Timberline meadows in Wells Gray Park, British Columbia, and their comparative geobotanical interpretation

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Orohemiarctic (subalpine) timberline meadows dominate or alternate with *Abies lasiocarpa-Picea engelmannii* stands at 1 600–2 000 m on Battle Mountain (Cariboo Mountains), Wells Gray Provincial Park, British Columbia. Lush, mesic to moist forb communities prevail, while heath communities are scarce. Judged from the floristic composition some of the communities have distinct counterparts in the North Cascade Range or in the Canadian Rocky Mountains, but some are clearly different.

The general timberline vegetation pattern in the northern hemisphere characterized by the abundance of forb meadows prevails in western North America south of ca Lat. 55° N and in various Eurasian mountains (e.g., Altai, Sayan, Tien Shan, Alai, Tarbagatay, the Himalayas, the Caucasus, and the South Ural Mountains). The other main timberline pattern, characterized by the dominance of heath vegetation, prevails in the other mountains and in the whole polar timberline area. The reasons for this duality are not fully understood, but the floristic history seems to offer the best explanation.

KEY INDEX WORDS: *floristic composition, subalpine, timberline meadows, vegetation pattern.*

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Introduction

A European botanist may find many striking phytogeographical features in western North America (Lüdi 1961; Faegri 1966, 1968). One of the most surprising phenomena is the timberline vegetation of extensive areas of the western North American mountains. In most parts of Europe, both latitudinal and altitudinal, native timberline vegetation usually consists of dwarf-shrub or grass heaths; lush mesic or moist meadows are restricted to the wet or very eutrophic habitats. In many parts of the Rocky Mountains and the Cascade Range in western North America the situation is quite opposite; the more or less luxuriant meadows often predominate at the timberline and the shrubby or grassy heaths are more scanty.

In July 1961, I studied the timberline vegetation of Battle Mountain in Wells Gray Provincial Park, British Columbia, and made some relevés. The visit to the mountain was interrupted by an extremely heavy rainfall. Battle Mountain was at that time difficult to reach and no other opportunity opened to supplement this study. However, I also visited another mountain with meadows, viz. Fish Lake Hill (outside Wells Gray Park, but near its SE corner). In 1967, I made observations on the timberlines in the mountains of northern British Columbia, the southern Yukon, and various parts of Alaska. This experience as well as visits to some Eurasian mountains (Japan, Scandinavia, Central Europe, and Yugoslavia) convinced me of the occurrence of an interesting duality and a remarkable physiognomic similarity of the timberline vegetation in both the continents of the northern hemisphere.

Though there are many excellent papers dealing with North American mountain vegetation (*see* Douglas and Bliss 1977), I have seen no published papers on the timberline vegetation in eastern British Columbia. My main purpose here is to indicate the diversity of this vegetation on Battle Mountain and outline the distribution of its counterpart communities in the northern hemisphere.

The material consists of 51 relevés, each of 25 m². They were chosen from larger homogeneous meadow stands, the sizes of which are indicated in the tables. The cover of the plant species in the field and ground layers and the cover of stones was estimated as percentages (+ means less than 0.25%), the exposure was determined with a compass, and the slope gradient with a clinometer. The humus layer and subsoil were estimated visually.

FIGURE 1. The timberline and timberline meadows in the orohemiarctic (subalpine) zone of Battle Mountain. The oroarctic (alpine) uppermost slope of the mountain is seen in the background.

The nomenclature of the vascular plants mainly follows Hämet-Ahti (1965*a*) but some small changes in accordance with Hultén (1967) and Hitchcock and Cronquist (1973) have been made. The more difficult bryophytes were determined by R. Fagerstén, by T. Lammes (hepatics), or by Dr. P. Isoviita (*Sphagnum*). The lichens were checked by Dr. T. Ahti.

Study area

Battle Mountain in Wells Gray Provincial Park occurs in the Cariboo Mountains, east-central British Columbia, approximately at Lat. 52° N and Long. 120° W. The highest peak of the mountain reaches 2 369 m but the study area surrounds Fight Lake[1] at about 1 750–1 850 m elevation. The size of the main study area is about 5 km in diameter. Although all the relevés are from the Fight Lake Meadow,[1] I also made observations outside this area.

The study area on Battle Mountain is an undulating upper plateau with gently sloping low heights and ridges. Much of the area is covered by thick glacial till but a few schistose and some volcanic rock outcrops emerge (*see* Goward 1977). The bedrock is obviously rather oligotrophic: for instance, no moss or lichen species indicating calcareous sites were found within the studied area on Battle Mountain.

No exact climatic data are available, but the area belongs to the Interior Wet Belt. The vegetation reveals that the annual precipitation must be fairly high: in the nearest valley (Hemp Creek, alt. 630 m) it is less than 600 mm, and on Battle Mountain it is evidently distinctly higher (*see* Hämet-Ahti 1965*a*).

There was almost no disturbance by human activities on the timberline vegetation in Battle Mountain (at least not in 1961!). That locality has never had any permanent settlement, and at the time there was only a small cabin for hunters, park-rangers, and fire patrolmen, who very occasionally visited the mountain. Very locally, disturbance by horse grazing caused by hunting parties since the 1920's may be noted (C. Shook and T. Goward, *in litt.* 1978). Re-

[1] Not an official name.

cently the adjacent Cariboo Meadows have been grazed bare by horses (Goward 1977).

There are a few papers dealing with the lichens (Ahti 1962; who also includes a preliminary classification of the subalpine meadows), the vascular plants (Hämet-Ahti 1965*a*), the forest vegetation (Hämet-Ahti 1965*b*), and the mosses (Ahti and Fagerstén 1967) of the Wells Gray Provincial Park, including the present study area.

Timberline vegetation on Battle Mountain

The timberline in the study area is at approximately 1 750 m. Between 1 600 and 2 000 m there is a distinct zone (orohemiarctic or subalpine) where extensive or limited tree stands are intermingled with large meadows (Figs. 1, 2). The tree stands are formed by *Picea engelmannii* and *Abies lasiocarpa* (*see* the description of their vegetation in Hämet-Ahti 1965*b*). Above 2 000 m the vegetation becomes oroarctic or alpine (Fig. 1): it is formed by low and sparsely growing herbs, grasses, and a few dwarf shrubs. The species are quite different from the zone dominated by meadows and tree stands (cf. Hämet-Ahti 1965*a*).

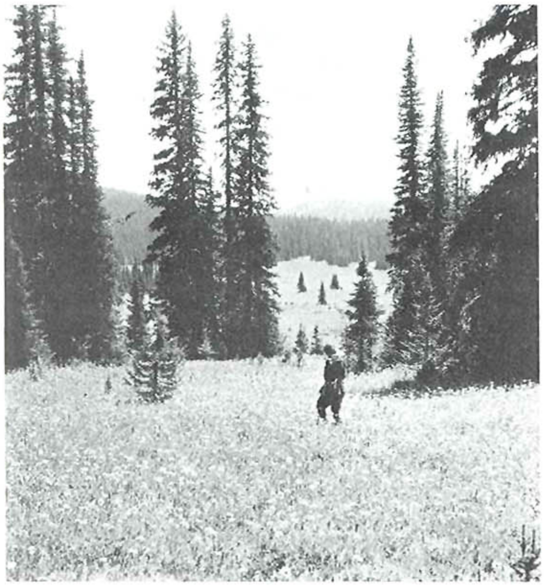

FIGURE 2. Mesic herb-rich meadows and *Abies lasiocarpa* stands. The dominating species are *Erigeron peregrinus* and *Valeriana sitchensis.*

The treeless vegetation consists mainly of various kinds of meadows but there are also some fens and small heaths. This vegetation superficially seems to consist of fairly large homogeneous communities, but closer examination reveals that it is ecologically often a rich mosaic with alternating wetter and drier habitats. Because the bedrock and soil are obviously fairly uniform the level and the movements of the water, the snow cover and its duration, the sloping of the surface, the exposure, and the distance from the forest stands seem to be the most important parameters for the species selection in the communities.

A podsol-like soil profile with distinct humus layer and fairly indistinct leached horizon was found only under the heath vegetation.

Heaths (Table I)

True heath vegetation surrounds some forest islands or tree stands as a fairly narrow (5 to 50 m) belt (Fig. 3). These communities are dominated by such dwarf shrubs as *Phyllodoce empetriformis, Diphasium sitchense, Cassiope mertensiana,* and *Vaccinium caespitosum.* Sometimes *Luetkea pectinata* is also abundant. The ground layer is not very rich because of heavy litter. There are some mosses (*Dicranum scoparium, D. fuscescens, D. muehlenbeckii*) or some lichens (*Cladonia ecmocyna* var. *intermedia, Cetraria subalpina, Lecidea granulosa, L. uliginosa* sensu lato) but they are not abundant.

The humus layer is rather peatlike but fairly rich in mineral soil; the leached horizon is fairly indistinct.

The heath-covered area on Battle Mountain is not very extensive. Heaths often occur on gently sloping southern exposures, where the snow cover evidently disappears fairly early but they are also on almost north-facing slopes.

There are several reports of similar heath vegetation in western North America, e.g., from the Bella Coola Region, B.C. (McAvoy 1931), from "far northern and northern Rocky Mountains" (Daubenmire 1943), from the Canadian Rocky Mountains (Heusser 1956), from Garibaldi Park (Brink 1959, Archer 1964, Brooke 1965, Brooke *et al.* 1970), from Glacier National Park (Choate and Habeck 1967), from the northern Cascade Range (Franklin and Trappe 1963; Douglas 1971, 1972; Douglas and Bliss 1977) and from the Olympic Mountains (Kuramoto and Bliss 1970). Most of these authors report that heaths are common but not very extensive within the investigated areas.

At least part of this heath vegetation apparently belongs to the alliance Phyllodoco-Cassiopion as circumscribed by Brooke (1965, Brooke *et al.* 1970) from the parkland subzone (= the orohemiarctic zone) of the subalpine mountain hemlock zone in Garibaldi Park, British Columbia. Henderson (1973) and Franklin and Dyrness (1973) reported a *Phyllodoce empetriformis—Vaccinium deliciosum* and a *Vaccinium deliciosum* community from western Washington but neither one is floristically similar to the heaths of Battle Mountain. The subalpine phase of the *Cassiope mertensiana* community reported by Douglas and Bliss (1977) from the North Cascade Range is more closely related.

Most authors also report that this kind of vegetation occurs particularly on southern exposures, but according to Kuramoto and Bliss (1970) it occurs also on the north-facing slopes in the Olympic Mountains.

TABLE I

Vegetation analyses of the heath communities in Fight Lake Meadow, Battle Mountain, British Columbia. Species are grouped into 1) dwarf shrubs, 2) herbs, 3) graminoids, 4) bryophytes, and 5) lichens. The vascular plant (field) layer is partially multistratose and therefore the total cover may exceed 100%. (Plot size 25 m^2; + = less than 0.25% cover.)

No. of relevé	1	2	3
Size of community (100 m^2)	1	1	1
Exposure	NE	S	SE
Slope gradient (degree)	2	—	5
Coverage of stones (%)	—	—	—
DWARF SHRUBS			
Abies lasiocarpa (Hook.) Nutt. (juv.)	10	2	—
Cassiope mertensiana (Bong.) D. Don	—	—	60
Diphasium sitchense (Rupr.) Löve & Löve	5	25	—
Gaultheria humifusa (Graham) Rydb.	0.5	5	—
Phyllodoce empetriformis (Sm.) D. Don	30	10	10
Vaccinium caespitosum Michx.	5	30	3
HERBS			
Anemone occidentalis S. Wats.	4	—	10
Antennaria lanata (Hook.) Greene	1	—	10
Arnica latifolia Bong.	+	—	5
Artemisia arctica Less.	+	—	—
Caltha leptosepala DC.	3	—	—
Epilobium anagallidifolium Lam.	+	—	—
Erigeron peregrinus (Pursh) Greene	—	—	2
Hieracium gracile Hook.	+	0.5	—
Luetkea pectinata (Pursh) Kuntze	—	30	—
Lupinus latifolius Agardh var. *subalpinus* (Piper & Robins.) C. P. Smith	0.25	+	—
Mitella breweri A. Gray	3	—	—
Pedicularis bracteosa Benth.	0.5	—	—
Valeriana sitchensis Bong.	15	—	0.5
Veratrum viride Ait.	0.25	0.5	+
Veronica wormskjoldii Roem. & Schult.	+	—	—
GRAMINOIDS			
Carex nigricans C. A. Meyer	3	—	—
C. spectabilis Dewey	+	—	2
Danthonia intermedia Vasey	0.25	1	—
Poa cusickii Vasey var. *epilis* (Scribn.) Hitchc.	—	—	—
Vahlodea atropurpurea (Wahlenb.) Fries	25	2	3
BRYOPHYTES			
Aulacomnium palustre (Hedw.) Schwaegr.	—	0.5	—
Dicranum fuscescens Turn.	5	0.25	0.25
D. muehlenbeckii B.S.G.	3	0.25	—
D. scoparium Hedw.	10	1	3
Lescuraea radicosa (Mitt.) Mönk.	0.25	—	+
Polytrichum commune Hedw.	0.25	—	+
P. juniperinum Hedw.	+	—	—
P. piliferum Hedw.	—	—	+
Barbilophozia floerkei (Web. & Mohr) Loeske	—	+	—
B. lycopodioides (Wallr.) Loeske	0.25	—	1
Hepaticae sp.	—	+	—

TABLE I—*Continued*

LICHENS			
Cetraria subalpina Imsh.	+	1	0.5
Cladonia bellidiflora (Ach.) Schaer.	—	0.5	—
C. ecmocyna Leight. var. *intermedia* (Robb.) Evans	0.5	1	—
C. pleurota (Flörke) Schaer.	—	+	—
Lecidea granulosa (Hoffm.) Ach.	—	3	—
L. uliginosa (Schrad.) Ach. s. lat.	—	4	—
Peltigera malacea (Ach.) Funck	—	+	+
P. polydactyla (Neck.) Hoffm.	—	+	—

Dry meadows (Table II)

These meadows occur on low ridges and dry gentle slopes and rarely ever very close to the tree stands (Fig. 3). The relevés 1–3 represent the vegetation occurring on the driest and often stony sites, usually on the tops or on the uppermost slopes of the low ridges.

The most characteristic plants are *Antennaria lanata,* which gives these meadows a grey colour, *Sibbaldia procumbens, Polytrichum juniperinum, P. piliferum,* and *Dicranum scoparium. Vaccinium caespitosum, Erigeron peregrinus, Carex spectabilis, Trisetum spicatum,* and *Vahlodea atropurpurea* are also frequent but they may occur in other meadows, too. The driest meadows have several lichens (*Cladonia ecmocyna* var. *intermedia* and other *Cladonia* species, *Cetraria subalpina,* etc.).

The uppermost soil layer is rich in raw, peat-like humus and there is no distinguishable leached horizon.

These meadows are common and fairly abundant on Battle Mountain. There are only a few published reports of this kind of vegetation: Knapik *et al.* (1973) mentioned *Antennaria lanata* meadows from the alpine (=oroarctic) zone of Banff National Park, Henderson (1973) an *Antennaria lanata* community from Mt. Rainier, and Douglas and Bliss (1977) from the North Cascade Range. In the North Cascades and on Mt. Rainier, the dry meadows seem to occur in habitats ecologically similar to those on Battle Mountain. On the other hand, in the coastal Garibaldi Park, Brooke *et al.* (1970) reported no community corresponding to these dry meadows on Battle Mountain. This kind of vegetation appears to be confined to the mountains of the eastern part of the North Cascade Range (cf. Douglas and Bliss 1977) and of the Interior Wet Belt, where the precipitation is not as high as in the coastal areas.

TABLE II

Vegetation analyses of the dry meadow communities. Species are grouped into 1) dwarf shrubs, 2) herbs, 3) graminoids, 4) mosses, 5) hepatics, and 6) lichens. (Plot size 25 m^2; + = less than 0.25% cover; cover may exceed 100%, *see* Table I).

No. of relevé	1	2	3	4	5	6	7	8	9	10	11	12
Size of community (100 m^2)	21	200	100	4.5	0.75	21	0.7	50	1	12	75	1.75
Exposure	E	—	W	W	S	—	—	SE	N	S	E	—
Slope gradient (degree)	2	—	2	1	2	—	—	2	1	1	3	—
Coverage of stones (%)	15	15	20	0.5	—	0.25	—	—	0.25	—	—	—
DWARF SHRUBS												
Vaccinium caespitosum Michx.	30	30	15	20	30	25	10	30	20	30	20	30
HERBS												
Agoseris aurantiaca (Hook.) Greene	—	—	—	—	—	—	—	+	—	—	7	+
Anemone occidentalis S. Wats.	—	—	0.5	+	—	—	—	—	—	+	—	—

TABLE II—*Continued*

HERBS—*Cont'd*												
Antennaria lanata (Hook.) Greene	60	30	70	60	60	40	10	10	40	20	20	2
Artemisia arctica Less.	—	20	—	—	4	30	—	25	4	20	—	50
Erigeron peregrinus (Pursh) Greene	5	3	+	7	10	20	5	40	10	10	0.25	40
Hieracium gracile Hook.	+	+	+	0.25	—	+	+	—	+	—	+	—
Pedicularis bracteosa Benth.	—	—	+	—	—	4	0.25	3	3	7	—	3
Potentilla diversifolia Lehm.	0.25	—	0.25	1	+	+	1	0.5	—	—	+	0.25
Sagina saginoides (L.) Karst.	+	+	+	—	—	+	—	—	—	—	—	—
Senecio triangularis Hook.	—	—	—	+	—	—	5	—	0.25	—	—	—
Sibbaldia procumbens L.	+	+	2	+	0.25	+	7	0.25	2	0.25	1	0.5
Stellaria monantha Hult.	—	+	—	—	—	—	—	+	—	—	—	—
Veronica wormskjoldii Roem. & Schult.	—	—	+	—	—	0.25	+	1	+	+	—	+
GRAMINOIDS												
Calamagrostis canadensis (Michx.) Beauv.	0.25	—	—	—	—	—	3	—	—	—	+	3
Carex illota Bailey	—	—	—	—	+	—	—	+	—	0.5	—	—
C. nigricans C. A. Meyer	2	3	0.5	5	1	1	25	0.5	1	—	60	4
C. spectabilis Dewey	2	10	10	3	5	15	20	10	1	5	1	3
Danthonia intermedia Vasey	—	7	—	—	30	—	—	10	5	10	—	—
Festuca brachyphylla Schultes	+	+	—	—	—	—	—	—	—	—	—	—
Luzula spicata (L.) DC.	+	+	—	—	—	—	—	—	—	—	—	—
Phleum alpinum L.	+	+	0.25	—	—	0.25	—	2	+	+	—	0.25
Poa cusickii Vasey var. *epilis* (Scribn.) Hitchc.	+	+	+	—	—	5	—	+	—	+	—	—
Trisetum spicatum (L.) Richt.	0.25	—	3	0.5	—	+	0.25	0.25	—	—	2	0.25
Vahlodea atropurpurea (Wahlenb.) Fries	—	2	2	2	2	0.25	0.25	+	3	3	3	+
Other species				(1)		(2)			(3)		(4)	(5)
MOSSES												
Aulacomnium palustre (Hedw.) Schwaegr.	—	—	—	—	—	5	—	—	—	—	5	—
Brachythecium albicans (Hedw.) B.S.G.	—	—	—	0.25	—	0.5	—	—	+	+	—	—
Bryum sp.	—	0.25	—	—	—	—	0.25	—	—	—	—	—
Dicranum scoparium Hedw.	1	10	+	10	5	0.25	+	1	5	0.25	+	+
Kiaeria starkei (Web. & Mohr) I. Hag.	—	—	5	1	—	—	—	—	—	—	30	—

TABLE II—*Continued*

MOSSES—*Cont'd*												
Lescuraea radicosa (Mitt.) Mönk.	—	+	—	+	—	—	—	0.5	—	+	—	3
Pohlia nutans (Hedw.) Lindb.	—	+	—	+	—	+	—	+	—	—	—	—
Polytrichum commune Hedw.	—	—	20	7	+	—	50	—	—	—	40	20
P. juniperinum Hedw.	0.5	20	—	25	20	5	+	5	75	10	—	30
P. piliferum Hedw.	50	5	3	0.25	5	50	—	40	—	20	—	2
Other species				(6)		(7)					(8)	
HEPATICS												
Barbilophozia floerkei (Web. & Mohr) Loeske	—	—	—	0.5	—	—	3	—	5	—	+	—
B. hatcheri (Evans) Loeske	+	—	—	—	—	—	—	+	—	—	—	—
B. lycopodioides (Wallr.) Loeske	—	1	—	—	—	+	—	—	—	+	—	+
Other species	(9)					(10)				(11)		
LICHENS												
Cladonia bellidiflora (Ach.) Schaer.	+	+	—	0.25	+	0.25	—	—	—	—	—	—
C. carneola (Fr.) Fr.	—	+	—	+	+	+	+	—	+	—	—	—
C. chlorophaea (Sommerf.) Spreng.	+	—	—	—	—	+	—	+	0.25	+	—	+
C. ecmocyna Leight. var. *intermedia* (Robb.) Evans	1	5	20	40	50	20	30	5	—	—	—	—
C. macrophyllodes Nyl.	0.5	+	0.5	+	—	0.5	—	4	—	5	—	+
C. mitis Sandst.	—	20	—	—	—	—	—	—	—	—	—	—
C. pleurota (Flörke) Schaer.	0.5	+	2	1	+	0.25	0.25	—	—	—	—	—
Cetraria ericetorum Opiz	0.5	1	—	—	—	—	—	—	—	—	—	—
C. islandica (L.) Ach.	—	—	—	—	—	0.25	+	—	—	—	—	—
C. subalpina Imsh.	2	2	0.5	0.25	5	+	+	3	1	1	—	+
Lecidea granulosa (Hoffm.) Ach.	—	—	1	1	—	0.5	+	—	—	—	—	—
L. uliginosa (Schrad.) Ach. s. lat.	—	—	+	+	—	+	0.5	—	—	—	—	—
Lepraria arctica (Lynge) Wetm.	10	—	10	—	+	—	—	—	—	—	—	—

TABLE II—*Continued*

LICHENS—*Cont'd*												
Peltigera malacea (Ach.) Funck	+	+	+	+	+	+	+	1	+	—	—	—
P. rufescens (Weis) Humb.	+	+	+	—	+	+	—	+	+	—	—	—
Psoroma hypnorum (Vahl) S. F. Gray	—	+	—	—	—	+	—	—	—	—	—	—
Solorina crocea (L.) Ach.	2	—	0.5	—	—	—	—	—	—	—	—	—
Other species	(12)	(13)		(14)		(15)						

Other species. [1] *Epilobium anagallidifolium* Lam. +, *Gentiana glauca* Pall. 1, *Gaultheria humifusa* (Graham) Rydb. 0.25. [2] *Diphasium sitchense* (Rupr.) Löve & Löve +, *Senecio integerrimus* Nutt. +, *Valeriana sitchensis* Bong. 1. [3] *Juncus drummondii* E. Meyer +. [4] *Arnica mollis* Hook. +, *Caltha leptosepala* DC. 2. [5] *Achillea millefolium* L. ssp. *lanulosa* (Nutt.) Piper var. *alpicola* (Rydb.) Garrett +, *Castilleja rhexifolia* Rydb. 0.5, *Thalictrum occidentale* A. Gray 0.5. [6] *Bryum* cf. *capillare* Hedw. +. [7] *Climacium dendroides* (Hedw.) Web. & Mohr +, *Tortula ruralis* (Hedw.) Gaertn. *et al.* 1. [8] *Rhacomitrium ericoides* (Hedw.) Brid. 1. [9] *Hepaticae* sp. +. [10] *Anastrophyllum michauxii* (Web.) Buch. 5. [11] *Marsupella* sp. +. [12] *Lecidea demissa* (Rutstr.) Ach. 0.25. [13] *Cladonia cenotea* (Ach.) Schar. +, *Peltigera polydactyla* (Neck.) Hoffm. +. [14] *Cladonia phyllophora* Hoffm. +, *C. gonecha* (Ach.) Asah. +. [15] *Cladonia pyxidata* (L.) Hoffm. +, *Pertusaria* sp. +.

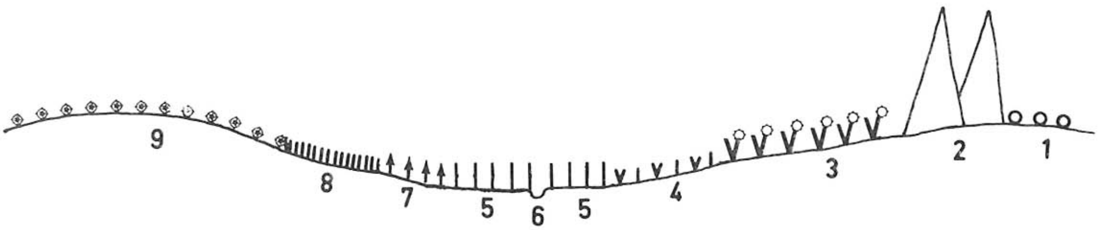

FIGURE 3. A scheme of the sequence of different kinds of meadows on Battle Mountain. **1,** Heath. **2,** Tree stand (*Abies lasiocarpa*). **3,** Mesic meadow (*Erigeron peregrinus, Valeriana sitchensis,* etc.). **4,** Moist mesotrophic meadow (*Senecio triangularis, Juncus drummondii,* etc.). **5,** Shallow marsh (*Eriophorum angustifolium,* etc.). **6,** Fen (*Carex physocarpa*). **7,** Wet meadow (*Carex spectabilis,* etc.). **8,** Moist oligotrophic meadow (*Carex nigricans*). **9,** Dry meadow (*Antennaria lanata,* etc.).

Mesic meadows (Table III)

Mesic sites, especially on gently sloping northern but also other exposures are occupied by lush herb-rich meadows (Figs. 2, 3) often preferring the vicinity of the tree stands. They are dominated by *Valeriana sitchensis, Erigeron peregrinus, Senecio triangularis, Vahlodea atropurpurea, Lupinus latifolius* var. *subalpinus* and *Carex spectabilis.* Among these *Castilleja occidentalis, C. rhexifolia, Anemone occidentalis* and *Arnica mollis* may be often fairly abundant. Those meadows, which are situated rather close to the tree stands or the forest border, have some species more commonly associated with forest vegetation, e.g., *Mitella breweri* and *Arnica latifolia.* The height of the herb layer is ca. 500 mm.

The ground layer may consist of some mosses, the most abundant one being *Lescuraea radicosa.*

The soil is dark brown sandy till and the uppermost layer (200–300 mm) is very rich in humus.

These attractive and luxuriant herb meadows are common and abundant on Battle Mountain. They also seem to be common in many mountains of western North America: they are reported, for instance, by Kirkwood (1927) from Bitter Root Mountains, by McAvoy (1931) from the Bella Coola Region, by Heusser (1956) from the Canadian Rocky

Mountains, by Brink (1956: "forb meadows") and by Archer (1964: "Valerianetum sitchensis") from Garibaldi Park, by Franklin and Trappe (1963), Douglas (1971, 1972: "*Valeriana sitchensis-Veratrum viride* community") and Douglas and Bliss (1977: "*Lipinus latifolius* community") from the North Cascade Range, by Habeck (1969) from the Glacier National Park, by Kuramoto and Bliss (1970) from the Olympic Mountains and by Henderson (1973) from Mt. Rainier. However, floristically many of these only slightly resemble the meadows of Battle Mountain. According to Franklin and Dyrness (1973) this lush herbaceous community occurs most commonly on steep, well-watered slopes which are subjected to recurring avalanches in Washington and Oregon. On Battle Mountain this is not true: the habitats of the herb-rich meadows are obviously well-watered but they are only on gently facing slopes and the occurrence of the avalanches is not likely.

TABLE III

Vegetation analyses of the mesic meadow communities. Species are grouped into 1) shrubs, 2) herbs, 3) graminoids, and 4) bryophytes. (Plot size 25 m²; + = less than 0.25% cover; cover may exceed 100%, *see* Table I).

No. of relevé	1	2	3	4	5	6	7
Size of community (100 m²)	2	200	2	1	60	?	1
Exposure	E	N	N	N	E	S	S
Slope gradient (degree)	3	7	7	9	5	2	3
Coverage of stones (%)	—	+	—	—	1	—	2
SHRUBS							
Abies lasiocarpa (Hook.) Nutt. (juv.)	—	—	—	—	0.5	2	1
HERBS							
Agoseris aurantiaca (Hook.) Greene	—	+	+	+	—	—	—
Anemone occidentalis S. Wats.	2	1	—	40	3	+	—
Arnica mollis Hook.	2	5	0.5	—	0.25	—	—
A. latifolia Bong.	—	—	—	—	0.25	—	20
Castilleja occidentalis Torr.	1	+	+	—	+	—	—
C. rhexifolia Rydb.	3	0.25	0.5	1	+	+	—
Claytonia lanceolata Pursh	—	+	—	3	—	—	—
Erigeron peregrinus (Pursh) Greene	25	30	5	5	20	7	10
Lupinus latifolius Agardh var. *subalpinus* (Piper & Robins.) C. P. Smith	30	—	40	10	5	3	—
Mitella breweri A. Gray	—	—	0.25	0.25	—	—	5
Pedicularis bracteosa Benth.	1	—	+	0.5	0.25	0.25	—
Senecio triangularis Hook.	3	15	30	15	30	10	0.25
Valeriana sitchensis Bong.	50	50	60	60	60	30	60
Veratrum viride Ait.	—	—	0.5	2	15	—	—
Veronica wormskjoldii Roem. & Schult.	2	1	—	1	+	—	—

TABLE III—*Continued*

GRAMINOIDS							
Carex nigricans C. A. Meyer	+	1	—	—	—	—	—
C. spectabilis Dewey	0.5	7	15	5	5	60	10
Juncus drummondii E. Meyer	—	1	0.5	—	1	1	—
Phleum alpinum L.	+	10	1	3	—	—	—
Poa cusickii Vasey var. *epilis* (Scribn.) Hitchc.	+	—	—	+	—	—	—
P. pratensis L. s. lat.	+	—	—	—	+	—	—
Vahlodea atropurpurea (Wahlenb.) Fries	4	10	1	2	2	1	10
Other species	(1)	(2)	(3)	(4)	(5)		(5)
BRYOPHYTES							
Lescuraea radicosa (Mitt.) Mönk.	0.5	5	20	30	20	—	5
Polytrichum commune Hedw.	—	30	—	5	0.25	—	1
Rhytidiadelphus subpinnatus (Lindb.) T. Kop.	1	—	—	—	—	—	0.5
Roellia roellii (Broth.) Crum	—	1	0.5	+	—	—	—
Other species	(6)	(7)				(8)	

Other species. [1] *Vaccinium caespitosum* Michx. 2, *Polygonum viviparum* L. 0.25, *Calamagrostis canadensis* (Michx.) Beauv. 1, *Trisetum spicatum* (L.) Richt. +. [2] *Hieracium gracile* Hook. +. [3] *Ranunclus eschscholtzii* Schlecht. +. [4] *Antennaria lanata* (Hook.) Greene +, *Trollius laxus* Salisb. 3. [5] *Epilobium anagallidifolium* Lam. +. [6] *Polytrichum juniperinum* Hedw. +, *Hepaticae* sp. +. [7] *Barbilophozia kunzeana* (Hueb.) K. Muell. +. [8] *Barbilophozia hatcheri* (Evans) Loeske +.

Moist mesotrophic meadows (Table IV)

The sites irrigated by seepages, around springs or along brooks outside the marsh and fen zone are occupied by moist herb meadows (Fig. 3). The field layer in these meadows is lower growing (ca. 200–300 mm) and not as dense as in the mesic meadows. Several species occur in these moist habitats (e.g., *Senecio triangularis, Epilobium anagallidifolium, Juncus drummondii, Erigeron peregrinus, Calamagrostis canadensis, Vahlodea atropurpurea, Veronica wormskjoldii, Aulacomnium palustre, Polytrichum commune,* and *Rhytidiadelphus subpinnatus*) but some, e.g., *Trollius laxus* and *Caltha leptosepala,* are characteristic of the wettest seepages.

The subsoil is sandy till, covered by about 100 cm of a thick, dark peat-like humus layer.

The moist herb meadows do not belong to one vegetational or ecological unit but represent several slightly different types. These meadows are frequent but not very extensive in area on Battle Mountain.

Brooke *et al.* (1970) described a Leptarrheno-Calthetum leptosepalae association (the order Montio-Cardaminetalia) from Garibaldi Park, and by relevés 1–3 probably should be included in the same alliance (Leptarrhenion pyrolifoliae). McAvoy (1931) mentioned this kind of vegetation from the Bella Coola Region, and Henderson's (1973) "hygric or riparian communities" from Mount Rainier are very similar. Most authors evidently have included them in the *Carex nigricans* meadows or overlooked them completely, although they should be common in all mountainous areas on the coast or in the Interior Wet Belt of western North America.

TABLE IV

Vegetation analyses of the moist mesothrophic meadows. Species are grouped into 1) dwarf shrubs, 2) herbs, 3) graminoids, and 4) bryophytes and lichens. (Plot size 25 m^2; + = less than 0.25% cover; cover may exceed 100%, *see* Table I).

No. of relevé	1	2	3	4	5	6	7	8	9
Size of community (100 m^2)	10	2.5	20	0.7	20	15	30	4.5	2
Exposure	S	N	SE	S	—	S	SE	E	N
Slope gradient (degree)	1	7	3	3	—	2	7	3	5
Coverage of stones (%)	—	0.5	—	—	—	—	—	—	—
DWARF SHRUBS									
Salix barclayi Anders.	7	—	7	—	—	—	—	—	—
Vaccinium caespitosum Michx.	3	5	—	—	20	40	15	—	—
HERBS									
Agoseris aurantiaca (Hook.) Greene	+	10	5	—	—	3	—	30	25
Antennaria lanata S. Wats.	3	0.3	+	—	0.5	—	1	0.25	—
Arnica mollis Hook.	0.25	5	1	+	—	—	—	0.5	2
Artemisia arctica Less.	20	—	—	—	25	—	25	—	—
Caltha leptosepala DC.	10	30	30	40	—	0.25	—	15	—
Castilleja occidentalis Torr.	—	0.25	+	—	—	—	—	—	—
C. rhexifolia Rybd.	+	+	15	—	—	—	2	—	—
Epilobium anagallidifolium Lam.	+	0.25	+	3	—	2	—	0.25	0.5
Erigeron peregrinus (Pursh) Greene	40	20	40	3	5	30	25	5	5
Hieracium gracile Hook.	—	—	—	+	—	—	—	0.25	—
Lupinus latifolius Agardh var. *subalpinus* (Piper & Robins.) C. P. Smith	0.25	—	—	—	—	—	10	—	—
Mitella breweri A. Gray	—	—	0.25	7	—	+	—	—	—
Pedicularis bracteosa Hook.	1	—	—	—	—	—	5	—	—
Potentilla diversifolia Lehm.	1	—	+	—	2	1	2	+	—
Ranunculus eschscholtzii Schlecht.	+	+	—	—	—	—	—	—	+
Senecio triangularis Hook.	5	10	7	5	—	0.5	—	0.25	10
Sibbaldia procumbens L.	—	+	—	—	2	—	3	7	—
Stellaria monantha Hult.	+	—	—	—	+	—	+	—	—
Trollius laxus Salisb. var. *albiflorus* Gray	30	25	20	—	—	—	5	—	—
Valeriana sitchensis Bong.	1	—	1	5	—	25	5	0.25	—
Veronica serpyllifolia L.	—	—	—	+	—	+	—	—	—
V. wormskjoldii Roem. & Schult.	2	0.25	0.25	—	2	2	+	0.25	1

TABLE IV—*Continued*

GRAMINOIDS									
Agrostis thurberiana Hitchc.	+	—	0.25	5	—	7	—	+	—
Calamagrostis canadensis (Michx.) Beauv.	1	0.25	0.5	0.25	3	2	—	2	+
Carex nigricans C. A. Meyer	1	10	2	50	2	15	—	20	40
C. spectabilis Dewey	+	5	1	+	20	7	1	2	15
Danthonia intermedia Vasey	—	—	—	—	10	2	—	—	—
Juncus drummondii E. Meyer	0.5	0.5	1	0.5	—	0.5	—	0.25	+
J. mertensianus Bong.	—	—	1	—	—	—	—	0.25	—
Luzula parviflora (Ehrh.) Desv.	0.25	—	—	—	—	—	0.25	—	—
Phleum alpinum L.	0.5	1	+	—	1	—	1	3	0.25
Trisetum spicatum (L.) Richter	+	—	—	—	0.5	—	2	—	—
Vahlodea atropurpurea (Wahlenb.) Fries	15	5	20	5	+	5	2	20	1
Other species	(1)		(2)		(3)		(4)		
BRYOPHYTES AND LICHENS									
Aulacomnium palustre (Hedw.) Schwaegr.	20	70	75	60	5	60	—	30	25
Brachythecium albicans (Hedw.) B. S. G.	—	—	—	—	—	—	+	+	0.25
Dicranum scoparium Hedw.	+	0.5	10	+	—	+	+	—	+
Drepanocladus uncinatus (Hedw.) Warnst.	0.25	2	—	0.25	—	—	—	20	5
Lescuraea radicosa (Mitt.) Mönk.	—	—	0.25	+	—	—	—	—	—
Pohlia nutans (Hedw.) Lindb.	—	+	—	—	—	—	—	—	+
Polytrichum commune Hedw.	—	0.25	0.25	10	60	—	—	—	20
P. juniperinum Hedw.	0.25	—	—	—	+	+	30	0.25	0.25
Rhytidiadelphus subpinnatus (Lindb.) T. Kop.	30	+	10	1	—	1	—	0.25	+
Sphagnum compactum DC.	—	—	—	—	—	25	—	—	—
Barbilophozia lycopodioides (Wallr.) Loeske	—	—	—	—	+	—	+	—	+
Hepaticae sp.	+	—	—	—	—	—	—	+	—
Other species	(5)	(6)	(7)	(8)	(9)	(10)	(11)	—	—

Other species. [1] *Anemone occidentalis* S. Wats. +, *Equisetum palustre* L. +, *Polygonum viviparum* L. +, *Veratrum viride* Ait. +. [2] *Epilobium hornemannii* Reichenb. +, *Habenaria dilatata* (Pursh) Hook. +, *Stellaria calycanta* (Ledeb.) Bong. +. [3] *Achillea millefolium* L. ssp. *lanulosa* (Nutt.) Piper var. *alpicola* (Rydb.) Garrett +, *Carex illota* Bailey 3. [4] *Abies lasiocarpa* (Hook.) Nutt. (juv.) +, *Botrychium boreale* (Fr.) Milde 0.25, *Senecio integerrimus* Nutt. +, *Poa cusickii* Vasey var. *epilis* (Scribn.) Hitchc. 0.25. [5] *Marchantia alpestris* (Nees) Burgeff 1, *Scapania* sp. +. [6] *Barbilophozia kunzeana* (Hueb.) K. Muell. +, *Peltigera rufescens* (Weis) Humb. +. [7] *Bryum pseudotriquetrum* (Hedw.) Gaertn. *et al.* 3, *Philonotis* sp. +, *Scapania paludosa* (K. Muell.) K. Muell. [8] *Lophozia wenzelii* (Nees) Steph. +, *Peltigera polydactyla* (Neck.) Hoffm. +. [9] *Desmatodon latifolius* (Hedw.) Brid. +, *Peltigera aphthosa* (L.) Willd. 1. [10] *Scapania* cf. *irrigua* (Nees) Nees +. [11] *Tortula ruralis* (Hedw.) Gaertn. *et al.* +, *Barbilophozia hatcheri* (Evens) Loeske +, *Cladonia chlorophaea* (Sommerf.) Spreng. +, *C. macrophyllodes* Nyl. +.

Moist oligotrophic meadows (Table V)

Between the dry *Antennaria lanata*-dominated meadows and wet *Carex spectabilis* or *C. illota* meadows there are moist oligotrophic meadows (Fig. 3). They lie on flat or very slightly sloping (up to 3°) surfaces and are often seasonally covered by water.

The dominant species is *Carex nigricans,* often with high cover. *C. nigricans* occurs in many herb-rich meadows as well, but usually with low coverage.

The subsoil is sandy till and covered by 50–70 mm of thick humified peat.

These meadows are fairly extensive on Battle Mountain and they seem to be common in the Rocky Mountains and the Cascade Range. They are reported by Knapik *et al.* (1973) from the Banff National Park, by Brink (1959), Archer (1964), Brooke (1965), and Brooke *et al.* (1970) from Garibaldi Park, by Bliss (1969) and Kuramoto and Bliss (1970) from the Olympic Mountains, by Douglas (1971, 1972) and Douglas and Bliss (1977: *Carex nigricans* community) from the North Cascade Range. Obviously these meadows can be included in the Caricion nigricantis alliance described by Brooke (1965) and Brooke *et al.* (1970).

The *Carex nigricans*-dominated meadows are often reported to be associated with snow-bed habitats and therefore they have a very short-growing period (Brooke 1965, Brooke *et al.* 1970, Kuramoto and Bliss 1970, Douglas and Bliss 1977) but some of them occur along streams and in other permanently wet places which apparently have a longer growing season (cf. also Franklin and Dyrness 1973). On Battle Mountain these communities are not clearly associated with snow beds but often seem to prefer seasonal flooding.

TABLE V

Vegetation analyses of the moist oligotrophic meadows. Species are grouped into 1) dwarf shrubs, 2) herbs, 3) graminoids, 4) bryophytes, and 5) lichens. (Plot size 25 m^2; + = less than 0.25% cover; cover may exceed 100%, *see* Table I).

No. of relevé	1	2	3	4	5
Size of community (100 m^2)	0.4	7.5	1	6	30
Exposure	—	S	NE	NW	S
Slope gradient (degree)	—	1	2	2	2
Coverage of stones (%)	—	—	—	—	—
DWARF SHRUBS					
Vaccinium caespitosum Michx.	7	20	—	—	0.25
Kalmia microphylla (Hook.) Heller	—	—	—	—	3
HERBS					
Antennaria lanata S. Wats.	—	0.25	—	0.25	—
Caltha leptosepala DC.	—	—	15	—	25
Epilobium anagallidifolium Lam.	—	—	+	—	—
Erigeron peregrinus (Pursh) Greene	—	—	—	+	+
Gentiana glauca Pall.	—	0.25	—	—	—
Hieracium gracile Hook.	+	0.5	—	—	—
Potentilla diversifolia Lehm.	—	—	—	0.25	—
Senecio pauciflorus Pursh	—	+	—	—	—

TABLE V—*Continued*

HERBS—*Cont'd*					
S. triangularis Hook.	—	—	+	0.25	+
Sibbaldia procumbens L.	2	15	—	3	—
Veronica wormskjoldii Roem. & Schult.	—	—	+	—	—
GRAMINOIDS					
Agrostis thurberiana Hitchc.	—	—	—	—	0.25
Calamagrostis canadensis (Michx.) Beauv.	0.5	0.25	—	+	—
Carex illota Bailey	—	—	0.25	—	—
C. nigricans C. A. Meyer	90	80	90	90	70
C. praeceptorium Mack.	—	+	—	—	—
C. spectabilis Dewey	1	—	—	1	—
Eriophorum angustifolium Honck.	—	—	+	—	—
Phleum alpinum L.	—	+	+	2	—
Poa pratensis L. s. lat.	—	—	—	—	+
Trisetum spicatum (L.) Richt.	—	1	—	—	—
Vahlodea atropurpurea (Wahlenb.) Fries	0.25	—	0.25	—	10
BRYOPHYTES					
Aulacomnium palustre (Hedw.) Schwaegr.	5	7	80	5	5
Bryum weigelii Spreng.	—	—	0.25	—	—
Calliergon stramineum (Brid.) Kindb.	—	—	+	—	0.25
Drepanocladus uncinatus (Hedw.) Warnst.	—	—	0.5	—	—
Dicranum scoparium Hedw.	+	3	—	+	—
Philonotis sp.	—	—	0.25	—	—
Pohlia nutans (Hedw.) Lindb.	+	+	—	—	—
Polytrichum commune Hedw.	40	30	—	60	—
P. juniperinum Hedw.	5	—	—	—	—
P. strictum Brid.	—	—	—	—	1
Rhytidiadelphus subpinnatus (Lindb.) T. Kop.	—	—	2	—	—
Sphagnum compactum DC.	2	—	—	—	20
S. platyphyllum (Braithw.) Warnst.	—	—	—	—	3
S. russowii Warnst.	—	—	—	—	60
Barbilophozia floerkei (Web. & Mohr) Loeske	+	5	—	1	—
B. kunzeana (hueb.) K. Muell.	1	—	—	+	+
Lophozia wenzelii (Nees) Steph.	—	—	—	—	+
LICHENS					
Cetraria subalpina Imsh.	0.25	—	—	—	—
Cladonia pleurota (Flörke) Schaer.	+	—	—	—	—
Peltigera malacea (Ach.) Funck	—	+	—	—	—
P. polydactyla (Neck.) Hoffm.	0.25	1	—	—	—

Wet meadows (Table VI)

These meadows occur in rather wet and level sites. These habitats are wetter than the *Carex nigricans*-dominated meadows but drier than the fens proper and the shallow marshes (Fig. 3). They are fairly poor in species: the only abundant species are *Carex spectabilis* or *C. illota* and *Calamagrostis canadensis.* In some sites individuals of *Erigeron peregrinus, Senecio triangularis,* and other herbs may occur. The ground layer is almost bare and very poor in mosses. The humus layer is thin (20–40 mm) and formed by sedge peat rich in mineral soil.

There are some large wet meadows on Battle Mountain, but they are not very frequent.

Archer (1964, Caricetum spectabilis) mentioned ecologically rather similar meadows from Garibaldi Park, Kuramoto and Bliss (1970, under the name *Carex albonigra,* cf. Franklin and Dyrness, 1973), and Douglas and Bliss (1977) described them from the North Cascade Range. However, all these meadows differ floristically to some extent from those on Battle Mountain.

TABLE VI

Vegetation analyses of the wet meadows. Species are grouped into 1) herbs, 2) graminoids, and 3) mosses. (Plot size 25 m²; + = less than 0.25% cover; cover may exceed 100%, *see* Table I.)

No. of relevé	1	2	3
Size of community (100 m²)	2.5	1	20
Exposure	S	—	S
Slope gradient (degree)	1	—	1
Coverage of stones (%)	+	—	—
HERBS			
Agoseris aurantiaca (Hook.) Greene	—	+	+
Caltha leptosepala DC.	—	—	0.5
Erigeron peregrinus (Pursh) Greene	1	5	3
Potentilla diversifolia Lehm.	1	—	—
Senecio triangularis Hook.	0.25	—	25
Valeriana sitchensis Bong.	—	—	2
Veronica wormskjoldii Roem. & Schult.	—	+	1
GRAMINOIDS			
Calamagrostis canadensis (Michx.) Beauv.	5	5	10
Carex illota Bailey	40	1	15
C. nigricans C. A. Meyer	+	—	—
C. spectabilis Dewey	50	90	40
Phleum alpinum L.	—	+	3
Trisetum spicatum (L.) Richt.	—	+	—
Vahlodea atropurpurea (Wahlenb.) Fries	—	—	10
MOSSES			
Bryum weigelii Spreng.	+	—	—
Lescurea radicosa (Mitt.) Mönk.	+	—	1

Shallow marshes and fens (Table VII)

On Battle Mountain, this kind of vegetation is rather common along the brooks and in depressions (Fig. 3) but it does not cover extensive areas. It is poor in species and obviously rather oligotrophic. Unfortunately my revelés only give a poor idea about it.

Shallow marshes (relevés 1–3) are covered by water for fairly long periods, evidently up to the end of July. The ground layer is covered by dense *Polytrichum commune* mixed with *Aulacomnium palustre* or sometimes by *A. palustre* alone. The field layer is not dense and it contains sedges and grasses (*Carex paupercula, Eriophorum angustifolium,* and *Calamagrostis canadensis*). The herbs are rare and scanty. The soil is covered by thin (20–30 mm) fairly unhumified peat.

Fens (relevés 4–12) are wetter than shallow marshes and at least some of them are covered by fairly deep water (up to 100–200 mm) apparently for most of the summer. The dominant species in several (mesotrophic) fens is *Carex physocarpa,* which may grow alone or with some mosses (e.g., with *Drepanocladus* spp.). It also occurs in fens dominated by *Eriophorum angustifolium* or *Calamagrostis canadensis.* The thin (20–30 mm) humus layer is formed by slightly humified sedge peat.

The Eriophoro-Sphagnetum described by Brooke *et al.* (1970) from Garibaldi Park and four hygric communities described by Campbell

(1973) from Mount Jefferson are not similar to these communities of Battle Mountain. Shallow marshes and fens resembling these are not often mentioned by western North American authors, who usually include them in the "sedge meadows" (e.g., Brink 1959, from Garibaldi Park) or overlook them. Shallow marshes and fens are expected to be rather common along creeks and ponds in gentle sloping mountain areas at the timberline.

TABLE VII

Vegetation analyses of the shallow marshes (Plots 1–3) and the fens (Plots 4–12). Species are grouped into 1) herbs, 2) graminoids, and 3) bryophytes and lichens. (Plot size 25 m^2; + = less than 0.25% cover; cover may exceed 100%, *see* Table I).

	MARSHES			*FENS*								
No. of relevé	1	2	3	4	5	6	7	8	9	10	11	12
Size of community (100 m^2)	50	5	150	30	25	10	0.6	10	0.5	2	3.75	0.5
Exposure	—	—	—	—	—	—	—	—	—	—	—	—
Slope gradient (degree)	—	—	—	—	—	—	—	—	—	—	—	—
Coverage of stones (%)	—	—	—	—	—	—	—	—	—	—	—	—
HERBS												
Agoseris aurantiaca (Hook.) Greene	—	—	—	—	—	—	—	—	+	—	—	—
Epilobium anagallidifolium Lam.	—	—	—	—	—	—	—	0.25	—	—	—	—
Galium trifidum L.	+	—	—	—	—	—	—	—	—	—	—	—
Potentilla diversifolia Lehm.	—	—	+	—	—	—	—	—	—	—	—	—
P. palustris (L.) Scop.	+	—	—	—	—	—	—	—	—	—	—	—
Ranunculus eschscholtzii Schlecht.	—	—	0.25	—	—	—	—	—	—	—	—	—
R. reptans L.	—	—	0.25	—	—	—	—	—	—	—	—	—
Senecio pauciflorus Pursh	—	—	—	—	—	—	—	0.25	—	—	—	—
Sibbaldia procumbens L.	+	—	—	—	—	—	—	—	—	—	—	—
Veronica serpyllifolia L. var. *humifusa* (Dicks.) Vahl	—	—	+	—	—	—	—	—	—	—	—	—
V. wormskjoldii Roem. & Schult.	+	—	—	—	—	—	—	+	—	—	—	—
GRAMINOIDS												
Calamagrostis canadensis (Michx.) Beauv.	10	5	50	—	—	—	—	30	—	0.25	—	—
Carex illota Bailey	—	—	3	—	—	2	—	1	3	—	—	—
C. nigricans C. A. Meyer	2	1	1	—	—	—	—	50	—	—	—	—
C. paupercula Michx.	3	30	—	40	—	30	+	—	—	—	—	—
C. physocarpa Presl (incl. *C. physocarpa* x *rostrata* Stokes)	10	—	20	15	2	—	—	—	90	90	50	40

TABLE VII—*Continued*

	MARSHES			*FENS*								
GRAMINOIDS—*Cont'd*												
Eriophorum angustifolium Honck.	0.25	20	—	10	40	40	50	3	—	—	10	—
Juncus filiformis L.	2	—	—	—	—	—	—	—	—	—	—	—
Phleum alpinum L.	5	—	—	—	—	—	—	0.5	—	—	—	—
Poa pratensis L. s. lat.	10	—	—	—	—	—	—	—	—	—	—	—
BRYOPHYTES AND LICHENS												
Aulacomnium palustre (Hedw.) Schwaegr.	60	3	—	—	—	—	—	90	—	—	—	—
Bryum weigelii Spreng.	—	—	—	—	—	—	—	—	—	+	—	—
Calliergon stramineum (Brid.) Kindb.	—	1	—	30	+	40	0.5	—	—	—	—	—
Drepanocladus exannulatus (B.S.G.) Warnst.	—	—	—	30	60	—	—	—	—	—	—	—
D. fluitans (Hedw.) Warnst.	—	—	—	—	—	30	30	0.25	—	—	—	—
D. procerus (Ren. & H. Arn.) Warnst.	—	—	—	—	—	—	—	—	—	—	—	60
Polytrichum commune Hedw.	30	60	60	—	—	—	—	+	—	—	—	—
Sphagnum compactum DC.	—	—	—	—	—	—	+	—	—	—	—	—
S. platyphyllum (Braithw.) Warnst.	—	—	—	—	—	—	—	—	—	—	1	—
Barbilophozia kunzeana (Hueb.) K. Muell.	—	25	—	—	—	—	—	—	—	—	—	—
Gymnocolea inflata (Huds.) Dum.	—	—	—	10	—	—	—	—	—	—	—	—
Lophozia wenzelii (Nees) Steph.	—	+	—	—	—	—	—	—	—	—	—	—
Scapania paludicola Loeske & K. Muell.	—	—	—	—	—	+	—	—	—	—	—	—
Scapania sp.	—	—	—	+	—	—	—	—	—	—	—	—
Peltigera polydactyla (Neck.) Hoffm.	0.25	—	—	—	—	—	—	3	—	—	—	—
P. rufescens (Weis) Humb.	0.25	—	—	—	—	—	—	—	—	—	—	—

Timberline meadows of the mountains in the northern hemisphere

There are numerous papers dealing with the tree species of the northern latitudinal and altitudinal timberlines in Eurasia and North America (e.g., Hermes 1955, Hustich 1966, Wardle 1974). However, there is little published information on the floristic composition of the vegetation in the field and ground layer at timberline.

Arctic

The understory vegetation of the whole arctic timberline of both continents seems to be formed mainly by various heaths dominated by dwarf shrubs or low-growing graminoids (Soczava 1956*a*; Soczava and Gorodkov 1956; Bliss 1956, 1971; Larsen 1965, 1971, 1972, 1973, 1974).

North America

In eastern and northwestern North American mountains as well as in the northernmost Rocky Mountains the timberline vegetation is also composed mainly of dwarf shrub or grass heaths (Raup 1934, 1947; Daubenmire 1943; Porsild 1945, 1951; Griggs 1946; Moss 1955; Woodin 1959; Lüdi 1961; Bliss 1963, 1966; Knapp 1970; Hoefs *et al.* 1976). For instance, at Summit Lake, in the Rocky Mountains, of northern British Columbia, there are almost no timberline meadows but shrubby and grassy heaths.

But in western North America, southwards from 55° N latitude, a pronounced change takes place: the timberline heaths are often replaced by rich meadows. The northernmost timberline meadows, which are, not as luxuriant as those in the more southern areas, are reported from the Jasper and Banff National Parks in Alberta (Moss 1955, Lüdi 1961, Knapik *et al.* 1973). In British Columbia, timberline meadows are very common and well-developed in the mountains of the middle and southern parts of the province (Brink 1959, Archer 1964, Brooke 1965, McLean 1970, Brooke *et al.* 1970). In the United States they occur along the Rocky Mountains south to at least Colorado and Utah (Rydberg 1915*a*, 1915*b*, Ellison 1954, Marr 1961). In the high mountains of Oregon and Washington, herb-rich meadows are common at timberline (Franklin and Dyrness 1973). Their occurrence southwards from these areas is uncertain. However, Beaman and Andresen (1966) described physiognomically similar "subalpine" vegetation from Cerro Potosi, Mexico, and Lauer (1973) from the central Mexican highlands. In the eastern slopes of the Rocky Mountains and the Cascade Range these herb-rich meadows seem to turn into fairly arid graminoid communities (Ellison 1954, Marr 1961, Kuramoto and Bliss 1970, Root and Habeck 1972, Franklin and Dyrness 1973, Douglas and Bliss 1977).

Eurasia

In most parts of Europe and northern Asia, the timberline vegetation of the mountains is composed mainly of dwarf-shrub and grass heaths[1] (Lüdi 1935, Kalliola 1939, Popov 1949, Braun-Blanquet *et al.* 1954, Soczava 1956*a*, Schubert 1960, Igoshina 1961, 1964; Holtmeier 1963, Rune 1965, Schiechtl 1967, Ahti *et al.* 1968). Some small meadows in southeastern Carpathians (Soczava 1956*b*) may be included in these timberline meadows, but in the central and southern parts of the Ural Mountains (Igoshina 1961, 1964; Gorchakovskiy 1966, 1967, 1975) and particularly in western and Central Caucasus (Leskov 1932, Grossheim 1948, Sokolova *et al.* 1956, Agababyan and Vanetsyan 1966, Zimina 1973, Zimina *et al.* 1973), and in some parts of the Altai and Sayan Mountains (Printz 1921, Soczava 1956*a*, Krasnoborov 1966, Stanyukovich 1973) herb-rich meadows, physiognomically very similar to those of the Rocky Mountains, dominate at the timberline. Obviously there are also some herb-rich meadows in parts of the Tien Shan (M. V. Kultiasov 1922, Leskov 1932, I. M. Kultiasov 1955, Sokolova *et al.* 1956, Vykhodtsev 1956, 1966; Stepanova 1962, Sharashova and Lebedeva 1966, Agakhanyants 1967, Kotov 1967, Zimina 1973) but they seem to dominate only on slopes receiving large amounts of precipitation. In more arid areas, steppe-like graminoid communities dominate, being similar to those in western North America.

In many parts of the Himalayas there are evidently large meadows along the timberline (Kingdon Ward 1934, 1936; Schweinfurth 1957, Troll 1967, Kaul and Sarin 1971, Stainton 1972).

In the mountains of easternmost Asia, the timberline meadows are largely lacking or occur either only locally along streams or in other wet places like at the polar timberline.

[1] The famous "alpine meadows" of the Alps are essentially man-made, grazed clearings in originally forested areas and do not belong to this vegetation at all.

In Japan the *Pinus pumila* thickets and dwarf-shrub heaths predominate at the timberline (Ishizuka 1974, Hämet-Ahti *et al.* 1974) and meadows occur only in alluvial or other wet habitats. Timberline vegetation patterns in the mountains of the eastern continental Soviet Union (Soczava 1944, 1945*a*, 1945*b*; Soczava and Lukicheva 1953, Stanyukovich 1973, Vasil'ev and Kolesnikov 1974) and China (Wang 1961, Danert *et al.* 1961) seem to be like those in Japan. The herb-rich meadows of Kamchatka (Hultén 1972) and Sakhalin (Schwind 1942, Stepanova 1956, Tolmachev 1956) do not occur at the altitudinal timberline.

Heaths versus meadows

It seems clear that the dominant vegetation at the uppermost altitudinal timberlines in the mountains of Eurasia and North America comprises two main groups: (1) dwarf-shrub or grass heaths and (2) timberline meadows, which have different distribution patterns (Fig. 4).

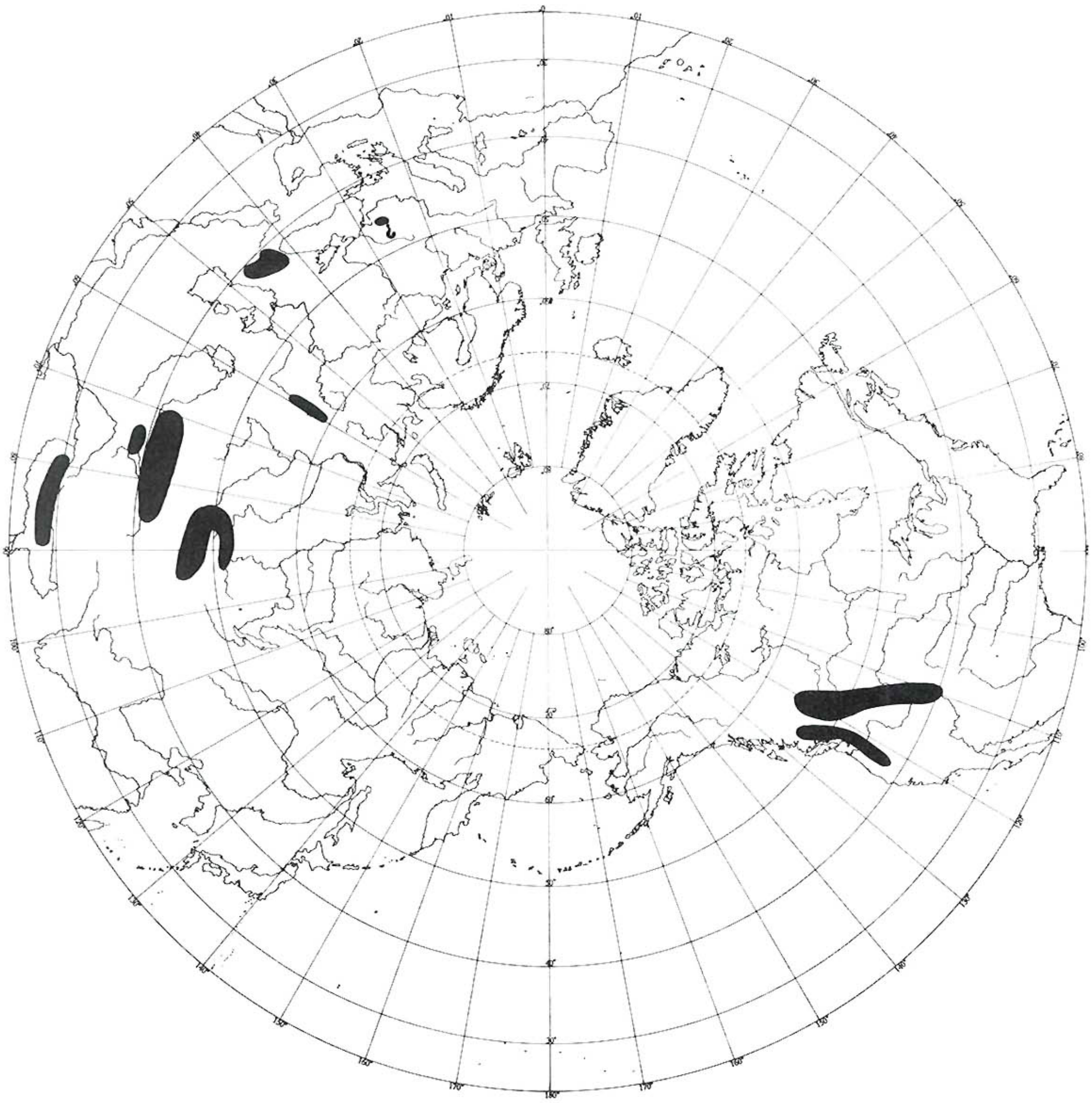

FIGURE 4. Regions in the northern hemisphere (blackened) where extensive natural meadow vegetation dominates at the altitudinal (upper) timberlines. (Polar projection.)

What is the reason for this distinct duality of the mountain timberline vegetation in the northern hemisphere? The dwarf-shrub and grass heaths are evidently more northern in distribution than the meadows. They also seem to be fairly similar to the vegetation at the polar timberline. In the arctic zone truly natural meadows only occur along rivers and lakes or in other wet places (Tikhomirov 1946, Soczava and Gorodkov 1956). The same is true in the hemiarctic (forest tundra) zone, the meadows belong to local rather than zonal vegetation. The dwarf-shrub heaths are replaced by meadows south of about the 60° N latitude in the Ural Mountains and at about the 55° N latitude in western North American mountains. The same change is also seen in the species composition of the uppermost forests. The circumboreal dwarf-shrub species which predominate in the field layer are replaced by herb and grass species not usually present in more northern forests. The same phenomenon occurs in the oroarctic (alpine) vegetation: chamaephytes are replaced by hemicryptophytes (Bliss 1956, Soczava and Gorodkov 1956). *Salix* thickets which are typical of the polar timberline as well as in some mountains (e.g., in Scandinavia, Alaska, and the northern Rocky Mountains) are less developed in the areas where the timberline meadows dominate.

This problem has not been completely overlooked by ecologists. Bliss (1956) pointed out the difference between the North American Arctic, where the evergreens dominate, and the oroarctic (alpine) zone of Wyoming, which has few evergreens. Later he (Bliss 1963) pointed out that the alpine vegetation of the Presidential Range, New Hampshire, is more similar to the vegetation of the Arctic and of the Scandinavian and Central European mountains than to the mountains of western North America. Soczava (1956*a*) outlined in a map the distribution of these two different types of timberline vegetation in Russia and North America and Lüdi (1961) has also noted the peculiarity of the timberline meadow vegetation of the Rocky Mountains.

Soczava (1956*a*) considered the main cause for the herb-rich meadow vegetation to be climatic. Rainy cyclones from the Atlantic promote this vegetation in Eurasia and comparable precipitation patterns from the Pacific in western North America. However, the explanation cannot be climatic alone, though some of the meadow areas are situated in the oceanic areas and are very rich in snow in winter (e.g., in western North America). In fact, on the more continental slopes (like on the east slopes of the Rocky Mountains, in the eastern Caucasus or western Tien Shan) the herb-rich meadows are not replaced by heath vegetation but steppe-like meadows. On the other hand, in the north there are dwarf-shrub heaths at the timberlines both in oceanic (e.g., Scandinavia, the Alps, Kamchatka, Japan, southern Alaska) and continental areas (e.g., interior Alaska, the northern Rocky Mountains).

The bedrock and soil cannot be the only decisive factors, either, because both the timberline vegetation patterns can be found on either oligotrophic or eutrophic habitats. The edaphic conditions naturally have a great effect on the floristic composition but not the over-all pattern.

Human activities could be expected to be one explanation of this vegetational duality. In Asia and in some parts of the Rocky Mountains these meadows are being used or they have been used as pastures, an activity which has perhaps expanded them locally, but originally they were not man-made. So although they physiognomically greatly resemble the European "Alpine meadows," they are not the same phenomenon. In North America there are extensive tracts of timberline meadow (excellent natural pastures) which were never grazed by domesticated animals.

The grazing pressure of the native ungulates on the timberline meadows must also be negligible. The ground squirrels and other rodents common in meadow vegetation on both continents also occur in timberline heaths, e.g., in Alaska, and so they cannot be an important cause. Certainly they have some effect on species composition of certain local meadow community types.

Fire, natural or man-made, modifies the limits of the meadows and tree stands at timberlines and has also been suggested as a reason for vegetation differences (Billings 1969, Douglas and Ballard 1971). Franklin *et al.* (1971), however, believe it a significant cause only locally.

Zonal position

The zonal position of these timberline meadows is a complicated and interesting problem. They are usually called "subalpine" by most North American and Soviet authors. Many Siberian authors call them the "podgoltsy" meadows which actually means the same as "subalpine." Krajina (1959, 1964, 1965) and his students (e.g., Brooke *et al.* 1970) have a different opinion. They do include the lower timberline meadows (in British Columbia) with scattered trees and tree stands in the "subalpine zone" as a "subalpine parkland subzone" but consider the upper meadows without (essentially) any trees in the "alpine zone."

On Battle Mountain I have included all the timberline meadows in the orohemiarctic[2] zone, i.e., the transitional zone (mountain forest-tundra ecotone) between the uppermost oroboreal fully forested zone and the absolutely treeless lower oroarctic (low-alpine) zone (*see* Hämet-Ahti 1965*a*, 1965*b*; and terminology in Ahti *et al.* 1968 and Hämet-Ahti *et al.* 1974). Thus the timberline of Battle Mountain is actually a band of gradual transition situated in this orohemiarctic (sub)zone rather than a single line.

However, all the timberline meadows in the northern hemisphere are not necessarily orohemiarctic, because the timberline may lie in any zone below the lower oroarctic zone (Hermes 1955, Troll 1973, Hämet-Ahti *et al.* 1974). The timberline meadows may be orohemiarctic, oroboreal or even orotemperate, depending on the mountain range and the ecology of the timberline tree species. Among the timberline meadows in North American and Eurasian mountains all these zones are probably represented. Unfortunately, the studies available do not always allow the determination of their zones exactly, but certainly their zonal position does not explain the duality of the timberline vegetation and, at least, is not the main reason for it.

Floristic history

It seems that we should seek to find the answer from the history of the flora and vegetation in these areas. All those areas where meadow vegetation prevails have good continuous or almost continuous mountain connections to the south. This is true especially in the Rocky Mountains but also with the Asian areas (Sayan, Altai, etc.). The only rather separate area is in the southern Ural Mountains but, in fact, it is not very far from the Caucasus Range.

The common circumboreal dwarf shrubs (e.g., *Vaccinium vitis-idaea* sensu lato, *V. uliginosum* sensu lato, *Empetrum nigrum* sensu lato, *Linnaea borealis* sensu lato,) and mosses are an important part of vegetation outside their circumboreal range, for instance in the Alps, but they play a small role in the Rocky Mountains south of the 55° N latitude or in the southern Ural Mountains, Caucasus, Sayan or Altai Mountains (cf. Hultén 1970). Weber (1965) emphasizes the floristic relationship between the southern Rocky Mountains and the Altai Mountains; obviously they also have some common features in their vegetation pattern.

In any case, although the historical features seem to offer the best explanations for the present range of the herb-rich timberline meadows, the problem is still largely open and needs further studies using the methods of comparative geobotany.

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[2] I am avoiding the term subalpine proposed by Löve (1970), because it is applied in many different meanings in different regions (cf. Hämet-Ahti *et al.* 1974).

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