

Yukon Taiga – Past, Present and Future

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1. Introduction

“This land-mass, which I shall hereinafter call Beringia, must have been a good refugium for the biota during the glacial period.” Hultén, 1937 (p. 34).

Summary: Primeval Yukon Beringia comprises subalpine taiga over mountainous landscape extending from the Alaska border south-eastward to Mount Nansen and northward to the Arctic Ocean. It is proposed that persistence of populations of *Picea glauca*, *P. mariana* and *Pinus contorta* on subarctic permafrost soils of this never-glaciated region has its explanation in *in situ* ancestries and physio-genetic constitutions, the exceptional morphological diversity and survival fitness tracing back to ancient stock and successive periods of climate change. Based on preliminary chloroplast DNA (cpDNA) evidence, Yukon Beringia’s upland conifers were a source of post-glacial reinstatement of subarctic boreal conifers of northwestern North America.

1.1 Objectives

Early explorers observed that northwestern North America and northeastern Siberia lacked evidence, widespread elsewhere in North America and Eurasia, for having been modified by overriding ice sheets (Hayes, 1892; Kryshstofovich, 1935; Bostock, 1936). Hultén (1937) named this region Beringia and, aware of the concept of glacial refugia (Blytt, 1882; Warming, 1888), considered known circumpolar distributions of ~ 2000 arctic and subarctic plant species in relation to perceived postglacial reestablishment east and west of Beringia (Fig. 1). The primary objective here is to highlight the scientific value of populations of spruce trees (*Picea* spp.) in Canada’s Yukon Beringia. Although supporting scientific data are wanting, there is nevertheless reason to doubt that interior boreal forest provenances if transplanted into subarctic taiga could display survival fitness comparable to that of Beringia’s hardy taiga trees. Thus, major concerns in relation to North American spruce taiga reduce to ancestral lineage and physiology. Are Beringia trees the ancestors of North American taiga conifers? What is the physiological basis for their exceptional subarctic fitness? Answers may well reside in trees populating a never-glaciated portion of ‘Primeval’ Beringia spanning 62.5 °N to 64.5 °N along the boundary between Yukon Canada and Alaska USA, and extending southeastward to Mount Nansen (Fig. 1).

2. Current state of knowledge

2.1 Geological past of East Beringia

The continental plate containing North America and Eurasia had moved northward from the southern hemisphere to north of the equator ~ 330 million years ago (~ 330 Ma), and during the Mesozoic mountains of East Beringia's Yukon - Tanana Terrane had begun being uplifted (Mortensen, 1992). Subsequent volcanic extrusions, weathering and erosion over millions of years produced the non-glaciated mountainous landscape encountered at present within Yukon Primeval Beringia (Fig. 1). When the Atlantic Ocean began forming and distancing Eurasian and North American continents, ~ 170 Ma, they were approaching their present-day latitudes and shapes. Although Late Cretaceous (~ 100 Ma) brought global warming (Steuber et al., 2005), cold arctic winters followed for 30 million years (Davies et al., 2009).

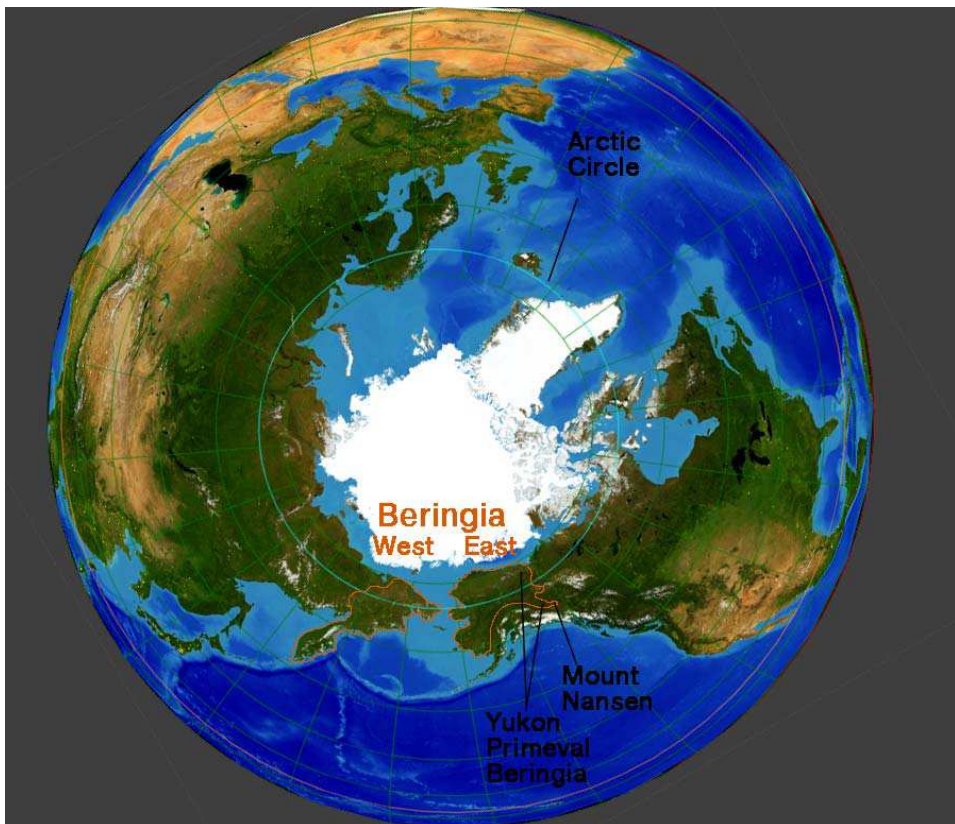


Fig. 1. The outlines of the bounds of West and East Beringia indicate regions where terrestrial refugia could have existed during the Last Glacial Maximum. Approximately 2.9 million years ago (~ 2.9 Ma), Mount Nansen near the southeastern tip of East Beringia stood at the edge of the first and most northwesterly advance of Cordilleran ice sheets toward Yukon Primeval Beringia, a never-glaciated landscape that probably held ancestors of postglacial ecosystem reinstatement eastward across North America.

Relatively warm conditions again prevailed in the Arctic from 70 to 40 Ma, and ~ 45 Ma the high Arctic supported lush temperate to tropical forests containing palms, flowering broadleaved trees and various conifers, including *Picea* spp. (Andrews et al., 1965; Hills et al., 1974; Francis, 1991; LePage, 2001; Jahren, 2007; Taylor et al., 2009). Those ancient forested ecosystems stood far north of the Arctic Circle where present-day tundra is entirely barren of trees. Isotopic data point to the existence during Middle Eocene of a global climate system conducive to warm temperatures and an Arctic Ocean that remained unfrozen even during its extended winter dark period (Jahren et al., 2009). It is probable that changes associated with the Earth's mantle and extraterrestrial cycles affecting axial tilt, precession, and eccentricity of the elliptical orbit of Earth were contributing factors (Milankovitch, 1941; Foulger, 2010).

Stockey and Wiebe (2008) described *Picea*-like fossil needles in Early Cretaceous sediments of Vancouver Island, Canada, evidence that spruce was evolving distantly south of the polar region much earlier than ~45 Ma, an earlier deduction based on Arctic fossil finds (Lepage, 2001). Based on chloroplast DNA (cpDNA) sequences, Ran et al. (2006) suggested that the world distribution of spruce reflects two dispersals to Asia via a Bering Strait land bridge during glacial periods; however, additional scientific data are needed to substantiate such a global hypothesis. Nothing is yet known of ecosystems which existed in the domain of Beringia when lush forests were growing in the high Arctic ~ 45 Ma, nor of how temperate trees subsequently acquired the fitness needed to survive contemporary subarctic conditions (Namroud et al., 2008). Those secrets may yet be discovered within Yukon's Primeval Beringia.

2.2 Glacial periods and Primeval Beringia within East Beringia

Early geologists recognized that Yukon glaciations involved several ice sheets (Hayes, 1892; Bostock 1936, 1966). In Table 1, three principal glacial periods of the Yukon are listed. Those three comprise eight ice-sheet advances, each of which moved northwest toward East Beringia beginning ~2.9 Ma (Duk-Rodkin, 1999; Barendregt & Duk-Rodkin, 2004).

| Glacial Period | Glacial Maxima (Ma) | Geomagnetic Polarity CHRON | CHRON timespan (Ma) | Unglaciaded terrain to the northwest from coordinates (°N, °W): |
|-----------------------|----------------------------|-----------------------------------|----------------------------|--|
| pre-Reid | 2.90-0.78 | GAUSS / MATUYAMA | 3.58-2.58 2.58-0.78 | (61.72, -138.10) |
| Reid | ±0.200 | BRUNHES | 0.78-0.13 | (61.55, -136.92) |
| McConnell | 0.022 | BRUNHES | 0.13-0.00 | (61.32, -136.63) |

Table 1. Chronology of Late Cenozoic Cordilleran ice sheet advances toward East Beringia's southeast tip (after Duk-Rodkin, 1999; Barendregt & Duk-Rodkin, 2004).

East Beringia frequently has been considered in relation to landscape modifications produced at the Last Glacial Maximum (LGM) approximately 22,000 years ago (~ 22 ka). However, it is apparent in Table 1 that the bounds of unglaciaded East Beringia depend on the timeframe of interest. Occupying a relatively small area of East Beringia on the east side

of the Alaska-Yukon boundary is never-glaciated Yukon 'Primeval' Beringia, a mountainous region including Nisling Terrane, Yukon-Tanana Uplands and lands northward along the Alaska boundary to the Firth River and Beaufort Sea (Fig. 1, Table 1). Hayes (1892) was first to note the non-glaciated character of this region. The farthest glacial advances across Nisling Terrane into the Yukon-Tanana Uplands were subsequently found by Bostock (1936) to have terminated in the vicinity of Mount Nansen (62.1064 °N, 137.3031 °W), between the southeastern tip of Primeval Beringia to the northwest and Reid/McConnell terrain to the south and east (Fig. 1; see also Fig. 5). Those advances were referred to by Bostock (1966) as 'Nansen - Klaza' glaciations, and he associated them with the earliest northwestern advance of a Cordilleran ice sheet. That first Cordilleran ice sheet and associated mountain glacial events occurred ~ 2.9 Ma and became known as 'pre-Reid' glaciations (Duk-Rodkin et al., 2004). The pre-Reid glacial period spans two million years (Table 1), and the number and extents of glaciations within its time range remain to be better characterized (Bostock, 1966; Lebarge, 1995; Duk-Rodkin, 1999; Duk-Rodkin et al., 2004).

There is no obvious surficial evidence for Primeval Beringia having ever been altered by overriding glaciers. However, it cannot be concluded that mountain valleys were never affected by major snow accumulations or localized piedmont or valley bottom glaciers. Beringia in general experiences winter and summer extremes. Snag (62.383333 °N, 140.366667 °W) within Yukon lowland Beringia experienced the lowest recorded temperature (-63 °C) in North America (Wahl et al., 1987), and Oymyakon (63.450765 °N, 142.803188 °W) not far west of West Beringia experienced the coldest recorded temperature (-71 °C) in the northern hemisphere (Takahashi et al., 2011). East Beringia is largely semi-arid, shielded from heavy Pacific Ocean precipitation by high mountain ranges in southwestern Yukon. Ongoing uplift of those mountains is probably the principal explanation for progressive reductions in the volume of precipitation hence for concomitant decreases in northwestward advances of Cordilleran ice sheets during successive glacial periods (Armentrout, 1983). In addition, dry arctic winds flowing over East Beringia encourage sublimation, and summers bring long days and temperatures on south-facing slopes reaching to 40 °C. Thus, although glaciers stood in valley bottoms near Mount Nansen as recently as 1970 (R. A. Savidge, unpublished data), it is doubtful that high altitude slopes and mountain tops remained perennially buried beneath snow and ice even during the most severe pre-Reid glacial period.

Angular and only partially rounded cobblestones occur in mineral excavations made in valley bottoms near Mount Nansen (Bostock, 1936; Lebarge, 1995). High altitude cirques exist particularly on northern aspects of some Yukon-Tanana mountains and, evidently, piedmont lobes advanced down slopes and along subalpine valleys (Duk-Rodkin, 1999). The elevations achieved by valley glaciers remain conspicuously marked by tors at > 1400 m a.s.l. (e.g., see Fig. 7C). The pre-Reid ended ~ 0.78 Ma, and an extended interglacial period followed (Duk-Rodkin et al., 2004). Reid glaciations peaked ~ 200 ka; and most recently McConnell glaciations of the Wisconsinan followed (Table 1). Figure 2A indicates the extent of North American Wisconsinan ice sheet coverage 21.4 ka, approximating the LGM for the continent.

During the McConnell glacial period leading to the LGM, both Laurentide and Cordilleran ice sheets of northwestern Canada experienced climate-change episodes when rate of melting exceeded rate of growth, leading to multiple advances and retreats. Coalescence of the two ice sheets occurred in some places (Bednarski, 2008), but at other locations the two

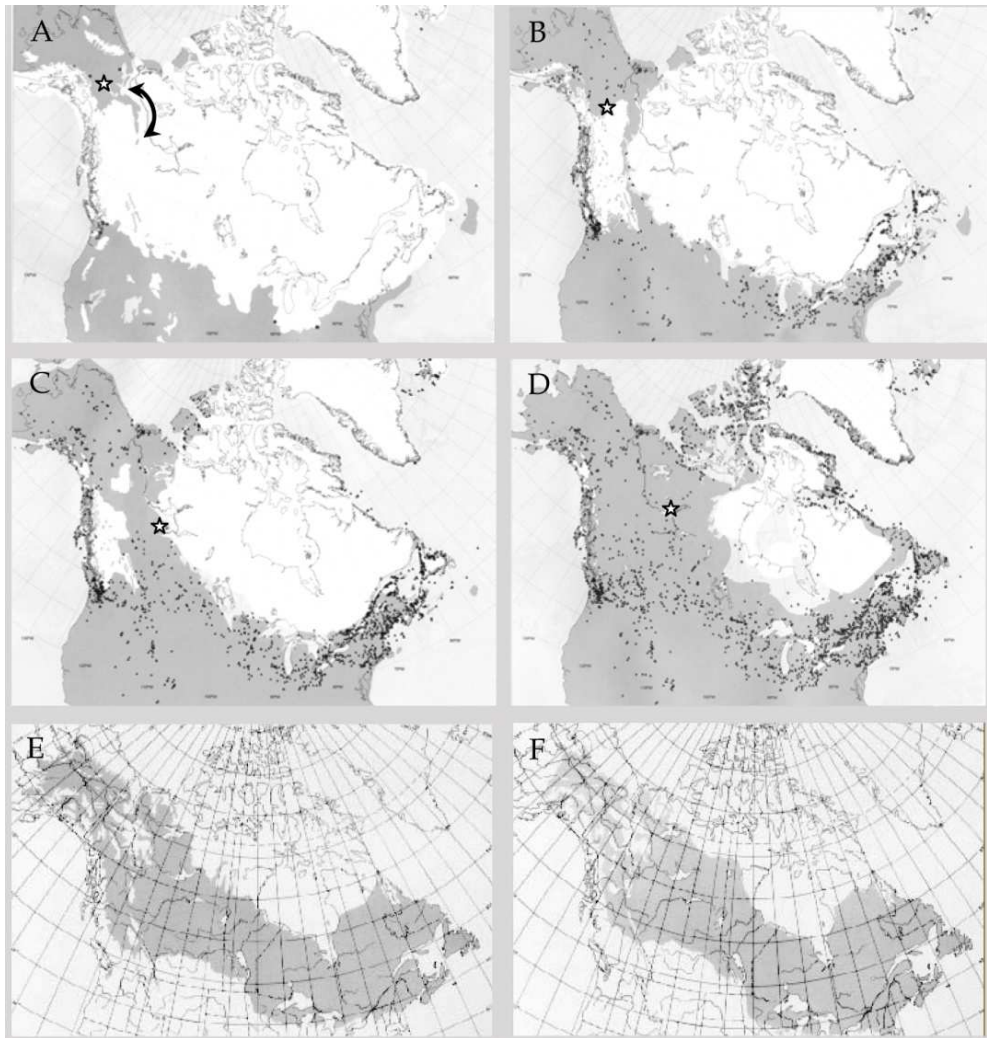


Fig. 2. A-D: Positions of North American ice sheets (white) at successive stages of Wisconsinan deglaciation (after Dyke, 2004). E, F: Native range maps (dark grey) of two boreal forest spruce species. A) 21.4 ka; the star indicates the Klotassin River realm in Yukon Primeval Beringia; the curved double-arrowheaded line indicates a hypothetical ice-free corridor between Cordilleran and Laurentide ice sheets, possibly a refugium for subalpine conifers derived from Beringia. B) 14.1 ka; terrain of the Carmacks region (star) had become available for taiga reestablishment. C) 12.70 ka; terrain of High Level, Alberta (star) had become available for repopulation. D) 8.45 ka; deglaciation was extensive throughout North America, but Yellowknife (star) remained beneath a glacial lake. E) White spruce (after Nienstadt & Zasada, 1990). F) Black spruce (after Viereck & Johnston, 1990). (Maps A, B, C, D © Department of Natural Resources Canada. All rights reserved.)

fronts evidently remained apart (Catto et al., 1996). Consequently, in addition to plausible existence of refugia within Yukon Primeval Beringia, in ice-free corridors and on mountainous nunataks, spots at various locations between Laurentide and Cordilleran ice sheets may have supported 'cryptic' refugia. Before an advancing ice sheet had covered a spot, if the opposing ice-sheet margin melted back to expose barren ground, populations could have shifted position. Thus, sites that today clearly testify to having been glaciated may at one time have sustained cryptic refugia of mobile organisms, and perhaps also of tundra plants and trees (Geml et al., 2006; Loehr et al., 2006; Stewart & Dalén, 2008).

Deglaciation maps based on data compiled by Dyke (2004) illustrate how post-Wisconsinan withdrawal of ice sheets proceeded gradually over thousands of years following the LGM (Figs. 2A-2D). Those data and knowledge of the ranges of conifers within the boreal forest (e.g., Figs. 2E, 2F) provide clues about where and when boreal forest of North America reinstated following the LGM. Barren Canadian landscape to the south of the receding continental ice sheets, in continental USA, undoubtedly began to form new soil for reforestation starting ~ 18 ka. Some subarctic locations remained beneath ice/water for thousands of years thereafter; for example, Yellowknife and the Hudson's Bay region are both part of Canada's present taiga, and both were still beneath ice until ~ 8 ka (Fig. 2D).

At the LGM, an 'ice-free' corridor is thought to have extended between Cordilleran and Laurentide ice sheets from East Beringia to the southern end of the Mackenzie Mountain Range (Fig. 2A). Mackenzie Mountain peaks evidently protruded as an extensive nunatak 'island chain' above the Laurentide ice sheet during the LGM (Szeicz and MacDonald, 2001). The Richardson Mountains of northern Yukon are a plausible alternative connection between Yukon Beringia and the northern terminus of the Mackenzie Mountains (Catto, 1996). Ongoing deglaciation extended that corridor southward along mountainous terrain, to where at ~ 14 ka it was about to merge with another ice-free corridor extending northward along the eastern slope of the Canadian Rocky Mountains (Fig. 2B). Considerable uncertainty attends the assumed LGM nature of the northern ice-free corridor; when and where it actually existed before 13 ka remain open questions (Catto, 1996; Levson & Rutter, 1996; MacDonald & McLeod, 1996; McLeod & MacDonald, 1997; Mandryk et al., 2001). However, the geological evidence indicates that by 12.7 ka a wide north-south ice-free corridor was in place (Fig. 2C). Thus, it can be assumed that generations of conifers had been advancing northward starting ~ 18 ka from seed sources in the south; conceivably, trees had advanced as far north as High Level, Alberta, by 12.7 ka (Fig. 2C). Based on native range maps (Figs. 2E, 2F), with ongoing deglaciation a considerable area of boreal forest that presently is co-occupied by white spruce (*Picea glauca* (Moench) Voss) and black spruce (*P. mariana* (Mill.) BSP) had become available for repopulation by 8 ka.

The glaciation history associated with North American taiga and East Beringia remains to be well elucidated, but the preceding considerations raise the possibility that microbes, fungi and plants existing today in North American boreal forest may have very ancient ancestry extending to Yukon's Primeval Beringia. Predecessors of organisms within Primeval Beringia presumably experienced a temperate climate similar to that supporting mixed-wood forests 50 - 40 Ma, and subsequently the ensuing climate change that resulted in familiar frozen arctic environments. Their contribution to taiga remains uncertain, because East Beringia investigations into refugia have focused on accessible lowland Quaternary sites, and little is yet known about either extant organisms or paleobiology of Yukon

Primeval Beringia. Evidence presented below indicates that investigations in the uplands may well clarify many unresolved issues concerning ecosystems of the LGM, such as the plant species which remained available to herbivores (Bradshaw et al., 2003), and the persistent mycorrhizae which enabled plants to survive (Lydolph et al., 2005).

3. Tundra, taiga, and boreal forest

3.1 Tundra, taiga, forest-tundra ecotone and boreal forest nomenclature

‘Tundra’ refers to treeless arctic/subarctic terrains carpeted with ground vegetation. In common usage, ‘taiga’ is synonymous with boreal forest (Day, 2006); however, ‘boreal forest’ includes many distinct ecosystems covering much of northern North America and Eurasia as a circumpolar forested zone (Fig. 3). In other words, boreal forest is not a singular forest. The transitional zone between boreal forest’s closed-canopy interior ecosystems and arctic tundra has been called various names (Hustich, 1953) and presently it is referred to as the ‘forest-tundra ecotone’ (Walker, 2010; Harper et al., 2011). However, ‘taiga’ has served as a succinct designation (Hustich, 1953; Elliott-Fisk, 2000). For brevity, taiga is hereinafter used to refer specifically to the northern transitional zone of the boreal forest.

3.2 Boreal forest ecosystems

Green shading in the inset of Figure 3 provides an indication of the current approximate position of global boreal forests. LiDAR data of Figure 3 indicate approximate bounds and tree heights of interior boreal forest. Those LiDAR data had 500 m x 500 m pixal resolution (Lefsky, 2010) and, therefore, small trees whether solitary or as small populations are not portrayed.

Boreal forest comprises a plurality of forest ecosystems covering much of northern North America and Eurasia as a circumpolar forested zone (Fig. 3). Thus, although numerous published investigations refer to ‘boreal forest,’ its heterogeneity makes it doubtful that research findings at any one site have general relevance to the entire circumpolar forest (e.g., see Hustich, 1953; Harper et al., 2011; Viktora et al., 2011). Certainly, every taiga site of pixal area in Figure 3 can be expected to have unique microsite characteristics.

The North American subarctic is a vast taiga domain of which only a very small fraction has been closely investigated. Spruce trees occur distantly north of the Arctic Circle in northwestern Canada and Alaska (Hustich, 1953; MacKay, 1958; Hansell et al., 1971; Cooper, 1986; Cody, 2000; Lloyd et al., 2005). The Firth River valley (mouth 69.5 °N, 139.5 °W) of East Beringia’s Ivvavik National Park supports the most northerly spruce populations (Welsh and Rigby, 1971). The record altitude for taiga spruce evidently is held by a small lone specimen on a Yukon mountaintop near Mount Nansen at 1675 m (5495 feet) a.s.l. (Fig. 4D), far above the Yukon’s variable spruce timberline of 1220 - 1370 m (4000 - 4500 feet - Bostock, 1936) and well above the “maximum” altitude of 1520 m recorded for interior boreal forest white spruce in the Canadian Rocky Mountains (Nienstadt & Zasada, 1990).

3.3 Evidence for refugia

Two questions of considerable importance in relation to understanding not only the ancestral foundation of boreal forest but also how best to manage it over the long term concern whether upland East Beringian conifers survived the LGM and, if so, whether their

progeny propagated outward in all directions, as appears to have been possible (Figs. 1, 2). If East Beringia in fact was a conifer refugium, postglacial reinstatement of taiga may have taken place relatively rapidly by conifer populations already in possession of the physiological hardiness needed for survival in subarctic environments. Alternatively, the possibility exists that East Beringia conditions during the LGM were so stressful that conifers could not survive there.

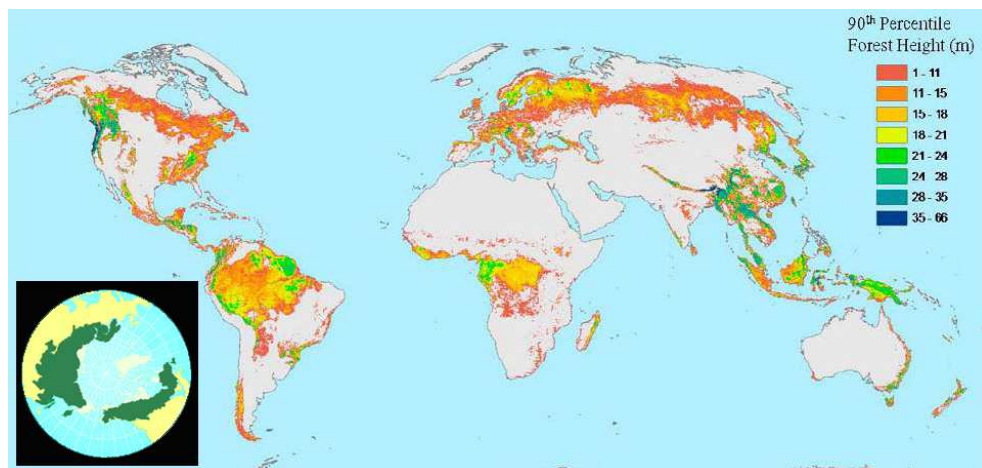


Fig. 3. Global forests in the first decade of the 21st century, indicated by light detection and ranging (LiDAR) technology from the Ice, Cloud and Land Elevation Satellite. Canopy heights are represented by different colours (reproduced courtesy of M.A. Lefsky - see Lefsky, 2010). Inset: North Pole centered view of Earth's boreal forest zone (dark green).

If conifers were entirely eliminated from subarctic taiga during the LGM, boreal forest today must have arisen by northward-only emigration of successive progeny starting from 'mother' trees that survived south of the Wisconsinan ice sheet (Fig. 2A). This northward-only hypothesis has found support in an absence of LGM conifer pollen in cores taken from small lakes in lowland Beringia of the Yukon (Cwynar & Ritchie, 1980; Cwynar 1982, 1988; Ritchie, 1984, 1987; Ritchie & MacDonald, 1986; Pisaric et al., 2001; Brubaker et al., 2005). Further, Hopkins (1982) concluded on the basis of fossil wood ages that white and black spruce and "tree birch" discovered in Alaska and Yukon Beringian lowland sediments evidently were all exterminated ~ 30 ka, trees not reappearing within East Beringia until deglaciation permitted dispersal of new populations northward. Zazula et al. (2006) found evidence for East Beringia spruce trees from 26.0 - 24.5 ka, but continuing existence through the LGM was considered doubtful, perhaps occurring in "rare valley-bottom habitats."

Most investigators of Yukon and Alaska East Beringia have concluded that only steppe vegetation existed following the LGM. MacDonald & McLeod (1996) proposed that boreal forest development was initiated by rapid northward spread of spruce trees starting from western mountains and eastern plains, North America's boreal forest achieving similar occupation to that in existence today ~ 8 ka.

It is not inconceivable that progeny of southern conifers through natural selection gradually acquired the needed fitness to survive extreme subarctic environments while progressively,

generation after generation, reinstating denuded postglacial landscapes to the north (e.g., see Delcourt & Delcourt, 1987). On the other hand, comparison of the LGM glacial limit (Fig. 2A) with present-day conifer range maps (Figs. 2E, 2F) reveals a puzzling incongruity about northward-only taiga reinstatement. Excepting regions south of the Great Lakes, current southern limits of black spruce occur well north of latitude 49 °N (Figs. 2E, 2F), whereas at the LGM the ice sheet's southern margin was south of 49 °N (Fig. 2A). If black spruce were non-existent south of the ice sheet in western North America, within the northward-only scenario LGM ancestors of Yukon taiga's spruce trees must have stood south of the Great Lakes or farther east, and their lineage should therefore trace back to ancestors which resided far to the southeast. There is no evidence for such ancestry (see below, section 3.4).

Negative evidence against conifer survival in Yukon throughout the LGM embodies the unstated assumption that, if trees were non-existent in lowlands of East Beringia, they must also have been non-existent everywhere in mountainous Primeval Beringia. However, mountain climatology within Beringia can be markedly distinct from that of lowland valleys. Cold air is denser and moves down mountain sides to pool in valleys and on plateaus; thus, lowlands experience the colder winter temperatures (Takahashi et al., 2011; R. A. Savidge, unpublished data). Relatively strong mountain winds result in variable snow depths, ranging from bare ground to deep drifts and, in general, snow accumulates to greater depths in forested lowlands. Wind-blown mountain slopes accumulate only modest amounts of snow, and it disappears from their south slopes relatively rapidly in springtime.

South-facing slopes and mountain tops extending northwest from Mount Nansen over the western Yukon Plateau presently support white spruce as upright trees, krummholz and ground mats at high altitudes (e.g., see Fig. 8). Moreover, among pre-Reid tors near Mount Nansen, upright white spruce trees of > 5 m height bear seed cones (Figs. 4A, 4B, 4C, 7C, 7D). If trees and other plants survived on southern aspects of nunataks as well as within Yukon Primeval Beringia throughout glacial periods, in effect refugia of Primeval Beringia could have extended southeastward across Yukon-Tanana high altitude terrain as far as Mount Nansen, also northward as far as the Richardson Mountains (Fig. 1). However, no fossil pollen investigations have been done in the uplands of Yukon Primeval Beringia.

White spruce ground mats in upland pre-Reid landscape begin as normal upright trees, and they may bear both male and female cones. On south-facing slopes, such trees not uncommonly reach several meters in height before their trunks die (Figs. 4A, 4B, 4C, 7D). Main-stem dieback evidently occurs when sun-warmed needles lose moisture that cannot be replenished during winter and spring months (R.A. Savidge, unpublished observations). Branches near the ground nevertheless survive beneath winter snow, and in summer those branches extend plagiotropically. The mat specimen shown in Figure 4D, discovered in 2011, had survived for > 20 years on thin soil over permanently frozen rock on a never-glaciated mountaintop at 1675 m a.s.l.

It will be apparent that palynological investigations in lowland East Beringia cannot fully account for presence/absence of conifers during either the LGM or earlier glacial periods. If Beringian lowlands experienced deep accumulations of (non-glacial) snow and ice during any glacial period, perennially buried lowland trees could not be expected to survive continual light exclusion. Trees positioned on south slopes of the uplands could nevertheless have survived and produced seed throughout the LGM, as well as throughout earlier glacial periods, as 'microrefugia' (cf. Holderegger and Thiel-Egenter, 2009). There are

no data on travel distances achievable by pollen and seeds as shed from small upright and ground mat trees within mountainous Primeval Beringia, but all sites so far investigated palynologically have been far removed (Williams et al., 2004).



Fig. 4. White spruce mats of Mount Nansen alpine terrain. A) 12 m² mat of plagiotropically growing branches. B) Male and C) female strobili found on the mat. D) A small white spruce mat, age estimated at 20 – 30 years, growing at 1675 m a.s.l.

3.4 DNA evidence for refugia

Genetic investigations into possible refugia supporting post-Wisconsinan reinstatement of subarctic populations of plants, animals and fungi from East Beringia, although increasing in number, remain small, and the findings are also controversial (Senjo et al., 1999; Goetcheus & Birks, 2001; Abbott and Brochmann, 2003; Brochmann et al., 2003; Cook et al., 2005; Edwards et al., 2005; Lydolph et al., 2005; Geml et al., 2006, 2010; Loehr et al. 2006; Politov et al., 2006; Zazula et al., 2006; Eidesen et al., 2007; Shilo et al., 2007, 2008; Waltari et al. 2007; Barnosky, 2008; Stewart and Dalén, 2008; Ickert-Bond et al., 2009; Levsen and Mort, 2009; Tsutsui et al. 2009; Carlsen et al., 2010; Gérardi et al., 2010; Nakonechnaya et al., 2010; Shafer et al., 2010; Stewart et al., 2010; Westergaard et al. 2010).

Chloroplast DNA (cpDNA) investigations provide insight into phylogenetic and biogeographic relatedness among populations of trees (Sigurgeirsson & Szmídt, 1993; Petit et al., 1997). Based on pollen investigations, refugia of *Salix* and *Betula* were abundantly, *Picea* and *Alnus* spottily, *Populus* questionably and *Pinus* plausibly present in eastern Beringia of Alaska at 21 ka (Williams et al., 2004). In agreement with this, Anderson et al. (2006) concluded on the basis of cpDNA evidence that white spruce in East Beringia of Alaska probably did survive the LGM within favourable microhabitats (of unidentified location).

We investigated the hypothesis that if the mountainous southeastern portion of Yukon Primeval Beringia (site KL in Fig. 5) served as ancestral seed source for progressive reinstatement of postglacial black spruce taiga from west to east across Canada's boreal zone, then diminishing genetic relatedness with increasing geographic distance should be observable (R. A. Savidge, M. Viktora and O.P. Rajora, unpublished). Seven populations were sampled (Fig. 5), using one-year-old needles gathered from 60 well-separated trees within each population. None of the seven investigated sites had been planted with black spruce, nor had any served as a source of seeds for reforestation elsewhere. In each of the 420 samples, cpDNA was probed using three microsatellite markers (loci Pt26081, Pt 63718 and Pt71936, Vendramin et al., 1996) and methods as described (Viktora et al., 2011). Each marker was found to be polymorphic, yielding for all populations 12 alleles for Pt26081, 4

for Pt 63718, and 8 for Pt71936. Three-loci combinations were considered to determine haplotype frequencies at the seven sites (Fig. 5).

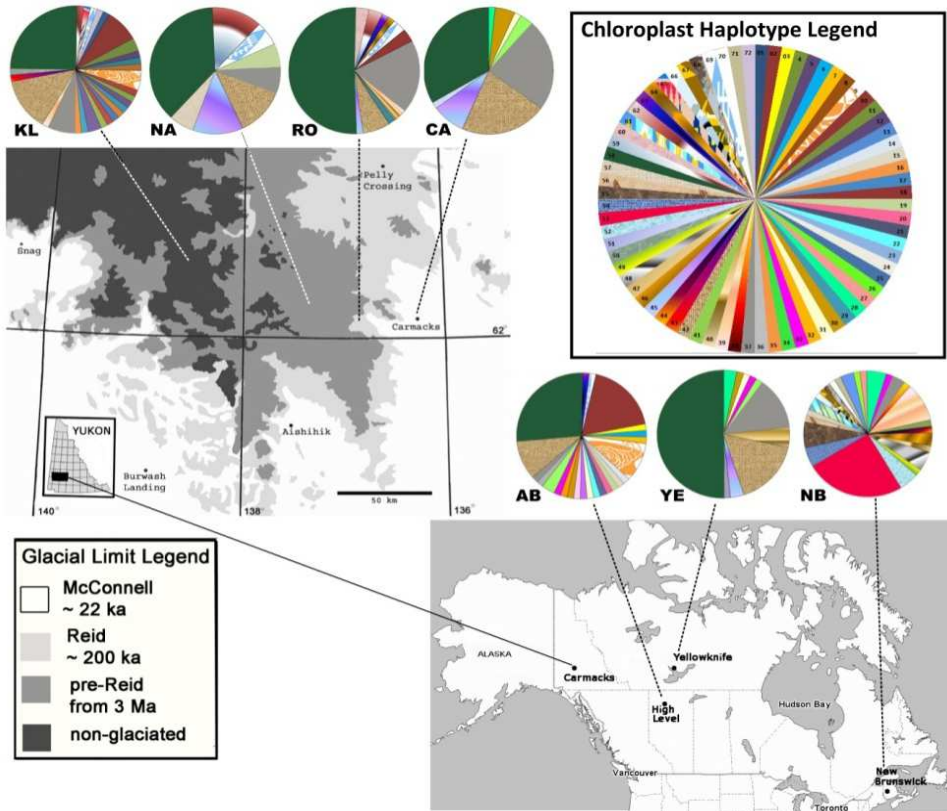


Fig. 5. Chloroplast DNA (cpDNA) haplotype frequencies within seven black spruce populations of Canada’s boreal forest, based on three microsatellite markers. KL, Klotassin River; NA, Mount Nansen; RO, Rowlinson Creek; CA, Carmacks; YK, Yellowknife; AB, High Level, Alberta; NB, New Brunswick. Each colour within the chloroplast pie chart legend represents a distinct haplotype, and areas within the pie charts associated with each of the seven indicated sites are relative frequencies of detected haplotypes. The region near Carmacks (see lower right map) is enlarged at upper left to show CA, RO, NA and KL sites sampled across a transect leading from recently glaciated (McConnell) to non-glaciated terrain (see section 2.2 text). Unpublished data of R. A. Savidge, M. Viktora and O.P. Rajora.

Our study was unexpectedly compromised by the fact that most of the 60 sampled Mount Nansen (NA) trees were clonal, yielding eight genets and only eight additional genotypes rather than the expected 60 (Viktora et al., 2011). Each of the eight genets stood on what evidently was never-disturbed tundra and, consequently, each occupied an extensive area. Although data for the NA population indicated it to be distinct from neighbouring populations (Fig. 5), additional sampling of NA is needed before drawing firm conclusions.

In agreement with studies by Juan et al. (2004) and Gérardi et al. (2010), but in disagreement with MacDonald and McLeod (1996), the New Brunswick (NB) population of southeastern Canada was unrelated to black spruce populations in northwestern Canada (Fig. 5). Our cpDNA data unexpectedly revealed the AB population near High Level, Alberta, to be paternally related to the KL population, more than to Rowlinson Creek (RO) and Carmacks (CA) populations, despite RO and CA sites being geographically between KL and AB. Within the northward-only hypothesis for subarctic postglacial spruce taiga reinstatement, assuming that AB was the first populated of the sampled northwestern populations, CA, RO and NA locations were in geographic line for repopulation before KL, and the greater affinity between KL and AB seems to argue against northward-only reinstatement. Thus, data of Figure 5 constitute the first evidence that Yukon Primeval Beringia was a source for post-glacial taiga re-establishment of northwestern Canada's boreal black spruce forest.

As indicated in Figure 5, YE was more related to RO than to other sites, despite the fact that YE remained beneath a glacial lake for several thousand years after AB had been deglaciated (compare Figs. 2C and 2D). Thus, existence of the RO - YE relationship is an indication that RO progeny had earlier established in the Richardson or Mackenzie Mountains and thereafter survived the LGM as refugia with priority access to barren YE ground. At the LGM, widespread Cordilleran, Laurentide and local glaciers affected Richardson and/or Mackenzie Mountains at somewhat higher altitudes than those reached by lobes of the Mount Nansen region's piedmont glaciers, but the fact that spruce mats can grow at 1675 m a.s.l. (Fig. 4D) is evidence that subalpine/alpine south slopes of the Richardson and Mackenzie Mountains could also have contained nunatak refugia genetically related to the hardy conifers currently standing within Primeval Beringia.

Ongoing phylogenetic investigations in the mountains of Primeval Beringia are needed to answer the crucial still controversial question: Did conifers such as those represented by the KL population persist on Yukon Primeval Beringia soil during the LGM? With informed selection of sites, it can be predicted that the answer will eventually be found to be in the affirmative. If this proves to be the case, there will be incentive to probe even deeper into the past, eventually perhaps linking Primeval Beringia to high Arctic Eocene fossil conifers (Gugerli et al., 2005).

3.5 Phenotypic variation

Spruce trees are almost the only conifer species in the Mount Nansen region, where mature white spruce phenotypes are remarkably and conspicuously diversified (Figs. 6A, 6B), and similar variation also exists within black spruce. If crown form is in fact inherited rather than controlled by environment (Kärki & Tigerstedt, 1985), spruce manifests broad genetic diversity.

In addition to spruce trees, encountered rarely in upland pre-Reid landscape are scattered century-old (by annual ring counts - R. A. Savidge, unpublished data) pine trees similar to *Pinus contorta* Dougl. (Fig. 6C). Those high altitude pines stand on pre-Reid landscape and are geographically far removed from relatively young pine stands of McConnell-glaciated terrain to the east. Cones of upland pre-Reid pine trees are notably shorter than those of lowland lodgepole pine trees (Fig. 6D); however, both upland and lowland trees display three-needled as well as two-needled fascicles, a trait exclusive to Yukon lodgepole pine.

Although lowland pollen data indicated that lodgepole pine entered the Yukon from the south only recently (MacDonald & Cwynar, 1985; Cwynar & MacDonald, 1987), it remains possible that the actual ancestral source was Yukon Primeval Beringia.

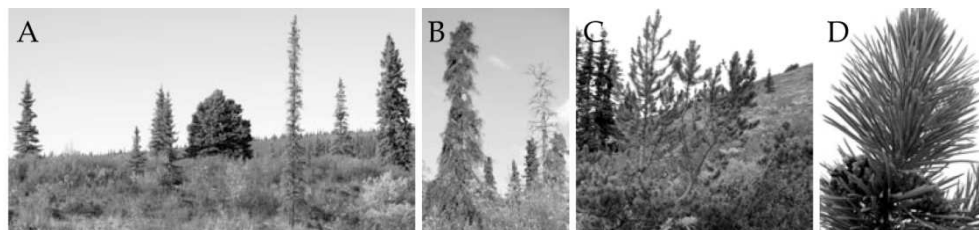


Fig. 6. Conifers of pre-Reid landscape near Mount Nansen. A) Varied white spruce crown forms at 1200 m a.s.l.; B) White spruce downswept branch form at 1330 m a.s.l.; C) Upland pine at 1430 m a.s.l.; white spruce in background; D) Pine seed cones and needles.

4. Taiga population fitness and soils

4.1 Taiga overview

Figures 7A and 7B demonstrate that the transitional zone between taiga and tundra can be readily if coarsely distinguished. Taiga skirts the northern boundary of the interior boreal forests and has a circumpolar length exceeding 14,000 km (Figs. 1, 3). Taiga boundaries are presently moving in response to climate change (Harper et al., 2011), and the total areas occupied by both taiga and tundra are therefore uncertain.

Considered in longitudinal section, boreal forest everywhere displays four distinct conifer subzones which, in effect, constitute community-level phenotypes. Proceeding from north southward, Hustich (1953) described those four zones as A) limit of species, B) treeline, C) biological limit of forest, and D) economic limit of forest. Emphasizing ecophysiology, the four zones are seen as: 1) The northern zone where tundra transitions southward into widely spaced small individual conifers; 2) A zone comprising variably sized patches of forest within tundra, otherwise seen as islands or populations of conifers having 100% live crowns but nevertheless lacking closed-canopy state at maturity; 3) A broad zone of interior boreal forest ecosystems where broadleaved tree species commonly co-occur with mature closed-crown conifers, and where lower spreading branches of conifers die and abscise in response to light exclusion by the closed canopy; and 4) A southern transitional zone, where dominantly coniferous old growth closed-canopy ecosystems merge with temperate-zone mixed-wood or steppe ecosystems. Similarly, in alpine regions, a timberline to tundra transitional taiga zone is found high on mountain slopes, and at lower altitudes are more or less widely spaced full-crowned conifers (Figs. 7A, 7B). Subalpine slopes often grade at lower altitude into closed-canopy stands having a broadleaved tree component; however, taiga valleys rarely if ever display ecosystems akin to those of boreal forest southern latitude transitional regions. Valley bottoms in mountain taiga tend to be devoid of conifers, evidently a response to accumulation of heavier cold air and freezing of boggy soils. Willows nevertheless survive in such locations.

Depending on how taiga and tundra are distinguished – for example, based on arbitrary values for ‘tree’ height (commonly 3 m), between-tree spacing distance for a ‘stand’, and area for a ‘forest’ – taiga’s northern boundary can be delineated on high resolution satellite

images (Fig. 7A). However, ground proofing of hyperspectral images (nominally 0.6 m resolution, Fig. 7B) revealed that > 50% of actually present taiga conifers having heights ≤ 5 m were not detectable on such images, nor could broadleaved trees standing as solitary individuals in tundra be resolved. Clumps of closely spaced small trees were discernible on images, but within clumps many trees of similar size and form to those shown in Figure 7C could not be resolved. Solitary upland trees such as that shown in Figure 7D were generally overlooked (R. A. Savidge, unpublished data). It remains no minor concern, particularly in relation to understanding effects of climate change on taiga dynamics, that immense areas of tundra and taiga remain to be resolved at small-tree resolution using either airborne or satellite imagery. In other words, mapping the distributions of small conifers, whether young or old within taiga and tundra, continues to require on-the-ground surveys.

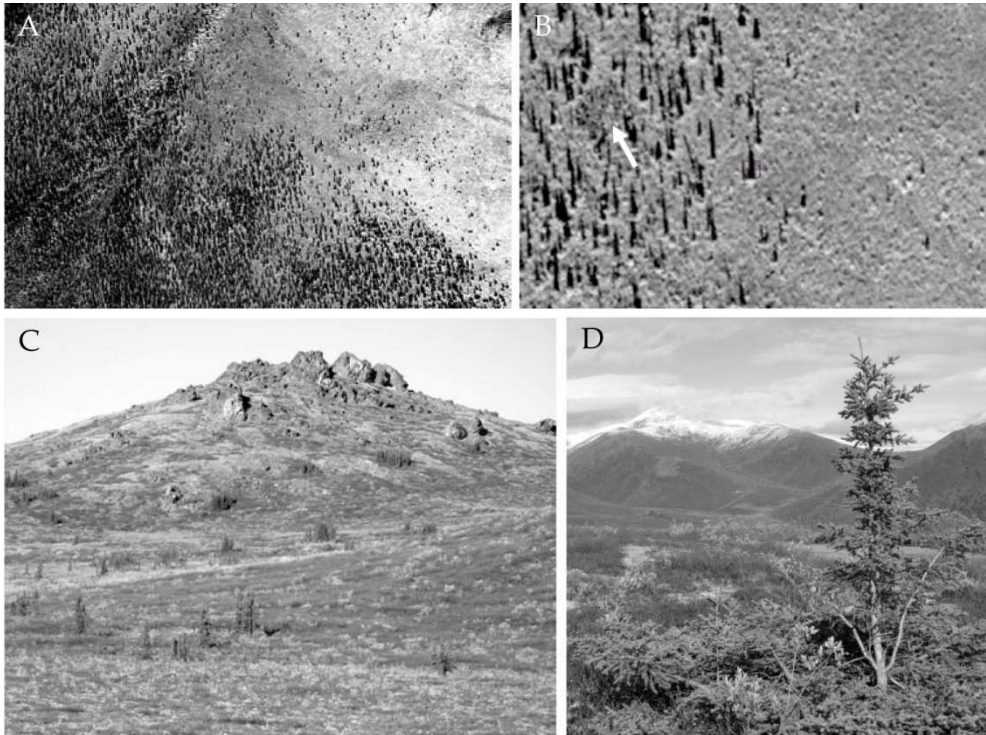


Fig. 7. Yukon taiga on the southeastern edge of Primeval Beringia. A) High resolution (0.6 m) QuickBird satellite overview, and B) close-up of white spruce (*Picea glauca*) treeline at approximately 1330 m a.s.l. The white arrow indicates a clone of *Picea mariana* within a white spruce population (cf. Viktora et al., 2011). C) White spruce at > 1400 m a.s.l. near a tor; D, Alpine white spruce at > 1500 m a.s.l. (satellite data provided by DigitalGlobe, Inc.).

In relation to defining the taiga treeline within North America, conifers because of their evergreen visibility have received the greater attention. However, willows (*Salix* spp.) and birches (*Betula* spp.) occur as shrubs and, arguably (depending on one's definition of 'tree'), also as trees at latitudes far north of conifer treelines, and also at taiga altitudes well above

alpine timberline (Polunin, 1948; Porsild 1955, 1964; MacKay, 1958; Beschel & Webb, 1963; Kuc, 1974). Where conifers for whatever reason cannot establish independently in tundra, willows and birches aid in subsequent conifer establishment (Nilsson, 2005). Both willows and birches contribute organic matter, hence aiding topsoil development. Willows beyond conifer treeline may exceed several metres in height and as such, they give the impression of being the hardiest of all northern trees. Willows are engendered with high levels of salicylic acid, a compound conferring disease resistance and serving in internal heat generation (Raskin, 1992). Thus, in relation to physiological tolerance of subarctic and far-northern environments, it would seem to follow that where willows cannot survive, conifers cannot be expected to.

Tree species diversity within Yukon Primeval Beringia is greater than that within upland pre-Reid populations (Fig. 8). Primeval Beringia timberline at ~ 1300 m a.s.l. on southern aspects occurs as a mixture of spruce, poplars (*Populus tremuloides* and *P. balsamifera* ssp. *trichocarpa*), birches and willows (Fig. 8A). As is the case for pre-Reid terrain, white spruce dominates (Figs. 8B, 8C), but small-diameter black spruce trees occur as monotypic populations on muskeg flats. On well-drained valley soils, mixtures of *P. glauca* var. *albertiana*, *P. glauca* var. *porsildii*, poplars, willows and alders occur. Most spruce species hybridise where ranges overlap (Farjon, 1990), but a hybridisation barrier evidently exists between the *albertiana* and *porsildii* varieties of white spruce, as the two co-exist side by side in Yukon Primeval Beringia as distinct phenotypes.



Fig. 8. Examples of September landscapes within Yukon Primeval Beringia. A) White spruce on patchy carpets of birch-willow vegetation on tallus slopes; B) Conifer populations as discrete aggregates scattered over the uplands; C) Lined 'streams' of conifers aligned by slope solifluction; D) Mixed woods at high altitudes in the Klotassin River valley.

North-facing slopes of both Primeval Beringia and pre-Reid landscapes at 1200 m a.s.l. and higher altitudes are generally devoid of all but short-branched, weakly foliated, widely spaced, single-stemmed, small diameter columnar-form white spruce trees having heights commonly less than 5 m. Tree growth is influenced indirectly by, for example, the extent of activity possible within a cool root system (Wareing 1985, Junttila and Nilsen 1993), but it can also be a function of additional, microsite-dependent extrinsic factors (Germino et al. 2002). For example, growth may be limited if soil water potential is either too high or low, nutrient imbalance or deficiency arises, root-system integrity is altered by solifluction or frost heaving, allelopathic inhibition occurs, or soil microflora become imbalanced (Ivarson,

1965). Considerable microsite variation evidently is normal. For example, within- and between-tree annual increments of multi-centurion subalpine white spruce growing on a south-facing slope near Mount Nansen were poorly correlated chronologically (Yuan, 2012).

Since 1990, *Populus tremuloides* and *P. balsamifera* ssp. *trichocarpa* have invaded pre-Reid uplands from lower Reid and McConnell glaciated altitudes, and they now are found as tree-sized individuals in subalpine tundra above spruce timberline. Valleys in Yukon Primeval Beringia and relatively low altitude (<1200 m a.s.l.) terrain of Reid/McConnell glaciated landscapes also have abundant alders (*Alnus* spp.). However, in contrast to *Populus* movement, no alder of any species was found during either 1968-1971 or 2007 - 2010 investigations on pre-Reid uplands (R. A. Savidge, unpublished observations).

4.2 Population fitness

The populations of diverse cryptobiotic organisms which survive within regions such as Yukon Primeval Beringia manifest adaptation to processes of natural selection which evidently operated over very long time frames. Ecophysiological considerations related to the fitness of a tree species to survive in the subarctic include tree tolerance of the north's seasonally changing light extremes (spectrum, intensity, photoperiod), desiccation and winter abrasion by wind-blown ice particles, low water potentials particularly in relation to evapo-transpirational demands and albedo/sunscald-related responses during periods when soil or trunk xylem water is frozen, deleterious effects on the root system (e.g., low root-zone temperature, low pH, anaerobiosis, limiting nutrient(s) microflora and/or fauna, allelopathy), herbivory, and insect and disease challenges (Larcher, 1995).

Various explanations have been advanced to explain positions of treelines, but consensus for any has yet to be achieved. Air temperature hypotheses have long been a favoured avenue to explain climatic tolerance (Weiser, 1970; Coursolle et al., 1998; Arft et al., 1999; Körner, 2007; Brandt 2009). However, low winter temperature *per se* is an improbable factor, because a variety of tree species of good size occur at sites such as Snag, Yukon, and Oymyakon, Siberia, locations of record temperature minima in the northern hemisphere. There nevertheless is preponderant agreement that treeline position somehow correlates with growing-season air temperature. Dwarf shrubs, including krummholz conifers, supersede upright trees wherever mean air temperature of the warmest month is less than about 10 °C. Expressed another way, treeline usually occurs below that altitude or latitude where mean temperature of the growing season does not exceed 7 °C (Körner, 2007). As noted earlier, however, a focus on tree height in relation to the treeline and fitness overlooks advantages conferred to morphotypes that survive near the ground.

Larcher (1995) noted for arctic/subarctic plants that photosynthesis and respiration both continue at temperatures a few degrees below the freezing point. At lower temperatures, photosynthetic activity ceases whereas respiration continues. Compounding this, northern plants have relatively high respiration rates compared to plants of southern climes (Larcher, 1995). In addition, little if any photosynthesis occurs throughout long dark taiga winters, and for tree survival it is therefore essential that sufficient storage reserves are present by the end of each summer's growing season (Lloyd et al., 2002; Röser et al., 2002; Zarter et al., 2006). Following their long winter, subarctic conifers are further drained of vital stored chemical energy due to their intrinsic tendency to commence root and

cambium growth in late spring before buds have broken and new needles matured (Savidge & Förster, 1998). Standing dead trees (i.e., snags) are common in taiga and, in the absence of disease or obvious physical damage, it appears that the taiga-tundra treeline manifests that point where loss of metabolic reserves exceeds a tree's ability to support its respiratory needs. In other words, retention of 100% live crown by taiga trees probably is not merely incidental to their wide spacing, rather an essential survival attribute in order for the annual photosynthesis to respiration ratio of the whole tree to be maintained near or above unity.

Based on extensive researches done in more southern realms and limited investigations in the north, root-system survival during winter must surely be a critical factor for every subarctic tree. Root systems are more susceptible than above-ground organs to freezing-induced mortality (Tyron and Chapin, 1983; Wareing, 1985; Delucia, 1986; Husted and Lavender, 1989; Lopushinsky and Max, 1990; Camm and Harper, 1991; Junttila and Nilsen, 1993; Pregitzer et al., 2000). Not only snow cover but also the nature and depth of soil influence its ability to insulate the root system from extremely low air temperatures commonly experienced in the taiga zone during winter (see Fig. 10). The limits of root system tolerance of low temperatures by taiga trees remain poorly investigated but, as addressed further below, white and black spruce and lodgepole pine can survive and grow on permafrost despite always cold root systems.

Fitness to survive in the north undoubtedly involves many interacting environment and genetic factors, but physiological understanding remains incomplete. Considerable progress was made during the period 1950 - 2000 toward understanding how plants tolerate low temperatures and other stresses (Scholander et al., 1953; Billings & Mooney, 1968; Raskin, 1992; Larcher, 1995; Arft et al., 1999; Kimball et al., 2007). However, only a minor fraction of the investigations involved controlled experimentation with *in situ* taiga/tundra plants (Arft et al., 1999). Moreover, there exists a major gap between the impressive ability of molecular biology technologies to generate huge amounts of DNA data and science's quite limited ability to interpret those data such that they are relevant to ecophysiology. Phenomena of seed production, seed dormancy, seedling establishment, vegetative reproduction, photosynthesis, respiration, drought resistance, plant dormancy, storage reserve accumulation and utilization, growth, partitioning between shoot, root and reproductive systems, soil nutrient roles, tissue cold hardiness, flowering and pollination all remain fascinatingly curious and quite incompletely understood physio-genetic phenomena of taiga and tundra ecosystems.

Taiga is heterogeneous, but by definition its central unifying theme is that trees do survive and complete their lifecycles within it. Nature, in the absence of human intervention, has maintained healthy sustainable taiga forests by means of two mechanisms, intrinsic physiological fitness and genetic diversity. Physiological fitness is an individual attribute maintained through ongoing natural selection and propagated within both sexually reproductive and clonal populations. Combinations of physiological fitness and genetic diversity ensure that trees (and all forest organisms) are able to survive the ranges of interacting environmental factors they are exposed to throughout lifecycles in taiga. Again, however, it is still entirely unclear which intrinsic factors contribute to physiological fitness within taiga. Intrinsic tolerance and adaptability unique to each species and each individual plant are, in general, genetic/epigenetic attributes (Wareing 1985; Durzan 1993).

4.3 Taiga soils

Boreal forest presently holds more carbon per unit area than any other terrestrial area (Shiklomanov and Rodda, 2003; Carlson et al., 2009). Although carbon is abundantly present in tissues of trees and ground vegetation, most boreal forest carbon occurs as subsurface dead organic matter in cold peatlands, and in taiga and tundra soils.

Tundra and taiga vegetation exist as communities in precariously balanced struggles of survival, and their fitness to tolerate cold soils is a distinguishing attribute of all subarctic plants. Figure 8A provides an example of the obligatory relationship between taiga soil formation and ensuing establishment of conifers. In order for the sequence of tundra - taiga - forest succession to occur on barren rock, accumulation of organic matter in support of soil formation is essential. The process undoubtedly requires many decades, probably centuries, beginning with bedrock weathering, disintegration, and coating of rock fragments with bacteria, lichens and mosses. Hardy grasses, sedges, *Salix*, *Betula*, *Dryas* and other plant species occur in the high Arctic where no conifers are to be found (Polunin 1948, Beschel and Webb 1963, Porsild 1964, Kuc 1974), and there can be little doubt that establishment of such plants serves as preliminaries to the overall process of soil formation.

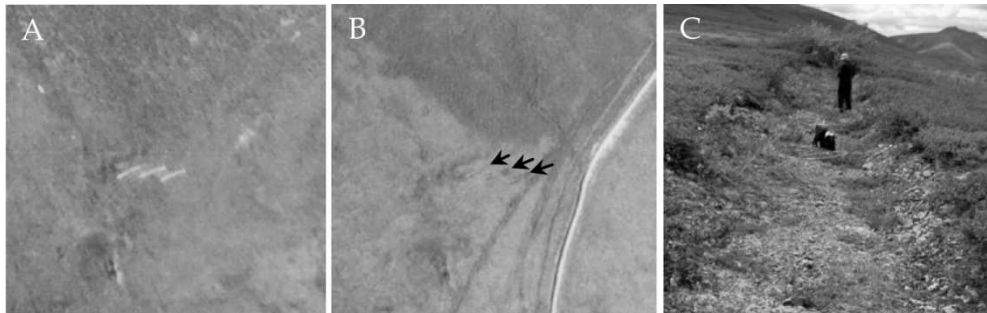


Fig. 9. Soil formation on exposed volcanic bedrock in upland taiga. A) Aerial view (A11069-92, National Air Photo Library - Natural Resources Canada) of three bulldozer trenches made at 62.0733 °N, 137.1666 °W prior to August 24, 1947; B) Same location on August 10, 2003 (A28501-106, National Air Photo Library - Natural Resources Canada), with positions of the three trenches arrowed. C) Ground inspection of one of the three trenches in 2008, showing patchy soil and incomplete establishment of ground vegetation.

Figure 9 provides direct evidence of the lengthy duration required for organic soil formation to occur on nutrient-rich volcanic rock fragments following disturbance of subalpine taiga ground vegetation. Three parallel shallow trenches were bulldozed some time before August 1947 at an altitude of 1400 m a.s.l., in a pre-Reid upland never-glaciated region near Mount Nansen (Fig. 9A). The excavations removed a pre-existing thin carpet of tundra vegetation and exposed frozen, weathered coarsely fragmented bedrock beneath. Analysis of air photographs taken in 2003 indicated that tundra healing was occurring (Fig. 9B). Field investigations around the perimeters of the trenches during 2008 revealed a remarkable diversity of densely packed broadleaved woody shrubs, vascular and non-vascular ground plants, fungi, and lichens. However, within the trenches only isolated patches of thin (< 1 cm) organic matter were found, and only a small fraction of the many tundra plant species

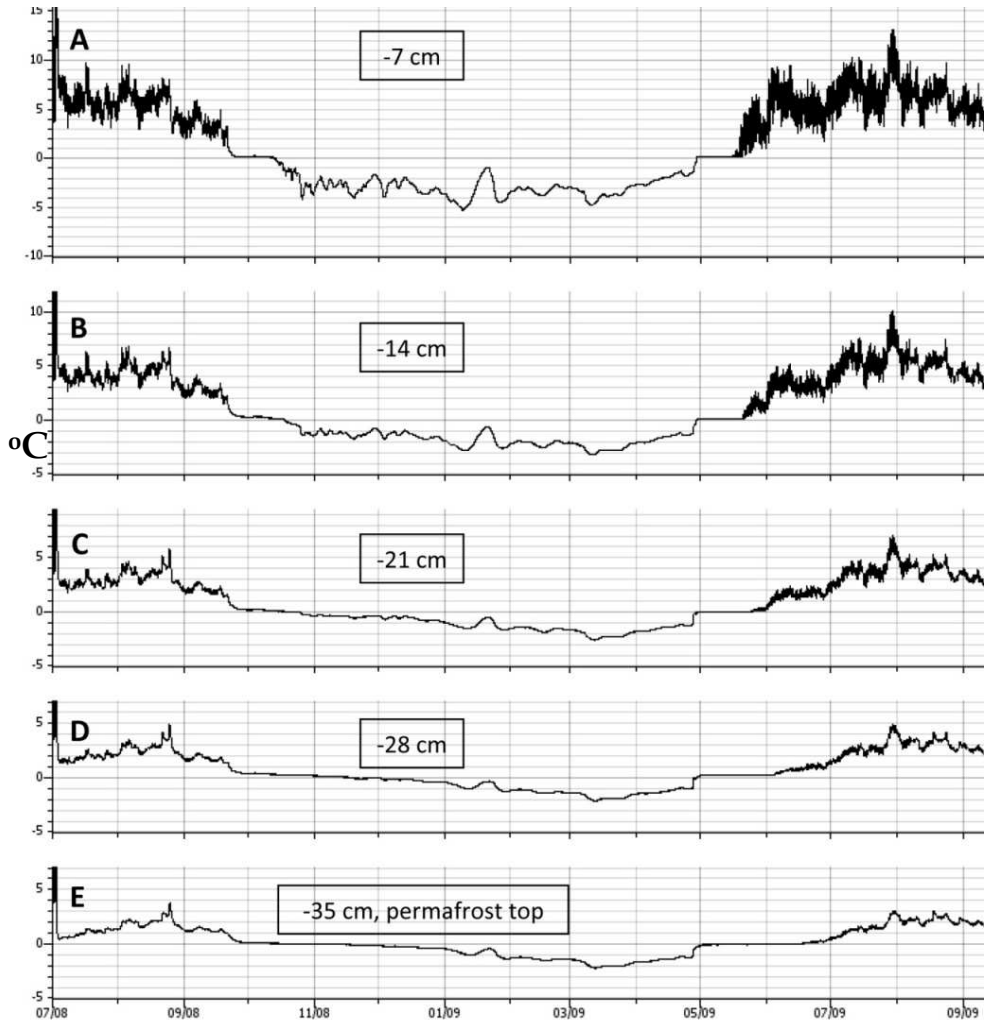


Fig. 10. Sub-surface temperatures at sequential vertical soil depths on a gentle south-facing slope of subalpine taiga (1320 m a.s.l.) underlain by permafrost and supporting a stand of mature white spruce trees near Mount Nansen, Yukon. Data loggers were placed at the gametophytic stem bases of live mosses (-7 cm), at the upper surface of the humic horizon (-14 cm), and progressively deeper into the humic horizon to where it was solidly frozen (-35 cm). The root zone consisted mainly of compacted brown humus at various stages of decay. Macro spruce tree roots nearby the excavation made to insert the data loggers existed only near the ground surface, probably because permafrost until recent decades extended to the ground surface (R. A. Savidge, unpublished data). Fine roots were most abundant in humic matter between 0 - 20 cm depths, but some were also present immediately above the -35 cm permafrost table (Fig. 10). Light data (not shown) served to verify that the data loggers had remained undisturbed throughout the monitoring period.

surrounding the trenches had established, covering < 50% of bedrock area within the trenches (Fig. 9C). Clearly, soil formation and plant establishment on barren rock fragments in a subarctic environment is a lengthy process even when a plethora of plant species and other soil-forming agents are already present nearby.

Closed-canopy interior boreal forest trees experience cold soil mainly during winter, whereas permafrost soils of tundra and taiga are perennially cold (Fig. 10). To gather the data of Figure 10, Pendant Hobo light/temperature data loggers (Onset Corp.) spaced 7 cm apart were inserted vertically into ground beneath a stand of mature subalpine white spruce of pre-Reid taiga landscape near Mount Nansen, logging ground temperatures every 20 minutes from early July 2008 to early September 2009. On the basis that soil water freezes near -3 °C, data of Figure 10 demonstrate that when the humus layer in taiga is sufficiently deep, water in liquid state is always available in the active layer over permafrost, not only in support of transpiration and photosynthesis during the growing season (Sugimoto et al., 2002), but even during winter periods. Taiga tree root systems evidently tolerate growing season soil temperatures that, farther south, would jeopardize tree survival (Stattin & Lindström, 2000).

Permafrost interfaces with an unfrozen active layer, but taiga tree roots in cold humic matter have little or no direct access to mineral soil nutrients. A similar deficiency undoubtedly also applies to plants growing on debris-covered glaciers (Fickert et al., 2007). Thus, fungal and bacterial associations are of great importance in determining nutrient uptake within taiga (Ivarson, 1965; Read et al., 2004). As noted above, scattered white spruce trees of unusual cylindrical phenotype grow on cold north slopes in pre-Reid and Primeval Beringia taiga. The trees grow slowly and produce only short branches. This may be a cold soil or limiting nutrient response; the precise physiological explanation remains wanting.

5. The future subarctic forest

If the present warming trend continues, much of what for centuries has been tundra will, in not very distant future, convert into taiga followed by mixed conifer – broadleaved forests. Similar climate change has happened before (Cwynar 1982, 1988; Burn, 1994). However, exploration and other human activities constitute unknown environmental impacts which introduce uncertainty into any prediction of what the future may hold, particularly in relation to the ability of taiga to retain the germplasm needed to survive through the next glacial period, an event that will undoubtedly occur sooner or later (Crucifix 2011).

In association with climate change and permafrost thawing, southern species are becoming more common and invasive in the north (Hickling et al., 2006). Boreal forest holds abundant fresh water in support of plant growth (Shiklomanov and Rodda, 2003) and, as refugial ecosystems within Yukon Primeval Beringia become increasingly disrupted by man, it can be predicted that those ecosystems will also be invaded by new species. However, landscape warming is likely to be the major catalyst for displacement of hardy indigenous populations from Beringia. Because there is no historical basis for understanding the impact on taiga populations of anthropogenic modifications in association with climate change, the future integrity of the taiga wilderness cannot be assumed to be sustainable. Until more has been

learned, the wisest option at present would be to manage locations such as Yukon Primeval Beringia as wilderness preservation sites. A related question concerns whether hardy northern germplasm can be conserved over the long term, for example in seed banks or as cryo-preserved micropropagules.

Testing progeny of a population in regions different from the one that the population is indigenous to is known as provenance testing (Hagman, 1993). Over the last two centuries, economic forestry practices in closed-crown boreal forest ecosystems have disrupted natural population structures, shuffling provenances and exerting still-uncertain effects on both physiological fitness and genetic diversity in relation to trees' abilities to tolerate environmental change. Northern taiga by virtue of its remoteness, harsh climate and small incentive for economic forestry exploitation has so far been largely exempted from those manipulations, and that inadvertent preservation may be the primary hope for reinstatement of boreal forest ecosystems following a future glacial period.

Provenance trials in relation to taiga remain a novelty (Walker, 2010). A noteworthy trial involved planting white spruce seeds and seedlings of a central Alaskan provenance at several locations north of treeline in northern Alaska, in a region where only tundra vegetation occurs. None of the white spruce seeds produced seedlings, and only two of 100 seedlings planted in calendar year 1968 were still alive when observed in 2001 (Wilmking and Ibendorf, 2004). Very little is yet understood about the physiology of taiga tree establishment (Walker, 2010).

6. Conclusions

Taiga is a highly complex transitional zone covering an immense circumpolar expanse and distinguished by exceptionally hardy widely spaced conifers that occupy both lowland and mountainous regions between the northern hemisphere's boreal forest and tundra. Although a major reservoir of sequestered carbon, fresh water and biodiverse ecosystems comprising species physiologically adapted to tolerate northern conditions, taiga remains an altogether mysterious realm holding secrets about past climate change and how its organisms acquired fitness to tolerate those changes. Within the taiga zone is Beringia landscape shielded from the Wisconsinan ice sheet advance, and deeper within East Beringia is never-glaciated Yukon Primeval Beringia. The latter is a relatively small area of mountainous taiga that may well hold the key to linking polar forests that existed in the high Arctic 45 million years ago with those of the present day, and to aiding in future management of the biosphere by enabling increased understanding of both the ancestry and the physio-genetic basis for survival of trees, and life in general, within the subarctic. Although its never glaciated character is potentially of immense scientific value, Yukon Primeval Beringia presently is an entirely virgin region in relation to scientific investigations aimed at deciphering the ancestry of North American boreal forests. Because the physiological basis for population fitness of both taiga and interior boreal forest trees remains unknown, it is difficult to estimate how important conservation of Yukon Primeval Beringia ecosystems could become when Earth approaches the next glacial period. Presently, taiga permafrost is thawing in response to rapid warming, and should this trend continue, it is expected that major modification of the taiga zone will occur over coming decades.

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8. References

- Abbott, R. J. & Brochmann, C. (2003). History and evolution of the arctic flora: in the footsteps of Eric Hultén. *Molecular Ecology* 12: 299-313.
- Anderson, L.L., Hu, F. S., Nelson, D. M., Petit, R. J. & Paige, K.N. (2006). Ice-age endurance: DNA evidence of a white spruce refugium in Alaska. *Proceedings of the National Academy of Sciences of the USA* 103: 12447-12450.
- Armentrout, J.M. (1983). Glacial lithofacies of the Neogene Yakataga Formation, Robinson Mountains, southern Alaska Coast Range, Alaska. In: *Glacial-Marine Sedimentation*. B. F. Molnia, (ed.), pp 629-665, Plenum Press, New York.
- Andrews, H.N., Phillips, T.L. & Radforth, N.W. (1965). Paleobotanical studies in Arctic Canada. 1. *Archaeopteris* from Ellesmere Island. *Canadian Journal of Botany* 43:545-556.
- Arft, A.M., Walker, M.D., Gurevitch, J., Alatalo, J.M., Bret-Harte, M.S., Dale, M., Diemer, M., Gugerli, F., Henry, G.H.R., Jones, M.H., Hollister, R.D. Jónsdóttir, I.S., Laine, K. Lévesque, E., Marion, G.M., Molau, U., Mølgaard, P. Nordenhäll, U., Raszhivin, V., Robinson, C.H., Starr, G., Stenström, A., Stenström, M., Totland, Ø. Turner, P.L., Walker, L.J., Webber, P.J., Welker, J.M. & Wookey, P.A. (1999). Response of tundra plants to experimental warming: meta-analysis of the International Tundra Experiment. *Ecological Monographs* 69:491-511.
- Barendregt, R. W. & Duk-Rodkin, A. (2004). Chronology and extent of Late Cenozoic ice sheets in North America: A magnetostratigraphic assessment. In *Quaternary Glaciations – Extent and Chronology, Part II*. J. Ehlers and P.L. Gibbard, (eds.), pp 1-7, Elsevier.
- Barnosky, A.D. (2008). Climatic change, refugia, and biodiversity: where do we go from here? An editorial comment. *Climatic Change* 86:29-32.
- Bednarski, J. M. (2008). Landform assemblages produced by the Laurentide Ice Sheet in northeastern British Columbia and adjacent Northwest Territories – constraints on glacial lakes and patterns of ice retreat. *Canadian Journal of Earth Sciences* 45:593-610.

- Beschel, R.E. & Webb, D. (1963). Growth ring studies on arctic willows, In: *Preliminary Report 1961-1962, Axel Heiberg Island Research Reports*, F. Müller, (ed.), pp 189-198, McGill U., Montreal.
- Billings, W.D. & Mooney, H.A. (1968). The ecology of Arctic and alpine plants. *Biological Reviews* 43: 481 – 529.
- Blytt, A. (1882). Die Theorie der wechselnden kontinentalen und insularen Klimate. *Botanische Jahrbücher* 2: 1-50.
- Bostock, H. S. (1966). Notes on glaciation in central Yukon Territory. *Geological Survey of Canada Paper* 65-56, 18 p.
- Bostock, H.S. (1936). *Carmacks District, Yukon*. Geological Survey Canada, Memoir 189, 67p.
- Bradshaw, R.H.W., Hannon, G.E. & Lister, A.M. (2003) A long-term perspective on ungulate-vegetation interactions. *Forest Ecology and Management* 181: 267-280.
- Brandt, J.P. (2009). The extent of the North American boreal zone. *Environmental Reviews* 17: 101-161.
- Brochmann, C., Gabrielsen, T.M., Nordal, I., Landvik, J. Y. & Elven, R. (2003). Glacial survival or tabula rasa? The history of North Atlantic biota revisited. *Taxon* 52: 417-450.
- Brubaker, L. B., Anderson, P. M., Edwards, M. E. and Lozhkin, A. V. (2005). Beringia as a glacial refugium for boreal trees and shrubs: new perspectives from mapped pollen data. *Journal of Biogeography* 32: 833-614 848.
- Burn, C.R. (1994). Permafrost, tectonics, and past and future regional climate change. Yukon and adjacent Northwest Territories. *Canadian Journal of Earth Science* 31: 182-191.
- Camm, E.L. & Harper, G.J. (1991). Temporal variations in cold sensitivity of root growth in cold-stored white spruce seedlings. *Tree Physiology* 9:425-431.
- Carlsen, T., Reidar, E. & Brochmann, C. (2010). The evolutionary history of Beringian *Smelowskia* (Brassicaceae) inferred from combined microsatellite and DNA sequence data. *Taxon* 59:427-438.
- Carlson, M. Wells, J. and Roberts, D. (2009). *The Carbon the World Forgot: Conserving the Capacity of Canada's Boreal Forest Region to Mitigate and Adapt to Climate Change*. Boreal Songbird Initiative and Canadian Boreal Initiative, Seattle, WA and Ottawa, 33 pp.
- Catto, N. R. (1996). Richardson Mountains, Yukon-Northwest Territories: the northern portal of the postulated 'ice-free corridor'. *Quaternary International* 32: 3-19.
- Catto, N.R., Liverman, D.G.E., Bobrowsky, P.T. & Rutter, N. (1996). Laurentide, Cordilleran, and montane glaciations in the western Peace River - Grande Praisie region, Alberta and British Columbia, Canada. *Quaternary International* 32: 21-32.
- Cody, W. J. (2000). *Flora of the Yukon Territory, 2nd ed.* NRC Research Press, Ottawa.
- Cook, J. A., Hoberg, E.P., Koehler, A., Henttonen, H., Wickström, L., Haukialmi, V., Galbreath, K., Chernyavski, F., Dokuchaev, N., Lahzuhtkin, A., MacDonald, S.O., Hope, A., Waltari, E., Runck, A., Veitch, A., Popko, R., Jenkins, E., Kutz, S. & Eckerlin, R. (2005). Beringia: Intercontinental exchange and diversification of high latitude mammals and their parasites during the Pliocene and Quaternary. *Mammal Study* 30: 533-544.
- Cooper, D. J. (1986). White spruce above and beyond treeline in the Arrigetch Peaks region, Brooks Range, Alaska. *Arctic* 39: 247-252.

- Coursolle, C., Bigras, F.J. & Margolis, H.A. (1998). Frost tolerance and hardening capacity during the germination and early developmental stages of four white spruce (*Picea glauca*) provenances. *Canadian Journal of Botany* 76: 122-129.
- Crucifix, M. (2011). How can a glacial inception be predicted? *Holocene* 21:831-842.
- Cwynar, L.C. (1982). A Late-Quaternary vegetation history from Hanging Lake, northern Yukon. *Ecological Monographs* 52: 1-24. 622
- Cwynar, L.C. (1988). Late Quaternary vegetation history of Kettlehole Pond, southwestern Yukon. *Canadian Journal of Earth Science* 18: 1270- 1279.
- Cwynar, L. C. & MacDonald, G. M. (1987). Geographical variation of lodgepole pine in relation to population history. *American Naturalist* 129:463-469.
- Cwynar, L.C. & Ritchie, J.C. (1980). Arctic steppe-tundra: a Yukon perspective. *Science* 208: 1375-1377.
- Davies, A., Kemp, A. S. & Pike, J. (2009). Late Cretaceous seasonal ocean variability from the Arctic. *Nature* 460: 254-258.
- Day, T. (2006). *Taiga*. Chelsea House, New York, ISBN-10:0-8160-5329-4.
- Delcourt, P. A. & Delcourt, H.R. (1987). *Long-term Forest Dynamics of the Temperate Zone. A Case Study of Late-Quaternary Forest in Eastern North America*. Ecological Studies 63, Springer-Verlag, ISBN 3-540-96495-9. 439 p.
- Delucia, E.H. (1986). Effect of low root temperature on net photosynthesis, stomatal conductance and carbohydrate concentration in Engelmann spruce (*Picea engelmannii* Parry ex Engelm.) seedlings. *Tree Physiology* 2:143-154.
- Duk-Rodkin, A. (1999). *Glacial limits map of Yukon Territory*. Geological Survey of Canada, Open File 3694, Indian and Northern Affairs Canada Geoscience Map 1999-2, scale 1:1000000.
- Duk-Rodkin, A., Barendregt, R.W., Froese, D.G., Weber, F., Enkin, R., Smith, I.R., Zazula, G.D., Waters, P. & Klassen, R. (2004). Timing and extent of Plio-Pleistocene glaciations in north-western Canada and east-central Alaska. In *Quaternary Glaciations – Extent and Chronology, Part II*. J. Ehlers and P.L. Gibbard, (eds.), pp 313-335, Elsevier.
- Durzan, D. J. (1993). Molecular bases for adaptation of coniferous trees to cold climates. In: *Forest Development in Cold Climates*. Alden, J., Mastrantonio, J. L., Odum, S. (eds.), pp 15-42, Plenum Press, New York and London, ISBN 0-306-44480-1.
- Dyke, A. S. (2004). An outline of North American deglaciation with emphasis on central and northern Canada. In *Quaternary Glaciations – Extent and Chronology, Part II*, eds. J. Ehlers and P.L. Gibbard, Elsevier B.V., pp 373 – 424.
- Edwards, M.E., Brubaker, L.B., Lozhkin, A.V. & Anderson, P.M. (2005). Structurally novel biomes: a response to past warming in Beringia. *Ecology* 86: 1696-1703.
- Eidesen, P.B., Carlsen, T., Molau, U. & Brochmann, C. (2007). Repeatedly out of Beringia: *Cassiope tetragona* embraces the arctic. *Journal of Biogeography* 34: 1559-1574.
- Elliott-Fisk, D. L. (2000). The taiga and boreal forest. In *North American Terrestrial Vegetation*, 2nd ed. M. G. Barbour and W. D. Billings (eds), pp 41-74, Cambridge University Press, Cambridge, U.K.
- Farjon, A. (1990). Pinaceae: drawings and descriptions of the genera *Abies*, *Cedrus*, *Pseudolarix*, *Keteleeria*, *Nothotsuga*, *Tsuga*, *Cathaya*, *Pseudotsuga*, *Larix* and *Picea*. Koeltz Scientific Books, 633 Königstein.

- Fickert, T., Friend, D., Grüninger, F., Molnia, B. & Richter, M. (2007). Did debris-covered glaciers serve as Pleistocene refugia for plants? A new hypothesis derived from observation of recent plant growth on glacier surfaces. *Antarctic & Alpine Research* 39:245-257.
- Foulger, G.R. (2010). *Plates vs Plumes: A Geological Controversy*. Wiley-Blackwell, 364 pp., ISBN 978-1405161480.
- Francis, J.E. (1991). The dynamics of polar fossil forests: Tertiary fossil forests of Axel Heiberg Island, Canadian Arctic. In: *Fossil Forests of Tertiary age in the Canadian Arctic Archipelago*, Christie, R.L. and McMillan, N.J. (eds.), pp 29-38, Geological Survey of Canada, Bulletin 403.
- Geml, J., Laursen, G.A., O'Neill, K., Nusbaum, H.C. & Taylor, D.L. (2006) Beringian origins and cryptic speciation events in the fly agaric (*Amanita muscaria*). *Molecular Ecology* 15: 225-239.
- Geml, J., Kauff, F., Laursen, G.A. & Taylor, D. L. (2010). Genetic studies point to Beringia as a biodiversity hotspot for high-latitude fungi. *Alaska Park Science* 8: 37-41.
- Gérardi, S., Jaramillo-Correa, J.P., Beaulieu, J. & Bousquet, J. (2010). From glacial refugia to modern populations: new assemblages of organelle genomes generated by differential cytoplasmic gene flow in transcontinental black spruce. *Molecular Ecology* 19: 5265-5280.
- Germino, M.J., Smith, W.K. & Resor, A.C. (2002). Conifer seedling distribution and survival in an alpine-treeline ecotone. *Plant Ecology* 162:157-168.
- Goetcheus, V. G. & Birks, H. H. (2001). Full-glacial upland tundra vegetation preserved under tephra in the Beringia National Park, Seward Peninsula, Alaska. *Quaternary Science Reviews* 20: 135-147.
- Gugerli, F., Parnucci, L. & Petit, R. J. (2005). Ancient plant DNA: review and prospects. *New Phytologist* 166:409-418.
- Hagman, M. (1993). Potential species and provenances for forest development in cold climates. pp 251-263. In Alden, J., Mastrantonio, J. L., Odum, S. 1993. *Forest Development in Cold Climates*. Plenum Press, New York and London, ISBN 0-306-44480-1.
- Hansell, R.I.C, Chant, D.A. & Weintraub, J. (1971). Changes in the northern limit of spruce at Dubawnt Lake, N.W.T. *Arctic* 24:233-34.
- Harper, K.A., Danby, R.K., De Fields, D. L., Lewis, K.P., Trant, A.J., Starzomski, B.M., Savidge, R. & Hermanutz, L. (2011). Tree spatial pattern within the forest-tundra ecotone: a comparison of sites across Canada. *Canadian Journal of Forest Research* 41: 479-489.
- Hayes, C. W. (1892). An expedition through the Yukon district. *National Geographic Magazine* 4: 117-162, plates 18-20.
- Hickling, R, Roy, D.B., Hill, J.K, Fox, R. and Thomas, C.D. (2006). The distributions of wide-ranging taxonomic groups are expanding polewards. *Global Change Biology* 12: 450-455.
- Hills, L. V., Klovan, J.E. & Sweet, A.R. (1974). *Juglans eocinerea* n. sp., Beaufort Formation (Tertiary), southwestern Banks Island, Arctic Canada. *Canadian Journal of Botany* 52: 65-90.
- Holderegger, R. & Thiel-Egenter, C. (2009). A discussion of different types of glacial refugia used in mountain biogeography and phylogeography. *Journal of Biogeography* 36:476-480.

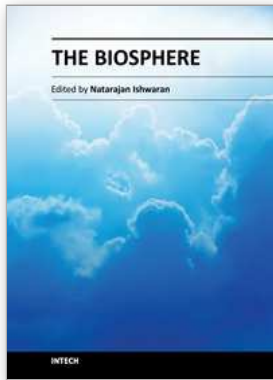
- Hopkins, D. M. (1982). Aspects of the paleogeography of Beringia during the Late Pleistocene, pp 3- 28 In *Paleoecology of Beringia*, ed. D. M. Hopkins, J. V. Matthews, C. E. Schweger and S. B. Young, Academic Press, 489 p.
- Hultén, E. (1937). *Outline of the History of Arctic and Boreal Biota During the Quaternary Period*. Lehre J. Cramer, Stockholm, New York, 168 pp.
- Husted, L. and Lavender, D.P. (1989). Effect of soil temperature upon the root growth and mycorrhizal formation of white spruce (*Picea glauca* (Moench) Voss) seedlings grown in controlled environments. *Annales des Sciences Forestières* 46:750s-753s.
- Hustich, I. (1953). The boreal limits of conifers. *Arctic* 62: 139-162.
- Ickert-Bond, S.M., Murray, D.F. & DeChaine, E. (2009). Contrasting patterns of plant distribution in Beringia. *Alaska Park Science* 8:26-32.
- Ivarson, K. C. (1965). The microbiology of some permafrost soils in the Mackenzie Valley, N.W.T. *Arctic* 18: 256-260.
- Jahren, A.H. (2007). The Arctic forest of the Middle Eocene. *Annual Reviews of Earth and Planetary Science* 35:509–540.
- Jahren, A.H., Byrne, M.C., Graham, H.V., Sternberg, L.S.L. & Summons, R.E. (2009). The environmental water of the middle Eocene Arctic: Evidence from δD , $\delta^{18}O$ and $\delta^{13}C$ within specific compounds. *Palaeogeography, Palaeoclimatology, Palaeoecology* 271: 96–103.
- Juan, P., Jaramillo, C., Jean, B. & Bousquet, J. (2004). Variation in mitochondrial DNA reveals multiple distant glacial refugia in black spruce (*Picea mariana*), a transcontinental North American conifer. *Molecular Ecology* 13: 2735-2747.
- Junttila, O. and Nilsen, J. (1993). Growth and development of northern forest trees as affected by temperature and light. In: *Forest Development in Cold Climates*. Alden, J., Mastrantonio, J. L., Odum, S. (eds.), pp 45-57, Plenum Press, New York and London, ISBN 0-306-44480-1.
- Kärki, L. & Tigerstedt, P.M.A. (1985). Definition and exploitation of forest tree ideotypes in Finland. In: *Attributes of Trees as Crop Plants*, Cannell, M.G.R. & Jackson, J.E. (eds.), pp 102-109, ITE, NERC, Abbots Ripton, England, ISBN 0-904282-83-X.
- Kimball, J.S., Zhao, M., McGuire, A.D. and Heinsch, F.A. (2007). Recent climate-driven increases in vegetation productivity for the western Arctic: Evidence of an acceleration of the northern terrestrial carbon cycle. *Earth Interactions* 11 (4): 1-30.
- Körner, C. (2007). Climatic treelines: conventions, global patterns, causes. *Erdkunde* 61:316-324.
- Kryshstofovich, A. N. (1935). A final link between the Tertiary floras of Asia and Europe. *New Phytologist* 34: 339-344.
- Kuc, M. (1974). Noteworthy plant records from southern Banks Island, N.W. T. *Arctic* 27:146-150.
- Larcher, W. (1995). *Physiological Plant Ecology*, 3rd ed. Springer-Verlag, Berlin Heidelberg New York, ISBN 3-540-58116-2 3, 506 p.
- Lebarge, W.P. (1995). *Sedimentology of Placer Gravels near Mt. Nansen, Central Yukon Territory*. Bulletin 4, Exploration and Geological Services Division, Northern Affairs Program, Yukon Region, Whitehorse, 155 p.
- Lefsky, M. A. (2010). A global forest canopy height map from the Moderate Resolution Imaging Spectroradiometer and the Geoscience Laser Altimeter System. *Geophysical Research Letters* 37, L15401: 1-5.

- LePage, B. A. (2001). New species of *Picea* A. Dietrich (Pinaceae) from the Middle Eocene of Axel Heiberg Island, Arctic Canada. *Botanical Journal of the Linnean Society* 135: 137-167.
- Levsen, N. D. & Mort, M. E. (2009). Inter-simple sequence repeat (ISSR) and morphological variation in the western North American range of *Chrysosplenium tetrandrum* (Saxifragaceae). *Botany* 87:780-790.
- Levson, V.M. & Rutter, N. W. (1996). Evidence of Cordilleran Late Wisconsinan glaciers in the 'ice-free corridor'. *Quaternary International* 32: 33-51.
- Lloyd, A.H., Wilson, A.E., Fastie, C.L. & Landis, R.M. (2005). Population dynamics of black and white spruce in the southern Brooks Range, Alaska. *Canadian Journal of Forest Research* 35:2073-2081.
- Lloyd, J., Shibistova, O., Zolotoukhine, D., Kolle, O., Arneth, A., Wirth, C., Styles, J.M., Tchebakova, N.M. & Schulze, E.D. (2002). Seasonal and annual variations in the photosynthetic productivity and carbon balance of a central Siberian pine forest. *Tellus* 54B: 590-610.
- Loehr, J., Worley, K., Grapputo, A., Carey, J., Veitch, A. & Coltman, D.W. (2006). Evidence for cryptic glacial refugia from North American mountain sheep mitochondrial DNA. *Journal of Evolutionary Biology* 19: 419-430.
- Lopushinsky, W. & Max, T.A. (1990). Effect of soil temperature on root and shoot growth and on budburst timing in conifer seedling transplants. *New Forests* 4:107-124.
- Lydolph, M.C., Jacobsen, J., Arctander, P., Gilbert, M.T.P., Gilichinsky, D.A., Hansen, A. J., Willerslev, E. & Lange, L. (2005). Beringian paleoecology inferred from permafrost-preserved fungal DNA. *Applied and Environmental Microbiology* 71: 1012-1017.
- Mackay, J. R. (1958). The valley of the lower Anderson River, N.W.T. *Geographical Bulletin* 11:37-56.
- MacDonald, G.M. & Cwynar, L. C. (1985). A fossil pollen based reconstruction of the late Quaternary history of lodgepole pine (*Pinus contorta* spp. *latifolia*) in the western interior of Canada. *Canadian Journal of Forest Research* 15: 1039-1044.
- MacDonald, G.M. & McLeod, T.K. (1996). The Holocene closing of the 'ice-free' corridor: a biogeographical perspective. *Quaternary International* 32: 87-95.
- Mandryk, C.A.S., Josenhans, H., Fedje, D.W. & Mathewes, R.W. (2001). Late Quaternary paleoenvironments of northwestern North America: implications for inland versus coastal migration routes. *Quaternary Science Reviews* 20:301-314.
- McLeod, T. K. & MacDonald, G. M. (1997). Postglacial range expansion and population growth of *Picea mariana*, *Picea glauca* and *Pinus banksiana* in the western interior of Canada. *Journal of Biogeography* 24: 865-881.
- Milankovitch, M. (1941). *Kanon der Erdbestrahlungen und seine Anwendung auf das Eiszeitenproblem*. (New English Translation (1998): *Canon of Insolation and the Ice Age Problem, with An Introduction and Biographical Essay by Nikola Pantic*, Alven Global, 636 pp.. ISBN 86-17-06619-9.)
- Mortensen, J.K. (1992). Pre-Mid-Mesozoic tectonic evolution of the Yukon-Tanana Terrane, Yukon and Alaska. *Tectonics* 11:836-853.
- Nakonechnaya, O.V., Kholina, A.B., Koren, O.G., Janeček, V., Kohutka, A., Gebauer, R. & Zhuravlev, Y.N. (2010). Characterization of gene pools of three *Pinus pumila* (Pall.) Regel populations at the range margins. *Russian Journal of Genetics* 46: 1417-1425.

- Namroud, M.-C., Beaulieu, J., Juge, N., Laroche, J. & Bousquet, J. (2008). Scanning the genome for gene single nucleotide polymorphisms involved in adaptive population differentiation in white spruce. *Molecular Ecology* 17: 3599-3613.
- Nienstaedt, H. & Zasada, J.C. (1990). *Picea glauca* (Moench) Voss, white spruce. In: *Silvics of North America 1. Conifers*, Burns, R.M. and Honkala, B.H. (eds.), 54 p, Agriculture Handbook 654, USDA Forest Service, Washington, D.C.
- Nilsson, M.C. (2005). Understory vegetation as a forest ecosystem driver, evidence from the northern Swedish boreal forest. *Frontiers in Ecology and the Environment* 3: 421-428.
- Pisaric, M.F.J., MacDonald, G.M., Velichko, A.A. & Cwynar, L.C. (2001). The lateglacial and postglacial vegetation history of the northwestern limits of Beringia, based on pollen, stomata and tree stump evidence. *Quaternary Science Reviews* 20: 235-245.
- Politov, D.V., Belokona, M.M & Belokon, Yu. S. (2006). Dynamics of allozyme heterozygosity in Siberian dwarf pine *Pinus pumila* (Pall.) Regel populations of the Russian far east: comparison of embryos and maternal plants. *Russian Journal of Genetics* 42: 1127-1136.
- Polunin, N.V. (1948). Botany of the Canadian Eastern Arctic, Part III; Vegetation and Ecology, *National Museum of Canada, Ottawa, Bulletin 104, Biological Series 32*, 304 p.
- Petit, R.J., Pineau, E., Demesure, B., Bacilieri, R., Ducouso, A. & Kremer, A. (1997). Chloroplast DNA footprints of postglacial recolonization by oaks. *Proceedings of the National Academy of Sciences USA* 94: 9996-10001.
- Porsild, A. E. (1955). The vascular plants of the western Canadian Arctic Archipelago. *National Museum of Canada, Ottawa, Bulletin 135, Biological Series 45*, 226 p.
- Porsild, A. E. (1964). *Illustrated Flora of the Canadian Arctic Archipelago*. National Museum of Canada, Ottawa, Bulletin 135, Biological Series 45, 226 p.
- Pregitzer, K.S., King, J.S., Burton, A.J. & Brown, S.E. (2000). Responses of tree fine roots to temperature. *New Phytologist* 147:105-115.
- Ran, J.-H., Wei, X.-X. & Wang, X.-Q. (2006). Molecular phylogeny and biogeography of *Picea* (Pinaceae): Implications for phylogeographical studies using cytoplasmic haplotypes. *Molecular Phylogeny and Evolution* 41: 405-419.
- Raskin, I. (1992). Role of salicylic acid in plants. *Annual Review of Plant Physiology* 43:439-463.
- Read, D.J., Leake, J.R. & Perez-Moreno, J. (2004). Mycorrhizal fungi as drivers of ecosystem processes in heathland and boreal forest biomes. *Canadian Journal of Botany* 82: 1243-1263.
- Ritchie, J. C. (1987). *Postglacial Vegetation of Canada*. Cambridge U. Press, Cambridge, ISBN 0 521 20868 2.
- Ritchie, J. C. (1984). *Past and Present Vegetation of the Far Northwest of Canada*. University of Toronto Press, Toronto.
- Ritchie, L.C. & MacDonald, G.M. (1986). The patterns of post-glacial spread of white spruce. *Journal of Biogeography* 13: 527-540.
- Röser, C., Montagnani, L., Schulze, E.D., Mollicone, D., Kolle, O., Meroni, M., Papale, D., Marchesini, L.B., Federici, S. & Valentini, R. (2002). Net CO₂ exchange rates in three different successional stages of the "Dark Taiga" of central Siberia. *Tellus* 54B:642-654.
- Savidge, R. A. & Förster, H. (1998). Seasonal activity of uridine 5'-diphosphoglucose : coniferyl alcohol glucosyltransferase in relation to cambial growth and dormancy in conifers. *Canadian Journal of Botany* 76.: 486 - 493.

- Scholander, P.F., Flagg, W., Hock, R.J. & Irving, L. (1953). Studies on the physiology of frozen plants and animals in the arctic. *Journal of Cellular and Comparative Physiology* 42 (S1): 1-56.
- Senjo, M., Kimura, K., Watano, Y., Ueda, K. & Shimizu, T. (1999). Extensive mitochondrial introgression from *Pinus pumila* to *P. parviflora* var. *pentaphylla* (Pinaceae). *Journal of Plant Research* 112: 97-105.
- Shafer, A. B. A., Côté, S. D. & Coltman, D. W. (2010). Hot spots of genetic diversity descended from multiple Pleistocene refugia in an alpine ungulate. *Evolution* 65: 125-138.
- Shiklomanov, I.A., & Rodda, J.C. (2003). *World Water Resources at the Beginning of the Twenty-first Century*. Cambridge, UK: Cambridge University Press.
- Shilo, N.A., Lozhkin, A.V., Anderson, P.M., Brown, T.A., Pakhomov, A. Yu. & Solomatkina, T.B. (2007). Glacial refugium of *Pinus pumila* (Pall.) Regel in northeastern Siberia. *Doklady Earth Sciences* 412:122-124.
- Shilo, N.A., Lozhkin, A.V., Anderson, P.M., Vazhenina, L.N., Glushkova, O. Yu. & Matrosova, T.V. (2008). First data on the expansion of *Larix gmelinii* (Rupr.) Rupr. into arctic regions of Beringia during the Early Holocene. *Doklady Earth Sciences* 423:1265-1267.
- Sigurgeirsson, A. & Szmidt, A. E. (1993). Phylogenetic and biogeographic implications of chloroplast DNA variation in *Picea*. *Nordic Journal of Botany* 13: 233-246.
- Stattin, E. & Lindström, A. (2000). Influence of soil temperature on root freezing tolerance of Scots pine (*Pinus sylvestris* L.) seedlings. In: *The Supporting Roots of Trees and Woody Plants: Form, Function and Physiology*, A. Stokes (ed.), pp 259-268, Kluwer, Dordrecht.
- Steuber, T., Rauch, M., Masse, J.-P., Graaf, J. & Malkoč, M. (2005). Low-latitude seasonality of Cretaceous temperatures in warm and cold episodes. *Nature* 437: 1341-1344.
- Stewart, J. R. & Dalén, L. (2008). Is the glacial refugium concept relevant for northern species? A comment on Pruett and Winker 2005. *Climatic Change* 86:19-22.
- Stewart, J.R., Lister, A.M., Barnes, I. & Dalén, L. (2010). Refugia revisited: individualistic responses of species in space and time. *Proceedings of the Royal Society B* 277: 661-671.
- Stockey, R. A. & Wiebe, N.J.P. (2008). Lower Cretaceous conifers from Apple Bay, Vancouver Island: *Picea*-like leaves, *Midoriphyllum piceoides* gen. et sp. nov. (Pinaceae). *Canadian Journal of Botany* 86: 649-657.
- Sugimoto, A., Yanagisawa, N., Naito, D., Fujita, N. & Maximov, T.C. (2002). Importance of permafrost as a source of water for plants in east Siberian taiga. *Ecological Research* 17: 493-503.
- Szeicz, J. M. & MacDonald, G.M. (2001). Montane climate and vegetation dynamics in easternmost Beringia during the Late Quaternary. *Quaternary Science Reviews* 20:247-257.
- Takahashi, S., Sugiura, K., Kameda, T., Enomoto, H., Kononov, Y., Ananicheva, M.D. & Kapustin, G. (2011). Response of glaciers in the Suntar-Khayata range, eastern Siberia, to climate change. *Annals of Glaciology* 52: 182-192.
- Taylor, T.N., Taylor, E.L. & Krings, M. (2009). *Paleobotany: the Biology and Evolution of Fossil Plants*, 2nd ed., Elsevier, ISBN: 978-0-12-373972-8.
- Tsutsui, K., Suwa, A., Sawada, K., Kato, T., Ohsawa, T.A. & Watano, Y. (2009). Incongruence among mitochondrial, chloroplast and nuclear gene trees in *Pinus* subgenus *Strobus* (Pinaceae). *Journal of Plant Research* 122:509-521.

- Tyron, P.R. & Chapin, F.S. (1983). Temperature control over root growth and root biomass in taiga forest trees. *Canadian Journal of Forest Research* 13:827-833.
- Vendramin, G.G., Lelli, L., Rossi, P & Morgante, M. (1996). A set of primers for the amplification of 20 chloroplast microsatellites in Pinaceae. *Molecular Ecology* 5: 595-598.
- Viereck, L.A. & Johnston, W.F. (1990) *Picea mariana* (Mill.) B.S.P, black spruce. In: *Silvics of North America 1. Conifers*, Burns, R.M. and Honkala, B.H. (eds.), Agriculture Handbook 654: 227-237, USDA Forest Service, Washington, D.C.
- Viktora, M., Savidge, R. A. & Rajora, O. P. (2011). Clonal and nonclonal genetic structure of subarctic black spruce (*Picea mariana*) populations in Yukon territory. *Botany* 89: 133-140.
- Wahl, E.E., Fraser, D.B., Harvey, R.C. & Maxwell, J.B. (1987). *Climate of Yukon*. Climatological Studies, 40. Environment Canada, Atmospheric Environment Service, 313p.
- Walker, X. (2010). The reproduction, establishment, and growth of white spruce in the forest tundra ecotone of the Inuvik-Tuktoyaktuk region. M.Sc. thesis, University of British Columbia, Vancouver, B.C.
- Waltari, E., Hoberg, E. P., Lessa, E. P. & Cook, J.A. (2007). Eastward ho: phylogeographical perspectives on colonization of hosts and parasites across the Beringian nexus. *Journal of Biogeography* 34: 561-574.
- Wareing, P. F. (1985). Tree growth at cool temperatures and prospects for improvement by breeding. In: *Attributes of Trees as Crop Plants*, M.G.R. Cannell and J. E. Jackson (eds.), pp 80-88, ITE, NERC Press, Abbots Ripton, England. ISBN 0-904282-83-X.
- Warming, E. (1888). Om Grønlands vegetation. *Meddelelser om Grønland* 12: 1-245.
- Weiser, C.J. (1970). Cold resistance and injury in woody plants. *Science* 169:1269-1278.
- Welsh, S.L. & Rigby, J.K. (1971). Botanical and physiographic reconnaissance of northern Yukon. *Brigham Young University, Science Bulletin, Biological Series* 14(2), 64 p.
- Westergaard, K. B., Jørgensen, M.H., Gabrielsen, T.M., Alsos, I.G. & Brochmann, C. (2010). The extreme Beringian/Atlantic disjunction in *Saxifraga rivularis* (Saxifragaceae) has formed at least twice. *Journal of Biogeography* 37:1262-1276.
- Williams, J.W., Shuman, B.N., Webb, T., Bartlein, P.J. & Leduc, P.L. (2004). Late Quaternary vegetation dynamics in North America: scaling from taxa to biomes. *Ecological Monographs* 74: 309-334.
- Wilmking, M. & Ibendorf, J. (2004). An early tree-line experiment by a wilderness advocate: Bob Marshall's legacy in the Brooks Range, Alaska. *Arctic* 57: 106-113.
- Yuan, X. (2012). Growth patterns of timberline *Picea glauca* on a site in the Yukon Plateau: Correlations within tree and between trees. M.Sc.F. thesis, University of New Brunswick, Fredericton, Canada.
- Zarter, C.R., Demmig-Adams, B., Ebbert, V., Adamska, I. & Adams, W.W. III. (2006). Photosynthetic capacity and light harvesting efficiency during the winter-to-spring transition in subalpine conifers. *New Phytologist* 172: 283-292.
- Zazula, G.D., Telka, A.M., Harington, C.R., Schweger, C.E. & Mathewes, R.W. (2006). New spruce (*Picea* spp.) macrofossils from Yukon territory: implications for Late Pleistocene refugia in Eastern Beringia. *Arctic* 59: 391-400.



The Biosphere

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In this book entitled "The Biosphere", researchers from all regions of the world report on their findings to explore the origins, evolution, ecosystems and resource utilization patterns of the biosphere. Some describe the complexities and challenges that humanity faces in its efforts to experiment and establish a new partnership with nature in places designated as biosphere reserves by UNESCO under its Man and the Biosphere (MAB) Programme. At the dawn of the 21st century humanity is ever more aware and conscious of the adverse consequences that it has brought upon global climate change and biodiversity loss. We are at a critical moment of reflection and action to work out a new compact with the biosphere that sustains our own wellbeing and that of our planetary companions. This book is a modest attempt to enrich and enable that special moment and its march ahead in human history.

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