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Review

Site factors controlling epiphytic lichen abundance in northern coniferous forests

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ABSTRACT

Epiphytic lichens are an important part of the vegetation of northern coniferous forests of Eurasia and North America. Much progress has been made during recent decades at disentangling relevant site factors, which control the diversity and distribution of epiphytic lichens in boreal and oroboreal forests. The present paper aims at summarizing the present state of knowledge. Relevant site factors include the microclimate, nutrient supply, structural diversity and, if applicable, air pollution. The continuity of site conditions decides over the presence of species with dispersal limitations. The effects of fire on epiphytic lichens are largely unstudied, although fire is an important ecological factor in boreal forests.

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Introduction

The northern coniferous forests include vast areas of the boreal zones of Eurasia and North America occupying around one third of the world's forest area (Schultz, 2000). South of the boreal zone, oroboreal forests form extrazonal vegetation in cold mountain sites of the temperate belt. The cool–moist conditions of most of these forests favor a rich epiphytic lichen vegetation. The present paper discusses the main site factors controlling the diversity and distribution of epiphytic lichens within the northern coniferous forests. Though it aims at providing a balanced view on the site ecology of lichens in boreal and oroboreal forests of the northern hemisphere, the paper may have some bias to link the author's own work to the relevant literature of other groups.

Diversity and abundance of epiphytic lichens in the northern coniferous forests

Information on the lichen diversity of northern coniferous forests is strongly different between regions. While the lichen flora of forests from Scandinavia and Scotland and the mountain forests of central Europe is well-known (Santesson et al., 2004; Smith et al., 2009; Tønsberg, 1992; Wirth, 1995), the knowledge of the lichen species composition of the most extended areas of coniferous forests in the Eurosiberian taiga and North America is far from being complete. This is apparent from the high number of epiphytic lichens described, for example, in recent years from coniferous forests of western North America (e.g. Spribille

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Table 1
Distribution types of boreal lichens with exemplary species (modified after Ahti, 1977).

Distribution types with characteristic examples of lichen species
1. Circumpolar
Throughout the boreal zones of Eurasia and North America (*Bryoria fuscescens*, *Hypogymnia physodes*, *Lecanora circumborealis*, *Lepraria jackii*, *Melanohalea septentrionalis*, *Ramboldia cinnabarina*, *Tuckermanopsis sepincola*, *Usnea cavernosa*, *U. dasypoga*)
2. Oceanic, incompletely circumpolar
Oceanic western and eastern parts of Eurasia and North America (*Cavernularia hultenii*, *Platismatia norvegica*, *Alectoria sarmentosa*, *Dolichousnea longissima*, *Hypogymnia tubulosa*, *Platismatia glauca*)
3. Amphi-Atlantic
Along the coasts of eastern North America and western Europe (*Erioderma pedicellatum*)
4. Western Eurasian-western North American
Oceanic to slightly continental parts of western Eurasia and North America (*Bryoria fremontii*, *Letharia vulpina*, *Thorluna dissimilis*, *Tuckermanopsis chlorophylla*)
5. Interior Eurasian-interior North American
Continental species of the arid inner parts of continents in vicinity to steppes or not (*Melanelixia albertana*, *Evernia mesomorpha*, *Hypogymnia bitteri*, *Bryoria furcellata*, *Flavopunctelia soredica*)
6. Western North American
Temperate to boreal parts of western North America, especially in coastal rain forests (*Cavernularia lophyrea*, *Hypogymnia duplicata*, *Lobaria oregana*, *Pseudocyphellaria anomala*, *P. anthraspis*, *Ramboldia gowardiana*)
7. Eastern North American
Temperate to boreal parts of eastern North America (*Pseudevernia cladonia*, *P. consocians*, *Hypogymnia krogiae*, *Imshaugia placorodia*)
8. Western Eurasian
Mainly temperate, marginal in the boreal zone (*Pseudevernia furfuracea*)
9. Eastern Eurasian
Mainly temperate, marginal in the boreal zone (*Hypogymnia mundata*, *H. fragillima*)
10. Eastern Eurasian-eastern North American
Mainly temperate, marginal in the boreal zone (*Parmelia squarrosa*)

and Hauck, 2003; Spribille and Printzen, 2007; Wedin et al., 2009). Taxonomic research activities on lichens from coniferous forests of Siberia and central Asia are less extensive than in Europe and North America. Nevertheless, case studies examining the species composition of epiphytic lichen vegetation and the dominance of individual species have been published from many areas of the northern coniferous forest belt. The state of knowledge on lichens from the northern coniferous forests clearly benefits from the fact that many boreal or boreal–temperate species have a circumpolar distribution and can thus also be easily recognized in lichenologically little explored regions. Ahti (1977) estimated that two thirds of the boreal macrolichen flora consist of circumpolar species. This high proportion of circumpolar species among the known boreal lichens probably decreased slightly during the past 30 years due to the description of new species with limited ranges. The biological cause for the existence of many circumpolar lichen species is their ability to disperse more easily over long time scales than vascular plants (Printzen, 2008). Many other species are limited either to oceanic or continental boreal forests or to one of the continents (Table 1). Ahti (1977) classified a total of 13 different distribution types of boreal lichens, from which are 10 relevant to epiphytes (Table 1). Some lichen species are strictly limited to boreal and oroboreal forests, whereas many other species occur both in the boreal and temperate zones.

Quantitative data on the epiphytic lichen vegetation analyzing the abundance of individual species have been published from various regions, e.g. Scandinavia (Esseen, 1981; Gauslaa and Holien, 1998; Gauslaa et al., 1998; Hilmo et al., 2009; Hilmo, 1994), central Europe (Hauck and Runge, 2002; Köstner and Lange, 1986), northeastern Asia (Biazrov, 1974; Hauck and Javkhlan, 2009), western (Bunnell et al., 2008; Hauck and Spribille, 2005) and eastern (Lang et al., 1980; Schmull et al., 2002) North America. Many other studies include species lists and specifications of preferred substrata, like many studies from Siberia (Makryi, 1990; Plikina, 2003; Sedelnikova and Lashchinskiy, 1991; Urbanavichene, 2001). Dominant epiphytes from the trunks of conifers from different boreal and oroboreal forests of Eurasia and North America are compiled in Table 2.

Several studies aim at estimating the biomass of epiphytic lichens in boreal forests. This is of special interest for fruticose–pendulous (alectorioid) lichens (*Alectoria*, *Bryoria*, *Usnea*), which contribute much to the epiphytic lichen biomass of the upper canopy, especially in areas with high precipitation and frequent fog events (Arseneau et al., 1998; Campbell and Coxson, 2001; Ellyson and Sillett, 2003; Kermit and Gauslaa, 2001). The relative significance of alectorioid lichens varies with the climatic conditions and the land use history. In moist unmanaged old-growth stands of *Picea abies* in Scandinavia, the biomass of alectorioid species was found to exceed that of foliose lichens (primarily Parmeliaceae species) by the factor 3–7 (Esseen and Renhorn, 1996). In managed stands, foliose lichens dominated over alectorioid lichens; the ratio of alectorioid to foliose lichen biomass varied between 0.1 and 1 (Esseen and Renhorn, 1996; Kermit and Gauslaa, 2001). Epiphytic lichen biomass is usually higher in unmanaged old-growth forests than in managed stands (McCune, 1993). Dead branches often harbor a particularly high lichen biomass (Liu et al., 2000). On the stand level, epiphytic lichen biomass of northern coniferous forests can reach several hundred to a few thousand kg/ha (Edwards et al., 1960; Lang et al., 1980; Rhoades, 1981).

Many epiphytic lichens of the northern coniferous forests share related photobionts. The unicellular green alga *Trebouxia simplex* and related species (Doering and Piercey-Normore, 2009; Hauck et al., 2007a; Kroken and Taylor, 2009) as well as *Trebouxia* species of the *Asterochloris* group (Rambold et al., 1998), namely *T. erici* (Gärtner, 1985), *T. excentrica* (Gärtner, 1985; Hildreth and Ahmadjian, 1981) and *T. glomerata* s.l. (Friedl, 1989; Piercey-Normore and DePriest, 2001), are most common among boreal epiphytes. Further relevant green algae include the genera *Dictyochloropsis* and *Stichococcus* (Tibell, 2001; Tschermak-Woess, 1978, 1980), which are associated, e.g. with *Chaenotheca*.

Site factors

Light

The availability of light is an important factor controlling the within-stand variation of epiphytic lichens. The lower tree trunks of dense forests receive much less light than the upper canopy or standing deadwood. Bark furrows, as found in old larch and pine trees, are both dark and dry habitats, which are inhabited by calicioid and leprarioid lichens (Rikkinen, 1995). Overall lichen