

ISSN 1432-9840, Volume 13, Number 3



**This article was published in the above mentioned Springer issue.
The material, including all portions thereof, is protected by copyright;
all rights are held exclusively by Springer Science + Business Media.
The material is for personal use only;
commercial use is not permitted.
Unauthorized reproduction, transfer and/or use
may be a violation of criminal as well as civil law.**

Dead Wood is Buried and Preserved in a Labrador Boreal Forest

Martin Thomas Moroni,^{1,2*} Ulrike Hagemann,³
and David Wesley Beilman^{4,5}

¹Natural Resources Canada, Canadian Forest Service – Atlantic Forestry Centre, PO Box 960, Corner Brook, Newfoundland and Labrador A2H 6J3, Canada; ²Forestry Tasmania, 79 Melville Street, Hobart, Tasmania 7000, Australia; ³Institute of Soil Science and Site Ecology, Faculty of Forest, Geo and Hydro Sciences, Dresden University of Technology, Piennner Str. 19, 01737 Tharandt, Germany; ⁴CHRONO Centre for Climate, the Environment and Chronology, Queen's University Belfast, Belfast BT9 6AX, UK; ⁵Department of Geography, University of Hawai'i Mānoa, Honolulu, Hawaii 96822-2223, USA

ABSTRACT

Large amounts (36.4 Mg ha⁻¹ or 179 m³ ha⁻¹) of buried dead wood were found in overmature (146–204-year-old) black spruce (*Picea mariana* (Mill.) B.S.P.) forests in the high boreal region of eastern Canada. Amounts of this size indicate that burial reduces rates of wood decay producing an important component of long-term carbon (C) storage. Radiocarbon-derived ages of black spruce stems buried near the bottom of the organic soil horizon at three old-growth sites were up to 515 years old. Together with information on current stand age, this suggests that the stems have been dead for more than 250 years. Most aboveground dead wood decays or becomes fragmented within about

70 years of tree death in these forests. The presence of old yet well-preserved buried wood suggests that decay rates are greatly reduced when downed dead wood is quickly overgrown by moss. Thus, the nature and type of ground-layer vegetation influences the accumulation of organic matter in these forests. This process of dead wood burial and the resultant addition to a large and long-enduring belowground C pool should be considered when estimating dead wood abundance for habitat or forest C accounting and cycling.

Key words: biomass; black spruce; carbon; necromass; *Picea mariana*; snags; woody debris.

INTRODUCTION

Dead wood (DW) is integral to a range of ecosystem functions, including provision of habitat for numerous species (for example, Harmon and others 2004; Simon and others 2002) and carbon (C) and nutrient cycling (for example, Kurz and Apps 1993; Laiho and Prescott 2004; Harmon and others 2004; Manies and others 2005). The few studies that report buried wood abundance show a wide

range of buried downed DW biomass storage, 0.2–36.4 Mg ha⁻¹, amounts often equivalent to or greater than unburied downed DW (3–1674%; Brais and others 2005; Hagemann and others 2009; Lang and others 1981; Manies and others 2005; Moroni 2006), with the largest amounts (36.4 Mg ha⁻¹ or 179 m³ ha⁻¹; 23–725% unburied downed DW biomass; Figure 1) from boreal black spruce (*Picea mariana* (Mill.) B.S.P.) forests in Labrador, Canada (Hagemann and others 2009).

Large amounts of buried wood in Labrador black spruce forests is indicative of long-term storage where rates of decay appear suppressed (Hagemann and others 2009). Burial of woody debris in the organic layer is promoted by the vigorous growth of bryophytes in the groundcover layer (Hagemann

Received 28 October 2009; accepted 10 March 2010;
published online 15 April 2010

Author Contributions: MTM wrote paper, and conceived and designed study; UH conceived and designed study, performed research; DWB contributed ¹⁴C method and conceived and designed this component, performed research and analyzed data.

*Corresponding author; e-mail: martin.moroni@forestrytas.com.au



Figure 1. ^{14}C -derived age of buried tree stems compared to the buried wood C pool in three old-growth black spruce sites in central Labrador, Canada. Horizontal bars show 2σ age uncertainties (Stuiver and Reimer 1993) and open squares are the medians of each 2σ age distribution (Table 1). Solid bars show ages older than current mean stand age (indicated) and filled bars show ages younger than current mean stand age.

and others 2009), typical of many coniferous forests (Wilton 1964; Bisbee and others 2001). Labrador experiences a cold wet environment (Environment Canada 2010) producing a cold wet organic layer, conditions enhanced by the presence of a bryophyte layer (Foster 1985; Kasischke and Johnstone 2005), likely resulting in buried DW decay rates that are dramatically lower than decay rates of unburied DW as suggested by other authors (Foster 1985; Manies and others 2005). Calculating decay rates of woody debris based on aboveground measurements of woody debris abundance may, therefore, overestimate decay rates as the potentially large component of DW that is quickly buried would be missed.

In this study, we measure the radiocarbon (^{14}C) age of buried wood excavated from the organic layer at the boundary between mineral and organic soil horizons in old-growth Labrador black spruce forests. We hypothesize that suppressed decay rates allow for substantial necromass to accumulate belowground, which would be evident in well-preserved buried wood that is centuries old.

MATERIALS AND METHODS

Site Selection and Description

The study area is near Goose Bay, Labrador, Canada in the “High-boreal Forest–Lake Melville”

Ecoregion (Ecosdistrict 452, Ecoregion 6; Ecoregions Working Group 1989), which is the easternmost extent of the Boreal Shield Ecozone and a narrow extension of the boreal forest into the Taiga Shield Ecozone. Forests on well-drained sites in the region are the most productive local forests and are dominated by black spruce mixed with balsam fir (*Abies balsamea* (L.)) and white birch (*Betula papyrifera* Marsh.) (Rowe 1972).

Three old-growth forest sites of stand type bS842M (Government of Newfoundland and Labrador, unpublished), the most common productive forest type in the region, were selected for study (Table 1). This forest type is dominated by black spruce (>75%) older than 140 years with an average height of 12–15 m, crown closure of 50–75%, and of medium productivity (for merchantable yield). The bS842M stand type typically attains a maximum gross merchantable volume (GMV) of about $140 \text{ m}^3 \text{ ha}^{-1}$ at stand ages of around 110–150 years, before going into gap dynamics at an average GMV of about $113 \text{ m}^3 \text{ ha}^{-1}$ (Table 2). Site elevation ranges from 161 to 257 m, and mean annual temperature is between -2.2 and -1.8°C (McKenney and others 2007). Mean annual precipitation of approximately 1,000 mm is well distributed throughout the year and is among the highest amounts for boreal North America (Foster 1985; Environment Canada 2010). Stand age at our study sites was estimated to be 146–204 years based on tree-ring counts from increment bores (Hagemann and others 2009).

Field and Laboratory Measurements

Field measurements and sampling were conducted in August 2008. Within each of the three forest sites, a 27-m-long trench was excavated to the bottom of the organic horizon to expose a vertical cross section of the organic layer and buried DW. Organic layer depth was measured every 27 cm within each trench. From each excavation, three or four individual buried stems (for a total of 10 stems) located near the interface of the organic layer and mineral soil with minimum diameters of 10 cm were sampled (Figure 2). Samples of approximately 150 cm^3 were excavated from the approximate center of each stem. Care was taken to avoid the exterior of the stem to prevent contamination of samples with modern C, as stems were often mixed with organic or mineral soil material and penetrated by roots and fungal hyphae.

Excavated 150 cm^3 stem samples were returned to the laboratory and air dried. Charcoal was identified on the surface of some buried wood from

Table 1. Site Characteristics, Buried wood ¹⁴C Ages, and Estimated Calendar Ages Following Calibration and Constraint by Current Stand Age

Site	Northing, Easting ^a	Organic layer depth (cm)	Forest age (years)	Sample	¹⁴ C age (¹⁴ C years BP)	Lab number	Median age (years before 2008) ^b	2-sigma age-ranges (years before 2008) ^b
Cape Caribou V	358200, 5936956	25 (2)	204 ± 20	a	306 ± 23	UB-11564	450	360–390, 405–515
				b	304 ± 22	UB-11566	450	360–390, 405–515
				c	146 ± 21	UB-11567	270	230–340
				d	63 ± 22	UB-11568	300	280–315
Arrowhead III	346964, 5941589	21 (2)	146 ± 20	a	184 ± 23	UB-11569	250	200–280, 320–350
				b	26 ± 22	UB-11571	290	175–185, 290–300
Arrowhead IV	348846, 5943983	17 (1)	148 ± 20	c	103 ± 23	UB-11572	200	150–200, 280–320
				a	61 ± 23	UB-11573	280	155–195, 280–315
				b	69 ± 24	UB-11574	280	150–195, 280–315
				c	1.0041 ± 0.0028 ^c	UB-11576	55	54–56

^aUTM coordinates, map datum NAD83, UTM Zone 20.^bCalendar age probabilities were determined using CALIB 5.1.0 (Stuiver and Reimer 1993) and IntCal04 data (Reimer and others 2004). Median ages and age ranges are derived from the probability distribution older than the current mean stand age.^cPost-homb ¹⁴C content is reported as F¹⁴C value. Parenthesis contains standard errors.**Table 2.** Description of Natural Resources Canada (2009) DW Decay Classes

Attribute	Decay class				
	1	2	3	4	5
Wood texture	Intact, hard	Intact, hard to partly decaying	Hard, large pieces, partly decaying	Small, blocky pieces	Many small pieces, soft portions
Portion on ground	Elevated on support points	Elevated but sagging slightly	Sagging near ground, or broken	All of log on ground, sinking	All of log on ground, partly sunken
Twigs <3 cm (if originally present)	Twigs present	No twigs	No twigs	No twigs	No twigs
Bark	Bark intact	Intact or partly missing	Trace bark	No bark	No bark
Shape	Round	Round	Round	Round to oval	Oval
Invading roots	None	None	In sapwood	In heartwood	In heartwood



Figure 2. Wood buried at Cape Caribou V showing (A) the sampled Cape Caribou Va buried stem laying on the mineral soil surface in a more than 20-cm-deep organic layer, (B) large amounts of wood buried in the organic layer, and (C) 450-year-old wood from Va and Vb; the three left most samples are charred. In all the samples, annual growth rings and blocky wood structure are clearly visible.

all sites and was visible on the Cape Caribou Va sample (Figure 2). Ingrown fungal mycelia and roots were removed by hand from buried wood under a stereo microscope before individual wood fragments were selected for ^{14}C measurement.

^{14}C Measurement

From each 150 cm³ stem sample, three or four small, randomly selected fragments of wood (about 100–200 mg each) were composited. Potential carbonate and humic acid contamination was removed from the composited wood by standard acid–base–acid pretreatment (65°C, 0.5 N HCl for 1 h, 0.5 N NaOH for 1 h, 0.5 N HCl for 4 h) at the ^{14}C CHRONO Centre, Queen’s University, Belfast. Samples were combusted to CO₂ at 900°C for 6 h in the presence of CuO and Ag in evacuated quartz tubes. An aliquot of CO₂ was cryogenically purified, then converted to graphite by hydrogen reduction for analysis by AMS. ^{14}C ages were calibrated to calendar ages using the IntCal04 curve and CALIB 5.1 (Reimer and others 2004; Stuiver and Reimer 1993). We report buried stem ages as years before excavation and measurement (before 2008 AD) and rounded off to the nearest decade. The buried wood sample Arrowhead IVc had greater than modern ^{14}C content (bomb carbon), and the calendar age corresponding to this level of ^{14}C was determined using CaliBomb (<http://intcal.qub.ac.uk/CALIBomb/frameset.html>).

RESULTS

The depth of the organic layer ranged from 17 to 25 cm (Table 1). The deepest organic layer was encountered at Cape Caribou V, which supported the oldest trees (204 ± 20 years). Arrowhead III and Arrowhead IV organic layer depth ranged from 17 to 21 cm deep under forests of similar age (146–148 ± 20 years). Portions of wood sampled from Cape Caribou Va and b were composed of small blocky pieces with clearly discernable wood structure (for example, rings; Figure 2) consistent with the description of wood of Decay Class 4 (Table 2).

The probability distributions for the ^{14}C -derived age of buried stems spanned 54–515 years before 2008, but were typically older than 200 years before 2008 (Table 1; Figure 1). Calibrated ^{14}C age uncertainties are particularly large between 50 and 380 years before 2008 owing to sharp increases and variable amounts of atmospheric $^{14}\text{CO}_2$ (Reimer and others 2004). To constrain age estimates, we conservatively assumed that buried DW is older than the living trees at these sites, and assigned a minimum age for buried stems at the current stand age. The median age of the remaining probability distribution, the constrained age, for each stem was between 240 and 450 years before 2008 (Table 1). Buried wood at the Cape Caribou V site was clearly very old, with some wood having been formed about 450 years ago. In contrast, the

Arrowhead IVc sample was found to contain anthropogenic bomb C (Table 1) indicating C fixed since 1952. Because this stem was located at the bottom of a well-developed 22-cm-deep organic layer in a stand with 148-year-old living trees, this sample is suspected to have been buried more than 50 years ago and subsequently contaminated with recently formed tissues, such as ingrown roots. If other stem ages were similarly influenced by younger C, then our ^{14}C -derived ages of buried wood are conservative. Well-preserved buried stems at old-growth black spruce sites in Labrador were likely fixed from atmospheric CO_2 200–450 years before 2008.

DISCUSSION

Radiocarbon measurements, tree demographics, and the presence of stems and charcoal near the interface of the organic and mineral soils provide evidence that wood buried has been dead for 250–500 years (Figure 1). Such buried DW longevity is far longer than aboveground DW is expected to persist. Following stand replacing natural disturbance of mature balsam fir or black spruce in Newfoundland and Labrador, dead trees fall to become woody debris that typically decays and fragments completely within 70 years (Moroni 2006; Hagemann and others 2009). Buried wood dead for 250–500 years is indicative of DW preservation upon burial.

The ^{14}C ages of buried DW reflect the time since wood C was photosynthetically fixed from atmospheric CO_2 , which our results indicate was up to 515 years before sampling. The average maximum lifespan of black spruce trees is about 200 years, but trees as old as 280 years have been reported (Fowells 1965; Vincent 1965). The oldest buried stems at Cape Caribou V have been dead for at least 170 years (450 years median age (Table 1)—280 years maximum black spruce age; Table 2), but probably not less than 250 years (450 years median age—200 years average maximum black spruce age). However, only wood removed from the center of the base of a buried tree would have been part of the living tree for its entire lifetime. At our study sites, all samples were taken from 10–15-cm-diameter horizontal-lying stems (Figure 2), that is, wood fixed sometime after the tree began to grow. In addition, buried trees of this stem size are not likely to have achieved their maximum age. Thus, buried trees from the Cape Caribou Va and b forests are likely to have been dead for more than 250 years and potentially as long as 515 years (Table 1).

Charcoal was identified on buried DW at all three sites, and was found on the surface of Cape Caribou V samples (Figure 2). Charred wood that is buried for centuries is indicative of significant original charring that likely resulted from intense stand-replacing fires that consumed the organic layer and allowed snags to fall to the mineral soil surface. These snags likely form much of the enormous abundance of buried wood encountered in the study sites (Table 1; Figure 1). The timing before present of the last stand-replacing fire at Cape Caribou V is clearly older than the age of the current forest (204 years). In addition, regeneration delays of decades are not unusual following intense fires in Labrador (compare Hagemann and others 2009). These forest dynamics support the ^{14}C -age evidence that buried wood has been dead for more than 250 years.

A surprising degree of preservation is required for wood that has been dead more than 250 years to remain at Decay Class 4 (Table 2). Further to this, rates of buried wood decay are likely slower than those indicated by this decay class and time since death, because DW probably decayed before it fell to the ground and became buried.

Snag longevity for black spruce is about 25 years in Labrador (Hagemann and others 2009) where a snag is likely to stand until it begins to lose structural integrity at approximately Decay Class 3 (Table 2). Once DW falls, burial appears to result from bryophyte groundcover overgrowth in Labrador (Hagemann and others 2009), a process requiring woody debris to make ground contact. Initially, fallen woody debris is often elevated from the forest floor and does not sag to the ground until it has significantly decomposed (Decay Class 3 or greater, Natural Resources Canada (2009); Table 2). Thus, even if DW fell relatively undecayed, it likely progressed to a higher Decay Class before burial. Cape Caribou Va and b samples likely progressed from Decay Class 1 to 3 in the first few decades following tree death as unburied DW, and from decay class 3 to 4 or higher in the following 2–5 centuries as buried wood.

In humid boreal forests, a combination of factors appears to favor enhanced preservation of buried wood including a cool growing season, high annual precipitation, microtopography that enhances moist conditions, a long fire-return interval, and vigorous bryophyte growth in the ground layer (Hagemann and others 2009). Bryophytes form a dense mat of groundcover in many boreal forests (Larsen 1980), which has been long recognized to decrease temperatures, increase moisture content, and reduce nutrient availability in soils (Tamm

1953; Oechel and van Cleve 1986). Vigorous moss growth is required to overgrow downed DW, which is further optimized in cool wet climates (Wilton 1964; Bisbee and others 2001). Microbial activity is slowed in cool conditions and wet bryophyte groundcover can further promote soil heat loss (Oechel and van Cleve 1986; Prescott and others 2000; Hermann and Prescott 2008). In addition, a wet organic layer can act as a fire retardant (Kasischke and Johnstone 2005; Manies and others 2005), increasing fire-return intervals and promoting DW preservation between fire events. Humid coniferous forests are common throughout the circumpolar boreal forests (Ahti and others 1968; Hämet-Ahti and others 1974; Ecoregions Working Group 1989) and at higher elevations south of the boreal biome (Clark and others 1998; Zielonka and Niklasson 2001). Thus, DW burial and long-term belowground persistence may be more common than previously considered. The presence or absence of a bryophyte ground layer and its associated characteristics may be overlooked as an important soil C stabilization factor (Swift and others 1979; Moore and others 1998; Prescott 2000).

In coniferous forests with small-diameter trees, DW is commonly reported to be a short-term C pool (for example, Moroni 2006). However, in cool humid coniferous ecosystems downed DW may become an important C store following burial. This mechanism and C pool have received little attention to date and the transfer of unburied woody debris stocks to buried DW has been previously attributed to decay and atmospheric flux. It may be important to consider the loss of aboveground DW habitat to burial in habitat availability studies (for example, for small birds in Labrador; Simon and others 2002), and to examine the role of buried wood as habitat for soil fauna or burrowing organisms, which to the authors' knowledge is yet to be described. We suggest that accounting for DW burial in black spruce forests and similar forest ecosystems would be a step toward accurate accounting and modeling of forest C cycles (Kurz and others 2009) in forests where buried wood is a potentially large and long-lived C pool.

ACKNOWLEDGMENT

We thank Darrell Harris for sample preparation.

REFERENCES

Ahti T, Hämet-Ahti L, Jalas J. 1968. Vegetation zones and their sections in northwestern Europe. *Ann Bot Fenn* 5:169–211.

Bisbee KE, Gower ST, Norman JM, Nordheim EV. 2001. Environmental controls on ground cover species composition and productivity in a black spruce boreal forest. *Oecologia* 129:261–70.

Brais S, Sadi F, Bergeron Y, Grenier Y. 2005. Coarse woody debris dynamics in a post-fire jack pine chronosequence and its relation with site productivity. *For Ecol Manag* 220:216–26.

Clark DF, Kneeshaw DD, Burton PJ, Antos JA. 1998. Coarse woody debris in sub-boreal spruce forests of west-central British Columbia. *Can J For Res* 28:284–90.

Ecoregions Working Group. 1989. Ecoclimatic regions of Canada: first approximation. Report and national map at 1:7 500 000 scale. Ecological Land Classification Series, No. 23. Ottawa, ON: Ecoregions Working Group, Canada Committee on Ecological Land Classification, Sustainable Development Branch, Canadian Wildlife Service, Conservation Protection, Environment Canada.

Environment Canada. 2010. Climate normals for Goose Bay Airport, Newfoundland and Labrador, 1971–2000. http://climate.weatheroffice.ec.gc.ca/climate_normals/index_e.html. Accessed January 2010.

Foster DR. 1985. Vegetation development following fire in *Picea mariana* (black spruce)–*Pleurozium* forests of south-eastern Labrador, Canada. *J Ecol* 73:517–34.

Fowells HA, compiler. 1965. Silvics of forest trees of the United States. Agriculture Handbook 271. Washington, DC: US Department of Agriculture.

Government of Newfoundland and Labrador. Unpublished. Forest inventory: data dictionary for district library, unpublished report.

Hagemann U, Moroni MT, Makeschin F. 2009. Dead wood abundance in Labrador high-boreal black spruce forests. *Can J For Res* 39:131–42.

Hämet-Ahti L, Ahti T, Koponen T. 1974. A scheme of vegetation zones for Japan and adjacent regions. *Ann Bot Fenn* 11:59–88.

Harmon ME, Franklin JF, Swanson FJ, Sollins P, Gregory SV, Lattin JD, Anderson NH, Cline SP, Aumen NG, Sedell JR, Lienkaemper GW, Cromack K Jr, Cummins KW. 2004. Ecology of woody debris in temperate ecosystems. *Adv Ecol Res* 34:59–234.

Hermann S, Prescott CE. 2008. Mass loss and nutrient dynamics of coarse woody debris in three Rocky Mountain coniferous forests; 21 year results. *Can J For Res* 38:125–32.

Kasischke ES, Johnstone JF. 2005. Variation in postfire organic layer thickness in a black spruce forest complex in interior Alaska and its effects on soil temperature and moisture. *Can J For Res* 35:2164–77.

Kurz WA, Apps MJ. 1993. Contribution of northern forests to the global C cycle: Canada as a case study. *Water Air Soil Pollut* 70:163–76.

Kurz WA, Dymond CC, White TM, Stinson G, Shaw CH, Rampley GJ, Smyth C, Simpson BN, Neilson ET, Trofymow JA, Metsaranta J, Apps MJ. 2009. CBM-CFS3: a model of carbon-dynamics in forestry and land-use change implementing IPCC standards. *Ecol Mod* 220:480–504.

Laiho R, Prescott CE. 2004. Decay and nutrient dynamics of coarse woody debris in northern coniferous forests: a synthesis. *Can J For Res* 34:763–77.

Lang GE, Cronan CS, Reiners WA. 1981. Organic matter and major elements of the forest floors and soils in subalpine balsam fir forests. *Can J For Res* 11:388–99.

- Larsen JA. 1980. The boreal forest ecosystem. New York: Academic Press.
- Manies K, Harden J, Bond-Lamberty B, O'Neill K. 2005. Woody debris along an upland chronosequence in boreal Manitoba and its impact on long-term carbon storage. *Can J For Res* 35:472–82.
- McKenney D, Papadopol P, Lawrence K, Campbell K, Hutchinson M. 2007. Customized spatial climate models for Canada. Technical Note 108. Sault Ste. Marie, ON: Natural Resources Canada, Canadian Forest Service – Great Lakes Forestry Centre.
- Moore TR, Roulet NT, Waddington JM. 1998. Uncertainty in predicting the effect of climatic change on the carbon cycling of Canadian peatlands. *Clim Change* 40:229–45.
- Moroni MT. 2006. Disturbance history affects dead wood abundance in Newfoundland boreal forests. *Can J For Res* 36:3194–208.
- Natural Resources Canada. 2009. Canada's National Forest Inventory and online database. Ottawa, ON: Natural Resources Canada, Canadian Forest Service – Headquarters, https://nfi.nfis.org/index_e.shtml. Accessed June 2009.
- Oechel WC, van Cleve K. 1986. The role of bryophytes in nutrient cycling in the taiga. In: van Cleve K, Chapin FSIII, Flanagan PW, Viereck LA, Dyrness CT, Eds. *Forest ecosystems in the Alaskan Taiga*. New York: Springer-Verlag. p 121–37.
- Prescott C, Maynard D, Laiho R. 2000. Humus in northern forests: friend or foe? *For Ecol Manag* 133:23–36.
- Reimer PJ, Baillie MGL, Bard E, Bayliss A, Beck JW, Bertrand CJH, Blackwell PG, Buck CE, Burr GS, Cutler KB, Damon PE, Edwards RL, Fairbanks RG, Friedrich M, Guilderson TP, Hogg AG, Hughen KA, Kromer B, McCormac G, Manning S, Ramsey CB, Reimer RW, Remmele S, Southon JR, Stuiver M, Talamo S, Taylor FW, van der Plicht J, Weyhenmeyer CE. 2004. IntCal04 Terrestrial radiocarbon age calibration, 26–0 ka BP. *Radiocarbon* 46:1029–58.
- Rowe JS. 1972. Forest regions of Canada. Publication No. 1300. Ottawa, ON: Department of the Environment, Canadian Forest Service.
- Simon NPP, Stratton CB, Forbes GJ, Schwab FE. 2002. Similarity of small mammal abundance in post-fire and clearcut forests. *For Ecol Manag* 165:163–72.
- Stuiver M, Reimer PJ. 1993. Extended 14C database and revised CALIB radiocarbon calibration program. *Radiocarbon* 35:215–30.
- Swift MJ, Heal OW, Anderson JM. 1979. *Decomposition in terrestrial ecosystems*. Oxford, UK: Blackwell Scientific.
- Tamm CO. 1953. Growth, yield and nutrition in carpets of a forest moss (*Hylocomium splendens*). *Meddelanden fran Statens Skogsforskningsinstitut* 43:1–140.
- Vincent AB. 1965. Black spruce: a review of its silvics, ecology and silviculture. Publication 1100. Ottawa, ON: Canada Department of Forestry, Forest Research Branch.
- Wilton W. 1964. The forests of Labrador. Ottawa, ON: Canada Department of Forestry, Forest Research Branch.
- Zielonka T, Niklasson M. 2001. Dynamics of dead wood and regeneration pattern in natural spruce forest in the Tatra Mountains, Poland. *Ecol Bull* 49:159–63.