ISSN 1067-4136, Russian Journal of Ecology, 2006, Vol. 37, No. 1, pp. 13–18. © Pleiades Publishing, Inc., 2006.
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Ecological Features and Trends in the Formation of the Flora of Liverworts under the Impact of Current Volcanic and Glacial Activities: The Example of Ushkovskii Volcano, Kamchatka

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Received February 17, 2005

Abstract—The flora of liverworts has been studied in the vicinity of the Bil'chenok glacier (the Ushkovskii volcano, Kamchatka), which is in a zone of volcanic ash fallout. Specific complexes of liverworts growing on young moraine and ash deposits have been identified. These complexes are dominated by thallose marchantioid species. Under the effect of periodic ash fallout (in the absence of glacial activity), communities are formed that contain increased proportions of xerophytes and species preferring sites with a disturbed ground vegetation cover.

DOI: 10.1134/S1067413606010036

Key words: ecology of liverworts, Kamchatka, volcanism, glaciers.

Volcanic activity has exerted an extraordinary effect on the formation of flora on the entire Kamchatka Peninsula (Komarov, 1951). Today, it largely determines the pattern of flora and vegetation in some regions of Kamchatka, mainly in its eastern part. Of the 29 active volcanoes recorded on the peninsula, 4 manifested explosive activity during the past five years (Kir'yanov *et al.*, 2003). The tops of seven volcanoes rise above 3000 m a.s.l. and are the present-day centers of glaciation. Trends in flora formation under the combined impact of volcanic and glacial activity have been described mainly as a secondary issue in large-scale floristic studies, and only a few publications have been devoted to the corresponding floristic complexes (Bylinkina, 1954). However, even these publications usually deal with vascular plants, while moss and lichen communities have escaped the attention of specialists in this field.

The purpose of this study was to describe the floristic groups of liverworts developing under the impact of a periodic fallout of volcanic ash and glacial activity in the vicinity of the Bil'chenok glacier on the Ushkovskii volcano (eastern Kamchatka).

MATERIAL AND METHODS

The Klyuchevskaya group of volcanoes extends over a large area (55°40′–56°15′ N, 160°15′ – 160°50′ E). The larger volcanoes of this group are the Ushkovskii, Krestovskii, Kamen', Oval'naya Zimina, Klyuchevskoi, Ostryi Tolbachik, and Bezymyannyi. The last three are currently more active than the others. The Shiveluch volcano, located north of the Klyuchevskaya group (55°40′ N, 161°33′ E), also has some impact on the study area. I studied liverworts in the vicinity of the Bil'chenok glacier located on the northern macroslope of Ushkovskii, a volcano whose current activity is low. Glaciologists distinguish between ice-cap and valley glaciers. The former develop in the zones where snow fails to melt during the warm season, accumulates, and gradually transforms into ice (in Kamchatka, usually at elevations above 2500 m a.s.l.). When the mass of ice exceeds a certain threshold level (specific to each case), it begins to flow down along depressions, forming the so-called valley glaciers. Bil'chenok belongs to the latter type. It flows from a large glacial lake (6 × 6 km) located on the top of a cone-shaped mountain and extends for 16 km, descending from 1900 to 750 m a.s.l. Periodically sliding abruptly downslope, the glacier produced a vast valley with moraine deposits on its sides. These deposits consist of crystalline rock debris brought by the glacier and mixed with volcanic ash.

During an explosive volcanic eruption, the ejected material, called tephra, may be transferred by air flows over large distances. For example, during the catastrophic eruption of Shiveluch in 1964, the city of Ust'-Kamchatsk located 200 km east of this volcano was covered with a 3-cm layer of ash within 3 h (Gorshkov and Dubik, 1969). Unfortunately, available data on the intensity and duration of ash fallouts are fragmentary and, with a few exceptions, concern urban areas (Petropavlovsk-Kamchatskii, Klyuchi, Ust'-Kamchatsk, etc.). In mountain regions near active volcanoes of the Klyuchevskaya group (i.e., in the zone of the heaviest fallout), only the total amounts of ash fallen over long periods of time (up to several years) is usually determined, and records are kept irregularly. Special studies are an exception, and the book by Gushchenko (1965) devoted to the comprehensive description of volcanic ash varieties in northern Kamchatka is of particular interest. It should be noted that the term "northern Kamchatka" in this case is applied to the Klyuchevskaya group of volcanoes and Shiveluch volcano, i.e., to the region referred to as eastern Kamchatka by Komarov (1951) and other authors.

In this book, the author presents a map of the accumulation of loose continental sediments. According to his data, sedimentation in the study region occurred at a rate of more than 6 cm per century, with more than 50% of them consisting of volcanic ash and dust that had not been redeposited. The bulk of deposits consist of the products ejected during the eruptions of Shiveluch, which account for 93% (430.25 billion metric tons) of loose pyroclasts produced by volcanoes of northern Kamchatka in the Holocene (Gushchenko, 1965). These data characterize pyroclastic deposits retrospectively, because they concern the compacted material. In fact, the vegetation of this region grows under the impact of loose ash, and the layers it forms on the soil surface are deeper than can be estimated by simply dividing the depth of the layer by its age in years. In 2003, for example, we examined a snowbank that proved to be covered with an approximately 1-cm ash layer, although no disastrous ash fallouts occurred in this year. The average diameter of pyroclastic particles in the study region varies from 0.05 to 0.1 mm, reaching 5 mm in deposits corresponding to the explosive eruptions of the Klyuchevskoi and Shiveluch volcanoes (Gushchenko, 1965).

Substrates formed by volcanic ash are, firstly, highly movable and poorly retain moisture and, secondly, have a specific chemical composition, so that the resulting soils are usually acid (pH_{H_2O} 3.2–3.8 to 5.5–6.8) (Gushchenko, 1965).

Volcanic ash is distributed over the surface nonuniformly. Its amount reaches 15–20 cm per year in depressions and approximately 1 cm per year in flat areas (beyond the periods of disastrous fallout), while steep slopes and bare rock outcrops remain virtually free from ash. When snow melts, streams running downslope wash channels through pyroclastic deposits in depressions, which gradually become gullies and ravines.

Glacial activity is another factor that has a significant effect on flora formation in the study region. The Bil'chenok valley glacier periodically moves rapidly (surges) down the slope at a variable speed, so that its margin advances for hundreds of meters within a few months. The interval between such surges is about 25 years (Vinogradov *et al.*, 1982). The last surge was recorded in 1980. The "inactive" glacier continues moving, although much slower. In such periods, the rate of ice melting in summer exceeds the rate of its advancement, which creates an impression that the glacier retreats.

The glacier forms fresh marginal moraines around its edges when it moves and deposits a new bare substrate (glacial till) on the bottom of the valley when it melts. Moreover, volcanic ash mixed with a coarser morainic material is deposited on the glacier itself, forming a layer several centimeters to several meters thick. This specific substrate, a product of both volcanic and glacial activities, is colonized by different plant groups, including liverworts.

Volcanic and glacial activities are the main but not the only factors influencing flora formation in the study region. Of major significance also are the differences in moistening, substrate density, and a set of biotic factors. All of them account for the unique mosaic pattern of this floristic complex.

The study area is at elevations of 750 to 1700 m a.s.l. Conditionally, it is located in the alpine belt, which is represented by different types of tundras and alpine short-grass meadows. Mountain pine and alder elfin wood occur sporadically.

The flora was studied together with botanists from the Komarov Botanical Institute and Kamchatka Branch of the Pacific Institute of Geography, Russian Academy of Sciences. In relatively flat areas with the tundra vegetation, complete geobotanical descriptions were made in 10 × 10-m plots to record the species composition, reproductive state, and coverage of liverworts. The plots were usually arranged along altitudinal transects passing through more or less stable tundra communities, but some descriptions of vegetation on fresh morainic substrates were also made. However, it was often impossible to find a lot with a more or less uniform plant cover in areas with crevices in rocks, on sloping banks and tuff outliers, etc. In such cases the synusial structure of liverwort communities was described.

The samples of liverworts that were impossible to identify in the field were processed in the laboratory by conventional anatomical–morphological methods. More than 350 such samples were studied.

After identification, the lists of liverworts found in different types of habitats were compiled.

INVOLVEMENT OF LIVERWORTS IN FLORA FORMATION

In most cases, the distribution of liverworts is determined not so much by vascular plants dominating in communities (dwarf shrubs, alder, etc.) as by the type of habitat characteristic of these communities (e.g., crumbling banks of streams). The types of habitats distinguished in the study region and the composition of liverworts in them are described below. Species names are given according to Bakalin (2003) or, for the species not included in this list, according to Konstantinova *et al.* (1992).

Morainic and pyroclastic deposits on the glacier body. This type of habitat is characterized by nonuniform and irregular moistening throughout the snow-free period, a low temperature of the substrate (0–5°C), and its mobility under the effect of wind, water, or sinking into thaw pools (microthermocarst). The dominant form is the thallose marchantioid species *Asterella saccata,* which is widespread and abundant. It is noteworthy that this species was described by Wahlenberg (1811) from the vicinity of Avachinskii Bay (*locus classicus* of the taxon) and has never been found since then. Apparently, its habitats in Kamchatka are confined to pyroclastic deposits (assuming that the habitat near Avachinskii Bay was on such a deposit produced by the Avachinskii volcano). Other liverworts found in habitats of this type were also marchantioids: *Conocephalum japonicum*, *Peltolepis quadrata*, *Sauteria alpina*, and *Preissia quadrata*.

Young moraines. This term refers to moraine deposits on bedrock, rather than on ice, that lack a closed plant cover. Plant communities on young moraines are at early stages of development but already include leafy jungermanniid liverworts, unlike the communities described above. This may be explained by the absence of thermocarst and resulting damage to the substrate. Liverworts are represented by *A. saccata* and very rare arctic species *Barbilophozia rubescens* and *Protolohozia debiliformis*. The taxonomic composition of their communities is poor because of insufficient moistening of well-drained moraine ridges and substrate mobility on their slopes.

Gullies (ravines) in pyroclastic deposits are a specific type of habitat not only for bryophytes, but in general. Their slopes consist of a material that is so light and movable that they do not allow the establishment of plants for more than one year. The only reliable substrate is provided by large boulders on the bottom. During floods or heavy rains, water carrying a large amount of suspended matter submerges these boulders, but bryophytes, including liverworts, manage to remain attached to them. When the water recedes, patches of bryophytes covered with a thick layer of ash mixed with silt emerge on the surface. The species diversity of these communities is relatively high. Based on ecological criteria, their constituent species may be divided into the following groups: (1) cryophilic species that often grow under conditions of high moistening along the banks of streams and in nival groups, such as *Anthelia juratzkana* and *Pleurocladula albescens*; (2) species growing on crystalline substrates in streams (*Jungermannia polaris, Marsupella commutata, M. memarginata*, and *Scapania subalpina*); (3) species often occurring on fine-grained substrates along the banks of streams (*Plectocolea hyalina, Pellia neesiana*, and *Scapania parvifolia*); and (4) the group of "random" species with different ecological preferences, such as eurytopic *Cephalozia bicuspidata*; *Lophozia wenzelii* var. *lapponica*, which prefers sites with a disturbed ground vegetation layer in the tundra belt; *Schistochilopsis opacifolia*, a species of moist tundras; and *Lophozia sudetica*, a mountain, mainly cryophilic species that is eurytopic in the tundra belt.

Banks of streams. Habitats of this type, being somewhat similar to those described above, differ from them in their regular moistening and much smaller amounts of suspended matter deposited by flowing water. Communities on the banks of streams are characterized by the highest floristic diversity. With respect to substrate, streams with light-soil (ash, sand, and peat) and stony banks can be conventionally distinguished.

Liverwort communities on stones consist of *Jungermannia pumila, Lophozia excisa, L. sudetica, L. ventricosa, L. wenzelii*, and *Scapania hyperborea*. Communities of peaty and sandy banks share the same group of dominant species: *Anthelia juratzkana, Nardia geoscyphus*, and *Pleurocladula albescens* (listed in order of decreasing significance). The proportions of other species in the synusiae are insignificant. *Lophozia sudetica, Scapania curta, Plectocolea subelliptica, Preissia quadrata*, and, rarely, *Aneura pinguis* and *Cephalozia ambigua* occur on sandy banks. Species growing on humus-rich ("peaty") banks include *Diplophyllum taxifolium, Lophozia ventricosa, L. savicziae, Scapania parvifolia, Tritomaria quinquedentata, Blepharostoma trichophyllum, Solenostoma confertissimum, Cephalozia bicuspidata*, and *Peltolepis quadrata.* Rarely, on compacted soils, *Marsupella commutata* and *M. sphacelata* can be found.

Nival habitats. This term refers to the sources and banks of small streams that flow from the glades on which snow melts after the summer flood is over (nival glades). Hence, the banks of these streams (unlike those described above) do not suffer from the powerful erosive action of floodwater. Liverwort communities in these habitats include *Jungermannia pumila, Eremonotus myriocarpus, Scapania mucronata, S. lingulata, S. hyperborea*, and *Hygrobiella laxifolia*. The flora of flat nival habitats with fine-grained (light) soils is markedly poorer and consists only of *Anthelia juratzkana* and *Pleurocladula albescens.* Moreover, the development of both these species is suppressed, because the plants are regularly covered with volcanic ash. In the areas where snow melts late, surface runoff is absent, and, hence, ash accumulates on the soil surface. The situation in this case is opposite to that with ravines: the substrate is not destroyed by flowing water but instead is covered with ash, which interferes with the development of vegetation.

Tundras. The entire study region is formally in the mountain tundra belt, but more or less well developed and stable tundra communities are found only beyond the valley occupied by the glacier and on moraines whose age exceeds 500 years according to tephra chronology (M.P. Vyatkina, personal communication). Depending on the intensity and regime of moistening, all tundra communities may be conventionally divided into three groups.

Firstly, there are areas with ground moistening in places where water released from melting permafrost comes to the surface. These are flat areas approximately 1000 m^2 in size with light soil and widely distributed moss–sedge hummocks. They may be conventionally referred to as degraded hummocky communities. Meltwater passing through pyroclastic deposits sometimes becomes slightly alkaline, and this is reflected in the composition of the flora. For example, *Saccobasis polita*, a very rare species in Kamchatka, appears in these communities. Liverworts growing on hummocks include *Cephalosia bicuspidata, Pleurocladula albescens, Blepharostoma trichophyllum, Scapania apludicola, Lophozia ventriculosa, Jungermannia pumila*, and *Scapania hyperborea.* Light soil between hummocks, which is mixed every year under the effect of freezing and thawing, is a substrate for *Anthelia juratzkana, Cephaloziella arctica, C. divaricata, Lophozia wenzelii* var. *lapponica, L. sudetica*, and *Nardia geoscyphus*. These liverworts form loose clusters that are not attached to the substrate with rhizoids. Hence, they are not damaged when the soil freezes, but, on the other hand, such clusters can develop only in very moist areas.

The other two types of tundra communities are characterized by surface moistening. The first type comprises moist tundras with different types of dwarf shrub–moss associations, in which liverworts grow on the sides of hummocks (*Blepharostoma trichophyllum* and *Leiocolea heterocolpos*) and in moist areas between them (*Orthocaulis quadrilobus, O. kunzeanus, Lophozia polaris*, and *Scapania paludicola*). *Marsupella commutata*, a rare species, sometimes occurs in small spots of light soil (approximately 1 dm^2).

The second type comprises different varieties of dry tundras. Among them, dwarf shrub–lichen stony tundras are most typical. In these communities, liverworts grow on the spots of light soil between dwarf shrubs of patches of lichens. Some species occupy narrow gaps in the lichen cover and emerge only when lichens dry and shrink. These are *Blepharostoma trichophyllum, Tritomaria quinquedentata, Orthocaulis quadrilobus, Ceophalozia bicuspidata, Cephaloziella divaricata*, and *Scapania hyperborea.* Liverworts growing between hummocks include *Barbilophozia rubescens, Lophozia polaris, Schistochilopsis grandiretis*, and *Diplophyllum taxifolium*. Finally, the spots of cryogenic light soil are colonized by species characteristic of habitats with a disturbed ground layer and multizonal species (*Solenostoma confertissimum*) along with cryoxerophilic species *Gymnomitrion concinnatum, G. coralloides, Prasanthus suecicus*, and *Marsupiella alpina* (the last three are rare in Kamchatka).

Burrows and holes made by animals. Zoogenic damage to the plant cover may be inflicted only once (holes) or repeatedly (almost constantly) but within a relatively short period of time, as animals rarely use the same burrow openings for more than one year. The difference in the degree and periodicity of damage between holes and areas near burrows accounts for the development of different complexes of liverworts. Species more or less tolerant to trampling by murine rodents grow near burrow openings. They include *Anthelia juratzkana, Cephalozia bicuspidata, Nardia geoscyphus*, and *Pleurocladula albescens* (note that these species are also components of the communities growing on the banks of streams). The complexes of liverworts in holes, which are usually moister than adjoining tundra areas, are formed by species growing in the surrounding cenoses, such as *Blepharostoma trichophyllum, Cephalozia bicuspidata, C. Pleniceps, Schistochilopsis incisa, Preissia quadrata*, and *Tritomaria quinquedentata.*

Crevices. Topographically, we distinguish crevices between stones in tundra stone streams and crevices in steep rocky walls of gorges (ravines). As a rule, habitats of the second group are characterized by stronger shading and less abundant moisture supply, but they do not suffer from ash fallouts (virtually no tephra is retained in almost vertical crevices). However, these parameters markedly vary in both groups of habitats.

In relatively dry tundra areas, *Gymnomitrion concinnatum* and *Sphenolobus minutus* are the typical liverworts growing in crevices between stones. Crevices with more abundant moisture supply (in increasing order) are favored by *Tritomaria quinquedentata, Diplophyllum taxifolium, Anthelia juratzkana*, and *Marsupella commutata.* The thallose species *Sauteria alpina* occurs in strongly shaded crevices.

The communities of dry crevices in rocky walls that receive different amounts of sunlight consist of the following species (in different combinations): *Athalamia hyalina, Preissia quadrata, Leiocolea heterocolpos, Blepharostoma trichophyllum, Eremonotus myriocarpus, Scapania gymnostomophyla, Plagiochila porelloides*, and *Protolophozia debiliformis.* In strongly shaded and moist crevices, *Calycularia laxa, Plectocolea subelliptica, Preissia quadrata*, and *Diplophyllum taxifolium* occur. The highest species diversity of liverworts is characteristic of moist and well-illuminated crevices: the spectrum of species is almost identical to that in local floras of similar mountain habitats in the areas of Kamchatka that are not exposed to volcanic ash fallout. This is explained by the fact that ash entering these crevices (if any) is quickly removed by flowing water. The corresponding communities include *Aneura pinguis, Anthelia juratzkana, Blepharostoma trichophyllum, Eremonotus myriocarpus, Nardia geoscyphus, Lophozia sudetica, Pleurocladula albescens, Plectocolea subelliptica, Preissia quadrata, Cephalozia pleniceps, Marsupella commutata*, and *Scapania curta.*

Of some interest are floristic complexes on light soils at the bases of tuff outliers and boulders in alder thickets, which develop under conditions of strong shading in summer. This factor suppresses the growth of plants but improves moisture supply by retarding evaporation. These communities have generally the same composition and include *Barbilophozia rubescens, Blepharostoma trichophyllum, Scapania parvifolia, S. curta, Tritomaria quinquedentata, Preissia quadrata*, and *Sauteria alpina*. *Diplophyllum taxifolium* is the only species that sometimes occurs above the soil surface, on the outliers.

Elfin wood. In the study area, elfin wood is represented mainly by alder, with mountain pine occurring rarely and in small areas (no more than 200 m^2). In both cases, *Ptilidium pulcherrimum* is the only liverwort species growing on tree bark. *Diplophyllum taxifolium* and *Barbilophozia hatcheri* occur on the spots of light soil shaded by alder.

DISCUSSION

The distribution of liverworts in the study area indicates that they may be divided into the ecological groups of species favoring regularly and strongly disturbed substrates, moderately disturbed substrates, and virtually undisturbed substrates.

Substrates of the first category are movable young moraines, morainic and pyroclastic deposits on the glacier surface, and sandy beds of streams and gullies. Thallose marchantioid liverworts are the absolute dominants or even the only members of corresponding communities. They are relatively large and have thick thalli, which makes them more effective in resisting substrate displacement and drying under conditions of irregular moistening. In general, this group plays a major role in the flora of liverworts in arid regions, such as the steppes, semideserts, and xerophytic mountain regions of Central Asia, Middle East, and the Mediterranean. Their presence in these regions is especially obvious as the species diversity of liverworts is low.

Substrates of the second category are flat areas in the tundras (stone streams, banks of slowly flowing water streams, nival habitats, etc.). They are permanently exposed to ash fallouts, but the amount of ash is insufficient for markedly affecting the development of liverworts. However, it accumulates in depressions, giving rise to the spots of noncryogenic light soil, and improves substrate drainage. As a consequence, the flora becomes slightly xerophilic (*Scapania* spp. and *Pleurocladula albescens* virtually disappear, being substituted by obvious xerophils such as *Prasanthus suecicus*), and "ruderal" species (*Nardia geoscyphus, Solenostoma confertissimum, Isopaches bicrenatus*, etc.) develop actively. Finally, ash fallouts affect floristic diversity. For example, *Tetralophozia setiformis* and *Macrodiplophyllum plicatum*, the species that occur in virtually all mountain regions of Kamchatka, have not been found in the study region despite our efforts. A probable explanation is that specific features of micro- and nanorelief allow the vegetation to survive in some places even after disastrous fallouts; during the subsequent fallouts, however, these "refugia" might be destroyed, whereas other places would be protected.

Therefore, when the flora of liverworts was formed, selection for the capacity for active and regular sexual reproduction was one of the main factors. Species that did not satisfy this requirement simply could not survive. This opinion is confirmed by data on insular floras: islands in the ocean were mainly colonized by species that reproduced sexually and, hence, had many more chances to arrive there due to the transfer of diaspores. A thorough search for some species (including the aforementioned *Tetralophozia setiformis*) in the flora of Bering Island, where climatic conditions are very similar to those in the tundra belt of the Klyuchevskaya group of volcanoes, was also ineffective.

The category of virtually undamaged habitats includes crevices in rocks and almost vertical slopes on which no ash is accumulated. Their relative area in the study region is small. But their role in the development of liverwort flora is significant. Communities of these habitats are similar to those developing beyond the zone of active volcanism in Kamchatka. It should be noted that these communities, being protected from the impact of pyroclastic fallout, are nevertheless exposed to other adverse factors, such as shading, insufficient moisture supply, and cold winds.

Thus, nine types of habitats for liverworts may be identified in the study region. They are not strictly delimited from each other with respect to physical and chemical parameters, and, hence, the boundaries of corresponding floristic complexes are also indistinct. The most specific type comprises young pyroclastic and morainic deposits on the glacier surface, where only thallose marchantioid liverworts grow. Crevices in rocks belong to the richest type, as their floristic complexes are very similar to those of corresponding habitats in other local floras that do not suffer from the effects of volcanic activity.

The flora of liverworts in the study region lacks some species that are widespread in the mountain tundras of Kamchatka but are incapable of continuous sexual and vegetative reproduction. Such species cannot survive in the ground vegetation layer regularly affected by pyroclastic fallouts.

Under the impact of continuous volcanic and glacial activities, the flora is not only impoverished but also acquires some specific features. We have found some species that are rare in the Far East (*Asterella saccata, Peltolepis quadrata, Prasanthus suecicus*, and others), and their presence in the study region is due to the availability of young substrates.

ACKNOWLEDGMENTS

This study was supported by the Russian Foundation for Basic research, project no. 03-04-49304, and by the Russian Science Support Foundation.

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