhi Reserve (Table 8.3).

Table 8.2 Species of tall herbaceous vegetation (Hochstaudenflur) (by Gagnidze 1974)

Aconitum nasutum
A. orientale
Angelica adzharica
A. pachyptera
A. tatianae
Anthriscus nemorosa
Cephalaria gigantea
C. procera
Campanula latifolia
Chaerophyllum maculatum
Cicerbita bourgaei
Cicerbita deltoidea
C. macrophylla
C. olgae
C. petiolata
C. prenanthoides
Cirsium aggregatum
C. albowianum
C. buschianum
C. czerkessicum
C. gagnidzei
C. hypoleucum
C. kuznetsowianum
C. oblongifolium
C. svaneticum
C. sychnosanthum
Delphinium bracteosum
D. buschianum
D. dasycarpum
D. dzavakhischwilii
D. fedorovii
D. flexuosum
D. ironorum
D. mariae
D. megalanthum
D. osseticum
D. prokhanovii
D. pyramidatum
D. speciosum
D. thamarae
Doronicum macrophyllum
Euphorbia macroceras
Gadellia lactiflora
Geranium kemulariae

(continued)

Table 8.2 (continued)

Grossheimia ossica
Heracleum aconitifolium
H. asperum
H. circassicum
H. colchicum
H. cyclocarpum
H. grossheimii
H. mantegazzianum
H. ponticum
H. sosnowskyi
H. trachyloma
H. wilhelmsii
Inula magnifica
Knautia montana
Ligusticum alatum
L. arafoe
L. physospermifolium
Lilium armenum
L. georgicum
L. kesselringianum
L. monadelphum
L. szovitsianum
Milium effusum
M. schmidtianum
Petasites albus
Prenanthes abietina
Pyrethrum macrophyllum
Senecio cladobotrys
S. othonnae
S. platyphylloides
S. pojarkovae
S. propinquus
S. rhombifolius
S. similiflorus
S. subfloccosus
Telekia speciosa
Valeriana alliariifolia
V. colchica
V. tiliifolia
Veratrum lobelianum
Xanthogalum purpurascens

Table 8.3 The phytosociological classification of the subalpine vegetation of the Lagodekhi reservation

Communities
Calamagrostis arundinacea + *Bromopsis variegata*
Calamagrostis arundinacea + *Poa longifolia*
Calamagrostis arundinacea + *Festuca varia*
Calamagrostis arundinacea + *Geranium ibericum*
Calamagrostis arundinacea + *Trollius ranunculinus*
Poa longifolia + *Calamagrostis arundinacea*
Poa longifolia + *Festuca varia*
Poa longifolia + *Agrostis planifolia*
Poa longifolia + *Geranium ibericum*
Poa longifolia + *Betonica macrantha*
Bromopsis variegata + *Calamagrostis arundinacea*
Bromopsis variegata + *Poa longifolia*
Agrostis planifolia + *Trifolium canescens*
Agrostis planifolia + *Alchemilla caucasica*
Inula orientalis + *Geranium ibericum*
Geranium ibericum + *Trollius ranunculinus*
Trollius ranunculinus + *Ranunculus caucasicus*
Festuca varia + *Chamaemelum caucasicum*
Festuca varia + *Betonica macrantha*
Festuca varia + *Nardus stricta*
Festuca varia + *Agrostis planifolia*
Nardus stricta + *Festuca varia*
Senecio platyphylloides + *Milium effusum*
Senecio platyphylloides + *Dactylis glomerata*
Heracleum sosnowskyi + *Telekia speciosa*
Telekia speciosa + *Heracleum sosnowskyi*
Telekia speciosa + *Athyrium filix-femina*
Athyrium filix-femina + *Gadellia lactiflora*
Rhododendron caucasicum + *Geranium ibericum*
Daphne glomerata + *Festuca varia*

8.1.2 Subalpine Meadows

The term "subalpine meadows" was proposed in 1898 by the well-known Caucasian botanist N. Busch. Subalpine meadows comprise all more or less mesic herbaceous communities which occupy the areas above timberline and are characterized by relatively high herbage (Dolukhanov et al. 1942; Nakhutsrishvili 1988). Caucasian subalpine meadows are very diverse floristically, phytocoenotically and display a large spectrum of life forms.

Further, we attempt to characterise the main types of subalpine meadows.

8.1.2.1 Grass Meadows

Bromopsieto (*Bromopsis variegata*); Agrostieta (*Agrostis tenuis, A. planifolia*). These communities occupy both dry and moist localities; they occur on skeletal cobble soils. Main components of the above-mentioned coenoses are *Trifolium ambiguum, Lotus caucasicus, Alchemilla sericata,* etc. The above communities are widespread in the Caucasian high-mountains and reach the altitude of 2,700 m. Tussocks are used as hay-meadows.

Hordeeta (*Hordeum violaceum*). *Hordeum* communities occupy the lower part of the subalpine belt (up to 2,000–2,200 m). Of the various coenoses of this formation special attention should be paid to *Hordeum* meadows with the predominance of such tall herbs as *Heracleum asperum, Anthriscus nemorosa, Seseli transcaucasica* (Table 8.4).

Calamogrostieta (*Calamogrostis arundinacea*). These coenoses occupy wet slopes. They are connected with forests and *Rhododendron* thickets floristically; *Calamagrostis* communities frequently occur on deforested areas. *Calamagrostis arundinacea* appears as a dominant of the herbaceous layer in subalpine oak (*Quercus macranthera*) forests, and a subdominant of variegated fescue *(Festuca varia)* communities.

Of the characteristic associations of West Transcaucasia the following should be mentioned:

1. Calamagrostideto-Betoniceta (*Betonica macrantha*),
2. Calamagrostideto-Geranieta (*Geranium ibericum*),
3. Calamagrostideto-Solidageta (*Solidago virgaurea*).

In western parts of Kavkasioni tussocks dominated by endemic *Festuca djimilensis* occupy both dry and moist localities. Meadows of *Sesleria anatolica* with high presence of *Brachypodium rupestre* and *Carex pontica* are restricted to the limestones of Colchis (Bzipi mountain ridge, Abkhazeti).

Poeta (*Poa longifolia*). These coenoses occupy clearings, forest margins, and wet stony slopes. Table 8.3 includes a list of several communities which are well represented in the Lagodekhi Reserve.

Deschampsieta (*Deschampsia caespitosa*) *Deschampsia* communities occur on pebbles near river banks and swampy places. Common plants of these coenoses include: *Equisetum arvense, Carex canescens, C. hirta, C. irrigua, Parnassia palustris,* etc. (Table 8.5).

Beckmanieta (*Beckmania eruciformis*) communities occur in moist and swampy localities of South Georgian Upland. According to Sh. Nakhutsrishvili (1966), the following bidominant communities populate this area:

1. Phleumeto (*Phleum pratense*) Festuceta (*Festuca pratensis*),
2. Agrostieto (*Agrostis alba*) Dactyleta (*Dactylis glomerata*).

The above-mentioned communities include many plants which are valuable for fodder.

Agrostieta (*Agrostis karsensis*). Communities involved in this group occupy banks of meandering streams in South Georgian Uplands (Nakhutsrishvili 1966).

Table 8.4 *Hordeeta* in Kazbegi

Height (m s. m.)	1,850
Exposition	S
Slope (°)	5
Cover (%)	100
Hordeum violaceum	5
Bromopsis riparia	2
B. variegata	2
Phleum pratense	2
Ph. phleoides	1
Agrostis planifolia	2
A. tenuis	2
Poa pratensis	4
Festuca pratensis	3
Koeleria gracilis	1
Tragopogon reticulatus	2
Rumex acetosa	1
Trifolium ambiguum	3
Myosotis alpestris	2
Rhinanthus minor	+
Lotus caucasicus	+
Pastinaca armena	2
Galium verum	1
Vicia grossheimii	2
Silene vulgaris	1
Trifolium fontanum	2
Ranunculus elegans	2
Seseli transcaucasica	4
Myosotis sylvatica	2
Cuscuta europaea	+
Anthriscus nemorosa	3
Alchemilla retinervis	2
Veronica gentianoides	2
Taraxacum confusum	2
Potentilla recta	+
Draba hispida	+
Leontodon hispidus	2
Pedicularis chroorryncha	2
Carum carvi	2
Euphrasia hirtella	+
Alchemilla sericata	1
Verbascum blattaria	+
Campanula trautvetteri	+
Polygonum alpinum	+
Cerastium arvense	+
Vicia alpestris	+

Table 8.5 *Deschampsieta* in Kazbegi

Height (m s. m.)	1,750
Exposition	W
Slope (°)	3
Cover (%)	80
Deschampsia cespitosa	5
Phragmites australis	4
Festuca arundinacea	2
Festuca pratensis	2
Agrostis planifolia	2
Phleum pratense	2
Carex aequivoca	3
Ranunculus elegans	3
Ranunculus buhsei	2
Rhinanthus minor	2
Cerastium arvense	2
Cerastium caespitosum	2
Linium catharticum	1
Trifolium fontanum	1
Equisetum palustre	4
Trifolium ambiguum	1
Leontodon hispidus	1
Lotus caucasicus	2
Cuscuta europaea	+
Euphrasia hirtella	+
Plantago caucasica	+
Trifolium repens	+
Vicia grossheimii	+
Carum carvi	+
Cruciata glabra	+
Ligularia sibirica	1
Seseli transcaucasica	+
Ranunculus acutilobus	+
Cirsium simplex	2
Geranium ruprechtii	+
Trifolium repens	+

8.1.2.2 Tussocks

***Festuceta variae* subsp.woronowii** occupy huge slopes of subalpine belt, where they form the first stage of succession. Under the influence of intensive grazing, *Calamagrostis arundinacea* communities become replaced by those of variegated fescue, but after grazing is forbidden, demutation of *Festuca* coenoses can be observed. *F. varia* forms large bunches; interspaces are populated by grasses *(Helictotrichon* *asiaticum, H. pubescens, Agrostis planifolia)*, sedges *(Carex meinshauseniana)* and forbs *(Betonica macrantha, Polygonum carneum,* etc.) (Table 8.6).

On wet slopes, *Festuca* communities are richer than those which occur on dry ones.

Jaroshenko (1942) and Geideman (1932) attributed variegated fescue meadows to steppe communities, while Busch (1935) and Magakian (1941) regarded them as typical meadows. Later Jaroshenko suggested, that *Festucetum variae* is a relic steppe, formed during the xerothermal period, and that since then, due to the further increase of climate humidity, the above-mentioned communities have been subject to the process of prairification. This opinion is shared by Grossheim.

Variegated fescue meadows are well-spread throughout the Caucasus. Though in South Georgian Uplands, unlike the Greater Caucasus, these communities occur on grazed areas of northern slopes.

Variegated fescue meadows include such widespread association as Festucetum caricosum *(Carex meinshauseniana)*.

***Festuceta valesiacae* steppe meadows** are confined to southern slopes. They are of a relatively simple structure (low herbage, low coverage percent, small number of coenoses). *Koeleria luerssenii, Bromopsis riparia, Agrostis tenuis, Carex buschiorum, Pulsatilla violacea, Thymus collinus* are the main components of these communities.

The driest eroded slopes of the subalpine belt are covered with communities dominated by *Bromopsis riparia, Festuca valesiaca, Koeleria luerssenii,* etc. They grow on thin, cobble and skeletal soils.

According to Tumajaniv (1980), forb-grass meadows observed in park forests of *Q. macranthera* in the eastern part of Kavkasioni, are steppificated. The following species are typical for these meadows: *Brachypodium pinnatum, Bromopsis riparia, Carex buschiorum* and *Onobrychis biebersteinii*.

8.1.2.3 Forb and Grass-Forb Meadows

Meadows of this group are abundant in the areas with moist temperate climate. Florogenetically, these communities are connected with the upper forest belt: they occur in thin park forests. It must be noted, that due to the dominant position of chionophytes, these meadows can rarely be found in the mountain massifs with a complex relief.

Meadows with *Woronowia speciosa* (= *Geum speciosum*) arise particular interest. They are very common in the western part of Kavkasioni (limestone-built mountains of Colchis). Usually, these communities populate the slopes with a sharply defined karst relief. *Woronowia speciosa* coenoses with a considerable admixture of *Carex pontica* occupy the same area.

Woronowia communities present the first stage of succession on karst funnels. Vital activity of *W. speciosa* results in the formation of soil, on which the other meadow elements start to crop up. *Woronowia* meadows are likely to have been more abundant in Colchis before. Due to the influence of grazing, in many areas, *W. speciosa* communities became substituted by those of *Nardus* and alpine carpet-like meadows.

Table 8.6 *Festuceta variae* in Kazbegi

Height (m s. m.)	2,000
Exposition	NW
Slope (°)	45
Cover (%)	100
Carex meinshauseniana	4
Agrostis planifolia	2
Bromopsis variegata	2
Festuca varia	5
Helictotrichon pubescens	2
Calamagrostis arundinacea	2
Poa longifolia	2
Anthoxanthum alpinum	2
Polygonum carneum	3
Vicia alpestris	3
Campanula collina	2
Alchemilla sericata	2
Trifolium ambiguum	1
Primula amoena	1
Betonica macrantha	2
Inula orientalis	2
Pedicularis chroorrhyncha	2
Silene ruprechtii	1
Ranunculus oreophilus	2
Ranunculus caucasicus	1
Pyrethrum roseum	2
Cuscuta europaea	+
Minuartia circassica	2
Minuartia imbricata	2
Scabiosa caucasica	2
Cirsium obvallatum	1
Trifolium trichocephalum	1
Myosotis alpestris	1
Polygala alpicola	1
Leontodon hispidus	2
Thymus nummularius	2
Lotus caucasicus	1
Anemonastrum fasciculatum	2
Alchemilla retinervis	2
Rhinanthus minor	1
Cerastium purpurascens	1
Carum alpinum	+
Centaurea cheiranthifolia	+
Coeloglossum viride	+
Cruciata glabra	+

(continued)

Table 8.6 (continued)

Gentiana septemfida	+
Polygonum alpinum	+
Selaginella helvetica	+
Viola odorata	+

Table 8.7 Subalpine *Galanthus* Meadow (grazed) near Jvari pass on the Georgian military highway over the central greater Caucasus (relevé G-10) (Box et al. 2000) (Location: Jvari Pass (2,394 m), Georgian Military Highway, south side (27 May 1999))

			2,300 m, Slope: 5° to SEE	
H	0.3 m	75 %	10 × 10 m KF, GN, *EB*, RJL	
H	3.4	*Galanthus platyphyllus*	3.3	*Alchemilla retinervis*
	2.2	*Rumex alpinus*	2.2	*Festuca supina*
	2.2	*Phleum alpinum*	2.2	*Rumex acetosa*
	1.2	*Sedum oppositifolium*	1.2	*Gagea supranivalis*
	1.2	*Veratrum lobelianum*	1.2	*Cirsium obavallatum*
	1.1	*Fritillaria latifolia*	+.2	*Ligusticum alatum*
	+.2	*Lamium album*	+.2	*Poa alpina*
	+.2	*Geranium ruprechtii*		

Meadows of *Trollius patulus* are very common in forest margins, thin park forests and elongated cavities.

Ranunculus caucasicus frequently occurs in these communities as a subdominant. Pure *Ranunculus* meadows have been formed under the influence of overgrazing (Grossheim 1948).

Geranieta (*Geranium gymnocaulon*) communities are confined chiefly to the alpine belt of the western part of the Greater Caucasus, though they also come down to the subalpine belt.

The distribution area of ***Geranium platypetalum*** meadows comprises Kavkasioni and the Lesser Caucasus. They are unavailable in South Colchis. These communities occur on stony substratum of moraines. With the development of soil cover, *G. platypetalum* communities are being replaced by other communities.

Forest margins, mountain slopes of medium steepness and flat areas are inhabited by *Geranium ibericum*, although as subdominant this species more frequently occurs in Calamagrostideta, Inuleta, Rhododendreta, etc.

Table 8.7 shows a sample of a (grazed) subalpine *Galanthus-Alchemilla* meadow near the Jvari Pass (2,300 m) on the Military Highway over the Greater Caucasus. The species total is again somewhat small, but the species are interesting local species from familiar Eurasian genera. At Kazbegi, at about 1,800 m on the north slope of the Greater Caucasus (Box et al. 2000).

Inuleta (*Inula orientalis*) coenosis are represented by pure thickets of *Inula*. It is very common in the high-mountains of the Caucasus. The following communities are characterized by predominance of this species:

Fig. 8.3 *Anemonetum fasciculatae*, Tskhratskaro Pass, Bakuriani region, Lesser Caucasus (Photo O. Abdaladze)

Inuletum geraniosum *(Geranium ibericum),*

Inuletum betonicetosum *(Betonica macrantha).*

In the western part of the Greater Caucasus, communities of *Inula grandiflora* usually occur on negative landforms where they replace tall herbs (Kolakovsky 1961). *Astrantia pontica* coenoses occupy screes and cobble substratum in limestone mountain ranges of Colchis (Abkhazeti).

Of the forb meadows, which are very rich in species, *Scabiosa caucasica* should be noted. These communities include such plants as *Helictotrichon pubescens, Inula orientalis, Agrostis planifolia, Betonica macrantha,* etc.

These meadows are very common in the Lesser Caucasus.

Betoniceta (*Betonica macrantha*) is a typical variant of subalpine meadows. It is well represented in the central and eastern parts of Kavkasioni and the Lesser Caucasus; the above-mentioned communities are rarely found in the western part of the Greater Caucasus.

Anemoneta (*Anemonastrum fasciculatum*) frequently populate slopes with optimal moisture and flat sites (Fig. 8.3). Slopes exposed to sunlight and cobble sites are occupied by communities of hemixerophytic *Hedysarum caucasicum.*

Subalpine meadows of *Veratrum lobelianum* are abundant in western and partly Central Kavkasioni, as well as in the Lesser Caucasus. *Veratrum lobelianum* is a poisonous pasture weed, usually rejected by animals; it is developed on the background of forb (*Trollius ranunculinus* (Fig. 8.4)*, Ranunculus caucasicus,* etc.) meadows.

Pulsatilleta (*Pulsatilla violacea*). These communities, typical for negligible areas, are confined to the slopes of northern exposure. *P. violacea* is frequently associated with hemixerophitic grasses (*Festuca ovina, Koeleria luerssenii*) and *Carex buschiorum* (Table 8.8).

Fig. 8.4 *Trollius ranunculinus*, Kazbegi, Central Caucasus (Photo G. Nakhutsrishvili)

Pulsatilleta (*Pulsatilla aurea*). These communities are very common in north-western Colchis. The distribution area of *P. albana* is more expansive.

Geranieto (*Geranium gymnocaulon*) – Woronowieta (*Woronowia speciosa*), **Geranieto-Inuleta (*Inula magnifica*)** illustrate subalpine mixed forb meadows, which often consist of 2–3 species and are found in Colchis. Pure forb communities are formed by *Euphorbia oblongifolia, E. scripta,* etc. Grass-forb meadows display high coenotical and floristic diversity. According to Kolakovsky (1961), the following species are very abundant in the above-mentioned meadows of Colchis: *Aquilegia olympica, Psephellus abchasicus, Kemulariella caucasica, Senecio aurantiacus,* etc.

Grossheimia polyphylla (*Asteraceae*) is a typical component of grass-forb meadows which are confined to the Lesser Caucasus and partly to western Kavkasioni.

The following plants frequently occur in subalpine grass-forb of the Caucasus: *Centaurea fischeri, C. cheiranthifolia, Vicia alpestris, Lotus caucasicus, Veronica gentianoides, Trifolium ambiguum, Leontodon hispidus, Ranunculus oreophilus,* etc.

Communities dominated by *Polygonum carneum* are worthy of notice; their area of distribution involves Kavkasioni and southern uplands. These meadows are of particular importance as natural grasslands. Under the influence of overgrazing, forb and grass-forb meadows become replaced by more resistant communities of compact-tussock grasses.

Astragaleta captiosus is characteristic of subalpine belt of the Central Caucasus and especially of Kazbegi region; these communities, formed by endemic *Astragalus captiosus*, occupy stony and pebble substratum.

8.1.3 Tragacanthic Vegetation

On the northern slopes of Kavkasioni, tragacanthic vegetation is sporadically distributed in dry inter-mountain vallies and hollows (Ivanishvili 1973).

Table 8.8 *Pulsatilleta* in Kazbegi

Height (m s. m.)	2,050
Exposition	S
Slope (°)	35
Cover (%)	90
Festuca rupicola	5
Carex buschiorum	4
Bromopsis variegata	2
Agrostis tenuis	2
Koeleria cristata	2
Koeleria caucasica	2
Bupleurum polyphyllum	2
Plantago caucasica	3
Pulsatilla violacea	4
Anthyllis variegata	2
Potentilla crantzii	2
Trifolium ambiguum	1
Ranunculus oreophilus	2
Selaginella selaginoides	1
Leontodon hispidus	2
Silene ruprechtii	1
Cerastium arvense	2
Veronica gentianoides	2
Thymus nummularius	2
Alchemilla sericata	2
Ranunculus acutilobus	1
Campanula collina	2
Euphrasia hirtella	1
Lotus caucasicus	1
Minuartia oreina	1
Ranunculus buhsei	+
Astragalus captiosus	+
Minuartia circassica	+
Pedicularis chroorrhyncha	+
Rhinanthus minor	+
Thesium procumbens	+
Campanula bellidifolia	+
Gentiana aquatica	+

Caucasian tragacanthic vegetation is a version of Asia Anterior–South-West Asia mountain-xerophytic vegetation; these communities are very rare in the Mediterranean mountains.

Astragaleta denudati (*Astragalus denudatus* (Fig. 8.5)) in Khevi (Central Caucasus) is restricted to the lower part of subalpine belt. These communities alternate with steppe-like meadows and saxicolous groupings; they occupy areas

Fig. 8.5 *Astragalus denudatus*, Kazbegi, Central Caucasus (Photo O. Abdaladze)

once populated by pine forests. In Daghestan (Eastern Caucasus) the above-mentioned coenoses can also be met in alpine belt; some individuals of *Astragalus aureus* penetrate even into the subnival zone (up to 3,150 m; Prima 1974).

Tragacanthic communities are dominated by plants, characterized by spiny cushion-like form. These communities also include the following plants:

- Dwarf subshrubs (species of *Artemisia, Thymus, Scutellaria*);
- Mountain steppe grasses (*Elytrigia gracillimum, Bromopsis riparia, Stipa tirsa,* etc.);
- *Carex buschiorum*;
- Hemixerophytic shrubs (*Juniperus hemisphaerica, J. sabina, Rhamnus tortuosa*).

The flora, formed on rocks has been enriched with lithophytes and chasmophytes, which involve many local endemics (Ivanishvili 1973).

The following is a concise list of species characteristic of one of tragacanthic communities:

Astragalus denudatus	*Stipa caucasica*
Berberis vulgaris	*Stipa tirsa*
Juniperus hemisphaerica	*Alopecurus vaginatus*
Spiraea hypericifolia	*Carex buschiorum*
Ephedra procera	*Oxytropis cyanea*
Artemisia chamaemelifolia	*Allium albidum*
Artemisia marschalliana	*Allium ruprechtii*
Artemisia splendens	*Asperula albovii*
Scutellaria leptostegia	*Astragalus kazbeki*
Agropyron gracillium	*Campanula hohenackeri*
Bromopsis riparia	*Dianthus cretaceus*

(continued)

Festuca valesiaca	*Onosma caucasica*
Koeleria cristata	*Myosotis arvensis*
Melica transsilvanica	

8.1.4 Microclimate and Energy Balance

A characteristic feature of high mountain ecosystems is their considerable variability within a relatively small area. As a result of particularly harsh climatic conditions (especially directed ones, like solar radiation and wind) and the relief of the high-mountains, a mosaic of various microhabitats emerges.

The microclimate and energetic conditions of phytocoenoses have been studied (by the method of Cernusca 1976) on the following objects, selected for this purpose:

- *Hordeeta*: (1,850 m a.s.l.) The meadow represents the *Hordeum violaceum-Poa pratensis-Anthriscus nemorosa* community with a very rich composition, including up to 70 species (Table 8.4).
- *Festuceta*: (2,000 m a.s.l.) The pasture meadow occupies extremely slanting and rocky slopes of a south-western exposure. The *Festuca varia-Carex meinshauseniana* community is widespread in the subalpine and alpine belts of the Central Greater Caucasus (Table 8.6).
- *Deschampsieta*: (1,750 m a.s.l.) These hay meadows are found on well-moistened habitats. Dominating species are *Deschampsia cespitosa* and *Equisetum palustre*, with regular occurrence of *Phragmites australis* (Table 8.5).
- *Pulsatilleta*: (2,050 m a.s.l.) Is part of an intensively grazed vast pasture. This is *Pulsatilla violacea-Festuca rupicola-Carex buschiorum* community (Table 8.8).
- *Dryeta*: (2,050 m a.s.l.) The community is found on an extremely slanted north-western slope. As a result of intensive grazing, the substrate is characterized as "step" relief. The dominants are *Dryas caucasica*, *Deschampsia flexuosa* and *Daphne glomerata* (Table 8.13).
- *Heracleeta*: (2,200 m a.s.l.) This tall herbaceous phytocoenosis is found on gently slanting northern slopes, in a highly humid substrate. Dominating species, *Heracleum sosnowskyi*, grows 2.4 m in height. The remaining seven species are rather scarce.
- *Kobresieta*: (2,175 m a.s.l.) Is found on gently slanting north-western slopes. The dominants are *Kobresia capilliformis*, *C. persica* and *Carex buschiorum* (Table 8.11).
- *Rhododendreta*: (2,200 m a.s.l.) Is found on steep north-western slopes. It is *Rhododendron caucasicum* and *Vaccinium myrtillus* community. The former is more developed (Table 8.12).

Analysis of the canopy structure and spatial orientation of leaves; microclimatic characteristics, profiles of soil, canopy and air temperature and humidity, falling

Table 8.9 Distribution of photosynthetically active radiation (RhAR) in different plant communities (Tappeiner et al. 1989)

Community	Recorded radiation %	Albedo %	Photosynthesizing parts of plants (leaves, green, shoods, etc.) %	Non-photosynthesizing parts of plants (trigs, dead matter, etc.) %	Soil %
Hordeeta (*H. violaceum*)	100	5	84	10	1
Festuceta (*F. varia*)	100	4	30	65	1
Deschampsieta (*D. cespitosa*)	100	5	84	5	6
Festuceta (*F. ovina*)	100	7	53	14	26
Dryeta (*D. caucasica*)	100	7	65	25	3
Heracleeta (*H. sosnowskyi*)	100	5	88	7	0
Rhododendreta (*Rh. caucasicum*)	100	3	92	5	0

and reflected radiation, net radiation, soil and convective heat flows and evapotranspiration have been made on the previously measured sites, which are described above.

As a result of this investigation of the structure of phytomass, the incident angle and the spatial orientation of leaves, three types of canopy have been relieved (Tappeiner et al. 1989).

1. Canopy with uniform leaf orientation (on different slopes), the phytomass concentrated in the lower parts of canopy.
2. Canopy with uniform distribution of phytomass in height and with basically erectophile leaf orientation in all canopy layers.
3. Canopy with a “storey” distribution of the phytomass and mainly planophile leaf orientation. Individual plant species are dominant.

Dryeta, Pulsatilleta and Kobresieta can be attributed to the first type of canopy. The basic layer of radiation exchange in these phytocoenoses is close to the ground. The second type involves Festuceta and Deschampsieta with low absorption of radiation, observable in the upper layers of the phytocoenosis and almost linear absorption of radiation in the lower part of the canopy. Hordeeta, Heracleeta and Rhododendreta communities, which belong to the third type, reveal absolutely different strategy of adaptation to radiation. The bulk of the biomass and the assimilative ingredients are accumulated in the upper layers of the canopy, thus providing maximum utilisation of the PhAR by their assimilating organs.

As shown in Table 8.9, intensively grazed phytocoenoses are the least utilizers of falling PhAR (Hordeeta pasture; Pulsatilleta; Kobresieta).

Measurements of vertical temperature profiles prove that irregularities between the temperature of the canopy and that of surrounding air are being smoothed.

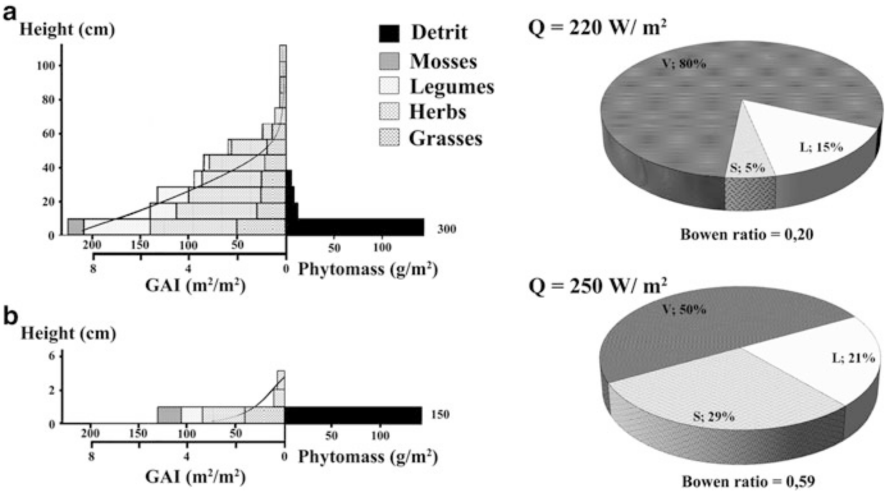


Fig. 8.6 Canopy structure and energy budget in Hordeetum community

Regarding the energy balance of these phytocoenoses, a similar (post-grazing) tendency of utilisation of the absorbed solar energy into heat exchange and transpiration is evident. On all pastures, the ratio of evapotranspiration (20–40 %) in the net radiation is reduced, while the ratio of convective and soil heat flows considerably grows demonstrates the canopy structure (Fig. 8.6), PhAR absorption and the energetic pattern of Hordeeta – both in preserve and on pasture. All these obvious modifications (often irreversible) have been caused by strong human impact.

Every high-mountain phytocoenoses in its natural development, acquires a special strategy of adaptation to environmental conditions, expressed in a definite spatial canopy structure (leaf orientation, distribution of LAI, etc.), which provokes a specific course of radiation energetic processes within the canopy. Heavy exploitation of the phytocoenoses (extensive haymaking, grazing) may stimulate irreversible processes, destroying habitual organisation of the canopy, leading to alterations in the direction of successive processes and moreover, arise dangerous erosion processes in the complex high-mountain relief. Therefore, exploitation of community should be subject to time limitation so as to prevent any such consequences and also to preserve the unique originality of high-mountain ecosystems.

8.1.5 Water Relations

An integral part of investigations into plant ecology is the study of the most important indicator of the vital activity of plants water relations. Water relations in the high-mountain plants of the Central Caucasus have been subject to intensive and long-term observations since the beginning of 1960s. Results of the analysis have been published in Georgia and abroad. However, the purpose of our further investigations is not only to expand the spectrum of the areas studied, but also to reconsider certain problems of water relations in high-mountain vegetation in view of availability of highly sensitive and compact field measuring devices and owing to new conceptions in plant ecology.

Our investigations confined the thesis that the indices of water relations in plants, i.e. water contents in leaves, xylem water potential and leaf transpiration, studied in order to determine their characteristic features, present three interrelated and complementary physiological parameters, giving an accurate picture of the water relations in plants. The determination of the diffusion resistance of leaves allowed us to judge of the function of stomatal apparatus in this vital process (Körner and Cernusca 1988). In order to obtain structural characteristics of water relation, we had to study various anatomical and morphological peculiarities of leaves; for ecological purposes – the phytoclimate and other environmental factors, controlling water relations. The soil moisture has also been carefully examined.

Particular attention was paid to the analysis of regulation mechanisms of the water relations in high-mountain meadow plants. By recent observations even in the subalpine belt of the Central Caucasus, where hydrothermal conditions are most favourable, water evaporation in plants is frequently magnified according to the considerable rise of air temperature and PhAR in the afternoon. Consequently, water contents and xylem water potential noticeably diminish. These conditions stimulate leaf diffusion resistance, hence normal water supply is quickly restored (Fig. 8.7). It should be noted, that physiological regulation by transpiration is expressed rather differently in species of various ecological groups and life forms.

Stomatal regulation of water exchange in plants of the subnival belt of the central Caucasus is much more pronounced. Due to extreme ecological conditions, plants of this belt sharply diminish water release in the afternoon (88–97 %) reducing transpiration to insignificant values as a result of intensification of leaf diffusion resistance.

However, the most important part of the stomata apparatus of leaves in the regulation of water relations of subalpine meadow plants becomes more evident by the end of summer, during the late-summer phase of seasonal development of plants in the course of long-term (10–15 days) drought periods, when the soil is almost devoid of moisture.

During this period the value of leaf moisture and xylem water potential considerably decrease. This situation provides sharp diurnal fluctuations of leaf diffusion resistance, followed by sudden (55–70 %) expansion of xylem water potential. Consequently, plants restore their normal level of tissue water contents (Fig. 8.8).

Considering the ecological fragility of high-mountain biomes, various aspects of the impact of human factor arise particular interest. On the basis of studies on the effect of grass-mowing and grazing on water exchange in high-mountain plants, the most favourable exploitation regime applicable to subalpine meadows has been determined, i.e. a systematic, regular (2–3 times per year) grass-mowing. Grazing or complete reservation, which cause gradual reduction of the green phytomass, seem inexpedient.

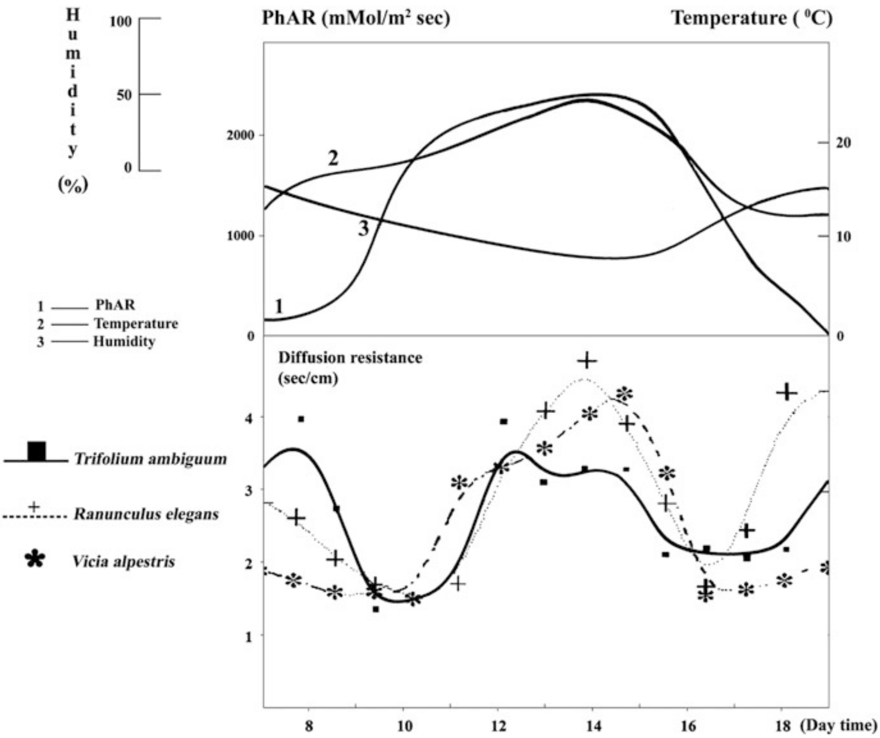


Fig. 8.7 Diurnal course of leaf diffusion resistance of subalpine plants (Sanadiradze, 1986)

8.1.6 Pigment Content

Content of chlorophyll and carotinoid pigments in leaves of more than 100 species of Central Caucasus plants has been subject to analysis in various habitat conditions at the altitudes of 1,800–3,000 m. The pigment content and distribution in different layers of phytocoenoses has been carefully studied. Chlorophyll content in leaves was determined spectrophotometrically (Khetsuriani, Chiboshvili 1998).

By their chlorophyll and carotinoid content, the examined species clearly differ from each other as to their habitat and phytocoenoses, so within a single phytocoenosis. Results of our investigations are illustrated here by the variegated fescue community, found in moderately humid habitats of the north-western slope exposure (1,950 m a.s.l.).

We selected 20 most typical species out of 60 plant species from this phytocoenosis, for close observation during the flowering phase.

Low chlorophyll content (2.66 mg g of dry mass) is typical for the dominant edificator *Festuca varia*, and the maximum (11.8 mg) – for *Vicia alpestris*. The low content of chlorophyll in dominant species can be accounted for by almost erectophyile orientation of leaves, unshaded by other plants.

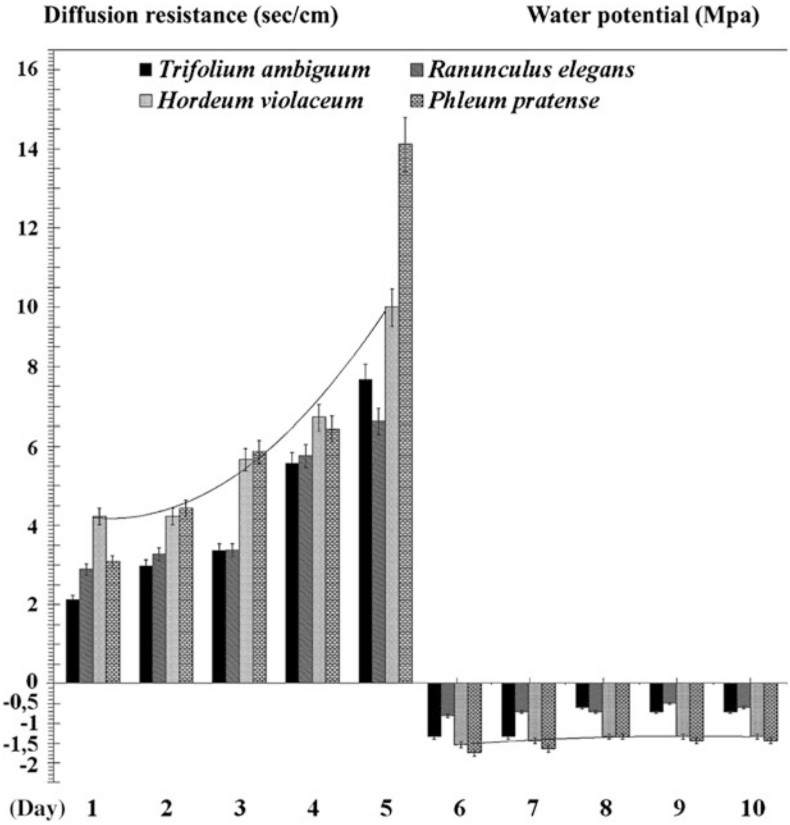


Fig. 8.8 Oscillation of plant water potential

Spring-flowering plants (*Anemonastrum fasciculatum, Primula amoena, Fritillaria lutea*) and other plants of variegated fescue community start their pigmentation synthesis when still under snow. They differ very little by chlorophyll content and the quantity of carotinoids. Though vernal plants develop in heavy ecological conditions, they accumulate as much pigment during their flowering phase as codominant *Carex meinshauseniana*, and twice as much as *Festuca varia.*

Comparison of the quantity of chlorophyll (mg per sq.m) and green mass (g. sq.m) in each species reveals a direct relation between chlorophyll content and biomass production in the majority of these species.

Variability of communities is also determined by their pigment content. Hence the difference between hay and pasture meadows.

Allocation of pigments depends on the height of phytocoenosis, e.g. pigment measurement in every 10 cm layer of the stand (herb-barley meadow) shows that max. amount of pigments (5.75 mg) is accumulated in the 50–60 cm layer and min. (1.00 mg) – in the first (90–100 cm) stand layer.

Consequently, the content of pigments in high-mountain phytocoenoses depends on the complexity of vegetation community structure, which in its turn predetermines the microclimate of the given phytocoenosis. Further, pigment content displays specific variety as a genetic property, in terms of plant species.

8.1.7 CO_2-Gas Exchange in Plants

8.1.7.1 Materials and Methods

Investigations were carried out in 13 different and most characteristic habitats of the Central Greater and Lesser Caucasus. 61 species of flowering plants have been studied for this purpose.

CO_2-gas exchange of intact plant leaves proceeded in under field conditions with infrared gas analyser techniques. The studies were conducted in the open system according to the universally accepted procedure (Abdaladze 1994).

8.1.7.2 Plant CO_2-Gas Exchange in Different Communities

Most intensive CO_2-assimilation in plants is observed in Hordeeta (moderate moist meadow) communities. In Pulsatilleta (dry meadow) and Deschampsieta (moist meadow) communities, the intensity of photosynthesis is slightly lower, whereas in *Rhododendron* communities it is considerably suppressed. CO_2-gas exchange in plants in the communities Festuceta (except *Festuca varia*) on dry south-western mountain side is strongly depressed. Particularly, net-photosynthesis midday depression frequency, duration and capacity are substantially increased and net-primary productivity-decreased.

CO_2-gas exchange in *Festuca varia* (tussock grass with rigid and rolly peinomorphic leaves) is very steady: net-photosynthesis midday depression frequency is extremely low (5–8 %), as well as the coefficient of variation of CO_2-gas exchange (22–25 %). It should be noted, that all parameters in this species display an amazingly constant character on moderately moist slope, on relatively dry slope and at the upper boundary of distribution area of these species (3,000 m a.s.l.), where *Festuca varia* is not a dominant species and is represented by isolated specimen. The CO_2-gas exchange character in *Festuca varia* can be considered as the ecophysiological basis of increased biological activity of this strong dominant, that promotes (particularly in the anthropogenic conditions) its intrusion into different coenoses – “capture” and “holding” of various territories.

Succulent species *Sedum oppositifolium* and *Sempervivum pumilum* are highly adapted to extreme temperature relations of their microhabitats. These succulents assimilate CO_2 by the CAM pathway, which is the most economical way of adaptation for their CO_2-gas exchange.

C3-type of carbon assimilation is typical for *Saxifraga juniperifolia* and *Sedum gracile*.

The obtained data shows that in winter, the evergreen shrub *Rhododendron caucasicum* blocks maximally the interaction with environment and entirely restricts metabolic processes. Net-photosynthesis is not detectable. Dark respiration rate is extremely low (0.2–0.5 mmol $CO_2/m^2.s$). In winter this species undergoes "deep resting" period.

Contrary to evergreen shrubs, summer-wintergreen herbs (*Plantago lanceolata, Phleum pratense, Trifolium alpestre, Carex sylvatica*) in winter are capable of CO_2 uptake. During thaw the diurnal balance of CO_2-gas exchange, is usually positive. Maximum values of net-photosynthesis on the plots free from snow reach 5.4–9.5 mmol $CO_2/m^2.s$ (37–50 % of vernal maximum). Under the snow cover CO_2 uptake is possible only for a short period of time (1–3 h a day).

8.1.7.3 Maximum Net-Photosynthesis

High net-photosynthesis maximum values show: the legumes – *Trifolium ambiguum, Trifolium fontanum, Vicia grossheimii,* etc. (17–20 mmol $CO_2/m^2.s$), *Ranunculus oreophilus, Pulsatilla violacea, Leontodon hispidus, Alchemilla sericata, Geranium gymnocaulon, Sibbaldia semiglabra* (18–22 mmol $CO_2/m^2.s$). The grasses (*Agrostis planifolia, Hordeum violaceum, Bromopsis riparia, Nardus stricta, Festuca ovina, F. varia,* etc.) show moderate values (10–15 mmol $CO_2/m^2.s$). Low maximums are characterized by C3 succulents, *Rhododendron caucasicum, Parnassia palustris* and the sedges (4.5–10 mmol $CO_2/m^2.s$).

8.1.7.4 Dark Respiration

High intensity of dark respiration at standard temperature (10 °C) is typical for meadow forbes and legumes (1.7–2.3 mmol $CO_2/m^2.s$). Sedges and C3-succulents reveal low values (0.9–1.3 mmol $CO_2/m^2.s$). Grasses show moderate values.

8.1.7.5 Influence of PhAR and Temperature on Plant CO_2-Gas Exchange

Typical shade-tolerant species are: *Saxifraga juniperifolia* and *Sedum gracile* (PhAR saturation intensity =450 mmol photons/m^2.s), *Betonica macrantha and Rhododendron caucasicum* (560–580 mmol photons/m^2.s). The most light-requiring species are: *Pulsatilla violacea, Trifolium ambiguum, Geranium gymnocaulon, Sibbaldia semiglabra* and some others (1,000–1,500 mmol photons/m^2.s; 42–48 % from full PhAR).

The majority of the investigated species are capable to assimilate CO_2 at negative air temperature (−4 to 0 °C). Maximum temperature limit for net-photosynthesis in subalpine and alpine meadow plants is rather high (37–44 °C). Wide temperature optimums for net-photosynthesis in *Festuca varia* (12–13 °C), *Saxifraga juniperifolia* (11–30 °C), *Sibbaldia semiglabra* (16–34 °C) and *Geranium gymnocaulon* (15–34 °C) attract special attention.

The ratio Q_{10} for dark respiration of investigated species equals approximately 2.0. At very high temperature (40 °C and more Q_{10} falls to 1.3–1.4).

8.1.7.6 Stress Factor in High Mountain and Plants CO_2-Gas Exchange

High mountains are stress dominated areas. The strongest negative effect, produced by the stress factor is a destroyed balance between photosynthesis and respiration. Reduction of the value photosynthesis/respiration in investigated species is caused by the increase of altitude above sea level. In heavy ecological conditions plants spend more energy on survival and adaptation.

Obviously, some herbs and shrublets in Rhododendreta become subject to stress caused by reduced PhAR. In cloudy weather relative illumination of leaves lowers to 0.5–1 % so that plants fail to assimilate CO_2.

By the end of spring, frosts reduce net-primary productivity in plants in Agrostieta on 80–85 %. In Festucetum (dry south-western slope) in all investigated species, except *Festuca varia*, net-primary productivity decreases for 11–35 %, because of high air temperature. Draught is a stress factor even for the plants growing under temperature conditions. The stronger is the draught, the greater is the influence of water stress on CO_2-gas exchange in *Hordeum violaceum* in Hordeeta.

As a result of thaw on the south slopes the photoinhibition, the freezing of plants at night and the "winter draught" phenomenon are observed. Therefore, strong and long-term thaws, provoking the activation of net-photosynthesis in herbs should be considered as unfavourable event.

No universal mechanism of plant CO_2-gas exchange adaptation to high mountain ecotope was revealed. CO_2-gas exchange shows the best adaptation to the main limiting ecological factor for a given biotope (Abdaladze 1994).

8.1.7.7 Phytocoenoses Effect on Plant CO_2-Gas Exchange

The survivability of canopy can be revealed experimentally: the protective effect of canopy on CO_2-gas exchange in *Trifolium ambiguum* has been investigated in Hordeetum. Separation, e.g. removal of vegetation around the experimental plants within the radius of 1 m, greatly effects the dependence of net-photosynthesis on PhAR and leaf temperature, suddenly narrowing ecological optimums of these factors. On sunny days for separated plants the highest values with negative index of correlation rate (net-photosynthesis-PhAR $= -0.93 \pm 0.14$; net-photosynthesis-leaf temperature $= -0.90 \pm 0.17$) are observed. It indicates the linear dependence on the net-photosynthesis depression from the illumination and leaf temperature. The correlation interactions of these dependencies are equal and this confirms the linear character of connection. In natural canopy the correlation rates have positive index. Moreover, it smoothed out the temperature fluctuations, which is expressed by net-photosynthesis ratio of variation reduction. Private correlation rate between leaf temperature and net-photosynthesis is approximately zero. It indicates, that canopy not only smoothes up the unfavourable factors but creates actively the optimal conditions for CO_2 uptake. Thus, temperature optimum in control plants equals to 17–26 °C, while an experimented one – 17–23 °C. Separation induces twice and a half times decrease of the net-photosynthesis maximums frequency. It also demonstrates the ability of vegetation cover to support favourable conditions temperature, air humidity, PhAR, etc.

This effect is directed against stress factors of the environment for support of optimal CO_2-gas exchange balance and is probably the result of a cooperative functioning of plants formed in the process of a long-standing joint evolution.

8.1.7.8 Anthropogenic Influence of Plant CO_2-Gas Exchange

Our investigations have been carried out in Hordeeta in the pasture, the hay and preserved plots. On intensively grazed meadow CO_2-gas exchange of plants is destabilised. Here, net-photosynthesis strong midday depressions are observed rather clearly (depression rate = 54–59 %). On preserved and hay meadows net-photosynthesis reduction at depressions does not exceed 38–45 %, whereas on pastures it is 78–81 %. On pastures, net-primary productivity and diurnal balance of CO_2-gas exchange are substantially depressed.

On hay meadows (once a year) optimal CO_2-gas exchange balance was observed (Abdaladze 1994).

8.1.8 Life Activity of High-Mountain Plants in Winter

Life activity of high-mountain plants in winter has been studied in the upper-forest and subalpine belts of the Lesser Caucasus. Our objective was to examine the strategies of hibernation of summer-winter-green meadow, herbaceous and evergreen shrub plants.

On the basis of the obtained data, winter evergreen shrubs usually hinder any interactions with the environment and entirely restrict metabolic processes. Therefore, leaf and air temperatures virtually remain immutable, water content in leaves slightly changes (1–2 %) compared to autumn, stomata are closed, transpiration and net-photosynthesis are imperceptible, respiration rate is extremely low. In profound dormancy, resistance of shrubs against various stress factors is much higher. Safe hibernation depends on snow protection, which prevents plants from desiccation and dehydration.

Contrary to evergreen shrubs, summer-winter-green herbaceous species are capable of vital activity at ever favourable opportunity in winter, particularly during thaw.

In free of snow areas, leaf temperature of the hibernating species amounts to high values on clear days, exceeding air temperature by 5.0–9.3 °C. Diurnal dynamics of water content, xylem water potential, transpiration intensities and net-photosynthesis are displayed rather clearly. During thaw the diurnal balance of CO_2-gas exchange is usually positive, whereas maximum intensity of the net-photosynthesis attains 37–50 % of vernal maxima. CO_2 assimilation under snow cover becomes possible only for a short period.

8.2 Alpine Vegetation

The alpine belt in the Caucasus extends from 2,400–2,500 up to 2,900–3,000 m a.s.l. (Fig. 8.9) It is characterized by the dominance of short grass meadows; carpet-like alpine meadows, alternating with *Rhododendron caucasicum* thickets and rock-scree vegetation are also well developed here.

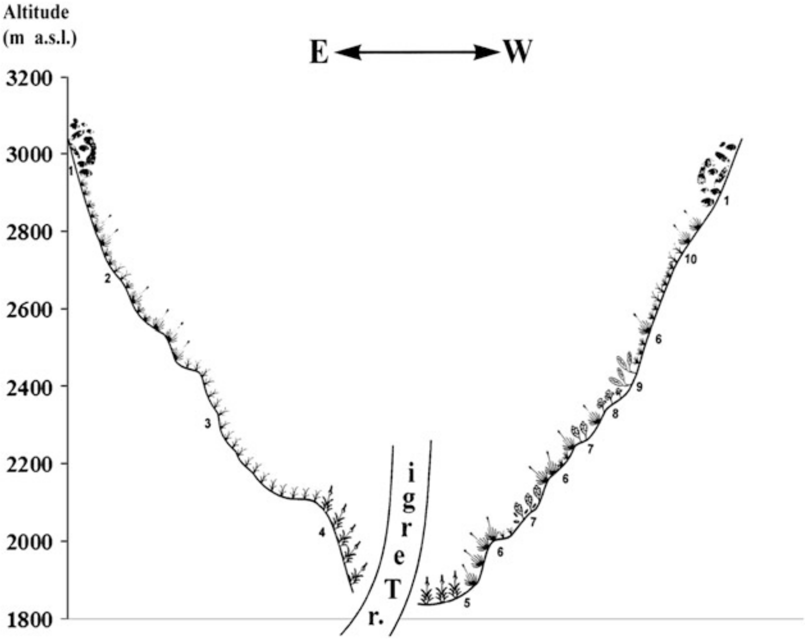


Fig. 8.9 Vegetation transect in Kazbegi region

8.2.1 Alpine Meadows

Alpine meadows occupy vast areas in Georgia. They are valuable natural grasslands. These communities mainly occur on mountain wetlands. Within the alpine meadows, it is possible to distinguish firm-bunch and sedge meadows, forb meadows and those dominated by tussock grasses and forbs. These groups of formations are typical for all geographical variants of the mountain-meadow vegetation of the Caucasus. The occurrence of local endemics is one of the floristic peculiarities of the above-mentioned communities (Bedoshvili 1985).

Information on the syntaxa of high-mountain vegetation (Svaneti region), including that of alpine belt is available in Table 8.10.

Festuceta variae, Festuceta supinae, Nardeta strictae, Cariceta tristis, Kobresieta capilliformis and K. persicae are the major formations of firm-bunch meadows.

Festuceta variae (*Festuca varia* subsp. *woronowii*). These communities are confined to steep slopes of southern exposure. Most frequently they occur in the eastern part of Kavkasioni.

Variegated fescue meadows are widespread in subalpine belt; they occupy areas, once populated by crook-stem forests, *Rhododendron* thickets and *Nardus* communities.

Nardeta. *Nardus* communities are very abundant throughout the Caucasus; they are restricted to the slopes of all exposures. Though due to the overgrazing, the secondary Nardus communities prevail here. Mixed communities of Nardeto-Festucetum variae

Table 8.10 The phytosociological classification of the vegetation of alpine belt of upper Svaneti (Dolukhanov et al. 1942)

Communities
1.1. *Sibbaldia parviflora* + *Carum meifolium*
2.1. *Sibbaldietum mixtoherbosum*
2.2. *Sibbaldia semiglabra* + *Geranium gymnocaulon*
2.3. *S. semiglabra* + *Festuca supina*
2.4. *S. semiglabra* + *Taraxacum stevenii*
2.5. *S. semiglabra* + *Ranunculus svaneticus*
2.6. *S. semiglabra* + *Pedicularis condensata*
2.7. *Sibbaldietum lichenoso–muscosum*
2.8. *Sibbaldia semiglabra* + *Campanula biebersteiniana*
2.9. *S. semiglabra* + *Ranunculus svaneticus* + *Gnaphalium supinum*
2.10. *S. semiglabra* + *Gnaphalium supinum*
2.11. *S. semiglabra* + *Carex micropodioides* + *Festuca supina*
3.1. *Ranunculus svanetici typicum*
3.2. *Ranunculus svaneticus* + *Gnaphalium supinum*
3.3. *R. svaneticus* + *Corydalis conorrhiza* + *Taraxacum stevenii*
3.4. *R. svaneticus* + *Pedicularis crassirostris*
4.1. *Caretum caucasici*
4.2. *Carum caucasicum* + *Trifolium ambiguum*
4.3. *C. caucasicum* + *Festuca supina*
5.1. *Minuartia colchica* + *Carum caucasicum*
5.2. *Minuartia aizoides* + *Campanula biebersteiniana*
5.3. *Plantago saxatilis* + *Festuca supina* + *Minuartia aizoides*
5.4. *Antennaria caucasica* + *Campanula saxifraga*
5.5. *Taraxacum stevenii* + *Gnaphalium supinum*
5.6. *Anthemis rudolphiana* + *Sibbaldia semiglabra*
5.7. *Festuca supina* + *Campanula saxifraga*
5.8. *Antennarietum caucasicae*
5.9. *Plantago saxatilis* + *Festuca supina*
5.10. *Antennaria caucasica* + *Alchemilla caucasica*
5.11. *Festuca supina* + *Chamaesciadium acaule* + *Plantago saxatilis*
6.1. *Alchemilletum caucasicae*
6.2. *Alchemilla caucasica* + *Antennaria caucasica* + *Festuca supina*
7.1. *Calamagrostis arundinacea* + *Betonica macrantha*
7.2. *Trollieto–Calamagrostidetum mixtoherbosum*
7.3. *Calamagrostidetum mixtoherbosum*
7.4. *Calamagrostis arundinacea* + *Anemonastrum fasciculatum*
8.1. *Deschampsieto–Calamagrostidetum mixtograminosum*
8.2. *Brometo–Calamagrostidetum mixtograminosum*
8.3. *Calamagrostis arundinacea* + *Trisetum pratense*
9.1. *Festuca djimilensis* + *Vaccinium myrtillus*
9.2. *Festuca djimilensis* + *Inula orientalis* + *Trollius ranunculinus*
10.1. *Trifolieto–Brometum mixtoherbosum*

(continued)

Table 8.10 (continued)

Communities
10.2. *Careto–Brometum mixtoherbosum*
11.1. *Trisetum pratense* + *Euphorbia abchasica* + *Polygonum carneum*
12.1. *Festuca djimilensis* + *Calamagrostis arundinacea* + *Geranium platypetalum* + *Vaccinium myrtillus*
12.2. *Calamagrostidetum arund. mixtograminoso–mixtoherbosum*
12.3. *Calamagrostidetum glaucae mixtograminoso–mixtoherbosum*
12.4. *Calamagrostis arundinacea* + *Festuca djimilensis* + *Anemonastrum fasciculatum* + *Betonica macrantha*
12.5. *Poetum longifoliae mixtoherbosum*
13.1. *Agrostis capillaris* + *Trifolium canescens*
14.1. *Trollius ranunculinus* + *Geranium gymnocaulon*
15.1. *Anemonastrum fasciculatum* + *Betonica macrantha*
16.1. *Alchemilla tredecimbola* + *Valeriana colchica*
16.2. *Alchemilletum tredecimlobae mixtoherbosum*
17.1. *Geranium typicum*
17.2. *Geranium gymnocaulon* + *Calamagrostis arundinacea*
18.1. *Geranium gymnocaulon* + *Carex aequivoca* + *Phleum alpinum* + *Anthoxanthum alpinum* + *Carum meifolium*
18.2. *Geranium gymnocaulon* + *Festuca supina* + *Senecio taraxacifolium* + *Aster caucasicus* + *Primula amoena*
18.3. *Triseto–Graminetum mixtoherbosum*
19.1. *Geranium gymnocaulon* + *Anemonastrum fasciculatum* + *Betonica macrantha*
19.2. *Geranium gymnocaulon mixtoherbosum*
19.3. *Geranium gymnocaulon* + *Trollius ranunculinus* + *Anemonastrum fasciculatum*
19.4. *Geranium gymnocaulon* + *Sibbaldia semiglabra*
19.5. *Geranium gymnocaulon* + *Campanula biebersteiniana*
19.6. *Geranium gymnocaulon* + *Trollius ranunculinus*
19.7. *Geranium gymnocaulon* + *Alchemilla sp.*
20.1. *Heracleetum (Heracleum aff. umbonatum Boiss.)*
20.2. *Ligusticetum alatae*
21.1. *Aconitum nasutum* + *Cephalaria gigantea* + *Heracleum aff. umbonatum*
21.2. *Senecio platyphyllus* + *Inula orientalis*
22.1. *Athyrium alpestris*
23.1. *Senecio platyphyllus* + *Rumex alpinus*
24.1. *Festucetum variae typicum*
25.1. *Festuca varia* + *Calamagrostis arundinacea*
25.2. *Festuca varia* + *Deschampsia flexuosa*
26.1. *Festuca varia* + *Alchemilla sp. div.*
26.2. *Festuca variae mixtoherbosum*
27.1. *Nardus stricta* + *Agrostis capillaris*
27.2. *Nardus stricta* + *Sibbaldia parviflora*
27.3. *Nardus stricta* + *Carum meifolium*
27.4. *Nardus stricta* + *Alchemilla sp.* + *Trifolium ambiguum*
27.5. *Nardus stricta* + *Plantago saxatilis*

(continued)

Table 8.10 (continued)

Communities
28.1. *Carex meinshauseniana + Anthemis rudolphiana*
28.2. *Caricetum typicum*
29.1. *Festuca supina + Carex meinshauseniana*
30.1. *Festuca ruprechtii + Geranium renardii*
31.1. *Deschampsia flexuosa + Geranium renardii*
32.1. *Deschampsia flexuosa + Festuca supina + Anthemis rudolphiana*
33.1. *Deschampsia flexuosa + Anthemis rudolphiana + Campanula saxifraga*
34.1. *Kobresieta schoenoides*
35.1. *Carex dacica + Primula auriculata*
35.2. *Carex dacica + Primula auriculata + Trifolium ambiguum*
36.1. *Alchemilla tredecymloba + Deschampsia cespitosa*
37.1. *Rhododendronetum typicum*
38.1. *Rhododendron caucasicum + Chamaenerium angustifolium*
38.2. *Rhododendron caucasicum + Geranium gymnocaulon*
38.3. *Rhododendron caucasicum + Athirium alpestre*
39.1. *Rhododendron caucasicum + Vaccinium myrtillus + Deschampsia flexuosa*

can be found in the central and eastern parts of the Greater Caucasus. Under the influence of pasturing hygrophytic *Nardus* communities have developed on swampy depressions of alpine belt.

Cariceta tristis. These coenoses are very abundant in the high-mountains of the Caucasus. Usually they inhibit prominent slopes exposed to winter winds. *Carex tristis* participates in the formation of sedge-fescue association *(Festuca supina-Carex tristis)*. The most typical communities are such, as: Cariceto-Alchemilleta *(Alchemilla caucasica)* and Cariceto-Kobresieta *(Kobresia capilliformis)*.

Kobresieta capilliformis. These communities like those of *K. persica* are found chiefly in the central and eastern parts of Kavkasioni and the southern upland of Georgia. They cover mountain ridges and prominent slopes. Coenoses, with Middle Asian-Himalayan *Kobresia capilliformis*, are very common in Georgia; the above-mentioned communities occur on marl-like shales and limestones of the Central Caucasus. Within variegated fescue meadows Kobresieta schoenoides occur on stony localities (Table 8.11).

Festuceta djimilensis. It belongs to the tussock grass-forb meadows, which have penetrated into the alpine belt from subalpine zone; Festuceta djimilensis is typical for both cobble and wet substratum (mostly in the western part of Kavkasioni).

Bromopsieta variegati, which enter the same group, are restricted to the southern slopes of alpine belt. In the high-mountains of Colchis, dry meadows occur on limestones; these meadows are formed by *Sesleria anatolica*, a grass with creeping rhizome.

Geranieta (*Geranium gymnocaulon*). These communities of forb meadows of alpine belt, are distributed in the western part of Kavkasioni. According to

Table 8.11 Kobresieta in Kazbegi

Height (m s. m.)	2,150
Exposition	N
Slope (°)	5
Cover (%)	90
Kobresia capilliformis	5
Kobresia persica	4
Carex buschiorum	2
Trifolium ambiguum	2
Trifolium repens	2
Trifolium fontanum	1
Trifolium canescens	1
Agrostis planifolia	1
Helictotrichon asiaticus	2
Bromopsis variegata	1
Lotus caucasicus	2
Polygonum viviparum	2
Antennaria caucasica	2
Campanula biebersteiniana	2
Leontodon danubialis	+
Taraxacum confusum	2
Plantago caucasica	2
Minuartia circassica	2
Minuartia oreina	2
Cerastium purpurascens	2
Draba hispida	1
Draba repens	1
Cirsium pugnax	+
Gnaphalium supinum	+
Thesium alpinum	+

Dolukhanov (1946), Onipchenko and Blnnikov 1994 *Geranium* communities extend from the low-alpine subzone to the upper limits of dense vegetation; these meadows merge into the subnival belt. They occur on mountain-meadow skeletal soils.

8.2.2 Carpet-Like Alpine Meadows

Carpet-like alpine meadows are a diverse group of formations. They occur in the upper part of the alpine belt. These coenoses are to be found among large stones.

The term "carpet-like alpine meadows" proposed by Grebenshikov (1965) coincides with "Dicotylen-Teppiche" of Ellenberg (1996). Alpine carpet-like meadows are composed of the following low rosetted and caespitose plants: *Campanula biebersteiniana, Carum caucasicum, Veronica gentianoides,* *Gnaphalium supinum, Pedicularis crassirostris, P. armena, Poa alpina, Taraxacum stevenii, T. porphyranthum, Sibbaldia semiglabra* etc.

These communities include such grasses as *Poa alpina, Phleum alpinum, Festuca supina,* etc.

Carpet-like alpine meadows differ from true meadows by their floristic composition and ecological peculiarities. Due to the lasting snow cover, they are characterized by short vegetative period. Herbage of the above-mentioned meadows does not exceed 3–4 cm. Eighty percentage of phytomass is accumulated in a 0–1 cm layer. As noted above, the carpet's sod belongs to the forb-type sod-forming. The typical carpet's sod has a two-layer structure. The main mass of the individual sod is concentrated in the upper layer (5–6 cm). The lower layer consists of separate deep roots (20–25 cm). Alpine carpet-like meadows are distinguished by large and brightly coloured flowers and inflorescences.

Some authors suggest considering alpine carpet-like meadows as Nanoherbeta, which belong to eumesophytic meadows.

Besides the climax carpet-like alpine meadows, secondary carpets, enriched by meadow elements (especially *Alchemilla* species), occupy considerable areas. Development of these secondary carpets is caused by overgrazing.

Sibbaldia semiglabra communities as well as those of *S. parviflora* are of particular interest. Pure *Sibbaldia* communities are very poor floristically.

These secondary communities occupy the most exploited pastures. Endemic carpet-like alpine meadows with *Ranunculus helenae* occur on limestone substratum in Colchis. Moist sites are occupied by carpets of *Carum caucasicum.* Pure stands of the above-mentioned plant are quite rare; usually it associates with *Taraxacum stevenii, Campanula biebersteiniana, Plantago saxatilis, Minuartia aizoides,* etc.

Carpet-like communities which are developed around the snow spots and at the edges of glaciers, include the following species: *Ranunculus oreophilus var. pumilus, R. baidarae, Primula algida, Gentiana djimilensis (= G. pyrenaica), G. angulosa, G. nivalis, Minuartia aizoides* and *Cerastium cerastoides.*

Of the plants growing at the banks of brooks, the following may be mentioned: *Pedicularis crassirostris, Primula auriculata, P. nordmanniana, Poa alpina,* etc.

8.2.3 Alpine Shrub

Steep northern slopes of alpine belt are inhibited by *Rhododendron caucasicum* thickets (dekiani). *Rhododendron* communities occur even at an altitude of 1,700–1,800 m (Table 8.12). According to Kolakovsky (1961), at greater altitudes *Rh. caucasicum* is restricted to cirques and valleys, which are characterized by high humidity and profound snow, protecting it from frost. The same scholar, attributes the present-day distribution of *Rh. caucasicum* in alpine belt to the lowering of upper forest margins, to which it has been confined before.

Rhododendron thickets occur on brownish-cinnamon bog soils, which are very rich in humus (usually skeletal) (Fig. 8.10).

Table 8.12 *Rhododendreta* i Kazbnegi

Height (m s. m.)	2,450
Exposition	N
Slope (°)	25
Cover (%)	100
Rhododendron caucasicum	5
Vaccinium myrtillus	3
Vaccinium vitis-idaea	2
Calamagrostis arundinacea	2
Pyrola minor	1
Agrostis planifolia	2
Anemonastrum fasciculatum	1
Geranium ibericum	1
Empetrum caucasicum	2
Luzula spicata	+
Carex tristis	+
Nardus stricta	+

Subshrub communities, formed by *Dryas caucasica* (Table 8.13) arise much interest. They favour cold stony slopes of northern exposure. In Colchis, *Dryas* communities are restricted to limestone rocks, rocky mountain ridges and stony slopes of northern exposure (Kolakovsky 1961).

Distribution area of elfin woods of *Juniperus hemisphaerica* and *J. sabina* extends throughout Kavkasioni. In Colchis, the fragments of *Juniperus* communities (Fig. 8.11) rarely intermingle with *Rhododendron* thickets. Juniper coenoses with *Woronowia speciosa (= Geum speciosum)* occupy limestone mountains (Kolakovsky 1961).

Chionophilic communities of *Daphne glomerata* are very characteristic of Kavkasioni. Coenoses of *D. albowiana* and *D. woronowii* are abundant in Colchis. It should be noted, that *D. woronowii* communities occur on limestones.

8.2.4 Alpine Saxicolous Plants

Of the saxicolous plants of alpine belt the following should be outlined: *Campanula mirabilis, C. dzaaku, Arenaria lychnidea, Draba bryoides, Albowiodoxa elegans, Symphyandra armena,* etc. The screes are occupied by *Heracleum calcareum, Campanula schistosa, Athyrium alpestre, Anthemis sosnovskyana, Barbarea minor,* etc.

8.2.5 Ecological Characteristics of Alpine Communities

Ecological characteristics of Nardeta strictae and Cariceta tristis are presented bellow. These communities are typical representatives of alpine vegetation of the

Fig. 8.10 *Rhododendron caucasicum* & *Betula litwinowii* at treeline, Kazbegi, Central Caucasus (Photo O. Abdaladze)

Caucasus. They are confined to the central part of the Greater Caucasus (Kazbegi region, 2,650 m).

8.2.5.1 Soils

Mother rocks of this area are of volcanic origin. Soils, formed by volcanic ash, are becoming andosols or Andept (the term proposed by North American pedologists). Soils populated by the afore-mentioned communities have A-B-C profile. Transition to A–C soils can be observed at greater altitudes. Soil pH of A layer is very acid, sandy loam and pierced through with roots. It appears that water content in phytocoenoses accounts for the changes of soil color; thus, when lacking water, the colour of soil becomes lighter.

Table 8.13 *Dryeta* in Kazbegi

Height (m s. m.)	2,050
Exposition	NW
Slope (°)	50
Cover (%)	100
Deschampsia flexuosa	3
Anthoxanthum alpinum	3
Carex meinshauseniana	3
Agrostis planifolia	2
Bromopsis variegata	2
Helictotrichon asiaticus	2
Nardus stricta	1
Poa alpina	1
Festuca supina	2
Daphne glomerata	2
Vaccinium vitis-idaea	1
Dryas caucasica	4
Carum caucasicum	3
Minuartia circassica	1
Trifolium ambiguum	2
Trifolium trichocephalum	1
Vicia alpestris	1
Primula amoena	1
Alchemilla sericata	1
Ranunculus caucasicus	1
Viola somchetica	1
Leontodon hispidus	1
Anemonastrum fasciculatum	1
Carum alpinum	1
Gentianella caucasica	1
Polygonum viviparum	2
Campanula collina	1
Betonica macrantha	1
Plantago caucasica	2
Selaginella selaginoides	1
Selaginella helvetica	1
Leontodon danubialis	1
Polygala alpicola	1
Polygonum carneum	1
Cirsium obvallatum	1
Ranunculus acutilobus	1
Cruciata laevipes	1
Pyrethrum roseum	1
Ranunculus oreophilus	2
Cirsium simplex	+

(continued)

Table 8.13 (continued)

Parnassia palustris	+
Silene ruprechtii	+
Rhinanthus minor	+
Cirsium pugnax	+
Taraxacum confusum	+
Cerastium purpurascens	+
Minuartia imbricata	+
Scabiosa caucasica	+
Inula orientalis	+

The content of organic water (17–20 %) is rather high in A layer of both phytocoenoses. However, at an altitude of 1,970 m, the same index is 14 %.

8.2.5.2 Temperature Regime

On sunny days the herbages of both phytocoenoses undergo overheating. In Cariceta the lower layers and soil surface represent the "active surface" of conductive heat exchange. For example, the mean diurnal temperature of soil surface is 9.4 °C higher than that of the air at the height of 2 m, and it is 10.5 °C higher – at 1 m.

When studying microclimate and energy balance, we have applied the methods of Cernusca (1976).

Maximum temperature of soil surface is 29 °C, more than that of the air at the height of 2 m.

In Nardeta the overheating of herbage is less than in Cariceta. Solar radiation is allocated over more expansive biomass, which accounts for less overheating. Maximum overheating is observed in the lower 3 cm layer of phytocoenoses. In this layer of herbage, the average diurnal temperature is 6.7 °C higher and maximum temperature is 19.4 °C higher than that of air at the altitude of 2 m. In Nardeta on soil surface the temperature reaches its maximum meaning 2 h later, than at 3 cm higher above soil. This must be provided by a rather thick layer of detritus over the soil, which is characterized by low heat conductivity.

The temperature of leaves is very important for photosynthesis, respiration and transpiration. By the peculiarities of temperature of leaves, both phytocoenoses are of two-layer structure: in lower warm layers of herbage (Cariceta 0–1 cm, Nardeta 0–5 cm) the temperature of leaves is below the air temperature. In Nardeta at the height of 0.5 cm leaves are cooled off on average 1.3 °C during the day, and in Nardeta at the height of 4 cm – on 2.6 °C. Under the influence of wind, intensive convective heat exchange takes place in the upper layer of phytocoenoses. The temperature of leaves here almost equals with that of the air. On the average, the temperature of leaves in Nardeta (height −3 cm) exceed that of the air just by 0.1 °C daily.

Air humidity, especially water vapour pressure gradients between leaves and their environment are very essential factors for many ecosystems.

Fig. 8.11 *Juniperus communis* (Photo O. Abdaladze) in Eastern Central Caucasus

The lack of water vapour pressure at different height levels from the surface of soil distinguishes two layers of phytocoenoses structure. In Cariceta tristis the layer above 1 cm is strongly influenced by wind and dry air; during the one hour (between 1.00 and 2.00 a.m.) the water vapour deficit amounts to 37.6 mbar at the height of 3 cm, whereas at 1 cm above the surface of soil water pressure deficit is only 17.2 mbar.

8.2.5.3 Solar Radiation Regime

On sunny days, daily global radiation equals to 562 cal. Cm^{-2}. In Cariceta tristis 21.9 % of this amount is reflected by leaves, while in Nardeta only 19.2 %. The value of albedo of Cariceta tristis coincides with that of Cariceta curvulae; these communities occur in Hohe Tauern (Cernusca 1976). In Cariceta 358 cal. Cm^{-2} is absorbed in the form of radiation balance, while in Nardeta 338 cal. cm^{-2}.

For Cariceta curvulae in the Hohe Tauern Mts. (Austrian Alps) the radiation balance makes up 66 % of global radiation.

In good weather, 44 % of absorbed solar energy (radiation balance) in *Cariceta* is spent on evapotranspiration, 40.7 % on air heating and 15.3 % on soil heat flow, correspondingly, in Nardeta it is 62.5 %, 28.7 % and 8.8 %.

Consequently, the soil heat flow in Cariceta is twice as much as in Nardeta. It can be accounted for by the fact, that a large amount of radiation is being absorbed in the lowest layers of phytocoenoses (0–0.5 cm) and in the soil surface. Whereas, in Nardeta radiation is absorbed in the upper layers. Besides, Nardeta has a rather dense layer of detritus, which retains the soil heat flow.

Results of the analysis confirm the conclusions based on the studies of dwarf shrub heaths in Patscherkofel (Tyrol) (Cernusca 1976) and alpine heaths in Hohe Tauern mts. Obviously, the structure of phytocoenose (orientation of leaves, shape, height of plants) and exposure have a great impact on the microclimate and energy balance of high-mountain ecosystems. Both of the studied phytocoenoses are of two-layer structure. The upper dry and relatively cool layers are more influenced by wind. The lower warm and moist layers are characterized by negligible wind speed. At the same time, we have found out that the structure of phytocoenose, microclimate and energy balance of Cariceta tristis in the Caucasus is similar to those of Caricetum curvulae in Hohe Tauern.

8.2.5.4 Water Potential

Alpine plants of the Caucasus are characterized by higher value of stomatal conductance than those of Alps (Körner 2003). Absence of stomata closing tendency, which is more pronounced in Nardeta, indicates at good water supply of both phytocoenoses. The values of stomatal conductance and water potential of leaves of *Carex tristis* seems to change in the opposite direction.

Extremely low values of maximum diffusion resistance speak of sufficient water supply and moist growth conditions of the plants, which occur in the alpine belt of Georgia.

8.3 Subnival Vegetation

The subnival belt is well represented in the Caucasus. It is situated between the belt of alpine meadows and that of firm fields at the altitude from 2,900–3,000 up to 3,500–3,700 m a.s.l.

In the Greater Caucasus, lower limit of the above-mentioned belt varies in altitude between 2,900 and 3,100 m, increasing from west to east. Due to the low position of eternal snow line (about 2,800 m) in the western part of the Greater Caucasus, boundaries of subnival belt, represented here fragmentally, are not subject to classification.

8.3.1 Life Conditions in Subnival Zone

Subnival belt of the Caucasus is characterized by moist climate with short cold summer and long severe winter. On the basis of the data of observations by the meteorological station, situated at 3,656 m a.s.l. (Kazbegi), the subnival belt can be characterized by the following figures: mean annual temperature 6.1 °C, mean temperature of January −15 °C, mean temperature of the warmest months (July–August) –10 °C; extreme maximum +16 °C; extreme minimum −42 °C, annual amount of precipitation is 1,074 mm, mean annual wind speed 6.4 m/s.

In the extreme high-mountain conditions life activity of plants is mainly governed by the temperature of boundary air layer.

According to the represented tautochrones (Fig. 8.12) high air temperature during the daytime (from 12.00–13.00 to 16.00–17.00) is observed at 0–10 cm above the soil surface. Temperature of the earth surface runs to high values, but at the depth of 10–20 cm it remains relatively low during the whole day. In the morning, the soil surface temperature is almost always negative.

The role of temperature as a limiting factor becomes more important; excessive solar radiation raises the temperature of soil surface and of boundary air layer, daily temperature fluctuations and evapotranspiration also increase. The role of wind as an ecological factor should be particularly emphasized, as the character of distribution of plants and communities in subnival and nival belts in many respects is dependent on the direction and strength of wind.

According to Larcher (1980; Larcher et al. 2010), Körner (2003), wind direction in high-mountains determines great differences in habitats, water and temperature relations of plants and soil. In respect of the observations produced by the same scholar, rocks, ridges and mountain-sides exposed to wind are less intensively warmed up by sun rays than the elongated cavities and ditches, protected from wind. The efficiency of CO_2 assimilation amounts with the altitude.

The pattern of plant microgrouping distribution, temperature and water relations of habitats, the phenological rhythm type of plants in subnival and especially nival belts are also predetermined by snow cover. In high-mountains some species of plants (chionophobes) are well adapted to low temperatures and others (chionophiles) have low frost resistance (Larcher 1977, 1987; Sakai and Larcher 1987).

One of the clearly defined characteristic properties of high-mountain biomes of diverse globe zones, including subnival and nival belts of the Caucasus, is a great variety of ecological niches within even small territories. Metabolism and plant growth in the extreme conditions of high-mountains are mainly governed by characteristic properties of microclimate of these niches.

Another unfavourable environmental factor affecting the growth of plants at high altitudes, is the ultraviolet radiation. However, due to the high concentration of carotinoids and flavonoids, these plants are well adapted to this factor (Caldwell 1968, 1989).

Physical and geographical conditions of the subnival belt of the Caucasus are particularly extreme, but due to life strategy adaptations, for some plants, typical for this belt, such living conditions are quite optimal.

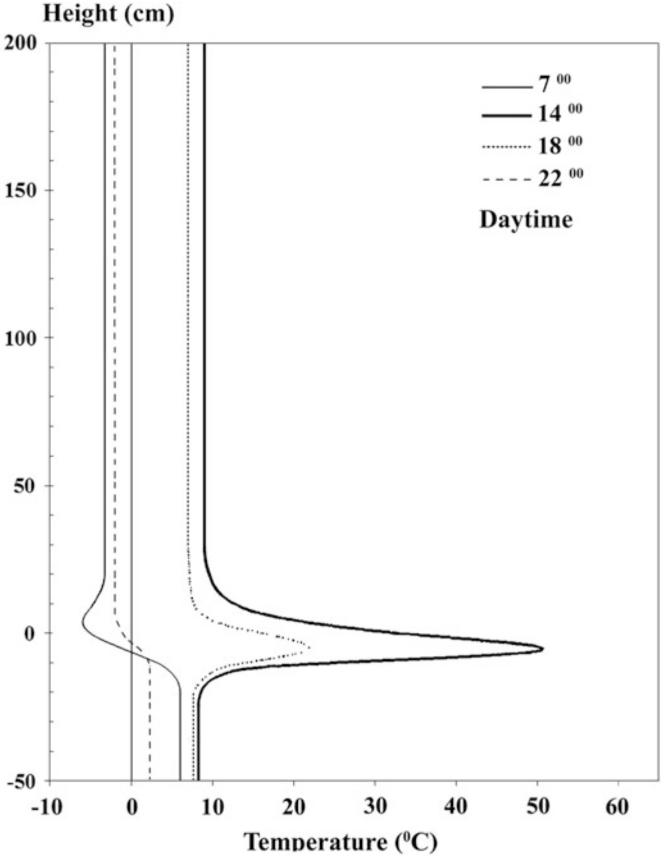


Fig. 8.12 Temperature tautochrones, Elbrus, 3.500 m.a.s.l.

In connection with the absence of terrains with more or less mature soil, almost all the plants of subnival ecosystems are rock and talus plants. Very high percentage of endemic, including also narrow-endemic species are prominent. Some of them fall into mono- or oligotype genera (*Pseudobetckea, Symphyoloma, Pseudovesicaria, Didymophysa, Trigonocaryum, Eunomia, Vavilovia*).

Severe climatic conditions dictate strict reglementation of population viability of every species, which has its own life strategy, habitat, favourable to development of individuals in every population, often scattered at considerable distances create quite often favourable conditions for the development of another one. In this connection, competition between populations of different species often seems to be masked or even eliminated by positive effect of different plant coexistence.

Fig. 8.13 *Cerastium kazbek*, the Central Caucasus (Photo Z. Kikodze)

Besides the peculiarities of climate, a lithologic composition of waste mantle and the degree of differences between high mountain conditions and the conditions similar to ones in edaphic and climatic respects, have a great impact on floristic composition of species, closely related to either rock, in the majority of cases have narrow area, whereas among the species indifferent to lithologic base of waste mantle, one can find fewer endemic species; the species with wide distribution predominate (Dolukhanov 1969).

A large amount of endemic species, which are typical representatives of subnival flora and even endemic genera, present enough grounds to suggest the existence of a suitable floristic complex, within the region, with analogues of high-mountain landscapes, in the geological past, far beyond the Pleistocene (Kharadze 1965).

8.3.2 Flora

Extreme environmental conditions appear in the subnival zone of the Caucasus. Nevertheless, more than 300 species occur here, among them plants which are typical for alpine and sometimes for subalpine belts (Table 8.14). Only 109 species are characteristic for the subnival zone (Kharadze 1965). Location of upper boundary of flowering plants distribution depends on the level of continental climate and on highness of mountain. For example in the highest region of the Greater Caucasus (Elbrus, Shkhara, Kazbegi) flowering plants reach 3,900–4,500 m a.s.l., while in continental Dagestan (East Greater Caucasus) (Prima 1974) and in mountain Aragatz (Lesser Caucasus) (Voskanyan 1976) they occur correspondingly at 3,300–4,000 m. At 4,000 m (Central Caucasus) appears *Cerastium kazbek* (Fig. 8.13) and at 4,000 m (Mt. Aragatz, Lesser Caucasus) *Draba araratica*. The following typical subnival

Table 8.14 List of plants growing in the subnival belt of Georgia

Apiaceae
Chaerophyllum humile
Symphyoloma graveolens
Asteraceae
Aetheopappus caucasicus
Antennaria caucasica
Anthemis iberica
Anthemis sosnovskyana
Erigeron uniflorus
Gnaphalium supinum
Jurinea filicifolia
Jurinella moschus
Jurinella subacaulis
Podospermum alpigenum
Podospermum meyeri
Senecio karjaginii
Senecio sosnovskyi
Senecio taraxacifolius
Taraxacum porphyranthum
Taraxacum stevenii
Tripleurospermum caucasicum
Tripleurospermum subnivale
Boraginaceae
Myosotis alpestris
Brassicaceae
Arabis kazbegi
Draba bryoides
Draba siliquosa
Draba supranivalis
Eunomia rotundifolia
Pseudovesicaria digitata
Thlaspi pumilum
Campanulaceae
Campanula saxifraga
Caryophyllaceae
Arenaria lychnidea
Cerastium cerastoides (=Dichodon cerastoides)
Cerastium kasbek
Cerastium multiflorum
Cerastium polymorphum
Cerastium undulatifolium
Minuartia imbricata
Minuartia inamoena
Minuartia ruprechtiana

(continued)

Table 8.14 (continued)

Minuartia trautvetteriana
Silene humilis
Silene lychnidea
Silene marcowiczii
Crassulaceae
Sedum involucratum
Sedum tenellum
Sedum stevenianum
Cyperaceae
Carex tristis
Fabaceae
Trifolium polyphyllum
Fumariaceae
Corydalis alpestris
Corydalis emanuelii
Murbeckiella huetii
Iridaceae
Crocus scharojanii
Juncaceae
Luzula spicata
Lamiaceae
Lamium tomentosum
Nepeta supina
Thymus nummularius
Ziziphora puschkinii
Ziziphora subnivalis
Liliaceae
Lloydia serotina
Poaceae
Alopecurus dasyanthus
Alopecurus glacialis
Alopecurus vaginatus
Colpodium versicolor
Festuca supina
Poa alpina
Poa caucasica
Trisetum buschianum
Trisetum spicatum
Primulaceae
Androsace albana
Primula bayernii
Ranunculaceae
Delphinium caucasicum

(continued)

Table 8.14 (continued)

Rosaceae
Alchemilla chlorosericea
Alchemilla sericea
Alchemilla caucasica
Potentilla gelida
Sibbaldia semiglabra
Rubiaceae
Galium coronatum
Saxifragaceae
Saxifraga exarata
Saxifraga flagellaris
Saxifraga moschata
Saxifraga ruprechtiana
Saxifraga scleropoda var.nivalis
Saxifraga sibirica
Saxifraga subverticillata
Scrophulariaceae
Scrophularia minima
Veronica minuta
Valerianaceae
Valeriana alpestris
Valeriana saxicola
Pseudobetckea caucasica
Violaceae
Viola minuta

species are found at 3,300–3,800 m a.s.l.: *Saxifraga moschata, S. exarata, S. flagellaris, S. sibirica, Tripleurospermum subnivale, Colpodium versicolor, Alopecurus dasyanthus, Draba supranivalis, Veronica minuta, V. telephiifolia, Senecio karjagini, Cerastium pseudokasbek, Pseudovesicaria digitata.*

A number of endemic species and genera occur in the subnival zone: monotypic genera – *Pseudovesicaria* (Brassicaceae), *Symphyoloma* (Apiaceae), *Pseudobetckea* (Valerianaceae).

From Caucasian-Asia Anterior–South-West Asian genera there are found oligotypic *Coluteocarpus*, *Didymophysa* and *Eunomia* (Brassicaceae), *Vavilovia* (Fabaceae). They are mainly distributed in high mountains of Lesser Caucasus and Asia Anterior–South-West Asia. Almost missing are Cyperaceae and shrubby plants. The same phenomenon is observed in polar deserts (Tikhomirov 1963; Aleksandrova 1983) the composition of the flora with respect to the soils is different. On the volcanic rocks of Keli Elevation has been established flora somehow different from one of mergel slates. High percentage of Caucasian endemics are connected with mergel slates (Dolukhanov 1969). Especially are distinguished limestone-built rocks of Western Caucasus where a number of local endemics appear (Nakhutsrishvili and Gagnidze 1999).

Fig. 8.14 *Delphinium caucasicum* (Photo O. Abdaladze)

8.3.3 Vegetation

Under subnival vegetation we consider the vegetation of a certain altitudinal zone placed between alpine low herbaceous meadows and nerve plain. Distribution of contagious vegetation is limited and open groups dominate mainly.

The following types of vegetation of the subnival zone are noticed.

1. Open groups are formed by one population or by few species of flowering plants, which are not contiguous to each other either by overground or by underground parts. Only biotope and environmental conditions are common for them.
2. Nanocoenoses or ultramicrocoenoses are dominated by individuals of vascular plants sprinking with turfs of certain plants or lichens. Plants contact with underground and overground parts. Nanocoenoses are spread in patches.
3. Fragments of turfy alpine meadows established by grasses and alpine carpets formed by various herbaceous plants. Fragments of alpine meadows have broad ecological amplitude, whereas "carpets" are found only at the snow edges. Overground and underground relationship between plants is well presented.

Large amount of mosses and lichens occur in all types of vegetation.

Mosses: *Bryum* sp., *Dicranum elongatum, Dicranoweisia crispula, Pohlia elongata, Pogonatum nanum, Tortulla tortuosa, Tortulla muralis* etc.

Lichens: *Thamnolia vermicularis, Hypogimnia encausta, Cetraria islandica, C. nivalis, Parmelia vagans, Umbilicaria virginis, Placolecanora melanophthalma, P. rubina, P. murilis, Stereocaulon alpinum, Caloplaca elegans, Umbilicaria cylindrica, Lecidea atrobrunnea, Rhizocarpon geographicum,* etc.

Species from open groups are presented in all biotopes of subnival zone with the exception of snow edges. For example on temporarily moving screes there occur: *Cerastium kasbek, Delphinium caucasicum* (Fig. 8.14); on weekly moving: *Veronica minuta, V. telephiifolia, Scrophularia minima* (Fig. 8.15), *Lamium tomentosum* (Fig. 8.16); – on fixed screes: *Aetheopappus caucasicus, Symphyoloma graveolens,*

Fig. 8.15 *Scrophularia minima* (Photo O. Abdaladze)

Fig. 8.16 *Lamium tomentosum* (Photo O. Abdaladze)

Jurinella subacaulis, J. moschus, Minuartia inamoena, Viola minuta (Fig. 8.17), *Eunomia rotundifolia* (Fig. 8.18); – on rocks: *Primula bayernii, Draba bryoides, Saxifraga moschata, S. exarata*. All these plants are chionophobes or hemichionophobes and are different from each other by living form. Espalier plants are: *Veronica minuta, V. telephiifolia*; – acaulescent rosette plants: *Scrophularia minima, Symphyoloma graveolens, Aetheopappus caucasicus*; – cushions: *Minuartia inamoena, M. trautvetteriana, Saxifraga moschata, S. exarata, Draba bryoides.*

Fig. 8.17 *Viola minuta* (Photo O. Abdaladze)

Fig. 8.18 *Eunomia rotundifolia* (Photo O. Abdaladze)

Almost all above-mentioned plants are typical representatives of the subnival zone and are well adapted to the extreme environmental conditions.

Nanocoenoses are spread in patches through the whole subnival zone of the Caucasus. Their dimensions sometimes are 15–20 cm^2. Number of plant rarely exceeds 4–5 species (Table 8.15). Nevertheless different aged populations are found there: sprouts, juvenils, immature and generative individuals with the whole seasonal cycle (Nakhutsrishvili 1974; Nakhutsrishvili and Gamtsemlidze 1984). Subnival and alpine species are present in all nanocoenoses which give possibility to alpine plants for successful survival and expansion of area.

Table 8.15 Nanocoenoses of the subnival belt (the Mamisoni pass in the central Caucasus)

Screes of southern slopes of 5–7°
Potentilla crantzii – Poa alpina – Symphyoloma graveolens
Poa alpina – Minuartia aizoides – Alchemilla sericea – Anthemis sosnovskyana
Alchemilla sericea – Poa alpina – Anthemis sosnowskyana
Minuartia inamoena – Poa alpina – Symphyoloma graveolens – Anthemis sosnovskyana – Taraxacum stevenii – Veronica gentianoides
Minuartia aizoides – Poa alpina – Symphyoloma graveolens
Arenaria lychnidea – Anthemis sosnovskyana
Minuartia inamoena – Campanula saxifraga – Potentilla gelida
Minuartia inamoena – Minuartia aizoides – Saxifraga exarata – Poa alpina
Minuartia inamoena – Saxifraga exarata – Symphyoloma graveolens – Anthemis sosnovskyana – Poa alpina – Taraxacum stevenii
Arenaria lychnidea – Campanula biebersteiniana – Saxifraga exarata – Taraxacum stevenii
Scree biotope of western exposure (10°) at 3,200 m
Jurinella subacaulis – Saxifraga sibirica
Alopecurus glacialis – Tripleurospermum subnivale – Erigeron uniflorus
Alopecurus glacialis – Tripleurospermum subnivale
Alopecurus glacialis – Sedum tenellum
Poa alpina – Tripleurospermum subnivale – Draba supranivalis
Alopecurus glacialis – Saxifraga moschata
Eunomia rotundifolia – turf of mosses and lichenes
Mergel slates of western exposure at 3,300 m
Saxifraga moschata – Tripleurospermum subnivale
3,350 m Stony scree biotope (Mt. Elbrus)
Potentilla gelida – Carum caucasicum
Potentilla gelida – Minuartia trautvetteriana – Saxifraga flagellaris – Veronica minuta
Minuartia trautvetteriana – Veronica telephiifolia
Tripleurospermum subnivale – Carum caucasicum – Cerastium cerastoides – Veronica telephiifolia – Senecio karjaginii
Tripleurospermum subnivale – Veronica telephiifolia – Senecio karjaginii – Saxifraga flagellaris – Cerastium cerastoides – Anthoxanthum alpinum
Potentilla gelida – Minuartia trautvetteriana – Veronica telephiifolia – Saxifraga flagellaris

Analysis of spatial relationships among species in the subnival zone of the Central Caucasus in 300 vegetation patches showed that 144 of the studied patches contained only one species, whereas the other 156 contained 2.36 ± 1.31 species, with species numbers distributed as follows: 59 patches with two species, 41 with three, 39 with four and 17 with five species.

In the multi-species patches, the 22 most frequent species were examined and 46 statistically significant species associations, 36 positive and 10 negative, were found. Ten of these 22 species were typical subnival plants very rarely occurring at lower altitudes. The other 12 species are “invaders” as they have broader altitudinal ranges of occurrence and are common in alpine and even in the subalpine zones. Contrary to the typical subnival species the invaders were found exclusively

Table 8.16 Basic nanocoenoses of the subnival belt of the Mamisoni pass bu the altitudinal gradient

3,000 m
Alchemilla sericea – Poa alpina – Sibbaldia semiglabra
Saxifraga moschata – Alchemilla sericea – Minuartia aizoides
Festuca supina – Campanula biebersteiniana – Carum caucasicum – Alchemilla sericea
3,200 m
Alopecurus dasyanthus – Saxifraga moschata – Minuartia inamoena
Tripleurospermum subnivale – Scrophularia minima – Delphinium caucasicum
Alopecurus dasyanthus – Tripleurospermum subnivale – Erigeron uniflorus
Alopecurus dasyanthus – Sedum tenellum
Taraxacum stevenii – Campanula biebersteiniana – Carum caucasicum
3,300 m
Saxifraga moschata – Tripleurospermum subnivale – Alopecurus dasyanthus
Alopecurus glacialis – Cerastium polymorphum
Erigeron uniflorus – Lamium tomentosum – Potentilla gelida
3,400 m
Delphinium caucasicum – Saxifraga moschata – Lamium tomentosum
Tripleurospermum subnivale – Colpodium versicolor – Ziziphora puschkinii
Eunomia rotundifolia – Tripleurospermum subnivale
Saxifraga moschata – Cerastium cerastoides
3,500 m
Saxifraga moschata – Eunomia rotundifolia – Senecio karjaginii
3,600 m
Saxifraga moschata – Cerastium kasbek

in the patches with more than one species. Invader species were significantly more associated with subnival species while they were significantly less associated with other species than expected by chance. An interpretation is that typical subnival species nurse plants from lower altitudes and facilitate their invasion to more adverse subnival environments (Kikvidze and Nakhutsrishvili 1998).

Nanocoenoses are presented almost in all biotopes of subnival zone especially in the schistous substrate.

They often reach great altitudes, for example in Mamisoni Pass nanocoenoses decrease only from 3,600 m a.s.l. (Table 8.16).

The floristic composition of nanocoenoses occurring on the same relief is very alike.

To assess the homogeneity of vegetation in horizontal structure was studied by the method of Raunkiaer (Braun-Blanquet 1964). Three sections of Mamisoni Pass and one section placed at the foot of Mt. Elbrus were explored. Was used circle (diameter 35.6 cm) restricting circle 1/100 m^2 of area 50 times. In brief, this method states that the vegetation of any surface is floristically homogeneous when the classes of higher frequency in the diagrams contain more number of species and the classes of lower frequency, accordingly, contain less number of species and vice versa.

The first section is located at 2,950 m on the western slope of 5–7°. General cover is 30–40 %. From typical subnivale species here occur: *Aetheopappus caucasicus*, *Symphyoloma graveolens*, *Jurinella subacaulis* etc. Mainly are dominated species from alpine zone. Homogeneity of vegetation is low. The following plants have the greatest frequency: *Minuartia oreina, Veronica gentianoides, Anthemis sosnovskyana.*

Second section is situated on southern slope of 5–6° at 3,000 m. Cover is 30–40 %. Here appear subnival species: *Aetheopappus caucasicus, Silene marcowiczii, Symphyoloma graveolens*. However, still dominate species from alpine zone. Homogeneity is low as well. Greatest frequency is observed for *Minuartia oreina* and for *Aetheopappus caucasicus* and *Campanula saxifraga.*

The third section is placed on western slope of 5–7° at 3,100 m. Cover of vegetation is 20–30 %.

There occur subnival species: *Alchemilla sericea, Saxifraga moschata, Symphyoloma graveolens*. Nevertheless, presence of alpine plants prevail over subnival ones. Homogeneity is low.

Fourth section is located at the foot of mt. Elbrus (3,350 m). Mesorelief is plane, strongly stoned. With the subnivale species – *Minuartia trautvetteriana, Saxifraga flagellaris, Veronica minuta* – there appear typical alpine plants: *Carum caucasicum, Poa alpina, Cerastium cerastoides*. The following species have the high frequency: *Carum* caucasicum, *Veronica minuta, Potentilla gelida, Minuartia trautvetteriana, Saxifraga flagellaris*. Consequently, a little more homogeneity is characteristic for subnival zone especially on the transitional places from alpine and subnival belt.

Fragments of turfy meadows and alpine carpets are well developed in subnival belt. Ellenberg (1996) calls these fragments “Rasenstьcke” and he considers that they are typical primary alpine meadows. Reisigl and Pitschmann (1958) call the above-mentioned fragments “Pionierrasen” and the zone of their distribution “Pionierrasenstufe”. Ellenberg accounts them as a formed and stabile climax association and refuses their farther development because of strongly restricted habitat. Composition of species very often remains to be stabile for the years.

Festuca varia, F. supina, Nardus stricta and other grasses form fragments of alpine meadows. Below is a list of some species appearing on the southern slope of 12–15° at 3,100 m (Mamisoni Pass, Greater Central Caucasus).

1. *Festuca varia*
Carex tristis
Poa alpina
Potentilla crantzii
Anthemis sosnovskyana
Campanula biebersteiniana
Anemone speciosa
2. *Festuca varia*
Alchemilla sericea

(continued)

Betonica macrantha
Poa alpina
Carex tristis
Anthemis sosnovskyana
Polygonum carneum
Taraxacum stevenii
Leontodon hispidus
3. *Festuca varia*
Poa alpina
Anthemis sosnovskyana
Aster alpinum
Veronica gentianoides
Campanula collina
4. *Festuca varia*
F. supina
Alchemilla caucasica
Carex tristis
Minuartia oreina
Veronica gentianoides
Polygonum carneum
*Leontodon hispidu*s
5. *Festuca supina*
Minuartia oreina
Poa alpina
Anthemis sosnovskyana
Campanula saxifraga
Taraxacum stevenii

One can notice that the species of alpine meadows dominate but there appear plants from alpine carpets – *Taraxacum stevenii*, *Campanula biebersteiniana*, from scree habitats – *Anthemis sosnovskyana* and typical subnival landscapes – *Alchemilla sericea*. As in nanocoenoses fragments are formed by a small number of species, however here they occur in a large amount rather than in nanocoenoses. In more extreme environmental conditions are established fragments dominated by *Kobresia schoenoides* and *Carex tristis* appearing mainly on windy slopes of subnival zone and by alpine species – *Campanula biebersteiniana, Gnaphalium supinum, Taraxacum stevenii, Poa alpina* etc.

Fragments of alpine carpets or “Dikotylen-Teppiche” by Ellenberg (1996), Onipchenko and Blinnikov (1994) are established on moist places especially where snowbeds remain for the long time. On snow free places plants occur in better temperature conditions. There dominate espalier (*Minuartia aizoides, Sibbaldia semiglabra*) and rosette life forms (*Taraxacum stevenii*, *Plantago saxatilis* etc.)

Below is a list of species collected at 3,250 m on the southern slope of Mamisoni Pass:

Poa alpina
Carex medwedewii
Minuartia aizoides
Sibbaldia semiglabra
Taraxacum stevenii
Luzula pseudosudetica
Campanula biebersteiniana
Carum caucasicum
Saxifraga flagellaris
Mosses
Dicranum elongatum
Pohlia elongata
Pogonatum nanum
Tortulla tortuosa
Lichenes
Thamnolia vermicularis
Cetraria islandica
C. nivalis
Parmelia vagans etc.

Vegetation of alpine carpets often develops between large stones and screes, where stones keep snowbeds and on snow free places as well. Stones protect plants from strong winds and after heating give them supplementary warmth (Aleksandrova 1983; Nakhutsrishvili 1998a, b; Nakhutsrishvili et al. 1990). Below is a list of species occurring among stones in the subnival zone of mt. Elbrus at 3,350 m a.s.l.:

Minuartia aizoides
Campanula biebersteiniana
Potentilla gelida
Veronica minuta
Festuca supina
Carum caucasicum
Saxifraga flagellaris
Draba siliquosa
Alchemilla chlorosericea
Senecio karjaginii

Fragments of alpine carpets and turfy meadows as well are distinguished from real alpine meadows and carpets by appearing of species of subnival zone such as: *Veronica minuta, Saxifraga flagellaris, Senecio karjaginii* etc.

At the 3,100–3,350 m one can notice such extrazonal phenomenon as appearing of *Salix kasbekensis* on morains, slopes in Truso gorge (Kazbegi) and in Mamisoni Pass. We consider that it is a result of local foehns, when temperature increases while relative moisture decreases.

8.3.4 Life Forms

In the process of a long evolution, subnival plants have developed, along with metabolic and biochemical adaptive mechanisms, pronounced morphological qualities aiding in maximum warmth consumption, water loss prevention, protection against wind, drying up and withering caused by high temperatures of substratum surface. There are many plants with widely spread vegetative shoots (*Symphyoloma graveolens, Pseudovesicaria digitata, Scrophularia minima*) in this belt. There are also many plants with shoots creeping along the ground (*Veronica telephiifolia var. glareosa, Lamium tomentosum, Tripleurospermum subnivale*). Trailing and widely spread shoots of plant should be undoubtedly regarded as a form of adaptation to several environmental conditions, in particular, as a response to overheating of the substratum and to strong winds.

Dense-cushion plants (*Saxifraga subverticillata, S. ruprechtiana, S. moschata, Draba bryoides*) and loose-cushion plants (*Minuartia brotherana, M. inamoena*) are typical for the high-mountains of the Caucasus (Nakhutsrishvili and Gamtsemlidze 1984). Plant propagation ability is of special importance in the subnival belt with a thinned plant cover. This undoubtedly depends on the individual mobility of one or another species. 28 out of 91 investigated species were qualified as vegetative immobile (*Symphyoloma graveolens, Scrophularia minima, Jurinella subacaulis)* (Fig. 8.19). The other 63 species are vegetative mobile (*Minuartia inamoena, Veronica minuta, Cerastium polymorphum*). Few species belong to the type of vegetative highly mobile species, such as the plants with slight horizontal mobility. Perhaps this regularity can be accounted by severity of these ecotopes and the corresponding high degree of insufficiency in vegetative mobility of species.

Two groups of plants can be singled out in accordance with the nature of leaf downiness. The first group includes plants with undowny leaves (45 species): *Phryne huetii, Corydalis emanueli, Viola minuta*. In the second group are plants with downy leaves (46 species): *Alchemilla sericea, Aetheopappus caucasicus, Lamium tomentosum, Cerastium kasbek*. Downiness of plants protects them from strong solar radiation and from sever overheating of leaves. Among the plants with undowny leaves there are species with succulent or semisucculent types of leaves. For example, *Eunomia rotundifolia, Pseudovesicaria digitata, Tripleurospermum subnivale* and all species of *Saxifraga*, as well as the species with twisted leaves (*Festuca supina, Trisetum buschianum, Arenaria lychnidea*).

Eighty three species of investigated subnival plants of the Central Caucasus appeared herbaceous. The other eight species (*Sibbaldia parviflora, Ziziphora puschkinii*) are semi-shrubs (Fig. 8.19).

There are 81 species of polycarpics among the investigated plants, the other 10 species are monocarpics. The latter can be subdivided into perennial and biennial plants (Fig. 8.19). According to the data presented by Gamtsemlidze (1977), monocarpic annual plants are unavailable in the subnival belt, although some monocarpic plants of this belt (*Senecio sosnovskyi*) behave as annual monocarpic plants.

According to Raunkiaer classification, hemicryptophytes prevail in the subnival belt (Fig. 8.19).

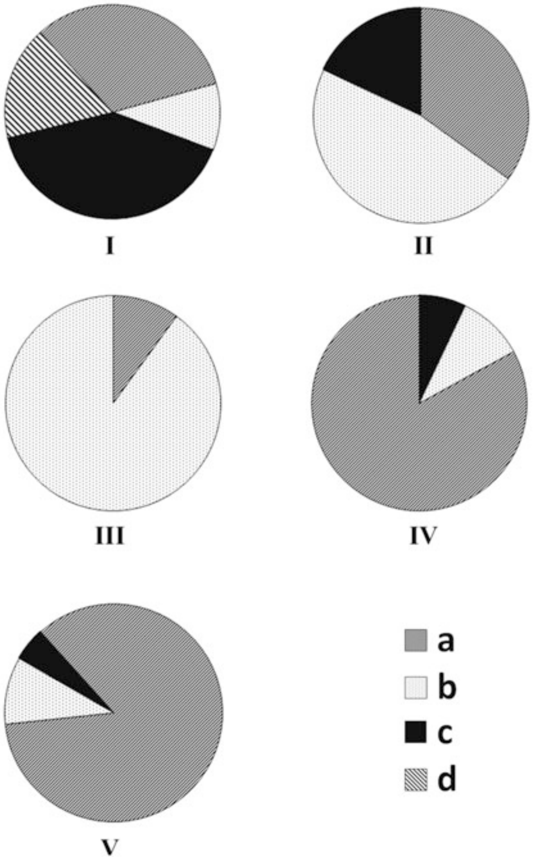


Fig. 8.19 Subnival plants comparison. Comparison of subnival plants with respect to the ecological-biomorphological indices: **I** - with respect to the way of specimen mobility: a - vegetatively immobile type; b - vegetatively poorly mobile type; c - vegetatively moderately mobile type; d - vegetatively intensively mobile type. **II** - with respect to the character of leaf downiness; a - plant leaves with downiness on both sides; b - plants with undowny leaves; c - plants with smooth upper and downy lower surface. **III** - with respect to shoot lignification: a - dwarf semi-shrubs; b - herbaceous plants. **IV** - with respect to lifespan: a - polycarpic; b - perennial monocarpic; c - biennial monocarpic. **V** - with respect to the type of plant reproductive bud position: a - hemicryptophyte; b - chamaephyte; c - geophyte (Nakhutsrishvili, Gamtsemlidze 1984)

Rhizome, taproot and rhizome-taproot plants are the most prevalent biomorphes in the subnival belt. There are much less mat-forming plants here. Tuberiferous plants are rarely found. Almost all the plants of this belt are characterized by intensive branching of underground organs near the surface of substratum.

Thus the subnival and nival belts are specified quite a large variety of life forms, notwithstanding their poor floristic composition; almost every species displays an independent life form. The variety of the life forms of plants, scattered on rocks, mounds and glaciers, enables them to use completely different ecological niches within a very restricted territory.

The most typical features of life forms of subnival belt plants are the following:

1. Out-spread, prostrate and cushion-shaped forms of the growth;
2. Miniaturization;
3. Not deeply penetrating into the ground downiness organs and widely branched near the substratum surface.

The out-spread and prostrated growth forms of the these plants promote:

(a) Maximum warmth consumption from the substratum surface warmed-up in sunny weather.
(b) Wind protection.
(c) Hibernating under snow cover which sometimes is not very thick.

Cushion-shaped plants form their microhabitat due to intensive orthotropic branching and spherical position of leaves and, thus, regulating the temperature relations and physiological processes under sever conditions of the belt.

Miniaturized life form “a very characteristic feature of humid alpine plants” is one of the important adaptive qualities for hibernating under a snow cover.

Downiness and succulence of leaves favour plant adaptation to the subnival and nival ecotopes with instable water relations protecting the stomatal apparatus from stress influence of wind and dry air, and establish an equalized water vapour concentration between leaves and the air around them (Larcher 1975; Cernusca 1976; Körner 2003). Besides leaf succulence ensures diurnal Crassulacean acid metabolism (CAM-plants), which under sharp temperature changes and in dry periods results in CO_2 uptake by plants at night.

Underground organs widely branched near a substratum surface provide active water absorbtion in the morning as soon as the soil begins to thaw. Another characteristic feature of underground organs of subnival and nival is their shallow rooting (about 15–20 cm) which protects them from cold lower layers (opposite data were obtained in the Alps (Körner 2003)). Even the longest underground organs at a certain level of depth (20–30 cm) begin to grow in horizontal direction (Nakhutsrishvili and Gamtsemlidze 1984).

8.3.5 Reproductive Buds

Buds of herbaceous plants may be bare (without special bud scales), protected (with spacial bud scales), and proleptic (with bud scales which in autumn begin to burst and new shoots leave their shells).

According to Gamtsemlidze (1979), in the subnival belt in severe winter conditions reproductive buds are covered by the residues of dead parts of plants and sheathes of dead leaves *(Jurinella subacaulis, Symphyoloma graveolens)*. But sometimes they occur in the surface layer of soil (*Lamium tomentosum, Cerastium polymorphum*) or deep in soil *(Delphinium caucasicum)*. Perennating buds of *Saxifraga sibirica* are covered by rosette-forming nodules which are partly in soil.

Reproductive buds of such wintergreen plants like *Saxifraga exarata, S. ruprechtiana* are protected by frame green leaves. A bud covering of plants which have protected proleptic buds is formed by solid bud scales and dead old leaves *(Scrophularia minima, Senecio karjaginii).*

It is characteristic that many subnival plants have stipules fitted closely to the base of stem and protect reproductive buds from damage *(Alchemilla sericea).*

Along with these adaptations for safe wintering of subnival plants snow cover protection is very important for reproductive buds. According to the data the biggest group of investigated plants is with bare buds (40 %), then the group with proleptic buds (35 %) and the smallest group is with protected buds (25 %).

The point is, what determines such a great amount of plants with bare reproductive buds in the subnival belt. There are a number of opinions on this problem. According to Serebriakov (1961): "The absence of bud scales in arctic and alpine plants is connected with fact that their scales are remetamorphosed into green assimilative leaves, which usually hibernate under the protection of a snow cover and partly under the protection of a cover of moss. One of the factors for the remetamorphosis of bud scales into green leaves in Tundra zone and high-mountain alpine belts was a considerable shortening of a vegetation period. Plants get an opportunity to extend the period of photosynthetic activity through remetomorphosis". Savile (1972) explains unprotection of reproductive buds with scales by the fact that hard scales hinder rapid spring development and hence, the plants are unable to adapt to short arctic vegetation period.

By the state of the next year shoot in reproductive buds at the end of the vegetation period, subnival plants could be divided into two groups: (1) plants with completely formed shoots in buds including not only vegetative organs but also inflorescenses and single flowers; (2) plants in the buds of which only the vegetative part of a shoot is formed, the inflorescence and flower germs appearing during the next vegetation period.

As much as 68 species out of 78 investigated subnival plants (88 %) possess generative shoots in reproductive buds which are born in the year before flowering (group 1) and only 10 species in the year of flowering (group 2).

According to the degree of flower development in reproductive buds the first group can be divided into three subgroups:

1. Next year flowers of reproductive buds are completely formed: sepales, a corolla, stamens, a pistil are developed (Fig. 8.20) (*Primula bayernii, Scrophularia minima*)*;*
2. Next year flowers of productive buds are formed incompletely: sepales, petales, stamens are developed completely, the pistil is unformed (Fig. 8.21) (*Saxifraga sibirica, Potentilla gelida, Alchemilla sericea, A. chlorosericea, Draba siliquosa, Jurinella subacaulis*)*;*
3. Inflorescenses and flowers of reproductive buds are not differentiated or start differentiating (Fig. 8.22) (*Senecio karjaginii, S. taraxacifolium, Tripleurospermum subnivale, Alopecurus glacialis, Delphinium caucasicum, Erigeron uniflorus*).

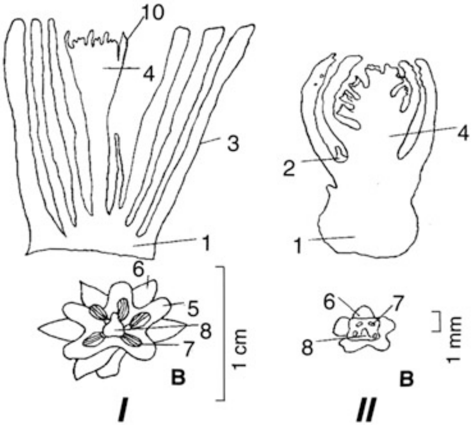


Fig. 8.20 *Primula bayernii*

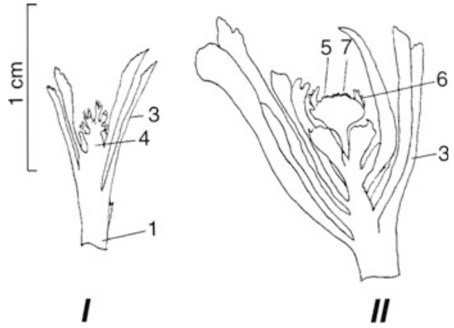


Fig. 8.21 *Alchemilla sericea* and *Potentilla gelida*

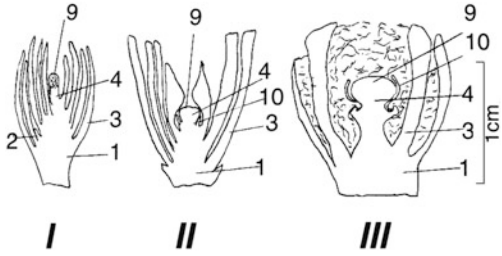


Fig. 8.22 *Alopecurus glacialis, Senecio taraxacifolius, S. karjaginii*

Profound studies of the subnival belt in the Tyrolean Alps (Ladinig and Wagner 2009; Steinacher and Wagner 2010) showed that flower differentiation in buds still continues except *Cerastium uniflorum*, in which flower emergence begins only 4–6 month prior to flowering and their opening is different in various species. For instance this period lasts 11 months in *Saxifraga oppositifolia*, 12–18 months in *Primula glutinosa* and *Saxifraga bryoides* and 24–26 months in *Ranunculus* *glacialis*. *R. glacialis* one of the flowering plants of the Alps extends to the highest zones. During the first year of the vegetation period stem buds appear at the base of old generative organs of the species, the flower cover and the first circle of stumen turn up before autumn. Next year the flower buds complete their development and in mid-August they turn into large closely situated flower buds (3–4 mm) and are ready to open with incompletely differentiated 1 year flower buds. Next spring the old buds open and the young ones continue to develop into new flower buds. *R. glacialis*, owing to such a periodical development of flowers retains the ability to flower every year in unfavourable conditions of vegetation.

Further development of flower buds of the plants, which are under snow cover during the whole summer stops for a while or at least slows down. Next year after the snow melts, these plants are able to bloom again, but their flowers will be plain and wretched. The plants (*R. glacialis*) covered by snow probably the germinated flowers perish. Such behaviour which is called "opportunistic" is contrary to the type of rapidly differentiating species (*Primula minima, P. glutinosa, Saxifraga oppositifolia*). Flower primordia of these species develop in July. In August, at the end of vegetation, the development of the originated flowers is completed, first of all among the plants located near the edge of glaciers. *S. oppositifolia* flowers immediately after the snow melting and just before the growth of vegetative parts begins. Under the conditions of habitat with much snow and extremely short period in comparison with the vegetative development is favourable, as due to high cold-resistance of flowers (10–15 °C), these species are able to enter a productive phase early and without any damage. Their seeds become ripe in cool summer. In the Pamirs (Steshenko 1967) it was also found that the majority of species have next year flowers and inflorescenses, originated in reproductive buds. High percentage of plants with previously originated inflorescenses and flowers can be observed in tundra (Nakhutsrishvili and Gamtsemlidze 1984).

8.3.6 Phenorhythmotypes

Phenorhythmotypes of the plants can be distinguished on the base of their phenological adaptation to environmental peculiarities. Taking into consideration a period favourable for vegetation in typical habitats, they can be distinguished by the behaviour of vegetative plants, that is, by the beginning and process of germination, by formation of leaves, their ageing, yellowing and defoliation, by the growth, germination and hibernation of buds (Borisova 1972; Larcher and Nakhutsrishvili 1982).

Below we give the phenorhythmotype classification of subnival plants.

A. Plants with Continuous Leafing

1. Evergreen plants: *Saxifraga ruprechtiana, S. scleropoda, S. exarata*
2. Summer-wintergreen plants:

Obligate summer-wintergreen plants: *Draba bryoides, Veronica minuta, Sedum tenellum, Saxifraga flagellaris, Antennaria caucasica*

Facultative summer-wintergreen plants: *Potentilla gelida, Viola minuta, Senecio karjaginii, Alopecurus glacialis, A. dasyanthus, Alchemilla sericea, Sibbaldia semiglabra, Ziziphora puschkinii, Tripleurospermum subnivale, Colpodium versicolor, Cerastium kasbek.*

B. Plants with Periodical Leafing

1. Summergreen plants with winter dormancy: *Scrophularia minima, Jurinella subacaulis, Phryne huetii, Chaerophillum humile, Valeriana saxicola, Silene marcowiczii, Minuartia inamoena, Anthemis sosnovskyana, Erigeron uniflorus, Delphinium caucasicum, Lamium tomentosum, Cerastium polymorphum, Symphyoloma graveolens, Aetheopappus caucasicus, Nepeta supina.*
2. Spring and early summergreen plants with the late summer-winter dormancy: *Corydalis alpestris, C. emanueli, Draba supranivalis, Primula bayernii, Arabis kazbegi.*
3. Late summergreen and autumn plants with summer-winter dormancy: *Crocus scharojanii, C. suworowianus.*

Among these groups summergreen plants with winter dormancy have the most widespreding (46.9 %), then come facultative summer-wintergreen (23.4 %), and spring-early summer-green with late summer-winter dormancy (9.4 %), the obligate summer-wintergreen (9.4 %), evergreen plants (7.8 %) and late summergreen-autumn (3.1 %) with summer-winter dormancy.

8.3.7 Temperature of Plants

Under extreme conditions of high-mountains the temperature of plants is one of the most important indicators of their life activity since it presents the true background for physiological processes when the amount of effective air temperature is small (Gorishina 1979; Körner and Larcher 1988).

Mountain plants show high leaf temperature and they should be included into the group of supratemperature plants which probably have high protoplasmic resistance. Such plants are identified as high temperature species (according to Kreeb 1974).

In the subnival belt of the Caucasus a very distinct surface temperature differentiation of species in accordance with surface temperature of plant organs is observed. Such species as *Potentilla gelida*, *Veronica minuta, Alopecurus dasyanthus* (Fig. 8.23), *Jurinella subacaulis*, have especially high temperature (29–30 °C). Leaf position of these plants in relation to the substratum is planophylic. All these species are spread to the upper line of flower plants. In comparison with other species *Potentilla gelida* is specified by the highest temperature in the West Pamirs, at the altitude of 4,750 m above sea level, as well as in the Caucasus (unpublished data by Gamtsemlidze and Chkhikvadze). Difference of leaf- air temperatures around the investigated plants amounts to 12–16 °C and 21–25 °C.

Fig. 8.23 *Alopecurus glacialis* (Photo O. Abdaladze)

Leaves of *Saxifraga moschata, S. kolenatiana*, semisucculent *Tripleurospermum subnivale* and leaves of plants with intensive downiness – *Anthemis sosnovskyana, Aetheopappus caucasicus* – warm-up relatively less. The lowest leaf temperature (23–25 °C) is recorded in coshion-plants – *Sibbaldia semiglabra, Minuartia inamoena*.

Plants with a high temperature of leaves also have the high temperature of flowers. In the investigated plants except cushion ones the temperature of flowers at noon is always lower than that of leaves. Very low temperatures of leaf surface (−4–6 °C) were registered early in the morning at great heights, when the plants turned into icicles. However, these plants thaw very slowly as they were shadowed by huge-boulders (otherwise they would have died). Temperature of leaves reached 28 °C and by 18–19 °C exceeded that of air. Subnival plants with prostrated and outstretched leaves over the substratum surface have to protect themselves against overheating when the temperature of leaves is much lower than that of substratum promoting normal water regulation and photosynthesis.

8.3.8 Structure of the Photosynthetic Apparatus

Structural adaptations related to photosynthetic activity play essential role in the adaptation of plants to habitat conditions, providing great ecological plasticity of the photosynthetic apparatus (Gorishina et al. 1985).

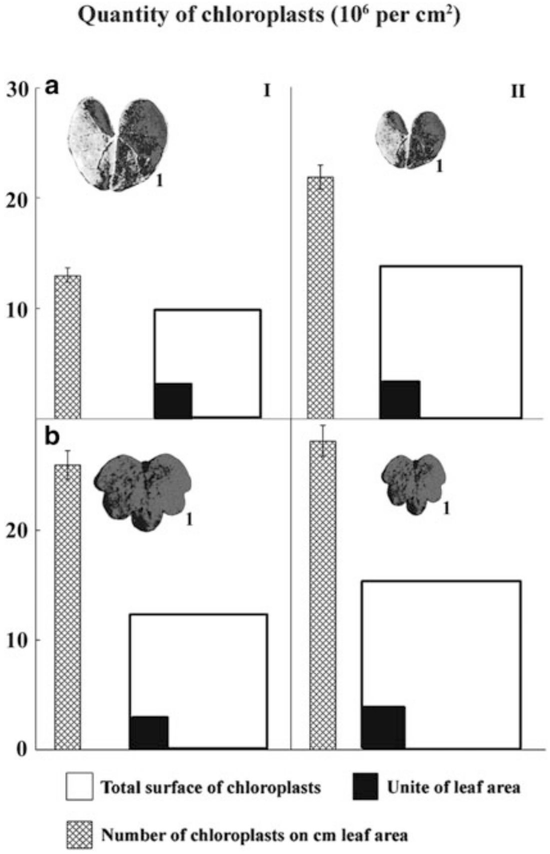
Among the investigated plants there are species with rather thin dorsivental lamellate leaves *(Oxyria elatior, Saxifraga sibirica)*, as well as with the isopalissade ones (*Astragalus kazbegi)* with the centric leaves of similar ones *(Arenaria lychnidea, Tripleurospermum subnivale)*, sometimes without clear differentiation of mesophyll between palissade and spongy tissues (*Ziziphora puschkinii*). The leaf structure of some species has distinct features of succulence. Leaf structure type is not closely connected with habitat conditions and shape of mesophyll cells. For instance, *O. elatior, S. sibirica* have narrow and elongated cells of palissade tissue, *S. juniperifolia*, has shorter and more rounded ones. As a rule, the cells of spongy tissue are round, the composition of the tissue being dense without big intercellural spaces. The cells of palissade tissue are packed very tight.

The investigated species are characterized by well-developed plastid apparatus. The mesophyll cells are filled densely with numerous chloroplasts, with their total volume being 10–30 % of the cell volume. The value of surface density of chloroplasts in leaves reaches 100,000–120,000/cm^2 accordingly the total surface chloroplasts is large. These peculiarities of the plastid apparatus are typical of the plants growing in habitats exposed to bright light. Such heliophilous plants grow in arid deserts, sea side littorals, deciduous forests in early spring as well as some in subalpine grasslands of the Caucasus. The values of the same indices in shade-requiring mesophytes are by an order more (Gorishina et al. 1985). Chloroplasts are usually small (*O. elatior* excluded) with very low chlorophyll content. This fact enables us to assume the presence of an ultrastructure with poorly developed system typical for the plants growing in the habitats exposed to bright-saturation. Chlorophyll content per unit of area and raw mass of the leaf is also not high (1.5–4 mg/dm^2 and 0.5–1.5 mg/g accordingly).

Light-requireness – “xerophilous” peculiarities of plants which can be called the “oreophytes” are expressed in different ways. They are best manifested in subnival oroxerophytes which inhabit rocks and talus and growing under the influence of substratum dryness and overheating. However, microhabitat conditions can be quite different even in these places. For example, the indices of plastid apparatus of *Saxifraga juniperifolia*, preferring more oversdaded and damp crevices, as a whole are mesophilous (small volume of chloroplasts in the cell and leaf, high concentration of chlorophyll in the chloroplast). The change reactions, e.g. under extreme conditions one of the orophil properties of the inner structure of leaves in plants, growing at the edges of a glacier or in hollows are expressed to a lesser degree. Only *Veronica telephiifolia var. glareosa*, having perennial green leaves and showing the trophorhythmotype of obligate-summer-winter green stands by itself (Larcher and Nakhutsrishvili 1982).

It was stated that the photosynthetical apparatus has considerable plasticity, manifested in the variability of leaf size and the indices of inner structure-surface density of chloroplasts etc. (Fig. 8.24). When the surface of a leaf varies in 3.5–4 times, the total reserve of plastids in the leaf varies in a more or less degree (1.5–2 times), as such diminution of the size of a leaf partially compensated by a considerable increase of the number of chloroplasts per unit of the leaf surface. That is to say, the plants growing in extreme conditions lose the reserve of chloroplasts in their leaves in a less degree in comparison with the loss of an assimilative surface that is important for the preservation of photosynthetic abilities of leaves. Chlorophyll content in chloroplasts differs substantially depending on a microhabitat (Fig. 8.25): both its total mass and concentration are slightly higher in species, growing in canopy.

Fig. 8.24 Change of leaf characteristics



8.3.9 CO_2-Gas Exchange

In extreme conditions of high-mountains in the Caucasus the assimilative period of anthophytes is short (60–70 days). However, even during this time the assimilation period can be interrupted by frost or draught. Plant species respond to such extreme ecological conditions by different CO_2 gas exchange reactions, e.g. under the extreme conditions one of the groups of species had adaptable type of gas exchange, while in others the process of CO_2-gas exchange was rather stable (Nakhutsrishvili and Gamtsemlidze 1984; Abdaladze and Kikvidze 1991; Abdaladze 1994).

The plants of the first type are characterized by "impulsive" diurnal dynamics of net-photosynthesis (Fig. 8.26), frequent depressions of the CO_2 assimilation process, being accompanied by raising of stomatal diffusion resistance. The values of net-photosynthesis, diurnal productivity of photosynthesis, diurnal balance of CO_2-gas exchange and photosynthesis efficiency (high percentage of absorbed light energy stored in chemical links carbohydrates) should be considered as the

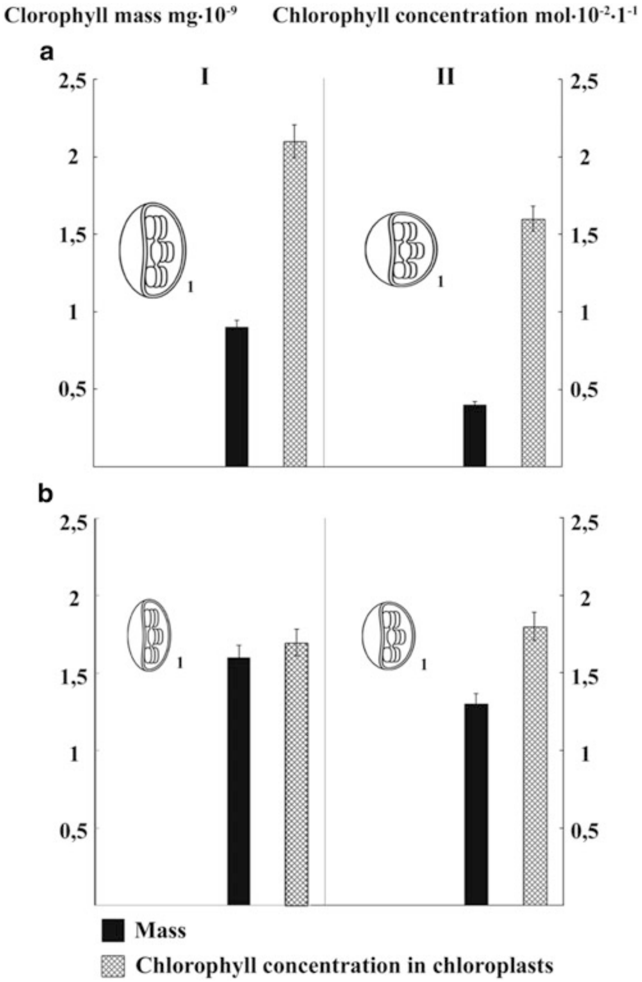


Fig. 8.25 Plant chloroplasts in different ecological microniches

distinguishing characteristic of the given type of CO_2 gas exchange. The plants showing the stable type of CO_2 gas exchange (succulent *Saxifraga kolenatiana),* cushion-shaped (*Minuartia inamoena*) are characterized by absolutely opposite indices (Table 8.17).

Subnival plants, as well as other mountain plants are characterized by a very high net-photosynthesis. It should be noted that plants which are not distinguished by high intensity of photosynthesis (e.g. *Saxifraga kolenatiana)* demonstrate their economy by way of moderate use of assimilants that is displayed in very low intensity of dark respiration (Fig. 8.27).

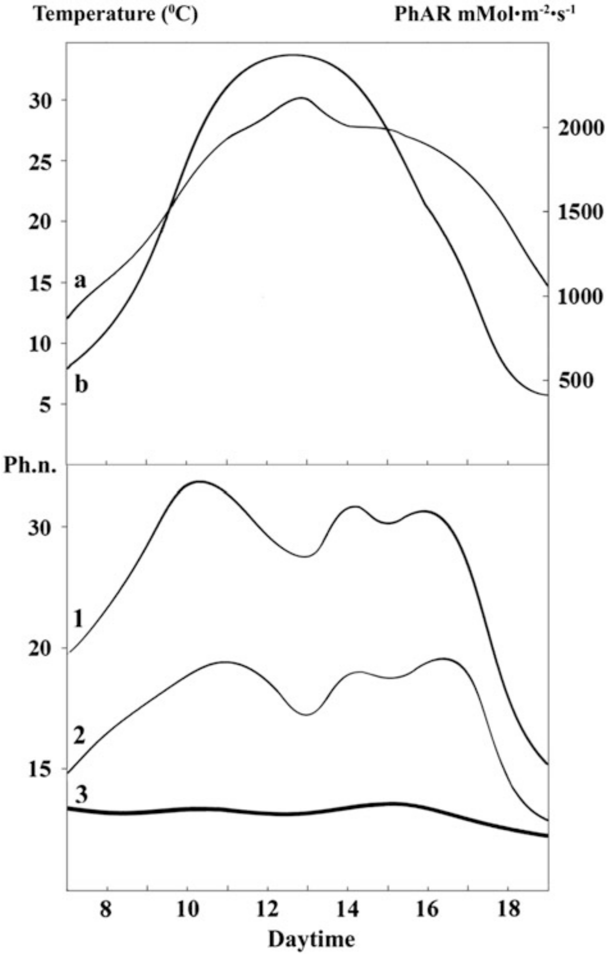


Fig. 8.26 Air temperature. PhAR and Net-Photosynthesis

Subnival plants are also characterized by wide temperature optimum of net-photosynthesis and well developed repair ability of assimilative apparatus (Moser 1973; Nakhutsrishvili and Gamtsemlidze 1984; Abdaladze 1994).

8.3.10 Diffusion Resistance of Leaves

"Xeromorphic" structure as well as trailing and cushion forms of plant growing promote stomatal apparatus regulation in the extreme conditions of high-mountains (Larcher 1975; Cernusca 1976; Körner 2003).

Table 8.17 CO_2-gas exchange of plants in the subnival belt of the Mamisoni pass at the altitude of 3,000 m s. m. (from Abdaladze 1994)

Species	Maximum net photosynthesis mg CO_2 dm^{-2} h^{-1}	Diurnal productivity mg CO_2 dm^{-2} per day	Daily balance of CO_2-gas exchange mg CO_2 md^{-2} 24 h	Photosynthesis efficiency %
Saxifraga kolenatiana	6,3	50	38	4,2
Arenaria lychnidea	42	277	230	20
Aetheopappus caucasicus	20	125	86	11
Alchemilla sericea	23	136	102	10
Minuartia inamoena	6,5	55	–	–

As is generally known, the higher the altitude the higher diffusive conductivity and duration of stomatal openings gaping. The main reason of this is lower pressure (Körner and Mayr 1980; Sanadiradze 1986; Körner 2003), responsible for the high level of plant evaporation at high altitudes.

Stomata diffusion resistance in the water relations and CO_2 gas exchange regulation of plants perform a very important function in the conditions of the subnival belt, where plants are isolated from each other and experience the impact of heavy dryness and heating of substratum. Diffusion conductivity in the majority of investigated subnival plants is rather high (1.5–1.7 cm s^{-1}).

As shown in Fig. 8.22, the highest level of conductivity of leaves with sharp fluctuations is observed in *Veronica minuta, Tripleurospermum subnivale, Senecio karjaginii* and *Potentilla gelida.* The *Saxifraga* species is characterized by low conductivity of leaves. No wonder that the values observed in this species *(Alopecurus dasyanthus)* are so small because of the ability of grasses to reduce the conductivity of water.

Majority of subnival plants are characterized by sharp diurnal water conductivity fluctuations. For example very often in the afternoon when high temperatures of substratum surface (50 °C and over), high levels of solar radiation (PhAR may extend up to 2,400–2,450 micromol m^2 s^{-1}) and in this respect the increased leaf temperatures (up to 300 C) occur, heavy depressions of water conductivity are observed. These depressions in different plants are manifested in different degrees.

Usually water conductivity in *Tripleurospermum subnivale* and *Veronica minuta* at noon compared to morning hours falls by 88–96 % (Fig. 8.28). Low midday deviations can be noticed in *Saxifraga* species, especially in *S. sibirica,* which at very high altitudes grows only under boulders. Almost flat curve of diurnal water conductivity was displayed by cushion-plants, e.g. *Sibbaldia semiglabra*, a dwarf

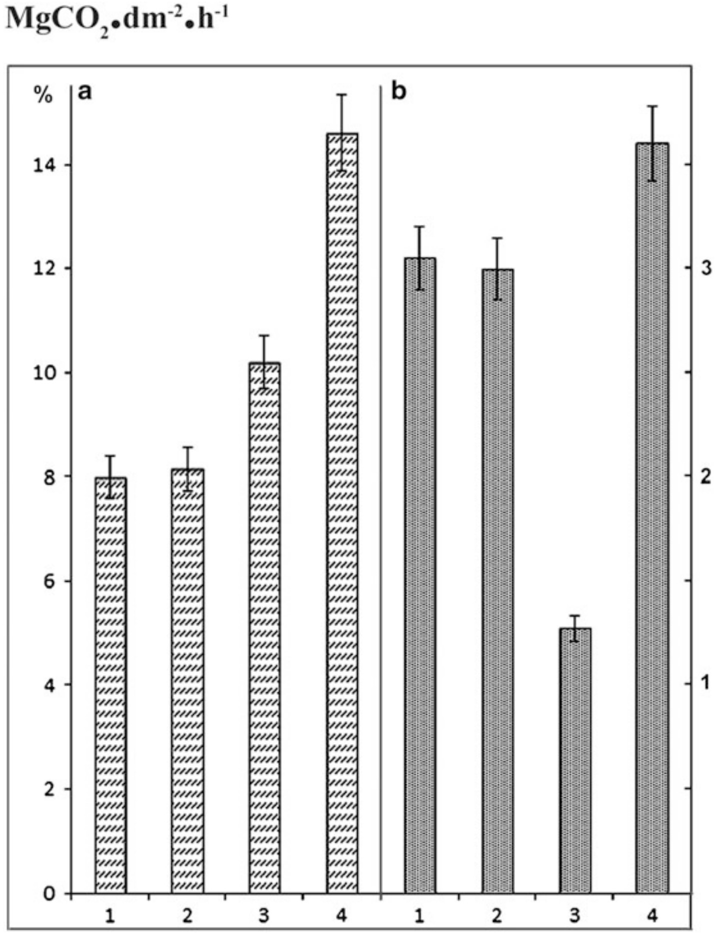


Fig. 8.27 Economical coefficient of Photosynthesis and dark respiration

subshrub. However at high altitudes in unclosed communities average diurnal conductivity of leaves falls.

Average values of total diffusion resistance of leaves in the subnival belt of the Elbrus (3,500 m a.s.l.) at low wind velocity.

Table 8.18 shows data on total water diffusion resistance (rt). So called leaf boundary layer resistance is very important for transpiration. Its share in investigated species except *Tripleurospermum subnivale* as compared to subalpine grasses is smaller than the share of stomatal resistance (rl). Thus in extreme life conditions (especially in the plants growing in open places exposed to strong winds) stomatal play the most vital role in water – relations of plants.

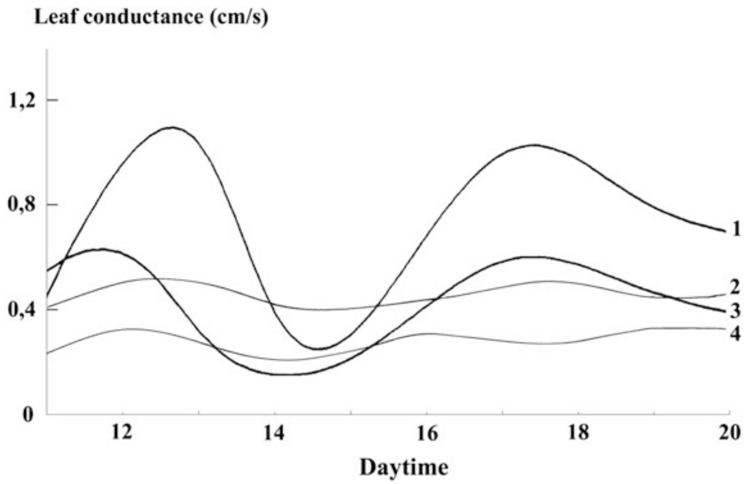


Fig. 8.28 Leaf conductivity of subnival plants

Table 8.18 Average values of the total diffusion resistance of the leaves of plants in the subnival belt of the Elbrus (3,500 m) at low wind velocity

Species	r_1	r_2	r
Veronica minuta	5.38	3.11	2.26
Tripleurospermum subnivale	3.6	1.52	1.50
Alopecurus dasyanthus	7.30	5.75	1.54

Plants growing in severe life conditions of high-mountains acquire reactivity potential after being exposed to extreme temperature (Semikhatova 1965; Larcher 1980; Zalensky 1982). This has been confirmed by the results obtained in the course of observations of diffusion resistance of stomata in morning hours, i.e. after the impact of negative temperature of air (−2.50 C), of substratum surface (−1.6 °C) and of leaf (−3.0 °C). In all species after sunrise (630–1,010 μmol m^{-2} s^{-1}) and with the increase of air temperature (10 °C) and substratum temperature (5.0 °C) leaf conductivity amounts up to 0.75–1.15 sm s^{-1}. Trailing plants, such as *Veronica minuta*, *Tripleurospermum subnivale* and the grass *Alopecurus dasyanthus* actively respond to the solar radiation and rise of temperature. Whereas *Senecio karjaginii* (plant with erect stalk and equally distributed leaves) reacts less actively and its leaf conductivity stays below 0.21 sm s^{-1}.

8.3.11 Leaf Water Potential of Plants

Plants of subnival belt possess high transpiration and water potential values (Nakhutsrishvili and Gamtsemlidze 1984). The question is whether water balance becomes equalized in the extreme conditions of high mountains. Larcher (1983) considers that water potential reflects any alterations in water balance as its tension immediately provokes loss of turgor and subsequent growth of water potential.

Very often the increase of PhAR and temperature of the boundary air layer and leaves results in the reduction of water potential of most subnival species. *Saxifraga* species are characterized by rather stable water potential, though.

A certain correlation has been observed between conductivity and water potential of leaves. Minimum conductivity of leaves corresponds to the minimum values of their water potential. In the diurnal course of water potential, we have noticed an interesting regularity, which is well manifested in the plants of highlands, after the morning temperature stress (Fig. 8.29). Water potential undergoes gradual reduction until quite low values at noon. It restores in the second half of the day, due to the growth of diffusion resistance.

It is interesting to compare leaf water potential of plants in the Central Caucasus and in the Pamirs. Observations carried out by Gamtsemlidze and Chkhikvadze (unpublished data) in the region of the Fortambek Glacier (north-west region of the Pamirs) at the height of 4,000–4,750 m above sea level, show that water potential of leaves in the Pamirs is 2–3 times lower than the same index in plants of the Caucasus (the Elbrus). The minimum water potential of plants in the Pamirs is 2.8–3.3 MPa. Water potential in *Potentilla gelida* in the Caucasus amounts to 5–11 MPa, whereas in the Pamirs it is 1.1–2.5 MPa. It should be noted, that at high altitudes of the Pamirs (4,750 m) water potential of leaves, which is rather low, can still reduce to 3.0 MPa, e.g. in *Waldheimia glabra*.

8.3.12 Discussion and Conclusions

Subnival and nival ecosystems (viz. microecosystems) scattered among rocks and mounds, consist of a small number of anthophyte species. Thanks to adaptation they can survive in severe life conditions. High-mountain inhabitants obtain the quality to resist such factors as low temperature and frosts during the vegetation period, warmed-up substratum, hurricane wind and besides, low carbon dioxide content and the pressure of water vapour in the air. These plants have a short vegetation period and a great deal of chionophiles stay under a thick snow cover during 18 months.

Apparently, evolution of plants here, in contrast to the alpine and subalpine belts is aimed at the selection of species with high resistance against heavy physical conditions; here competition seems to be less important for the selection of species.

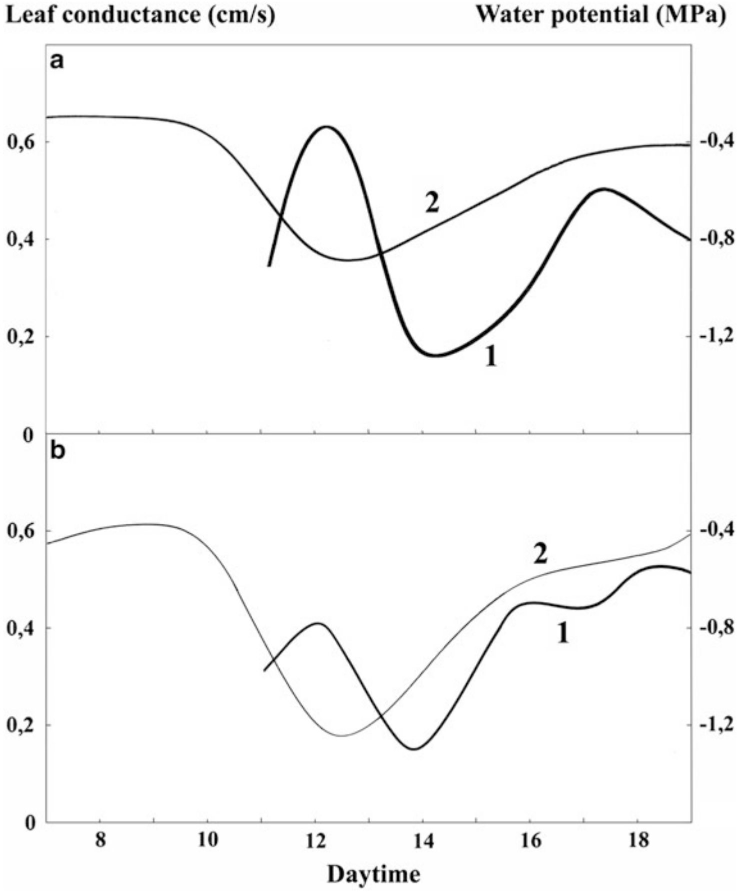


Fig. 8.29 Relations between leaf conductance and water potential

Severe climatic and edaphic conditions have a strong impact on the structure of plant cover. Vertical structure of plant groupings in the subnival and nival belts is characterized by the absence of stratum differentiation and unclosed horizontal structure. Unlike other altitudinal belts root systems here are closed only in case of penetration by one plant into the tufts of another, which leads to the formation of micro-and ultramicrogroupings.

Subnival belt displays a great variety of life forms, despite a restricted number of species; in extreme life conditions almost every species demonstrates an individual life form with its typical ecophysiological reaction to environmental changes. Probably, this accounts for the fact that various species of plants individually adapt to their existence within the same ecotope.

Analysis of life forms of plants of this belt revealed the prevalence of widely prostrate and cushion-plants with downy and semisucculent leaves. The subnival belt is also characterized by vegetative-movable plants, which form clumps and patches. They provide the security of widely represented rock-talus ecotopes. According to the Raunkiaer system the most frequent life forms here are illustrated by hemicryptophytes and chamaephytes. These life forms were caused by the adaptation of plants to the subnival ecotopes, which are subject to the impact of day-night temperature fluctuations and strong wind, the latter is of particular importance.

High-mountain biomes are very rich in diverse life forms, especially the mountains of the torrid zone. Every mountain system and every altitudinal belt involves specific life forms which are typical only for them. For example, mountains of the torrid zone are characterized by rosette-like megaphytes, large bunches of tussock grasses, downy and thorn plants; in arid high mountain regions prevail cushion and prostrate dwarf subshrubs and shrubby plants. Humid high mountain regions of temperate zones represent trailing shrubs and dense turf plants, small delicate grass species, and cushion-shaped, rosette-like, trailing and prostrate herbaceous plants which dominate in the extreme conditions of the subnival and nival belts. In alpine tundra the prevalent life forms are shrubs and small shrubs. In general, humid high-mountain regions of temperature and high latitude zones are characterized by tiny life forms as compared to the tropical and arid (low latitude) mountains (Nakhutsrishvili 1981)

Plants growing at high altitudes of both tropical and temperate zones are characterized by “xeromorphism” particularly by strong downiness, succulence, twisting of leaf, its thickening and substitution by thorn, etc. (Nakhutsrishvili 1974; Larcher 1975). These properties were regarded as a reaction of plants to water deficiency or poor mineral nutrition. The recent data advised by Larcher (1975) suggest that small pressure of water vapour and the state of stomata along with other factors, determine the “xeromorphism” of plants. Water deficiency, caused by freezing of soil is observed in different high-mountain biomes (Alps, Andes, Caucasus, etc.) occurring only at night or in the morning. During the rest of time, plants absorb water from soil.

Körner (2003) observed that the degree of stomatal opening is subject to the effect of dry air of high-mountain regions; various species react to dry winds (foehns) differently. Any increasing of the resistance of leaf boundary layer through their downiness, succulence, twisting protects the stomatal apparatus from strong influence of dry air and wind and establish a equalized concentration of water vapour of leaf and its environmental water. As a result of the scientific observation conducted by Cernusca (1976) it was found that the analogous effect was observed in the plants which have cushion and trailing growth forms. According to Larcher (1975) the ecological benefit of so called xeromorphic structure of high-mountain plants is in the levelling of air humidity fluctuations and, thus in maintaining (through the system of stomatal apparatus) the diffusion resistance of carbon dioxide gas and water at a comparatively optimum level.

Generative tissue, reproductive buds in particular, has decisive significance for plant adaptation to severe environmental conditions. Subnival plants are mainly characterized by bare and proleptic opening buds. Only a small number of species have closed ones. The majority of subnival plants have perennating reproductive buds in which flowers and inflorescences appear beforehand, that is one of the essential signs of adaptation of these plants to a very short period of vegetation.

The analysis of plants distribution in their habitat with different thickness of snow cover showed (Nakhutsrishvili and Gamtsemlidze 1984) that the number of species considerably increased from the minimum snow zone to the maximum one. The least number of species accounted for the maximum snow zone. Unlike other altitude belts in the subnival belt, there are the least number of chionophobous plants. In this belt as well as in tundra so called greenhouse effect is apparent in spring. It must be mentioned that in such "greenhouse" the vegetation period begins about 2 weeks earlier in comparison with one in the conditions of an open biotope.

The beginning of plant vegetation depends mainly on the periods of snow cover disappearance and so fluctuations have especially pronounced character at the beginning of it. Mass vegetation of plants in the subnival belt is observed only from the end of June till the end of September and the beginning of October (depends on snow fall). The first flowering species appear in the only in the second 10-day period of June reaching their culmination in the second half of July. The flowering period in the given belt is observed foe a rather long time, that lasts till the second half of September. During this period plants can hardly be found in the alpine and often in the lower subalpine belt.

Even the smallest territories of the subnival belt of the Greater Caucasus were rich in various phenorhythmotypes. Both, evergreen with summer-wintergreen species can be found there. Summergreen plants with winter dormancy were the prevailing phenorhythmotype of the subnival belt. Then comes facultative summer-wintergreen plants.

We came to the conclusion that plants growing at the highest altitudes were presented by high-temperature species which could survive in extreme conditions. Leaf temperature in sunny weather rises on average, than the ambient temperature and falls by the same degrees below the temperature of substratum surface over which leaves and shoots of subnival plants prostrate. The transpiration favours the hydrothermal regulation of plants not only in steppes and deserts but also in subnival conditions. In differentiation of plants in respect of temperature of their organs, the architectonics of plants, particularly the pattern of the position of their leaves in relation to the sun rays and highly warmed-up substratum is of high decisive importance. On the basis of example it is possible to consider the plants of cushion-shaped life from which is widely distributed almost in every biome with extreme conditions. According to our investigation the plants of such life form as opposed to many species are not overwarmed and at noon in sunny weather their leaf temperature is always optimal. Probably, such homeostasis is due to a ultramicrohabitat created by a specific form of growth of these plants. Their temperature conditions become favourable for active water exchange and carbon assimilation. The same function can be carried out by turf. Some of the plants not typical for the subnival belt and without such adaptive mechanisms, turn yellow and wither form intensive solar radiation in August.

Tolerance limits as to the temperature stress in the most subnival and nival plants are rather high, e.g. these plants may be due to their recover ability, leave the stress very quickly in spite of the fact that during a day leaf temperature varies from −2, −5 °C to +30, +34 °C. Specifically, diffusion resistant of leaves decreases, water exchange and assimilation activity of plants are restored.

Temperature conditions of plants and their environment have a large extent an impact of diffusion resistance of leaves. Almost all the species investigated were found to be sensitive to stomata regulation. Plant with erect stocks are subject to winter influence to a greater degree and during a day period their stomatal conductivity varies. As it is apparent, basically in extreme conditions of subnival belt, diffusion resistance of leaves has to perform the function of water balance and CO_2 gas exchange of plants.

As a whole a water relations of subnival plants is well regulated although the cases of considerable rise of water low level, considerable reduction of water content in leaves and water potential, elevation of osmotic pressure and water conductivity reduction are observed in many species. That is why all the subnival plants which have been investigated, except succulents, are included in the group with hydrolabile species and at the same time, with euryhydrous (Nakhutsrishvili and Gamtsemlidze 1984).

It is quite natural that peculiarities of water relations has an influence on carbon exchange of plants. For instance, the plants with low water content and high degree of water shortage are characterized by low intensity of photosynthesis. Midday depression of photosynthesis often observed at noon are mainly the result of increased diffusion resistance of leaves caused trees environmental conditions. Night frosts and midday depressions are the factors which limit day and seasonal course of photosynthesis. However, due to the recover ability of plants, their assimilation activity is restored rapidly after temperature stresses.

One of the most important strategies of plant survival in unfavourable conditions of high mountains is a high temperature optimum of net-photosynthesis. On the basis of our work we concluded that a short period of assimilation in extreme high-mountain conditions may be sufficient for a considerable carbon accumulation.

Thus, there are species with absolutely different mechanisms of adaptation to the habitat conditions within small territories, they are micro and ultramicrogroupings.

During a long period of evolution, high mountain plants have acquired ability to survive and reproduct in extreme conditions. The principal mechanism of plant adaptation are the following:

- Growing species via the medium of both caintagius and individual distribution of plants among rock, latus and glaciers.

- Formation of various specialized forms of growing resulted in the protection against the impact of unfavourable habitat conditions.
- Completion of seasonal development cycle of plants in a short period of vegetation.
- Early origination of almost all plant organs including all parts of flowers in reproductive buds.
- Final formation of leaves after more favourable ecological conditions coming.
- High leaf resistance to sharp daily fluctuations of temperature.
- High temperature of leaves with their thermoregulation capacity, which assure active assimilation activity and water exchange of plants.
- Regulation of physiological processes which manifest itself due to diffusion resistance of leaves.
- High temperature optimum for photosynthesis.
- High level of photosynthesis in the period between unfavourable weather conditions and low dark respiration in plants with poor photosynthetic activity resulting in economical expenditure of assimilants.
- Well developed recover capacity in plants after stress impact.
- The tendency to leaf succulence formation for optimum keeping of water balance and assimilation activity.
- Long under-snow-cover stay of plants due to considerable accumulation of organic matter reserve in underground organs.
- The variety of life forms, pheno-and trophorhythmotypes within the strongly limited territory demonstrating the species ability to occupy and develop their ecological niche.

In the conclusion we find it necessary to describe some distinctive characteristics of plants growing in extreme conditions of high-mountain regions of the Caucasus.

There are small or no such plants as bushes, dwarf shrubs, representative of sedge family in the subnival and nival ecosystems as opposed to alpine meadows having common border line with them. In such conditions root systems are closed very seldom and territory of unclosed vegetation cover; polygonal nature of relief –that is the most characteristic property of the alpine belt-is hardly marked. As the altitude increases the activity of species decreases. In the subnival and especially nival belts the species activity are not enough or inactive (e.g. *Cerastium kazbek*).

It must be outlined that the analogous regularity has been revealed by Aleksandrova (1983) as related to polar desert. This geobotanical region as well as the subnival and nival belts is characterized by small number of flowering plants, the absence of bushes and representatives of sedge family, the uncloseness of vegetation cover of species activity and etc.

When passing from the alpine belt to the subnival sharp changes of plant growth form is observed (cushion plants and prostrate ones predominate). In extreme conditions of high mountain regions the species with "xeromorphic" features hold a dominating position as opposed to mesophilous plants which are typical for the alpine belt.

Subnival and nival belt plants unlike the species of alpine belt are characterized by peculiar rhythmological features and physiological processes. For instance, they differ from each other by impulsive and peaked curves of efflorescence and two pronounced maxima of flowering. Diversity of aspects of ultramicrogroupings and aggregations is observed in the subnival belt even in the late summer phase of plant development while in the subalpine and alpine belts only some flower species. (Nakhutsrishvili and Gamtsemlidze 1984). Aspects change in vegetative groupings is expressed neither in extreme conditions of polar deserts nor in the nival belt (Aleksandrova 1983). Interrelations of physiological processes with environmental factors is more tense in subnival plants than e.g. in alpine or subalpine plants in the conditions of closed grass cover. In the first case, in spite of high species ability to adapt to the unfavourable conditions, strong overheating of assimilative surface of plants, photosynthesis depression and sharp increasing of leaf diffusion resistance are often observed.

Unlike the alpine belt, plant ecological stress in the subnival and nival belts becomes heavier due to the absence of closed vegetation cover (basically grass sods) promoting the development of various homeostatic mechanisms.

The species growing in the subnival and nival belts in the period of their formation experienced the climatic stresses caused both by sharp fall of temperature and its rise. Undoubtedly, these plants were witnesses of the period of volcanic activities when they had to adapt themselves to the existence conditions of extreme with high concentration of carbon dioxide gas, mobile and highly warmed-up substratum, etc.

Only such high adaptation ability of these plants to comparatively big number of external factors helps them to survive in conditions of extreme press. The plants adapted to such wide range of changing ecological conditions are the representatives of the most ancient flora of high mountain regions of the Caucasus.

8.4 High Mountain Plant Community Diversity

Vegetation of the humid climate orobiomes is characterized by high sensitivity and its irrational use frequently results in severe erosion. One example in point is Kazbegi region where plant diversity and endemism level are fairly high (Sakhokia and Khutsishvili 1975). Over 20 % of the Caucasian flora and all vertical zones of the Caucasus are represented here (Fig. 8.30); particularly high plant diversity is observed in the upper montane and subalpine zones.

The upper montane zone of Kazbegi region experiences strong anthropogenic stress, in particular, it is negatively influenced by urban areas, overgrazing, conversion of traditional hay fields to pastures, etc. Plants of almost all the vertical zones can be found there. A range of contrasting phytocoenoses is diverse including steppe, rock and scree tragacanth vegetation, of the one hand, and wetlands and meadows, on the other (Table 8.19). The majority of the coenoses are found on plain areas but some of them also occur on quite steep slopes. Meadows Bromopsieta variegatae, Hordeta violaceum Festuceta variae are distinguished by high specific diversity. Moist meadows Blysmo-Phragmitetum and eroded meadow-steppe Bromopsio-Festucetum contain relatively small number of species (Table 8.19).

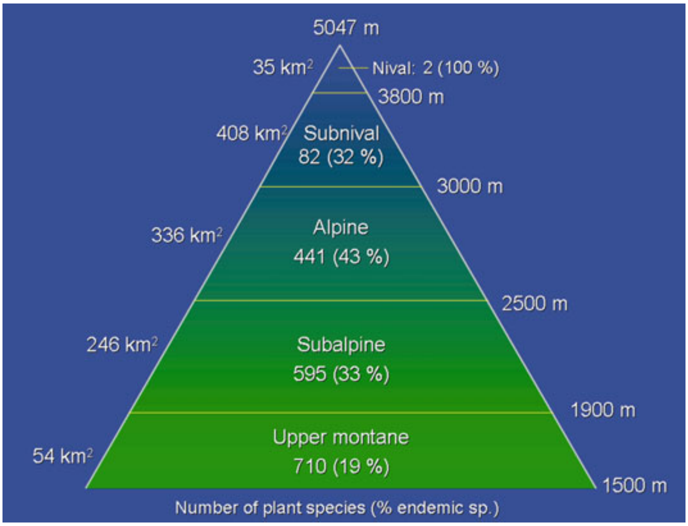


Fig. 8.30 Plant species diversity by altitudinal gradient in Kazbegi mountains

In subalpine zone Festuceta variae, Agrostio-Bromopsietum, Calamagrostieta are the coenoses with high number of species. It should be noted that meadow-steppes Festuceta ovinae, Koelerieta are also characterized by high floristic diversity (Table 8.19). The subalpine tall herb vegetation Heracletum is very poor in species.

In alpine zone the general vegetation background is similar to that in subalpine zone; floristically rich as well as poor coenoses can be found there. For instance, still Festuceta variae is the coenosis distinguished by high specific diversity. Nardeta is another floristically rich coenosis. Festuceta supinae, Kobresieta capiliformis contain small number of species.

Rhododendretum caucasici also does not contain high number of species.

Statistic analysis has shown that correlation between species richness (at 25m^2) and elevation is weak negative ($r=0.3$, p,0.05, $n=39$). It has revealed as well weak relationships between species richness and the following habitat parametres: community height, plant cover, slope inclination ($r=0.3$, $r=0.4$, and $r=0.4$, respectively; $p<0.05$, $n=39$). The number of species (per area unit) is abruptly dropped only above 2,800–2,900 m a.s.l.

8.5 A Comparative Analysis of the High Mountain Vegetation of the Caucasus and the Alps

The characteristic feature of high mountain vegetation of the Caucasus is the development of xero – and hemi-xerophytic vegetation, i.e. feather-grass steppes, steppe meadows, thorny cushion plant communities and meadows of the Lamiaceae family at the treeline and in the lower reaches of the alpine zone. These communities are not found in the high mountains of the Carpathians, the Alps

Table 8.19 Diversity of plant community of central Caucasus according to the altitude gradient

Plant communities	m.a.s.l. (m)	Inclination (°)	Exposition	Community height (cm)	Cover %	Number of species per 25 m
Upper montane belt						
Bromopsio – *Festucetum valesiacae*	1,740	0	O	40	70	25
Blysmo – *Phragmitetum australis*	1,740	0	O	60	80	20
Agrostio tenuis – Bromopsietum variagatae	1,750	0	O	40	95	20
Deschampsio cespitosae – Hordeetum violaceae	1,750	0	O	50	95	21
Triseteto rigidum – Festucetum ovinae	1,750	0	O	70	60	23
Festuco ovinae – Bromopsietum variegatae	1,750	5	W	50	90	21
Astragaletum denudatus	1,750	40	OS	70	60	23
Deschampsio flexuosae – Equisetetum arvense	1,750	0	O	30	90	21
Agrostio tenuis – Festucetum pratensis	1,800	0	O	100	100	30
Hordeetum violaceae	1,800	5	N	60	100	22
Hordeetum violaceae	1,800	2	S	100	100	28
Trisetetum rigidae	1,800	5	NO	50	70	27
Bromopsietum variegatae	1,800	15	NO	50	100	43
Poo pratensis – Hordeetum violaceae	1,800	2	W	70	100	27
Trifolio fontanum – Hordeetum violaceae	1,800	2	SW	70	100	27
Agrostio tenuis – Bromopsietum variegatae	1,850	25	NW	40	100	34
Agrostio tenuis – Bromopsietum variegatae	1,850	5	W	120	100	25
Hordeetum violaceae	1,850	5	W	160	100	25
Hordeetum violaceae	1,850	2	W	120	100	22
Hordeetum violaceae	1,850	3	W	15	70	22
Festucetum valesiacae	1,850	25	NW	60	95	38
Hordeetum violaceae	1,870	3	S	80	100	41
Agrostio tenuis – Bromopsietum variegatae	1,870	2	S	40	80	38

(continued)

Table 8.19 (continued)

Plant communities	m.a.s.l. (m)	Inclination (°)	Exposition	Community height (cm)	Cover %	Number of species per 25 m
Festuco ovinae – Agrostietum tenuis	1,870	0	O	50	80	23
Festucetum ovinae	1,897	15	S	70	95	33
Subalpine belt						
Cariceto meinshausenianae – Festucetum variae	1,900	30	W	70	100	32
Festucetum ovinae	1,900	5	S	50	100	27
Festucetum ovinae	1,900	5	S	20	90	26
Agriostio tenuis – Bromopsietum variegatae	1,900	5	S	50	100	29
Agrostio tenuis – Bromopsietum variegatae	1,900	5	S	50	95	33
Bromopsio variegatae – Agrostietum tenuis	1,900	25	SWS	50	90	33
Bromopsio variegatae – Koelerietum luerssenii	1,900	20	SWS	15	90	26
Bromopsio variegatae – Festucetum ovinae	1,900	30	S	50	70	23
Agrostio tenuis – Bromopsietum variegatae	1,900	20	SW	50	90	26
Agrostio tenuis – Bromopsietum variegatae	1,900	0	O	40	90	28
Agrostio tenuis – Bromopsietum variegatae	1,900	1	O	50	95	30
Bromopsio variegatae – Agrostietum tenuis	1,900	5	S	50	100	29
Agrostio tenuis – Bromopsietum variegatae	1,900	0	O	50	100	54
Bromopsio variegatae – Festucetum ovinae	1,900	10	S	40	70	21
Bromopsio variegatae – Festucetum ovinae	1,900	3	SO	40	80	23
Agrostio tenuis – Bromopsietum variegatae	1,900	15	NW	50	80	22
Bromopsio variegatae – Scabiosetum caucasici	1,900	5	S	50	100	22
Bromopsio variegatae – Agrostietum tenuis	1,910	3	S	40	90	41

(continued)

Table 8.19 (continued)

Plant communities	m.a.s.l. (m)	Inclination (°)	Exposition	Community height (cm)	Cover %	Number of species per 25 m
Agrostio tenuis–Festucetum ovinae	1,940	10	NW	50	90	43
Agrostio tenuis – Bromopsietum variegatae	1,945	3	SW	50	90	52
Cariceto meinshausenianae – Festucetum variae	1,950	35	NW	80	100	28
Cariceto meinshausenianae – Festucetum variae	1,950	40	SW	75	80	26
Cariceto meinshausenianae – Festucetum variae	1,950	30	WN	80	100	39
Cariceto meinshausenianae – Festucetum variae	1,950	35	SW	70	80	47
Cariceto meinshausenianae – Festucetum variae	1,950	30	WN	80	40	29
Nardetum strictae	1,950	9	NO	40	100	27
Nardetum strictae	1,950	10	NO	40	100	29
Agrostio tenuis – Bromopsietum variegatae	1,950	15	S	40	100	33
Helictotrichono asiaticus-Bromopsietum variegatae	1,950	10	S	40	95	28
Helictotrichono asiaticus-Bromopsietum variegatae	1,950	5	S	40	95	35
Bromopsio variegatae – Koelerietum luerssenii	1,950	15	S	50	95	25
Agrostio tenuis – Bromopsietum variegatae	1,950	20	SW	50	100	38
Agrostio tenuis – Bromopsietum variegatae	1,950	10	S	40	95	28
Agrostio tenuis – Bromopsietum variegatae	1,950	15	S	40	100	35
Cariceto meinshausenianae – Festucetum variae	1,950	35	NW	70	100	39

(continued)

Table 8.19 (continued)

Plant communities	m.a.s.l. (m)	Inclination (°)	Exposition	Community height (cm)	Cover %	Number of species per 25 m
Medicagini glutinosae – Bromopsietum variegatae	1,950	15	S	40	90	19
Bromopsio variegatae – Agrostietum tenuis	1,950	5	S	30	90	27
Festucetum ovinae	1,960	30	SW	40	90	40
Agrostio tenuis – Bromopsietum variegatae	1,970	30	N	70	100	38
Calamagrostietum arundinaceae	1,970	30	N	70	100	38
Festucetum ovinae	1,970	25	S	50	90	38
Agrostio tenuis-Bromopsietum variegatae	1,970	25	SW	50	90	38
Festucetum ovinae	1,980	20	S	50	95	27
Bromopsio variegatae – Festucetum ovinae	1,980	20	S	50	95	27
Bromopsio variegatae – Festucetum ovinae	1,980	20	S	50	90	24
Agrostio tenuis-Bromopsietum variegatae	1,980	20	S	30	95	27
Agrostio tenuis-Bromopsietum variegatae	1,980	20	S	50	95	24
Festucetum ovinae	1,987	20	SW	25	90	34
Festucetum ovinae	2,000	30	S	40	80	32
Agrostio tenuis-Bromopsietum variegatae	2,000	30	S	45	80	32
Nardetum strictae	2,000	15	SO	80	100	25
Bromopsio variegatae – Agrostietum tenuis	2,000	5	WNW	50	100	24
Festucetum ovinae	2,000	30	S	45	80	32
Agrostio tenuis-Bromopsietum variegatae	2,000	3	W	40	90	39
Pulsatillo – Festucetum ovinae	2,000	20	SO	40	90	30
Vicietum alpestris	2,000	5	S	40	90	20
Cariceto meinshausenianae – Festucetum variae	2,000	30	W	50	100	17

(continued)

Table 8.19 (continued)

Plant communities	m.a.s.l. (m)	Inclination (°)	Exposition	Community height (cm)	Cover %	Number of species per 25 m
Agrostio planifoliae – Bromopsietum variegatae	2,000	25	N	50	90	34
Bromopsio variegatae – Festucetum ovinae	2,000	15	S	40	90	20
Cariceto meinshausenianae – Festucetum variae	2,010	25	NO	60	100	28
Cariceto meinshausenianae – Festucetum variae	2,010	25	SW	60	100	39
Kobresio capilliformis – Festucetum ovinae	2,020	35	NO	20	90	42
Bromopsio variegatae – Kobresietum capilliformis	2,020	35	NO	30	90	42
Agrostio tenuis-Bromopsietum variegatae	2,025	20	SW	40	90	34
Festucetum variae	2,045	35	S	20–80	90	32
Bromopsio variegatae–Festucetum ovinae	2,050	10	SWS	50	100	26
Bromopsio variegatae–Festucetum ovinae	2,050	10	SWS	30	100	25
Bromopsio variegatae–Festucetum ovinae	2,050	10	SWS	10	90	28
Koelerietum luerssenii	2,050	5	SO	70	95	31
Koelerietum luerssenii	2,050	5	NW	40	95	26
Festucetum pratensis	2,050	0	O	80	100	28
Cariceto meinshausenianae – Festucetum variae	2,050	35	SW	100	90	21
Cariceto meinshausenianae – Festucetum variae	2,050	35	S	80	80	32
Cariceto meinshausenianae – Festucetum variae	2,050	30	NW	80	90	32
Cariceto meinshausenianae – Festucetum variae	2,050	30	NW	80	90	23
Festuco variae – Dryetum caucasici	2,050	35	NW	70	90	35
Festucetum ovinae	2,050	15	S	40	90	33
Festucetum ovinae	2,050	10	SO	30	95	20

(continued)

Table 8.19 (continued)

Plant communities	m.a.s.l. (m)	Inclination (°)	Exposition	Community height (cm)	Cover %	Number of species per 25 m
Pulsatilletum violaceae	2,050	35	SW	50	90	28
Festucetum ovinae	2,050	25	SW	25	90	37
Pulsatillo violaceae - Bromopsietum variegatae	2,050	35	SWS	50	90	28
Helictotrichono asiaticus– Bromopsietum variegatae	2,050	10	NWN	50	100	31
Bromopsio variegatae – Koelerietum luerssenii	2,050	5	S	70	95	31
Bromopsio variegatae – Koelerietum luerssenii	2,050	5	NW	40	95	26
Bromopsio variegatae – Koelerietum luerssenii	2,050	20	SO	30	95	24
Agrostio tenuis-Bromopsietum variegatae	2,050	15	S	30	90	27
Agrostio tenuis-Bromopsietum variegatae	2,050	0	O	60	100	27
Agrostio tenuis-Bromopsietum variegatae	2,050	3	N	40	100	24
Agrostio tenuis-Bromopsietum variegatae	2,050	10	NW	50	100	31
Agrostio tenuis-Bromopsietum variegatae	2,050	10	SO	30	95	31
Agrostio tenuis-Bromopsietum variegatae	2,050	5	SO	70	95	31
Agrostio tenuis-Bromopsietum variegatae	2,050	5	NW	40	90	26
Agrostio tenuis-Bromopsietum variegatae	2,050	20	SO	30	95	24
Nardo strictae – Deschampsietum flexuosae	2,050	5	W	30	90	24
Vicietum alpestris	2,050	15	SW	30	100	17
Caricetum meinshausenianae	2,050	20	W	25	100	27

(continued)

Table 8.19 (continued)

Plant communities	m.a.s.l. (m)	Inclination (°)	Exposition	Community height (cm)	Cover %	Number of species per 25 m
Cariceto buschiorum – Bromopsietum variegatae	2,050	0	O	30	90	20
Cariceto buschiorum – Bromopsietum variegatae	2,050	3	S	40	90	21
Cariceto meinshausenianae – Festucetum variae	2,055	30	S	100	80	16
Cariceto buschiorum – Festucetum ovinae	2,060	0	O	20	60	20
Helictotrichono asiaticus – Bromopsietum variegatae	2,060	15	NW	20	100	28
Festuco ovinae – Koelerietum luerssenii	2,060	0	O	20	90	20
Agrostio tenuis-Bromopsietum variegatae	2,060	15	NW	20	90	28
Trifolio ambiguum – Agrostietum planifoliae	2,080	30	NO	60	90	47
Trifolio ambiguum – Agrostietum planifoliae	2,080	30	NO	30	90	47
Nardetum strictae	2,100	20	S	50	100	31
Nardetum strictae	2,100	20	S	35	95	31
Trifolio ambiguum – Bromopsietum variegatae	2,100	25	SW	40	90	33
Agrostio tenuis – Poetum alpinae	2,100	30	N	60	90	28
Caricetum meinshausenianae	2,100	25	NW	30	90	33
Cariceto tristis – Festucetum variae	2,100	40	NW	60	80	39
Poetum alpinae	2,100	0	O	40	80	25
Festuco supinae – Sibbaldietum semiglabrae	2,105	0	O	20	70	40
Cariceto meinshausenianae – Festucetum variae	2,110	25	NO	70	100	50
Cariceto meinshausenianae – Festucetum variae	2,110	25	NO	60	100	50

(continued)

Table 8.19 (continued)

Plant communities	m.a.s.l. (m)	Inclination (°)	Exposition	Community height (cm)	Cover %	Number of species per 25 m
Cariceto meinshausenianae – Festucetum variae	2,120	35	NW	60	100	43
Agrostio tenuis – Festucetum ovinae	2,140	12	N	20	100	37
Festucetum supinae	2,150	20	SO	15–30	100	31
Kobresietum capilliformis	2,150	0	O	30	95	25
Kobresietum capilliformis	2,150	5	N	20	90	29
Blysmo – Deschampsietum flexuosae	2,150	0	O	40	80	25
Bromopsio variegatae – Kobresietum capilliformis	2,150	5	SO	30	100	27
Helictotrichono asiaticus – Festucetum ovinae	2,175	10	NO	30	90	44
Bromopsio variegatae – Kobresietum capilliformis	2,175	5	N	15	100	26
Anemonetum fasciculatae	2,190	20	SSW	30–40	95	22
Nardetum strictae	2,200	20	S	20	90	40
Nardetum strictae	2,200	20	S	30	90	40
Heracleetum sosnowskyi	2,200	0	O	200	80	7
Vaccinio myrtilli – Rhododendretum caucasici	2,200	20	N	60	100	16
Cariceto tristis – Anthennarietum caucasici	2,200	20	N	20	80	20
Alchemillo elisabethae – Kobresietum persica	2,200	15	SW	40	50	29
Trifolio ambiguum – Bromopsietum variegatae	2,200	10	SW	40	90	55
Kobresietum capilliformis	2,200	25	SO	20	100	28
Kobresio capilliformis-Nardetum strictae	2,200	10	N	25	100	27
Kobresio capilliformis-Bromopsietum variegatae	2,200	15	NO	30	100	38

(continued)

Table 8.19 (continued)

Plant communities	m.a.s.l. (m)	Inclination (°)	Exposition	Community height (cm)	Cover %	Number of species per 25 m
Cariceto meinshausenianae – Festucetum variae	2,220	25	O	60	90	31
Agrostio planifoliae – Nardetum strictae	2,220	5	NO	50	100	23
Deschampsietum cespitosae	2,250	0	O	100	100	13
Nardetum strictae	2,250	15	W	100	100	27
Nardetum strictae	2,250	5	SWS	25	95	27
Vaccinio myrtilli – Nardetum strictae	2,250	25	NW	30	90	39
Chamaesciadio acaule– Kobresietum capilliformis	2,250	5	SO	20	100	32
Daphno glomeratae – Festucetum ovinae	2,300	20	N	30	100	41
Pulsatillo violaceae– Festucetum ovinae	2,300	10	SW	20	90	33
Cariceto tristis – Festucetum variae	2,300	30	NW	60	90	40
Kobresietum capilliformis	2,300	10	SW	15	100	25
Nardeto strictae– Vaccinietum myrtilli	2,300	15	NO	35	100	30
Cariceto tristis – Festucetum variae	2,300	35	SO	50	80	27
Deschampsio flexuosum – Nardetum strictae	2,300	20	NO	30	100	47
Cariceto tristis – Festucetum variae	2,300	35	S	50	80	27
Cariceto meinshausenianae – Festucetum variae	2,330	20	S	30	80	25
Cariceto meinshausenianae – Festucetum variae	2,350	30	S	80	70	17
Nardetum strictae	2,350	25	SW	70	100	31
Bromopsietum variegatae	2,350	15	SO	50	100	34
Alchemillo sericatae – Festucetum ovinae	2,350	5	SO	30	90	40
Cariceto medwedewii – Nardetum strictae	2,390	5	NW	40	100	28
Alpine belt						
Sibbaldietum semiglabrae	2,400	10	N	80	100	26

(continued)

Table 8.19 (continued)

Plant communities	m.a.s.l. (m)	Inclination (°)	Exposition	Community height (cm)	Cover %	Number of species per 25 m
Nardetum strictae	2,400	0	O	40	100	24
Festuco variae – Rhododendretum caucasici	2,400	25	N	60	100	42
Pulsatillo violaceae – Festucetum ovinae	2,400	15	SW	20	90	26
Festuco variae – Rhododendretum caucasici	2,400	30	NW	70	100	38
Kobresietum capillifromis	2,410	0	O	15	80	22
Nardetum strictae	2,420	15	W	20	95	20
Sibbaldio parviflorae – Caricetum tristis	2,450	5	NW	30	90	25
Cariceto tristis – Festucetum variae	2,450	20	SW	50	100	43
Vaccinio myrtilli – Rhododendretum caucasici	2,450	20	N	30	100	27
Kobresietum capilliformis	2,450	0	O	15	90	26
Taraxacetum stevenii	2,500	5	N	20	90	18
Bromopsio variegatae – Caricetum tristis	2,500	5	NO	40	100	28
Deschampsio flexuosae – Nardetum strictae	2,500	5	N	40	100	35
Sibbaldio parviflorae – Nardetum strictae	2,500	5	N	25	100	35
Festuco variae – Dryadetum caucasici	2,500	40	N	70	100	33
Festuco supinae – Nardetum strictae	2,500	10	SO	20	100	41
Cariceto tristis – Alchemilletum elisabethae	2,550	5	NW	20	100	26
Sibbaldio semiglabrae – Caricetum medwedewii	2,550	0	O	15	90	16
Kobresietum capilliformis	2,550	10	SO	12	90	34
Sibbaldietum semiglabrae	2,560	10	N	30	100	19
Pulsatillo violaceae-Festucetum ovine	2,560	25	SO	40	100	23
Cariceto meinshausenianae – Festucetum variae	2,560	25	SO	40	100	39

(continued)

Table 8.19 (continued)

Plant communities	m.a.s.l. (m)	Inclination (°)	Exposition	Community height (cm)	Cover %	Number of species per 25 m
Festuco variae – Dryadetum caucasici	2,560	25	SO	40	100	23
Cariceto tristis – Festucetum variae	2,600	30	NO	50	100	31
Deschampsio flexuosae – Nardetum strictae	2,600	5	N	40	100	24
Cariceto tristis – Festucetum variae	2,600	20	NW	60	90	32
Festuco supinae – Kobresietum persica	2,600	20	SO	20	90	24
Deschampsio flexuosae – Nardetum strictae	2,650	5	SO	30	90	29
Festuco supinae – Kobresietum persica	2,700	0	O	15	80	13
Rhododendretum caucasici	2,700	25	N	30	80	22
Kobresio capilliformis – Caricetum tristis	2,700	15	SO	15	90	40
Poo alpinae – Nardetum strictae	2,700	15	SO	20	100	37
Festuco supinae – Caricetum tristis	2,700	15	NO	20	90	16
Festuco supinae – Nardetum strictae	2,700	15	SO	20	100	37
Rhododendretum caucasici	2,750	40	N	30	70	14
Kobresio capilliformis – Festucetum supinae	2,800	10	N	20	80	24
Kobresietum schoenoides	2,840	0	O	30	80	15
Festucetum variae	2,850	35	S	40	90	23
Kobresio schoenoides – Caricetum tristis	2,850	30	S	30	70	13
Kobresio schoenoides – Festucetum variae	2,850	15	SW	20	90	28
Kobresio capilliformis – Festucetum supinae	2,850	5	SO	15	90	22
Cariceto tristis – Festucetum supinae	2,900	10	N	30	70	16
Kobresio capilliformis – Festucetum supinae	2,900	0	O	15	80	29
Kobresietum capilliformis	2,950	20	S	15	95	20
Festucetum supinae	2,980	20	S	20	80	25

(continued)

Table 8.19 (continued)

Plant communities	m.a.s.l. (m)	Inclination (°)	Exposition	Community height (cm)	Cover %	Number of species per 25 m
Subnival belt						
Subnival –Nanocoenoses	3,200	0	O	5	20	5
Cerastium kazbek-Alopecurus dasyantus	4,000	0	O	5	1	2

and the Pyrenees (Franz 1979; Grabherr and Mucina 1993; Ellenberg 1996; Grabherr 1997; Ozenda 1985, 2002; Nakhutsrishvili and Ozenda 1998; Burga et al. 2004; Erschbamer et al. 2010; Pauli et al. 2011; Korner 2012).

In the Alps the treeline is mainly formed by conifers (*Pinus cembra, P. mugo, Larix decidua, Picea abies*) (Ozenda 1985, 2002), while in the Caucasus the same zone is dominated by broad-leaved trees (*Betula litwinowii, B. medwediewii, Acer trautvetteri, Sorbus caucasigena, Quercus macranthera*).

There is no analogue of Colchic per-humid relict vegetation in the Alps.

The tall herbaceous vegetation has no analogue in the Alps. Although some species of tall-herb vegetation are common to the Alps and the Caucasus (e.g. *Aconitum nasutum, Doronicum macrophyllum, Telekia speciosa*), the tall-herb vegetation of the Caucasus is unique in the number of species, level of endemism and stature. The *Betula-Adenostyles* tall-herb community of Ellenberg (1996) has little in common with the tall-herb vegetation of the Caucasus, which ecologically is more of an equivalent of the *Alnus viridis* scrub of the Alps (Nakhutsrishvili and Ozenda 1998).

Meadows of *Calamagrostis arundinacea, Festuca varia, Hordeum violaceum,* and *Trisetum flavescens* occur both in the Caucasus and in the Alps; however, in contrast to the Alps, *Arrhenatherum elatius* is not a characteristic grassland species in the Caucasus.

Dry meadows with *Bromopsis variegata* and diverse herb meadows with *Anemonastrum fasciculatum, Betonica macrantha, Geranium ibericum, Inula orientalis, Ranunculus caucasicus, R. oreophilus, Scabiosa caucasica,* and *Trollius patulus* are widespread in the Caucasus but are absent from the Alps. *Kobresia (= Elyna) myosuroides* (Alps) and *Kobresia capilliformis* (Caucasus) rush haths, *Woronowia speciosa-Carex pontica* (Caucasus, on limestines) and *Carex firma* (Alps, on limestones) sedge heaths can be regarded as vicarious communities.

The most important difference between the high mountain vegetation of the Alps and the Caucasus is that contrasting nature of the Caucasus plant cover including the per-humid relict plants (Colchis), on the one hand, and high mountain steppe and xerophilous scrub, on the other.

Many subnival plants in the Caucasus are local endemic species, which have phylogenetic relationships with species from Asia Anterior–South-West Asia or Asia Minor (Nakhutsrishvili and Gagnidze 1999), but unrelated to the species of the (sub) nival zone of the Alps. The vascular plant species of the Alps are widely distributed and occur in most European high mountain areas, while local endemism prevails in the Caucasus (Nakhutsrishvili 2003).