

Alterations of plant soil cover during reestablishment of bilberry-moss spruce forests

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Summary: We've been studying interactions between weed, small-shrub and moss species in spruce, birch and aspen forests. Alterations in tree layer are shown to affect the structure of plant soil cover via following factors (1) level of illumination, (2) amount and type of tree waste and (3) formation of the microrelief.

Zusammenfassung: Wir untersuchten Interaktionen zwischen Unkräutern, Zwergstäuchern und Moosen in Fichten-, Birken- und Espenwäldern. Änderungen der Baumschicht beeinflussen die Zusammensetzung der Pflanzendecke durch folgende Parameter: (1) Grad der Illumination, (2) Umfang und Typ des Baumverfalls und (3) Gestalt des Mikroreliefs.

Keywords: Taiga, forests, forest ecology, plant soil cover, spruce, *Picea abies*, *Vaccinium myrtillus*

Bilberry-moss spruce forests are very common spruce associations in the middle taiga of NW Russia. They mostly well correspond with ecotopic conditions of this zone and therefore are viewed as climax community (VASILEVICH 1983). In the weed and small-shrub layer of bilberry-moss spruce forests, *Vaccinium myrtillus* L. predominates with some addition of *Majanthemum bifolium* (L.) F.W. Schmidt, *Trientalis europaea* L., *Vaccinium vitis-idaea* L., *Oxalis acetosella* L. and *Linnaea borealis* L. The moss layer in these forests is well developed and usually represented by *Pleurozium schreberi* (Brid.) Mitt., *Hylocomium splendens* (Hedw.) B.S.G. and *Dicranum polysetum* Sw. Natural thinning of the tree canopy results in abundance of weed species like *Avenella flexuosa* (L.) Drejer and *Melampyrum pratense* L. In the sites where spruce is locally replaced by small-leaved trees, tall grass birch, aspen or alder forests are formed (NIZENKO 1960).

Reestablishment of bilberry-moss spruce forests after fellings and fires is shown to be possible in several ways. The first one occurs when disruption of the climax community does not affect spruce regrowth. In this way, reestablishment of bilberry-moss spruce forests takes place without alteration of edificator tree species (KAZIMIROV 1971). Another way of the reestablishment occurs through a set of secondary successions, namely, formation of pine, birch or aspen forests. Tree layer changes during this set of successions are described in details (MOROZOV 1930; SUKACHOV 1931). However, corresponding alterations of plant soil cover are studied very poorly.

In the present work, we investigated interrelations between different species in weed, small-shrub and moss layers in bilberry-moss spruce forests and different stages of its reestablishment.

Materials & Methods

Study area

The field studies were carried out in birch, aspen and spruce forests with well developed bilberry-moss layers situated at the first lake terrace in the West of Konevitsa island (SW of

Ladoga lake, Russia). The terrace surface is formed by sandy-boulder deposits. The studied areas' soil is podzolic.

Description of plant communities

In each plant community studied, one sample plot (20 x 20 m) has been established. By use of a net of coordinates, precise position of all trees and regrowth within certain plot was obtained. In addition, for every tree or regrowth, following parameters have been measured: (1) height, (2) stem diameter, (3) height of the crown attachment to the stem, (4) vertical projection of the crown and (5) horizontal projection of the crown.

Each sample plot was also described for plant soil cover. For this purpose, within every square meter of the sample plot, one mini-plot (0.1 m²) has been established. In each mini-plot, following parameters have been measured: (1) precise position in respect to the net of coordinates, (2) projective cover degree for different plant species, (3) total quantity of leaf fall, (4) percent equilibrium between leaf falls produced by different tree species and (5) properties of microrelief and illumination.

All mini-plots established in the same sample plot were subdivided in the following groups based on similar properties of the microrelief:

- flat areas out of the crown projections;
- small hollows out of the crown projections;
- small uplands out of the crown projections;
- near-stem uplands produced by different tree species (namely, spruce, birch and aspen);
- stumps.

For each group of the mini-plots, mean values of cover degree for different plant species were calculated.

Statistic analysis

Analysis of the data obtained was carried out by means of correlation (Pirson's correlation coefficient with 0.05 significance level) and dispersion analysis (ROHLF & SOKAL 1995).

Results & discussion

Birch forest

In this type of forest, several tree layers are well developed (Fig. 1). The first layer is represented by mature birch trees with high (approximately 30 m) stems and large (up to 9 m in diameter) crowns. The second layer is formed by media-height (about 10 m) spruce trees with lowly attached crowns. In the regrowth, both birch and spruce trees are present in approximately equal ratio. Mean density of the regrowth is about 1,500 per ha.

Characteristic plant soil cover of birch forest is formed predominantly by the weed and small-shrub layers: their joint mean projective cover degree is 57%. In these two layers, the most abundant species are *Oxalis acetosella*, *Avenella flexuosa*, *Vaccinium myrtillus*, *Stellaria holostea* and *Melampyrum pratense*. The role of mosses in plant soil cover is comparably low, their mean projective cover degree is only 22%. The most abundant species in the moss layer is *Brachythecium salebrosum* (Web.et Mohr) B.S.G. In addition, several other moss species (namely, *Tetraphis pellucida* Hedw. and *Plagiothecium cavifolium* (Brid.) Iwats.) are found preferably at near-stem uplands and fallen stems.

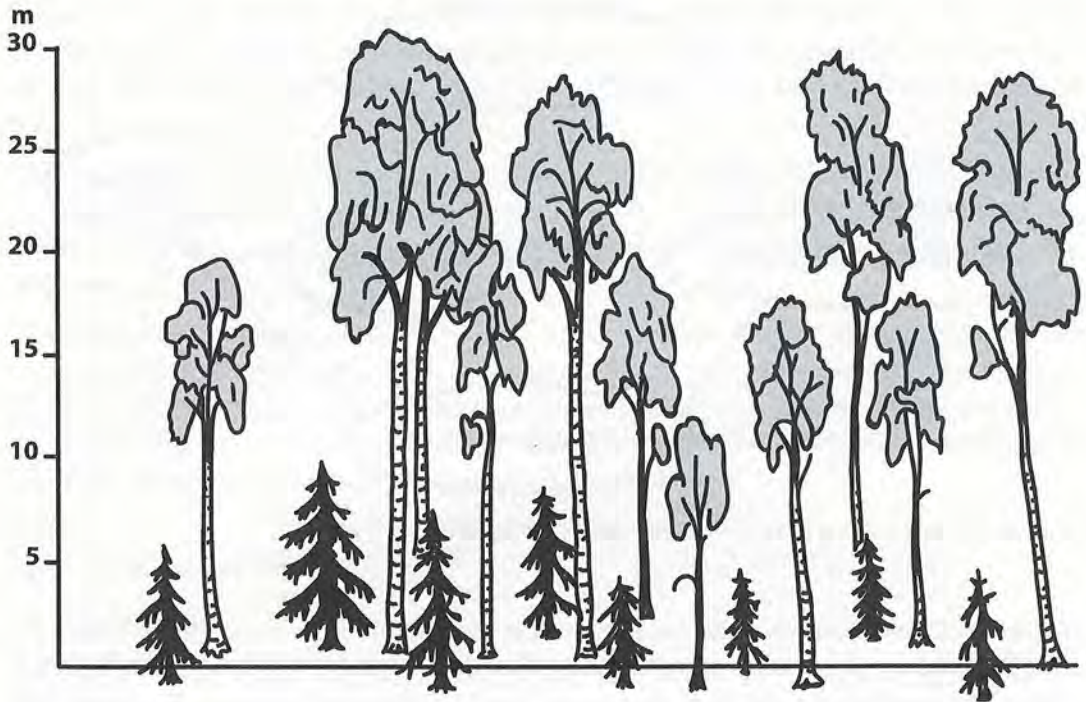


Figure 1. Birch forest (see text).

The leaf fall is quite extensive in this type of forest (projective cover degree is 85%) and is produced predominately by birch trees. Such leaf fall is shown to enrich the soil allowing formation of significant weed and small-shrub layers (SUKACHOV 1931; MELEKHOV 1980; BRANDTBERG et al. 2000).

In comparison with other investigated types of forests, birch forest have a high level of illumination (clear space in tree canopy is of 23%). We have shown that local increasing of illumination correlate with changes in leaf fall structure. Namely, in most illuminated sites, the portion of birch leaf fall is significantly higher compared with that of needles ($r = -0.50$), while most shadowed sites displayed the opposite equilibrium.

Studying plant soil cover in birch forests (Fig. 2), we have found positive correlations between:

- abundance of weeds/small-shrubs and value of clear space in tree canopy ($r = 0.32$);
- abundance of weeds/small-shrubs and portion of birch leaf fall in the soil cover ($r = 0.43$);
- abundance of mosses and value of clear space in tree canopy ($r = 0.16$);
- abundance of mosses and portion of birch leaf fall in the soil cover ($r = 0.43$).

As a result, species like *Avenella flexuosa*, *Melampyrum pratense*, *Vaccinium myrtillus*, *Majanthemum bifolium*, *Milium effusum*, *Stellaria holostea*, *Brachythecium salebrosum*, *Dicranum polysetum* and *Hylocomium splendens* are predominantly associated with highly illuminated sites of the birch forest. Projective cover degree of these species strongly decreases under spruce crowns where the level of illumination is low. Only *Oxalis acetosella* displays significant increase of its projective cover degree in the shady sites ($r = -0.14$). This species shows positive correlation with quantity of needles in the soil cover ($r = 0.22$). Our findings correspond well to the general rule that distribution of plant species in soil cover significantly depends on illumination level (TREMBLAY & LAROCQUE 2001).

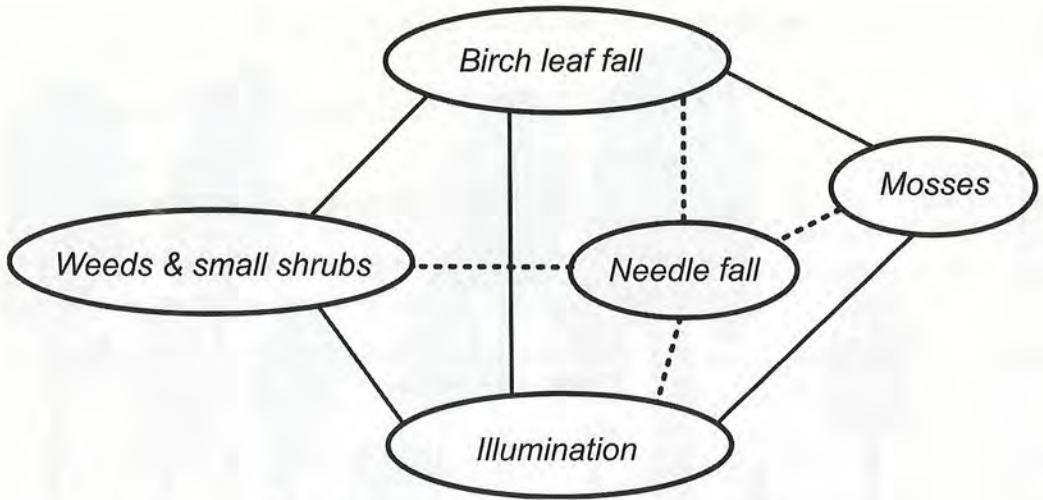


Figure 2. Correlation scheme in bilberry-moss birch forest.
 — positive Pirson's correlation negative Pirson's correlation

In plant soil cover characteristic for birch forest, we have found several groups of species (Fig. 3). The first group is only represented by *Vaccinium myrtillus*. This species is distributed in clones and predominates at well illuminated small uplands and stumps. We know that *V. myrtillus* is associated with micro-uplands of organic origin (MAZNAYA 1990) and often produces huge and dense clones which are able to inhibit spruce seedlings by root competition (JADERLUND et al. 1997). Some authors describe allelopathic influence of *V. myrtillus* leaves on spruce germination and micorrhiza (GALLET 1994). These data support our finding: *V. myrtillus* occupies a comparably independent position in birch forest community.

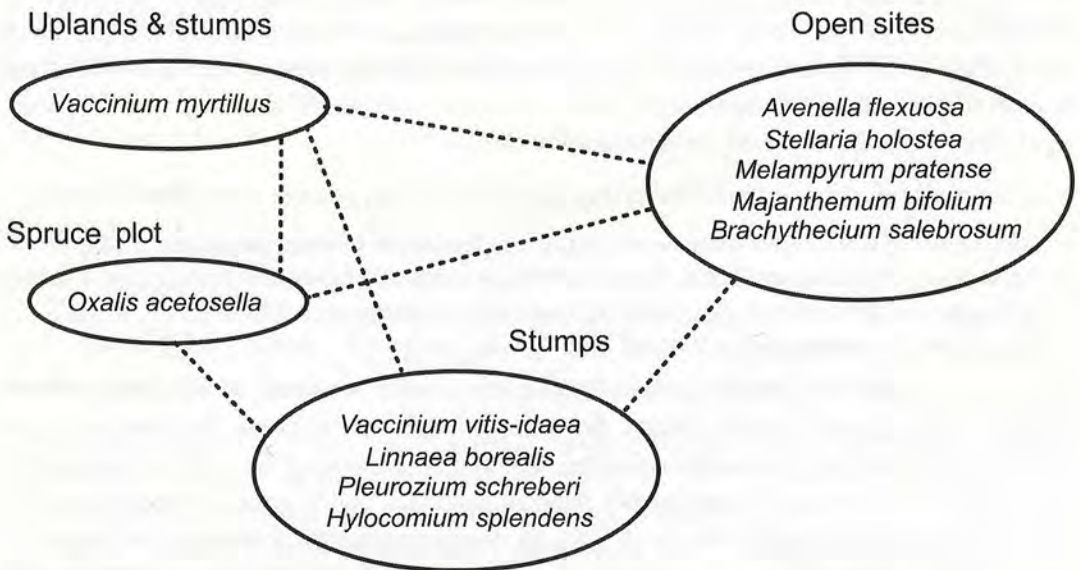


Figure 3. Groups of species in bilberry-moss birch forests
 (within groups, all species have positive correlations to each other).
 negative Pirson's correlation

The second group includes *Avenella flexuosa*, *Melampyrum pratense*, *Majanthemum bifolium*, *Milium effusum*, *Stellaria holostea* and *Brachythecium salebrosum* (coefficients of correlation vary from 0.12 to 0.38). The listed species are most abundant at well illuminated sites with almost no needle fall.

The third group is represented by *Vaccinium vitis-idaea*, *Linnaea borealis*, *Pleurozium schreberi*, *Hylocomium splendens* and *Dicranum scoparium* (coefficients of correlation vary from 0.18 to 0.36). These species have their highest projective cover degree at decomposing stumps and fallen tree stems.

In contrary to all species mentioned above, *Oxalis acetosella* is quite abundant in different environments including shady (the sites under spruce regrowth and near-stem uplands produced by birch trees) and well illuminated ones (stumps and the sites under rowan trees regrowth). This reflects high tolerance of *O. acetosella* to both, low and high illumination. There is a similar suggestion made by other authors (POLYAKOVA et al. 1981).

Thus in birch forest, the majority of moss, weed and small-shrub species is associated with open well illuminated flat sites or small uplands with a high portion of birch leaf fall.

Aspen forest

This type of forest shows a complex structure with several tree layers (Fig. 4). The first layer is formed by tall aspens (about 26 m in height) with sprawling large crowns (up to 9 m in diameter). Moreover in the lowest part of the first layer, birch trees and pines are also present but they are not so abundant compared to aspens. The second layer is represented by spruce trees of approximately 10 m height. Spruce trees are distributed not uniformly and make groups

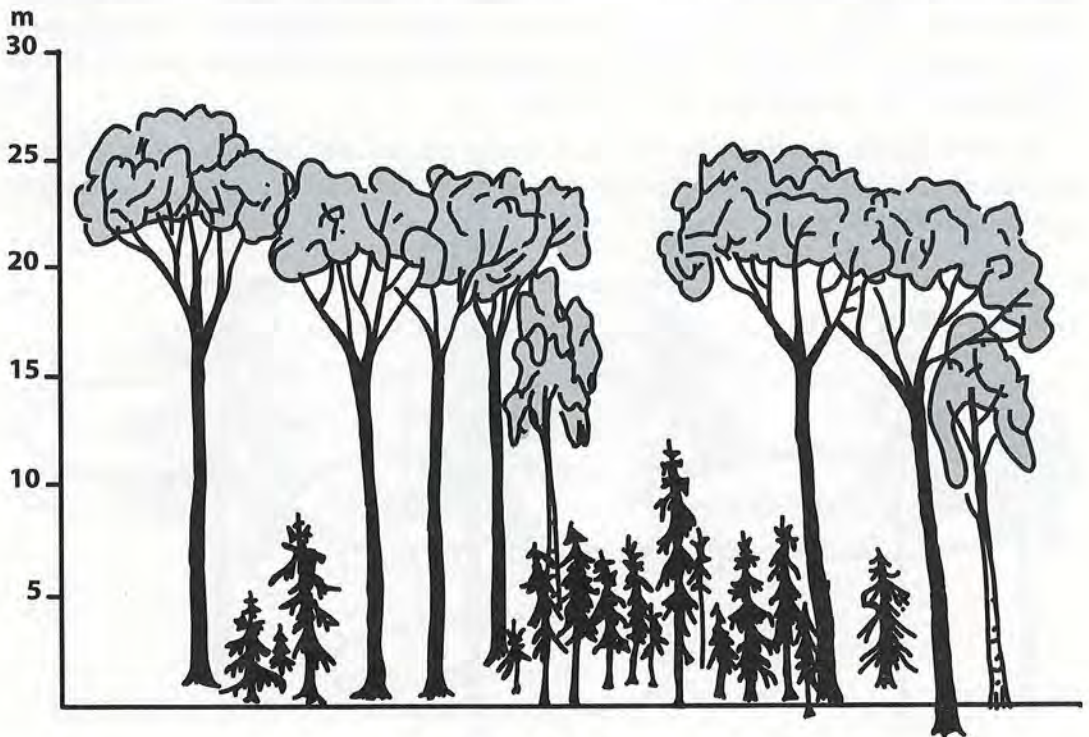


Figure 4. Aspen forest (see text).

in those sites of the forest where the first layer is significantly thinned. Here they form an independent synusium with low level of illumination and high amount of needles in soil cover. In the regrowth (its media density is about 1,000 per ha), spruce trees strongly predominate in addition with single birch and rowan trees.

Weed and small-shrub layers are poorly developed, their joint projective cover degree is only 33%. The most abundant species are *V. myrtillus* and *O. acetosella* with some presence of forest edge weeds (for example, *Viola canina* L., *Rubus saxatilis* L. and *Fragaria vesca* L.) at open well illuminated blanks. Moss layer predominantly comprises species like *Brachythecium salebrosum* and *Dicranum scoparium* and has even lower projective cover degree (6 %).

Perhaps poor development of plant soil cover in aspen forests is determined by high amounts of tree waste (its projective cover degree is 94 %). The main portion of tree waste is represented by aspen and birch leaf fall as well as needles (41%, 26% and 32%). Aspen leaf fall contains more ash nutrients. That's why it better enriches the soil than birch leaf fall (BANNIKOVA 1967). Therefore in aspen forest, the majority of weed and small-shrub species displays positive correlation with clear space in tree canopy ($r = 0.59$) and amount of aspen leaf fall ($r = 0.16$) but simultaneous negative correlation with amount of needles in soil cover ($r = -0.23$; Fig. 5). Moreover, many species (namely, *V. myrtillus*, *V. vitis-idaea*, *Linnaea borealis*, *Avenella flexuosa*, *Trientalis europaea*, *Melampyrum pratense*, *Oxalis acetosella*, *Stellaria holostea*, *Rubus saxatilis*, *Hylocomium splendens*, *Brachythecium salebrosum* and *Rhodobryum roseum*) are mostly abundant at open flat sites and small uplands with high illumination. The majority of these species is positively correlated to each other (coefficients of correlation vary from 0.12 to 0.48) producing a complex structure without clear groups.

In spruce synusium, clear space in tree canopy is low (16%) and the amount of needles in soil cover is high (45%). As a result, projective cover degrees of weed/small-shrub and moss layers decrease to 13% and 2%. The most abundant species in such environment is *O. acetosella* having comparably high tolerance to low illumination.

So in aspen forests, weeds, small-shrubs and mosses are generally associated with open well illuminated sites where the amount of leaf fall (aspen or birch) and tree waste is high whereas needle fall is nearly absent.

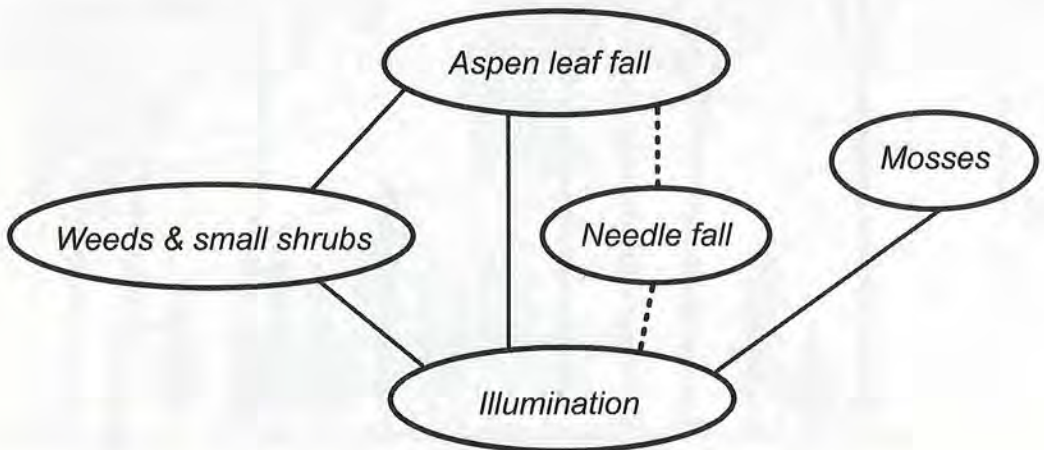


Figure 5. Correlation scheme in bilberry-moss aspen forest.
 — positive Pirson's correlation negative Pirson's correlation

Spruce forest

Tree layers in this type of forest are formed predominantly by about 100 year old spruce trees (30 m in height) with large (up to 9 m in diameter) and highly attached crowns (Fig. 6). The second generation of spruce is represented by rare 50 year old trees which are significantly inhibited and achieve not more than 8 m in height. The crowns of these trees are narrow, sharply asymmetric and highly attached. Single birch trees and pines are also present but they only grow in peripheral regions. The regrowth is represented by spruce with media density about 3,000 per ha and very rare rowan trees. It is distributed in groups associated with sites of first generation tree fall. This spruce forest is a mature climax community.

In plant soil cover, green mosses strongly predominate (projective cover degree is 75%) among which most abundant species are *Pleurozium schreberi*, *Dicranum scoparium* and *Hylocomium splendens*. Weed and small-shrub layer (joint projective cover degree is only 36%) is generally formed by *V. myrtillus* and *O. acetosella* completed by *Majanthemum bifolium*, *Avenella flexuosa* and *Linnaea borealis*. Amount of tree waste in soil cover is quite low, most of it (55%) is produced by spruce trees. Due to high crown attachment, the level of illumination of plant soil cover is comparably high (clear space in tree canopy is of 21%).

The majority of correlations found in spruce forest is opposite to those characteristic for birch and aspen ones. Namely, abundance of weed and small-shrub species is shown to correlate negatively with level of illumination ($r = -0.15$) but positively with amount of needle fall ($r = 0.19$; see Fig. 7). However, projective cover degree of mosses still correlates positively with illumination ($r = 0.27$) and negatively with total amount of tree waste ($r = -0.93$; for spruce needle fall, $r = -0.37$). So we have found negative correlation between abundance of weed/small-shrub species (for example, *V. myrtillus*, *V. vitis-idaea*, *Trientalis europaea*, *Oxalis acetosella*

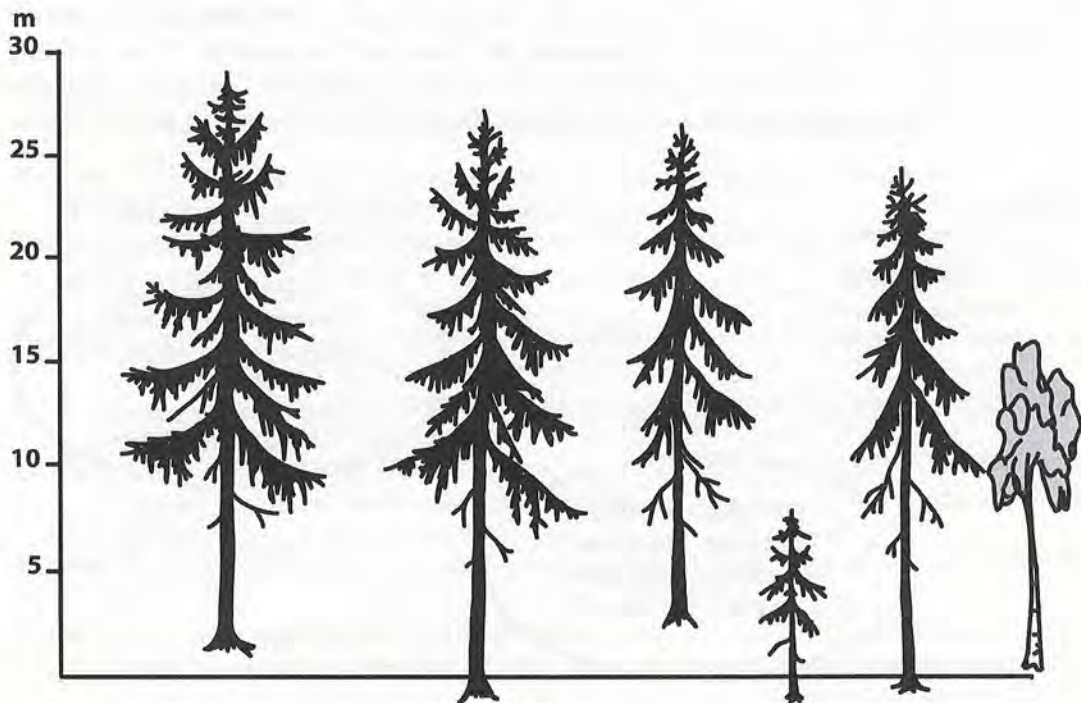


Figure 6. Spruce forest (see text).

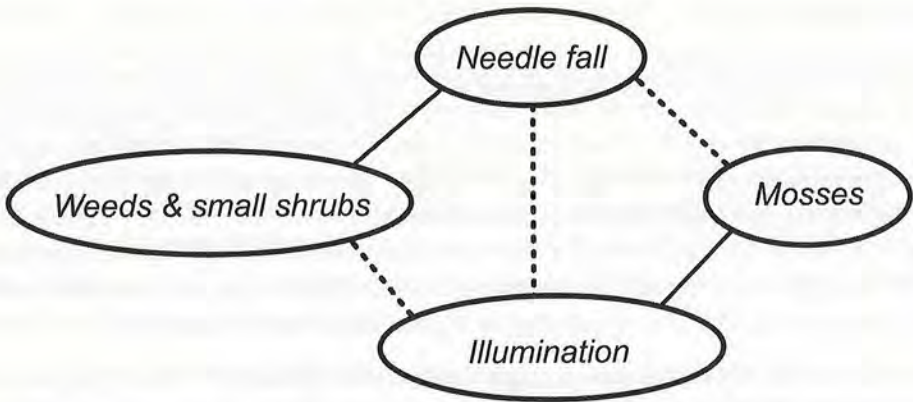


Figure 7. Correlation scheme in bilberry-moss spruce forest.
 — positive Pirson's correlation negative Pirson's correlation

and *Stellaria holostea*) and mosses ($r = -0.13$). Actually, weeds and small-shrubs are present in spruce forests predominantly at sites with high amount of needle fall which significantly inhibits the development of the moss layer.

This antagonism between weed/small-shrub and moss layers has been published several times. However, the majority of authors stresses out inhibition of one layer by another (KARPOV 1969; KARPOV & STAROSTINA 1969). According to our data, this antagonism is indirect and mainly determined by the tree layer and its waste.

Groups of species characteristic to spruce forests are presented in Fig. 8. The first group comprises several species (such as *Pleurozium schreberi*, *Avenella flexuosa*, *Melampyrum pratense*, *Majanthemum bifolium*, *Linnaea borealis* and *Luzula pilosa*; coefficients of correlation vary from 0.10 to 0.19) which are most abundant at flat sites, small uplands and stumps. The second group includes species that positively correlate with the amount of birch leaf fall and are generally associated with near-stem uplands produced by birch trees: *V. myrtillus*, *V. vitis-idaea*, *Hylocomium splendens* and *Rhytidiadelphus triquetrus* (coefficients of correlation vary from 0.13 to 0.23). These

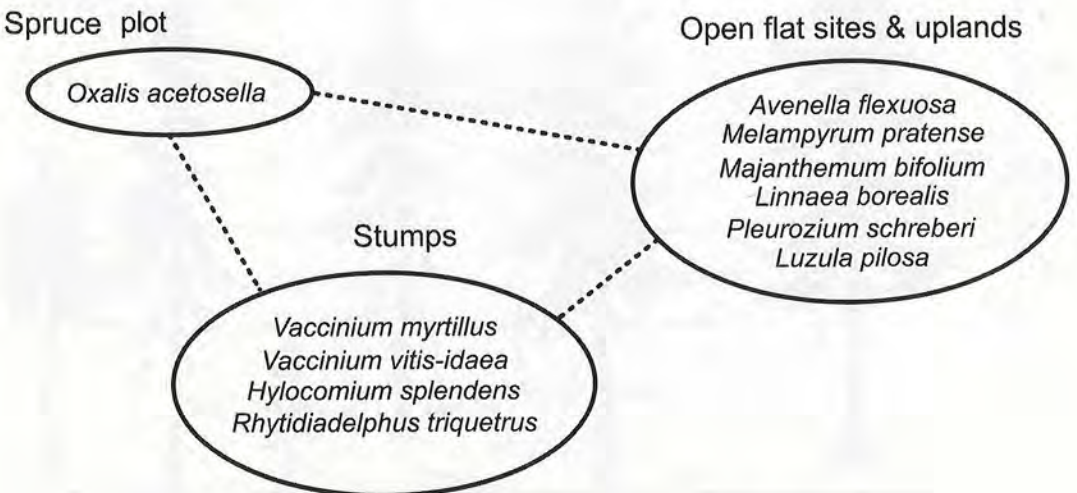


Figure 8. Groups of species in bilberry-moss spruce forests
 negative Pirson's correlation

species prefer rich and well drained soil. One more group is represented by *Oxalis acetosella*. This species correlates positively with the amount of spruce waste ($r = 0.30$) and low illumination ($r = -0.14$) and is most abundant at near-stem uplands produced by spruce trees. Similar data have been obtained by IPATOV & KIRIKOVA (1999). However, it should be stressed out that all groups mentioned above are not sharply divided and reflect general tendencies in distribution of plant soil cover species at different sites within spruce forest.

So the species from weed and small-shrub layers are generally associated in spruce forests with small uplands, stumps and near-stem uplands reflecting a significant role of the microrelief. Mosses prefer flat sites, small uplands and stumps. They seem to be inhibited by high amounts of tree waste and therefore they are associated with open and more illuminated sites. Weeds and small-shrubs are more tolerant of tree waste and even need it thus occupying more shadowed sites.

The influence of tree layer on plant soil cover structure

In all plant communities studied, the species from weed, small-shrub and moss layers are more abundant at various small uplands and stumps reflecting positive role of better drainage and high amount of organic compounds in the soil. In mature spruce forests where dense layer of mosses strongly predominate, weeds and small-shrubs occupy less illuminated sites as more tolerant to significant amounts of needles in soil cover. Fall of mature spruce trees results in their replace by birch or aspen trees, increase of illumination and enrichment of soil by the products of leaf fall decomposing. On its turn, this replacement leads to decrease of moss abundance. Simultaneously, various weeds and small-shrubs like *Vaccinium myrtillus*, *Avenella flexuosa*, *Melampyrum pratense* and *Stellaria holostea* actively penetrate into open, well illuminated sites and start to avoid shady sites under spruce regrowth (except *Oxalis acetosella* which is highly tolerant to low illumination and still retains under spruce crowns). Thus alterations in tree layer significantly affect the structure of plant soil cover via following factors (1) level of illumination, (2) amount and the type of tree waste and (3) formation of microrelief.

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