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Tamm review

Tamm review: The North-American lichen woodland

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ABSTRACT

The lichen woodland (LW) is an open-crown subarctic forest distributed principally in North America where it extends from Newfoundland in Atlantic Canada to the Yukon and Alaska. It is the main tree ecosystem of the LW zone north of the closed-crown boreal forest zone, and south of the forest-tundra zone where its cover diminishes progressively toward the Arctic tree line. Growth and development of LWs are closely dependent on dry-mesic, nutrient-poor podzolic soil environments largely distributed on the Canadian Precambrian Shield. The sun-exposed open structure and dominance of lichen species on the dry-mesic soils of LWs determine many of their functions. A diversified cryptogamic flora is thriving in LWs due to reduced competition from vascular plants unable to grow and survive on dry, nutrient-poor soils. Because of the reduced greenhouse effect caused by the open structure and dominance of pale-color lichen mats inducing a greater albedo, LWs exerts a negative microclimatic impact on the environment culminating in the reduction of the frost-free growth season and increase and intensity of frost events. A suite of common, often recurrent, sometime compounding, fine- and large-scale disturbances (including climate change) activates the successional dynamics of LWs and also their historical and present expansion and contraction across the boreal biome. Post-disturbance chronosequences induced by fire, wind and caribou trampling and grazing are producing similar seral communities converging toward the self-maintenance of the LW ecosystem. Long-term succession in southernmost LW sites possibly converges toward the closing of tree canopy and recovery of closed-crown conifer forests (CCCF) in absence of fire. The creation of LW occurred repeatedly during the late Holocene, as well as its extirpation from the northernmost sites (forest-tundra zone) with wildfire as the principal triggering mechanism. LWs are presently unable to transgress the tree line, except for minor advances in small confined sites. Current evidence of the dual distribution of LWs and CCCF in eastern Canada shows that the LW zone is expanding southward into the CCCF zone, where compound disturbances associated with epidemics followed by small to extensive fires are transforming dense forest stands to LWs, a process most likely independent of climate. In terms of ecosystem management, there are concerns about the maintenance of the southernmost LWs within the CCCF zone as poor carbon sinks. Projects involving LW plantation sites in the CCCF zone in eastern Canada are proposed to offset the increased emission of atmospheric gases and thus mitigate climate change.

1. Introduction

Lichen-dominated ecosystems cover approximately 8–10% of the earth's terrestrial surface, particularly in subarctic and arctic regions (Crittenden, 1999). Among these ecosystems, the lichen woodland (LW), an open-crown subarctic forest, stands as the second largest ecosystem of the North American boreal biome, covering about 2 million km^2 in Canada (Johnson and Miyanishi, 1999). LWs extend from the Atlantic coast to the Rocky Mountains and the Yukon (Hustich, 1951, 1966; Hare, 1950, 1959; Rousseau, 1952, 1968; Hare and Ritchie, 1972; Rowe, 1972, 1984; Payette, 1983, 1992; Timoney, 1988; Timoney and Wein, 1991; Sirois 1992; Timoney et al., 1993; Payette et al., 2001), where they progressively decline in extent (Fig. 1). The rare LWs in Alaska are located on dry, acid, glacial deposits of the Brooks Range (Christiansen, 1988). The zonal distribution of LWs lies north of the closed-crown conifer forest, the largest conifer ecosystem of the continent (Brandt, 2009), which is dominated by black spruce (*Picea mariana* (Mill. B.S.P.), white spruce (*Picea glauca* (Moench) Voss), tamarack (*Larix laricina* (Du Roi) K. Koch), jack pine (*Pinus banksiana* Lamb.), lodgepole pine (*Pinus contorta* Dougl. ex Loud.) and balsam fir (*Abies balsamea* (L.) Mill.). The LW is the main forest ecosystem of the LW zone north of the closed-crown forest zone, and south of the forest-tundra zone where its cover diminishes progressively toward the Arctic tree line. In the forest-tundra zone, LWs are forming a complex spatial

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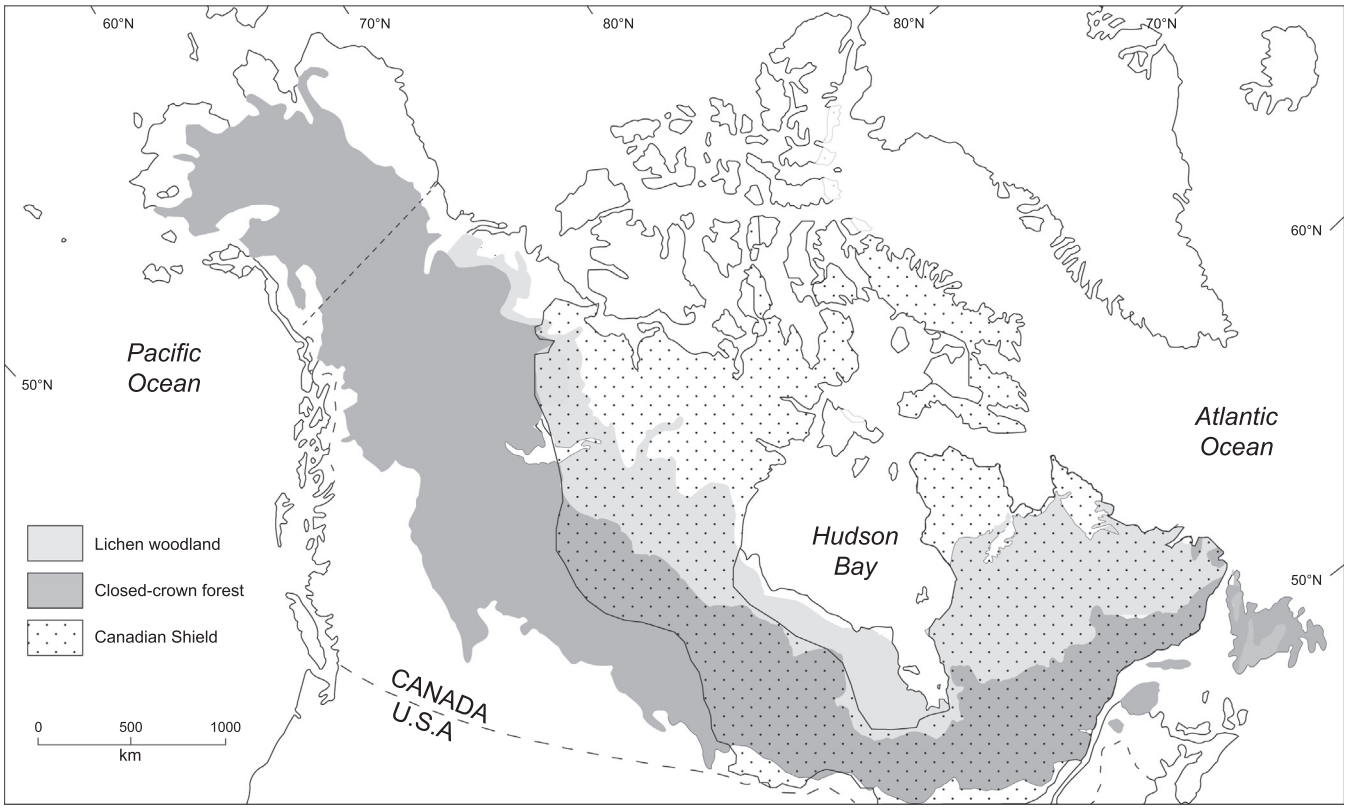

Fig. 1. Distribution of lichen woodlands in North America. Most lichen woodlands are growing on soils of the Precambrian Shield, except in Newfoundland, Yukon and a part of northern Ontario where Paleozoic rocks dominate.

pattern with lichen-tundra communities (Payette et al., 2001).

The LW zone extends northward to the Arctic treeline, and as such is a direct vegetational response to cold climatic conditions generated by moving air masses on both sides of the Arctic front (Bryson, 1966; Barry, 1967; Bryson and Hare, 1974; Johnson and Miyanishi, 1999). Yearly and seasonal precipitations do not appear to be the main causal factor of the distribution of lichen-dominated terrain across the continent. However, the boreal forest of northeastern North America receives more than twice the mean annual precipitation of its central and western counterparts (from 300 to 500 mm in central Canada to at least 600–1000 mm in Quebec-Labrador) (D'Orangeville et al., 2016). Even though the main geographical range of the LW is centered in the subarctic zone, its very existence is primarily dependent on the soil environment. This nutrient-poor ecosystem thrives on acid (pH < 4.5), relatively dry, coarse, sandy and rocky soils of the Canadian Precambrian Shield, and its continental distribution exceeds the boundaries of this major geological landmass only in the Yukon, northern Ontario and Newfoundland (Fig. 1). Outside North America, LWs are scattered across boreal Eurasia. Most LWs are dominated by Scots pine (*Pinus sylvestris* L.), mountain birch (*Betula pubescens* Ehrh.) and Siberian larch (*Larix sibirica* Ledeb.), on dry, coarse-grained soils of the Baltic Shield in northern Fennoscandia, and on acid and dry deposits of the Kola Peninsula and western Siberia (Steijlen et al., 1995; Tishkov, 2002; Tømmervik et al., 2004), respectively.

Conifer species growing in LWs are occasionally accompanied by broadleaf tree species such as paper birch (*Betula papyrifera* Marsh.) and trembling aspen (*Populus tremuloides* Michx.). The most extensive LWs are those occupied by black spruce and jack pine, whereas lodgepole pine, tamarack and white spruce LWs are less common (Figs. 2 and 3) (Morin and Payette, 1984; Rowe, 1984; Delwaide and Filion, 1988; Desponts and Payette, 1992; Coxson and Marsh, 2001; Houle and Filion, 2003; Laliberté and Payette, 2008). In eastern Canada, jack pine LWs generally grow outside the range of the subarctic LW zone (Rudolph and Laidly, 1990; Conkey et al., 1995; Barton and Grenier, 2008; Payette et al., 2017). Finally, pitch pine (*Pinus rigida* Mill.) LWs of the New Jersey pinelands are among the southernmost forest communities where lichens grow freely in close association with mosses (Sedia and Ehrenfeld, 2003).

In this review, we examine the main characteristics (structure, botanical composition, etc.), functions (microclimate, fire and animal interactions, spatiotemporal dynamics, etc.) and origin of LWs at several spatiotemporal scales. The regeneration potential and development of the LW ecosystem throughout the Holocene is assessed relative to its resilience to abiotic and biotic disturbances. Finally, we evaluate whether or not the geographical range of the LW ecosystem is changing relative to present climate warming. Conservation and management of LW are briefly discussed in the context of the C sink/source dynamics of boreal ecosystems.

2. Structure and plant composition of the lichen woodland

The floristic composition of LW includes a predominance of circumboreal and North-American boreal species. While no endemic species are exclusive to the LW ecosystem, a few arctic-alpine species currently grow in the northernmost exposed LWs at the Arctic treeline. The open structure of LW (generally 10–40% tree cover, including lichen parkland, with < 10% tree cover, Fig. 3) includes only a small number of mature trees compared to dense conifer forests, a contrasted difference of tree cover recorded in surface pollen assemblages across the boreal biome (King, 1993). Whereas the mean number of trees > 9 cm at breast height in > 100 year old dense spruce-moss forests is 1000–1050 stems ha^{-1} (based on a survey of 94 stands, Quebec Government Forest Surveys, 2013), the mean is only 560 stems ha^{-1} in LWs > 100 year old (based on a survey of 125 stands, Quebec Government Forest Surveys, 2013). These figures are similar to those of Rencz and Auclair (1978), who calculated a mean tree density of 556