Fine-root growth in a forested bog is seasonally dynamic, but shallowly distributed in nutrient-poor peat

Colleen M. Iversen · Joanne Childs · Richard J. Norby · Todd A. Ontl · Randall K. Kolka · Deanne J. Brice · Karis J. McFarlane · Paul J. Hanson

Abstract

Background and aims Fine roots contribute to ecosystem carbon, water, and nutrient fluxes through resource acquisition, respiration, exudation, and turnover, but are understudied in peatlands. We aimed to determine how the amount and timing of fine-root growth in a forested, ombrotrophic bog varied across gradients of vegetation density, peat microtopography, and changes in environmental conditions across the growing season and throughout the peat profile.

Methods We quantified fine-root peak standing crop and growth using non-destructive minirhizotron technology over a two-year period, focusing on the dominant woody species in the bog: *Picea mariana*, *Larix laricina*, *Rhododendron groenlandicum*, and *Chamaedaphne calyculata*.

Results The fine roots of trees and shrubs were concentrated in raised hummock microtopography, with more tree roots associated with greater tree densities and a unimodal peak in shrub roots at intermediate tree densities. Fine-root growth tended to be seasonally dynamic,

C. M. Iversen (✉) · J. Childs · R. J. Norby · D. J. Brice · P. J. Hanson
Climate Change Science Institute and Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, TN, USA
e-mail: iversencm@ornl.gov

J. Childs
e-mail: childsj@ornl.gov

R. J. Norby
e-mail: norbyrj@ornl.gov

D. J. Brice
e-mail: bricedj@ornl.gov

P. J. Hanson
e-mail: hansonpj@ornl.gov

T. A. Ontl
USDA Forest Service, Northern Research Station, Houghton, MI, USA
e-mail: tontl@fs.fed.us

R. K. Kolka
USDA Forest Service, Northern Research Station, Grand Rapids, MN, USA
e-mail: rkolka@fs.fed.us

K. J. McFarlane
Center for Accelerator Mass Spectrometry, Lawrence Livermore National Laboratory, Livermore, CA, USA
e-mail: mcfarlane3@llnl.gov

but shallowly distributed, in a thin layer of nutrient-poor, aerobic peat above the growing season water table level. *Conclusions* The dynamics and distribution of fine roots in this forested ombrotrophic bog varied across space and time in response to biological, edaphic, and climatic conditions, and we expect these relationships to be sensitive to projected environmental changes in northern peatlands.

Introduction

Peatlands cover less than 3% of the global land surface but store as much as one-third of global terrestrial soil carbon (C) in deep deposits of peat (Gorham 1991; Bridgham et al. 2006; Yu et al. 2010). This large C reserve may be vulnerable to global warming and associated drying (Bridgham et al. 2008), and relative to their land cover, peatlands could contribute a disproportionate amount of CO_2 and CH_4 to the atmosphere under projected climate scenarios, providing an important positive feedback to climatic change (Bridgham et al. 2006; Denman et al. 2007; McGuire et al. 2009).

While the accumulation of peat is driven in large part by the occurrence of mosses, especially those in the *Sphagnum* genus, vascular plants can also exert important controls over peat accumulation. Ephemeral, narrow-diameter, fine roots responsible for plant water and nutrient acquisition (Kramer 1969; Fitter 1982) have been estimated to comprise a large fraction of vascular plant annual net primary production (NPP) in peatlands (~25 to 75%; Reader and Stewart 1972; Backéus 1990; Weltzin et al. 2000; Wang et al. 2003; Bond-Lamberty et al. 2004; Wieder 2006). Fine roots contribute directly to peat formation through root turnover (Laiho et al. 2003), but living roots can also play a disproportionately important role in the release of carbon from ancient peat through interactions with the microbial consortia that facilitate the decomposition of soil organic matter under aerobic and anaerobic conditions (reviewed in Megonigal et al. 2004; Walker et al. 2016). Fine roots also contribute a significant portion of peatland CO_2 efflux (e.g., 35 to 45%, Silvola et al. 1996) through root respiration and rhizosphere CH_4 oxygenation, while aerenchymous roots formed by some graminoids also allow the passive transport of CH_4 to the atmosphere

(Silvola et al. 1996; Ruess et al. 2003; Megonigal et al. 2004; Chanton 2005; Crow and Wieder 2005; Ström et al. 2005; Laanbroek 2010). The timing of fine-root production throughout the year also exerts important controls over CO_2 and CH_4 efflux from peat, as well as peatland plant nutrient acquisition and root exudation (Silvola et al. 1996; Ström et al. 2005).

The activities of fine roots are a large source of uncertainty in projections of the relative proportion and amount of CO_2 and CH_4 released from organic soils across the globe (Frolking et al. 2010; Wania et al. 2010; Riley et al. 2011). This is because, compared with other patterns and processes in ecosystems underlain by organic soils, the distribution of fine roots across the landscape and throughout the soil profile and the relative amount and timing of root growth are understudied (Iversen et al. 2012; Bhuiyan et al. 2016).

Peatlands are highly heterogeneous, encompassing gradients of vegetation composition and density, topography, and environmental conditions that change over time and throughout the peat profile. Thus, the dynamics and distribution of fine roots could be affected by several processes. These include: (1) the relative abundance of trees compared with ericaceous shrubs, and their distribution across the landscape (Murphy et al. 2009b; Bhuiyan et al. 2016), (2) undulating peatland microtopography, where raised hummocks sit higher and drier than adjacent hollow depressions and typically have higher woody vegetation density and nutrient availability (Murphy et al. 2009b; Eppinga et al. 2010; Malhotra et al. 2016), (3) seasonal changes in environmental conditions, and accompanying changes in the carbon sink strength of leaves and wood that may limit the C available for allocation belowground (reviewed in Abramoff and Finzi 2015), and (4) changes in edaphic conditions throughout the peat profile, especially nutrient availability and depth to the water table (Kohzu et al. 2003).

Our limited knowledge of fine-root dynamics in peatlands has largely been based on extrapolation from relative aboveground growth rates, sequential soil coring, or root colonization of in-growth cores (Reader and Stewart 1972; Backéus 1990; Finér and Laine 1998; Weltzin et al. 2000; Bond-Lamberty et al. 2004; Wieder 2006; Murphy et al. 2009a; Murphy et al. 2009b; Murphy and Moore 2010; Bhuiyan et al. 2016). While these mainly destructive methods have emphasized the importance of the root component in these systems, they are unable to capture short-term patterns in the birth, death, and turnover of ephemeral fine roots.

Minirhizotrons, which are clear tubes inserted into the peat to allow camera access for repeated imaging of roots, provide a non-destructive way to capture the timing of fine-root birth and death, as well as the distribution of living fine roots throughout the peat profile. However, few studies have used minirhizotrons to examine fine-root growth and phenology—i.e., the pattern of root growth throughout the year—in ecosystems underlain by organic soils (Iversen et al. 2012).

We adapted minirhizotron technology to measure spatial and temporal patterns in the growth and distribution of fine roots across a forested, ombrotrophic bog. We hypothesized that: (1) fine-root peak standing crop and growth would vary spatially across the bog, with the greatest amount of biomass and growth in areas with the greatest tree density or shrub cover and also in raised hummocks compared with depressed hollows; (2) fine-root phenology would be driven by edaphic and environmental conditions such as peat temperature and photosynthetically active radiation, and would be offset in time from the growth of leaves and wood, and (3) newly-produced fine roots of the dominant woody plants would be shallowly distributed above the water table, limiting their access to nutrients available in deeper peat.

Materials and methods

Site characteristics

This study was conducted in the USDA Forest Service Marcell Experimental Forest (MEF) in Minnesota, USA, at the S1 bog ('Swamp 1', 47.50283 degrees latitude, −93.48283 degrees longitude). This forested, 8.1-ha bog is ombrotrophic, receiving inputs of water and nutrients from precipitation. The S1 bog ranges from 412.7 to 413.1 m above sea level in the subhumid continental climate of northern Minnesota, USA (Verry et al. 1988), and has a rich history of experimental research (Kolka et al. 2011). From 1961 through 2005, average annual air temperature was 3.3 °C, and average annual precipitation was 768 mm (Sebestyen et al. 2011). In recent years (2010 to 2014) mean annual air temperatures ranged from 1.6 °C to 5.1 °C, and annual rainfall ranged from 586 mm to 662 mm (Hanson et al. 2011). Snow free periods extend from day of year 112–128 in the spring to day of year 294–330 in the fall (~early May to ~early November). Water table depth ranged from +10 to +20 cm above the hollows directly

after snow melt to −50 cm below the hollows later in the growing season (the surface of the depressed hollow microtopography was considered to be 0 cm; positive numbers indicate raised hummock microtopography and negative numbers indicate depth below 0 cm in both hummocks and hollows). Poorly-decomposed peat with a pH ranging from ~3.8 in surface layers to ~5 in deeper layers (Iversen et al. 2014) reaches an average depth of ~2.5 m (Parsekian et al. 2012).

The dominant vascular species on the bog include 3- to 5-m tall trees *Picea mariana* (Mill.) Britton, Sterns & Poggenb. and *Larix laricina* (Du Roi) K. Koch, and an understory of woody ericaceous shrubs dominated by *Rhododendron groenlandicum* (Oeder) K.A. Kron & W.S. Judd and *Chamaedaphne calyculata* (L.) Moench. The forb *Maianthemum trifolium* (L.) Sloboda is found in the understory during summer months, while sedges *Eriophorum vaginatum* L. and *Carex trisperma* Dewey are sparsely distributed. A carpet of *Sphagnum* mosses blankets the ground surface; dominant species are *Sphagnum magellanicum* Brid., *Sphagnum angustifolium* (Warnst.) C.E.O. Jensen, and *Sphagnum fallax* H. Klinggr.

Much of our investigations were focused along gradients of raised hummock and depressed hollow microtopography as well as tree density. Trees were harvested in strip cuts from the S1 bog in 1969 and again 1974, and were allowed to naturally regenerate. A denser coverage of trees was found in the 1969 cuts that regenerated from mature *P. mariana* (Perala and Verry 2011), while 1974 cuts had sparser trees and more open canopy areas (i.e., shrub understory only), though there were also gradients of tree density within each cut. We also took advantage of newly-installed experimental plots in the 1974 cuts associated with the SPRUCE experiment (Spruce and Peatland Responses Under Climatic and Environmental change, http://mnspruce.ornl.gov/) for quantification of fine-root biomass in bulk peat and more extensive measurements of plant-available nutrients prior to the initiation of the SPRUCE experimental treatments.

Root morphology

Representative morphological specimens for each dominant vascular plant species (trees *P. mariana* and *L. laricina* and shrubs *R. groenlandicum* and *C. calyculata*) on the bog were collected in May, 2011. Root length and diameter were quantified by root order or root functional class for at least three replicate fine-root branches of each species as in Guo et al. (2008b).

We considered the first three fine-root orders as the functional class 'absorptive' fine roots, responsible for plant resource acquisition, and orders four and higher as the functional class 'transport' fine roots mainly responsible for resource transport (e.g., McCormack et al. 2015a). Subsamples were scanned for length and diameter using WinRhizo (Regent Instruments, Inc., Québec, Canada) at 1400 dpi to resolve the diameter of distal shrub fine roots that were often less than 100 μm. Roots were oven-dried at 70 °C and weighed to determine root biomass. Continuous relationships between fine-root diameter and specific root length (SRL, root length per unit biomass) were developed separately for trees and shrubs. With few exceptions, the diameter of the first three orders of fine roots was less than 200 μm for shrubs and greater than 200 μm for trees, and we used this diameter cutoff to distinguish shrub roots from tree roots in minirhizotron images (described below).

Fine-root growth and peak standing crop

Minirhizotrons We installed 24 cellulose acetate butyrate minirhizotrons (Bartz Technology, Santa Barbara, CA, USA) at a ~ 45° angle in the S1 bog in July, 2010, adjacent to wooden boardwalks. Twelve minirhizotrons were located in the southern portion of the bog near environmental monitoring stations, and twelve minirhizotrons were located adjacent to a long-term boardwalk used for a second series of monitoring stations in a more northerly section of the bog. In both the southern and northern portions of the bog, minirhizotrons were installed across a gradient of tree density, ranging from a dense coverage of trees to more open canopy areas (i.e., shrub understory only), taking advantage of differences in tree density across the 1969 and 1974 strip cuts but not focused in one or the other. In each location, minirhizotrons were installed in pairs, with one minirhizotron in raised hummock microtopography and one in an adjacent depressed hollow (n = 12 hummocks and 12 hollows, 24 minirhizotrons in total; on average, hollows were within 78 ± 25 cm of the hummock). See Online Resource 1 for additional details on the installation and anchorage of minirhizotrons, where we adapted upland minirhizotron technology for use in a waterlogged peatland ecosystem.

Images were collected from the minirhizotrons approximately weekly throughout the growing seasons of 2011 and 2012 (Table S1 in Online Resource 1) using a BTC-100× minirhizotron camera (Bartz Technology

Corporation, Carpinteria, CA). All images were analyzed by the same person to obtain root length and diameter per individual root per image area using RooTracker software (Duke University, Durham, NC, USA). See Online Resource 1 for additional details on image collection and interpretation.

Fine-root length production was calculated as the appearance of a new root, or the extension of an existing root, between imaging dates. One of the benefits of minirhizotron use in waterlogged peatlands with slow decomposition rates is the ability to pinpoint the birth of new roots, and to track them over time. This mitigates known issues with identifying living and dead roots in peat or ingrowth cores (Bhuiyan et al. 2016). In uplands, mortality would be calculated from minirhizotron images as the noticeable decomposition or disappearance (without subsequent reappearance) of a fine root between imaging dates. However, given the slow decomposition rates in peat which could impede our ability to determine when a root had died, we did not calculate fine-root mortality rates for the purposes of this study. Fine-root peak standing length was the maximum fine-root length observed for each minirhizotron tube during the growing seasons of 2011 and 2012.

We assigned each root observed in minirhizotron images to a plant functional type (shrub fine roots were less than 200 μm and tree fine roots were greater than 200 μm; roots with a diameter larger than 500 μm were carefully inspected to determine whether they were sedge roots, which have very different densities and chemistries, and do not follow the same allometry as the woody plant species). The assignment of a plant functional type was necessary because individual species cannot be distinguished in the minirhizotron images. We used relationships between fine-root diameter and SRL determined from species-specific voucher specimens to scale the fine-root diameter and length observed in minirhizotron images to fine-root biomass for each plant functional type, focusing on the first three root orders (i.e., the absorptive fine roots) because these are the roots generally quantified with minirhizotron technology (Guo et al. 2008a). Fine-root biomass production was scaled to a volume of soil by assuming that each minirhizotron image had a 2-mm depth of field (Johnson et al. 2001, Iversen et al. 2008) and scaled to soil area by taking into account the angle and depth of each minirhizotron tube. This scaling was necessary to provide an estimate of fine-root production for use in ecosystem C budgets and in models; we recognize that there is no perfect way to

quantify root biomass production (for further discussion on this topic, see in Vogt et al. 1998).

We focused on quantifying fine-root phenology in the generally aerobic top 20 cm of the hummock microtopography given that the majority of the fine-root standing crop was found in the hummocks (see *Results* section). For each plant functional type, fine-root growth phenology was calculated as the number of new roots at each imaging session (we counted the length extension of an existing root as a newly produced root for this analysis), divided by the number of days between imaging sessions. This number was then normalized by the maximum root number production rate for each tube throughout the growing season to allow comparisons across tubes, and also across years with differing root production rates (e.g., McCormack et al. 2015b). Two minirhizotron locations were excluded from phenology analyses in 2012 because fewer than two new roots were observed in the top 20 cm of the hummock for the entirety of the growing season.

Peat cores As a comparison against minirhizotron observations of fine-root peak standing crop, and to determine the potential age distribution of roots throughout the peat profile for comparison with minirhizotron observations of living roots, we sampled fine roots from peat cores that were collected to the mineral soil (~250 cm depth) from future SPRUCE experimental plots in August 2012 (further details are available in Iversen et al. 2014); here we focused on hummock and hollow microtopography from three plots, one in each of three transects associated with the future SPRUCE experimental plots. After collection, peat cores were immediately sectioned into depth increments of 10 cm (from 0 to −100 cm depth), 25 cm (from −100 to −150 cm depth) or 50 cm (from −150 to −300 cm depth), homogenized by increment, subsampled, and frozen at −20 °C until processing. After thawing overnight, a subsample of peat from each depth increment was meticulously sorted in the laboratory by floating fine roots in distilled water and identifying roots using jeweler's glasses. Fine roots were separated by individual tree species or by the shrub plant functional type, oven-dried at 70 °C, and weighed. In one plot, fine roots were sorted from all depth increments, but after ^{14}C analysis revealed that roots below −50 cm depth were likely dead but undecomposed, fine roots were only removed from the peat depths above −50 cm in the two remaining plots.

Calibrated ages were determined for a subset of shrub fine roots sampled from the peat cores (shrubs had the largest amount of fine-root biomass in the cores). Fine roots were combined across multiple depth increments in one hummock core and one hollow core to obtain enough material for analysis. Surface increments ranged from +20 to +10 cm and +10 to 0 cm in the hummock and from 0 to −30 cm in the hollow, and deeper increments ranged from −50 to −100 cm and −100 to −200 cm depths in both hummock and hollow. Unground root fragments comprising multiple fine roots were first subjected to an acid-base-acid pretreatment to ensure measurements corresponded to root structural carbon compounds rather than non-structural C compounds or C associated with the surrounding peat (Gaudinski et al. 2001). Samples were prepared for ^{14}C measurement by sealed-tube combustion to CO_2 in the presence of H_2 (Vogel et al. 1984) and measured in 2014. Prepared samples were analyzed on the Van de Graaff FN accelerator mass spectrometer at the Center for Accelerator Mass Spectrometry (CAMS) at Lawrence Livermore National Laboratory. Calibrated ages were determined by matching measured ^{14}C values to atmospheric ^{14}C calibration curves. Bomb-pulse radiocarbon dating, used for a number of different types of organic materials, has been found to be accurate within ~2 yr. (Spalding et al. 2005; Hua 2009).

Rooting depth distribution

A depth coefficient for 10-cm peat increments was fitted to fine-root length production quantified using minirhizotrons and fine-root standing biomass quantified from peat sampling (Gale and Grigal 1987, Jackson et al. 1996) using the NLIN procedure in SAS (Version 9.2, SAS Institute Inc., Cary, NC, USA). The formula is $Y = 1 - \beta^d$, where d is peat depth, and Y is the cumulative fraction of roots from the surface to depth d. Larger values of β indicate a larger fraction of fine roots in deeper peat. For this analysis, we excluded locations where no tree or shrub roots were observed throughout the peat profile, where there were no roots in surface peat, or where roots making up more than one third of the observed root length were 20 cm deeper than roots observed shallower in the profile.

Plant-available nutrients

Ion-exchange resin capsules (WECSA, LLC, Saint Ignatius, MT, USA) were used to monitor in situ changes

in plant-available nutrients (i.e., NH$_4$-N, NO$_3$-N, and PO$_4^{3-}$) in aerobic and anaerobic peat layers at approximately monthly intervals during the growing seasons of 2011 to 2013. Arrays of resin-access tubes (allowing repeated sampling of the same location over time; WECSA, LLC, Saint Ignatius, MT, USA) were installed across microtopographic positions at the south end of the bog and in the SPRUCE experimental plots. In May 2011, an array of three resin-access tubes were installed at a 30° angle from vertical to reach −10, −30, and −60 cm depths in hollow microtopography in three locations at the south end of the bog near minirhizotrons (n = 9 resin access tubes in total). In June 2013, arrays of six resin access tubes were similarly installed across a paired hummock-hollow surface in two locations in each of 16 SPRUCE experimental plots to capture microtopographic differences in nutrient availability (n = 12 tubes per plot). The tubes reached to −10 and −30 cm in the hollows and hummocks, and also to −10 and −30 cm from the hummock surface (∼ + 15 and +5, depending on hummock height, which averaged 25 cm above the hollow surface in sites where resin access tubes were installed).

At each collection, resin capsules were removed and replaced, and removed resins were rinsed free of peat using distilled water, air-dried, and serially extracted with 2 M KCl. The extractant was filtered through Whatman #1 filter paper and analyzed for NH$_4^+$, NO$_3^-$, and PO$_4^{3-}$ on a Lachat autoanalyzer (Hach Company, Loveland, CO). Nutrient adsorption was blank-corrected using resin capsules that were not incubated in the bog, and adsorption was standardized per unit of resin capsule surface area (11.4 cm^2) and per a 30 day interval. Here we present data from bi-weekly or month-long periods of in situ incubations during July–August in 2011, 2012, and 2013.

Tree basal area and vascular plant community composition

The number, basal area, and distance from the center point of all *P. mariana* and *L. laricina* trees within a 5-m radius of each minirhizotron pair was quantified in May 2011 (the mid-point between minirhizotron tubes was the center point for this measurement). While all saplings and trees were counted, circumference at breast height (1.3 m) was measured only on trees taller than 1 m. Tree density was the summed basal area (cm^2) of trees taller than 1 m within a circular plot of a given diameter.

Understory vascular plant community composition was surveyed in 1 m^2 areas at four cardinal directions adjacent to each pair of minirhizotrons in June 2011 (one survey plot to the north of the minirhizotron pair, one survey plot to the south, etc., for a total of four survey plots at each minirhizotron pair). Percent cover of each plant species (cover classes as in Hollingsworth et al. 2010) was visually estimated in four quadrants for each 1 m^2 area. The percent cover in each quadrant was averaged, and then averaged across the four cardinal directions.

Areal coverage of hummocks and hollows were estimated in July 2012 to scale stratified measurements collected in different microtopographic positions. Ten 4 m × 4 m plots were sampled along three 60-m transects (30 plots total). In each plot, microtopography was classified as hummock or hollow in 25 grid points sampled using a 1-m^2 point frame with adjustable-height legs placed in each quadrant of the larger plot (100 points total per plot). Hollows were defined as the lowest elevation within plots and were typically at or near the height of the water table; hummocks included area above hollows, including the sides of the hummocks.

Aboveground phenology

Dendrometers installed at 1.3 m tree height were used to measure stem growth during the growing seasons of 2011 and 2012 (May through September or October). In 2011, automatic tree dendrometers (DR26, EMS, Brno, Czech Republic) were installed on eight *P. mariana* trees (the basal area of *P. mariana* comprised 100% of the trees within a 1.5 m radius of each minirhizotron pair and 97 ± 5% of the tree basal area within a 5 m radius of each minirhizotron pair). Trees were chosen based on their proximity to the minirhizotrons. Initial stem circumference was measured, and the dendrometers logged the change in stem circumference every 30 min based on the tension in a stainless steel band encircling the stem. Circumference was converted to cross-sectional area, and daily stem growth (basal area increment, BAI) was calculated from the change in daily minimum basal area (the high temporal resolution of the logger captured diurnal shrinking and swelling). In 2012, weekly manual measurements of steel dendrobands installed on a second set of eight *P. mariana* trees were used to quantify stem growth (as in Norby et al. 2001). Leaf phenology of trees and

shrubs was estimated from manual observations and images captured daily with a phenology camera; data were available for trees in 2011 and 2012, and for shrubs in 2013 (Hanson et al. 2015).

Environmental monitoring

Ambient environmental monitoring stations were installed in the S1 bog in summer, 2010; two stations were co-located at the southern end of the bog, and one was located adjacent to an existing monitoring well in the mid- to northern portion of the bog (Hanson et al. 2011). At each monitoring station, standard sensors collected data on meteorological and soil variables. Here, we focused on photosynthetically active radiation at 2 m above the peat surface (PAR, 400–700 nm; Quantum Sensor, Li-Cor, Lincoln, Nebraska), peat temperatures in the upper 5 cm of hummocks using custom multipoint thermistor probes (W.H. Cooke & Co. Inc., Hanover, PA), and water table level (Trutrack Ltd. Christchurch, New Zealand; Part No. WT-VO2000). Automated sensors were queried every minute, and 30-min means were logged on an automated data logger (Campbell Scientific, Inc. Logan, UT; CR1000). Daily averages across all three monitoring stations of the S1 bog were used in the current analyses, with the exception of water table level, which was from one environmental monitoring station at the south end of the bog, supplemented with data from a long-term bog well in the northern section of the bog (Griffiths and Sebestyen 2016).

Statistical analyses

Our main objective was to measure spatial and temporal patterns in the growth and distribution of fine roots across a forested, ombrotrophic bog. Thus, much of our statistical analyses took advantage of regression or correlative approaches. Linear or non-linear relationships among fine-root morphological variables and between fine-root peak standing crop or growth, tree basal area, shrub percent cover, and environmental variables were analyzed by fitting curves using least-squares regression with the REG or NLIN procedures in SAS (Version 9.2, SAS Institute Inc., Cary, NC, USA). Potential correlations between the timing of fine-root growth in hummocks and hollows were assessed with the CORR procedure in SAS (Pearson product-moment correlation). Differences in nutrient availability between microtopographic positions and with peat depth in 2013

were analyzed using mixed-model ANOVAs with Tukey's post-hoc test using the MIXED procedure in SAS, where microtopography, peat depth, and their potential interaction were treated as fixed effects. Differences in nutrient availability with depth in hollows across 2011 and 2012 at the south end of the bog were analyzed using a repeated measures ANOVA using the MIXED procedure in SAS, where peat depth was treated as a fixed effect and year was treated as a random effect. Non-normal data were log-transformed prior to analysis, and effects were considered statistically significant at $P \leq 0.05$.

Results

Root morphology

The common woody vascular plant species in the bog encompassed a range of fine-root morphology (Fig. 1). The fine roots of ericaceous shrubs had a very narrow diameter relative to the tree species. For both trees and shrubs, the relationship between fine-root diameter and specific root length (SRL) followed a negative power function (Online Resource 2), similar to previous analyses of woody plant roots (Iversen et al. 2008).

Root dynamics

Fine-root length production assessed at the minirhizotron surface and extrapolated to a 1 m^2 ground area of peat varied across the bog. For tree fine roots, production ranged from 0 to 13 km fine roots m^{-2} ground area yr.$^{-1}$ in 2011 and from 0 to 5 km m^{-2} yr.$^{-1}$ in 2012. For shrub fine roots, production ranged from 0 to 21 km m^{-2} yr.$^{-1}$ in 2011 and from 0 to 5 km m^{-2} yr.$^{-1}$ in 2012 (Online Resource 3). Our estimates of '0' km m^{-2} yr.$^{-1}$ fine-root production in some locations on the bog do not necessarily indicate that there were no fine roots in the peat beneath a 1 m^2 ground area, but rather that fine roots were sparse enough in this location that we unable to view them at the minirhizotron surface. This caveat is also true of our reports of fine-root peak standing length estimated from minirhizotrons (*see below*). Fine-root length production was between three- and eight-fold greater in hummocks than in hollows in 2011 for trees and shrubs, respectively, though this difference was more muted in 2012 (two- and five-fold more root length production in hummocks

Fig. 1 Images of the fine roots of woody species in the S1 bog: trees *P. mariana* (**a**) and *L. laricina* (**b**), and ericaceous shrubs *R. groenlandicum* (**c**) and *C. calyculata* (**d**). Note the differences in diameter and mycorrhizal colonization between the trees and shrubs. These images were previously included in a letter (Iversen, 2014) and are reprinted here with permission from John Wiley and Sons
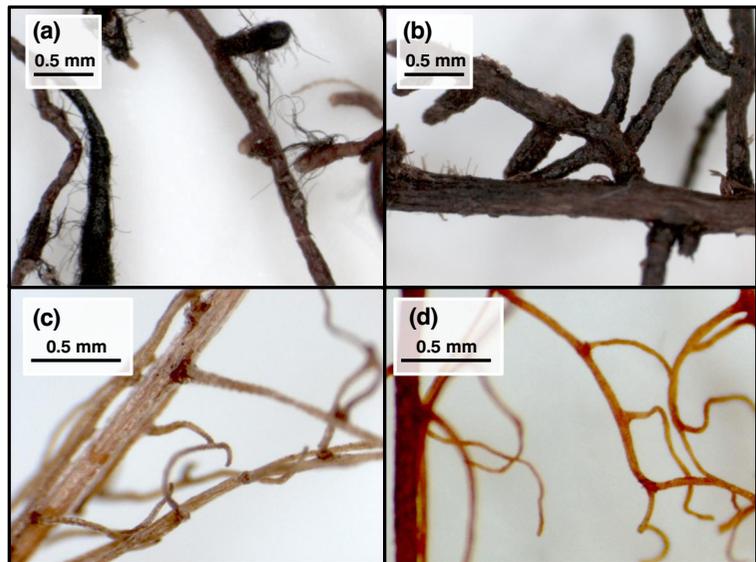
compared with hollows for trees and shrubs, respectively, Online Resource 3).

We calculated fine-root population turnover as the ratio of fine-root length production (i.e., roots newly produced during the period of minirhizotron observations) to fine-root peak standing length (where standing length was greater than 0) as in Gill and Jackson (2000), and found that turnover decreased from 2011 to 2012. Turnover (mean ± SD) averaged $1.04 ± 0.21$ yr.$^{-1}$ and $0.81 ± 0.30$ yr.$^{-1}$ for tree fine roots in 2011 and 2012, respectively, and averaged $1.25 ± 0.21$ yr.$^{-1}$ and $0.52 ± 0.40$ yr.$^{-1}$ for shrub fine roots in 2011 and 2012, respectively.

We observed multiple flushes in fine-root growth in the top 20 cm of the hummocks in 2011 (Online Resource 4) and in 2012 (Fig. 2). In 2011, patterns of fine-root growth phenology in the hummocks were correlated with the phenology of fine-root growth in the surface 20 cm of the hollows for both trees and shrubs ($R > 0.8$, $P < 0.001$; *data not shown*). This was not the case in 2012 ($R < 0.3$, $P > 0.4$; *data not shown*).

Standing root biomass

Fine-root peak standing length estimated from the minirhizotrons was similar across 2011 and 2012 for both trees and shrubs. Fine-root peak standing length varied across the bog, ranging from 0 to 12 km root /m^2 ground area for tree roots, and from 0 to 20 km root / m^2 ground area for shrub roots (Fig. 3a,b). Fine-root peak

standing length in hollows was on average $53 ± 64\%$ (SD) and $17 ± 21\%$ (SD) of that in adjacent hummocks for trees and shrubs, respectively, when averaged across 2011 and 2012 (Fig. 3a,b).

Fine-root standing biomass determined by meticulously removing all fine roots from peat cores taken in 2012 to a depth of ~2.5 m included a surprising amount of fine-root biomass in peat below the maximum summer water table level, especially for the shrub plant functional type (Fig. 4). Analysis of root tissue ^{14}C content indicated that fine roots in deeper peat were dead, but well-preserved, with C ages up to 5000 yr. old (Fig. 4; Online Resource 5).

Rooting depth distribution

The depth distribution of newly-produced, living tree and shrub fine roots observed with minirhizotrons was extremely shallow with respect to global estimates of rooting depth distribution (Fig. 5; Online Resource 6). In 2012, depth coefficients for fine-root production observed with minirhizotrons ranged from 0.726 to 0.886, where larger coefficients indicated a larger proportion of fine roots in deeper peat (Fig. 5; Online Resource 7). In contrast, rooting depth distributions across the globe ranged from shallow rooting depths in arctic tundra ($\beta = 0.914$) to deep rooting depths in temperate coniferous forest ($\beta = 0.976$) (Jackson et al. 1996).

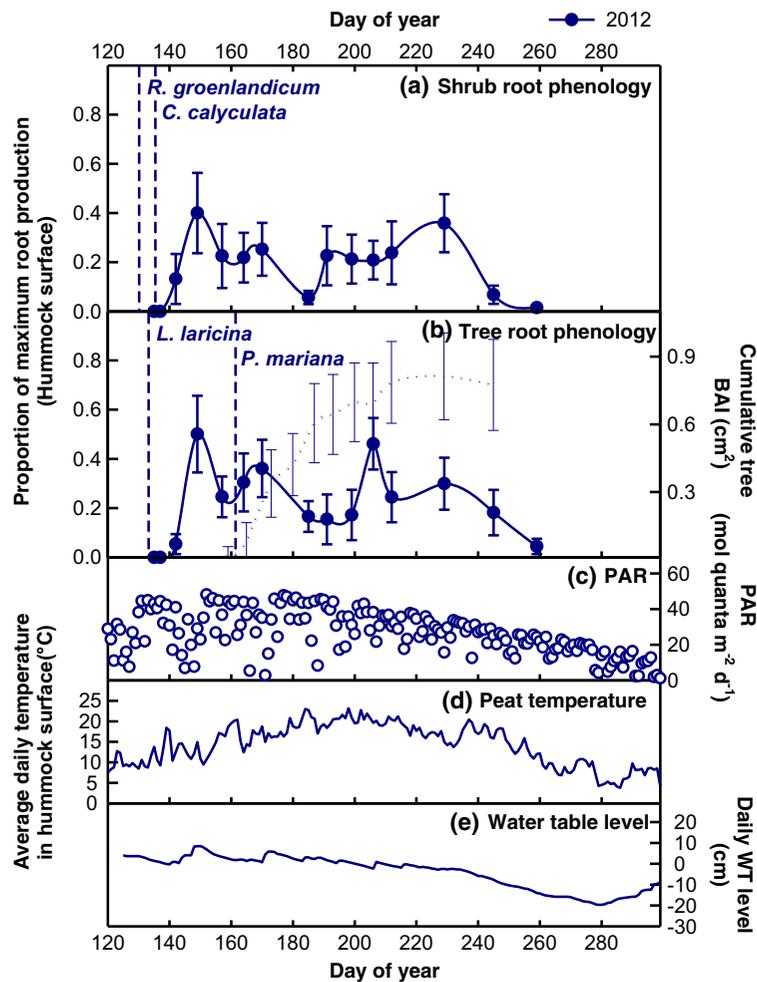Roots sampled from depressed hollow microtopography were more shallowly distributed than

Fig. 2 The timing of the production of new shrub fine roots and shrub leaf out (**a**) and the timing of the production of tree fine roots and wood, as well as tree leaf out (**b**) in 2012 (data from 2011 are in Online Resource 4). Data for fine roots and wood are presented as means ±1 standard error. Root growth phenology (solid lines in panels a and b) was determined from minirhizotron observations. The timing of leaf out was determined from manual observations and daily images (Hanson et al. 2015), represented as dashed lines for shrubs *R. groenlandicum* and *C. calyculata* (panel a) and trees *L. laricina* and *P. mariana* (panel b). The phenology of wood growth was determined from dendrobands, and cumulative tree basal area index (BAI) is indicated by a dotted line in panel b. Environmental data collected from nearby monitoring stations includes photosynthetically active radiation (PAR) measured at 2 m above the peat surface (**c**), peat temperature measured in the top 5 cm of hummocks (**d**), and water table level (WT) measured in a hollow (**e**), where 0 cm was the hollow surface (the surface of the hummocks where minirhizotrons were installed were on average 13 cm above the hollow surface)

those sampled from raised hummocks (Fig. 5), though the fit of the depth coefficient to the data was poorer in hollows because many hollow locations had roots only in the top 10 cm. The depth distribution of newly-produced roots tended to be shallower in 2012 than in 2011. By 2012, tree and shrub rooting depth distributions quantified using minirhizotrons were similar (overlapping standard errors, Online Resource 7; Fig. 5). Within a given microtopographic position, newly-produced fine roots observed with

minirhizotrons tended to be more shallowly distributed than those sampled from peat cores (Online Resource 7), likely due to the influence of preserved, dead roots on the rooting depth distribution in peat cores.

Nutrient availability with depth

The ion-exchange resins collected from hummocks and hollows in the SPRUCE experimental plots (Fig. 5, Online Resource 8) confirmed initial findings
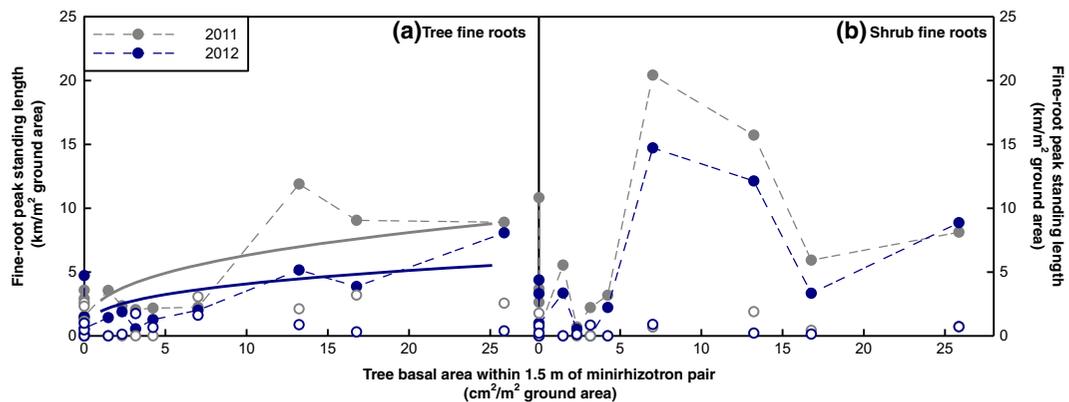
Fig. 3 Fine-root peak standing length of trees and shrubs across gradients of tree density in the S1 bog. (**a**) Data collected in 2011 are in grey; data collected in 2012 are in blue. Filled symbols connected by dashed lines are hummocks; open symbols are hollows. A significant portion of the variation in peak standing length of tree roots in the hummocks (dashed lines) was explained by nearby tree basal area density (i.e., trees within 1.5 m of paired minirhizotrons, Table 1). In 2011, (log) SC = 0.44 + 0.36 × (log) BA (Adj. R^2 = 0.50, P = 0.006) and in 2012, (log)

SC = 0.28 + 0.33 × (log) BA (Adj. R^2 = 0.35, P = 0.02), where SC is peak standing length for the tree roots (km/m²), and BA is nearby tree basal area per unit ground area (cm²/m²). Regressions are indicated by solid lines (back-transformed from log functions). The relationship between tree roots and nearby tree basal area in the hollows was weaker, and not significant (P > 0.28). (**b**) The peak standing crop of shrub fine roots had a unimodal relationship with nearby tree basal area density across hummocks and hollows
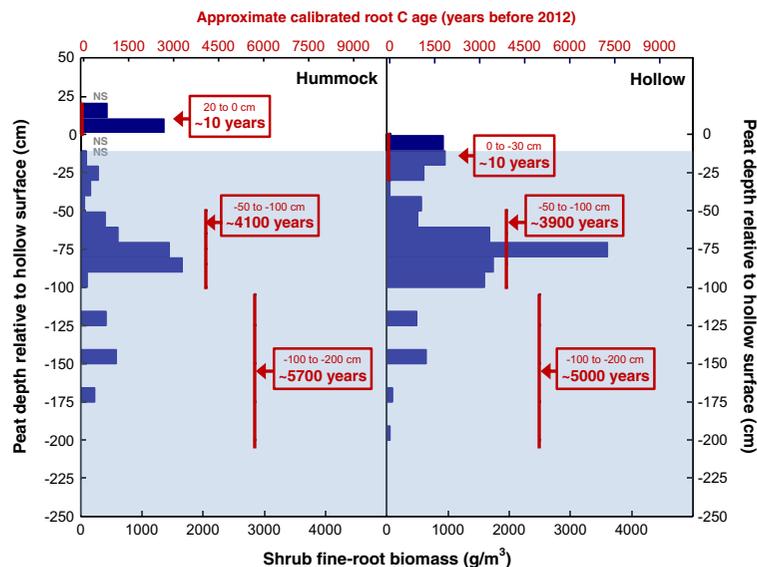

Fig. 4 Analysis of the ^{14}C content of shrub fine-root biomass sampled throughout the peat profile revealed that intact shrub roots found deeper than the maximum summer water table level (light blue shading) were ancient, dead roots with an approximate calibrated C age between 4000 and 6000 yr. before the peat sampling in 2012 (and ^{14}C measurement in 2014). The dark blue bars are shrub fine-root biomass sampled in a hummock and a hollow in one SPRUCE experimental plot (with biomass values found on the lower X-axis); the red lines and red boxes indicate C ages on the upper X-axis (approximate age before 2012, when the peat was sampled) for samples combined into surface roots and deeper roots

as described in the Methods (e.g., roots from −50 cm to −100 cm were combined in order to have enough biomass for the analysis). See Online Resource 5 for more specific radiocarbon age estimates, and for age estimates of *P. mariana* and *L. laricina* roots in surface peat. Absolute peat depths consider the surface of the depressed hollow microtopography to be 0 cm. Positive numbers indicate raised hummock microtopography, while negative numbers indicate depth below 0 in both hummocks and hollows. *NS* is not sampled, given a limited amount of peat in the shallowest hummock depths (only 3 cm thickness) or extremely low bulk density from 0 to −20 cm (0.01 g/cm³)
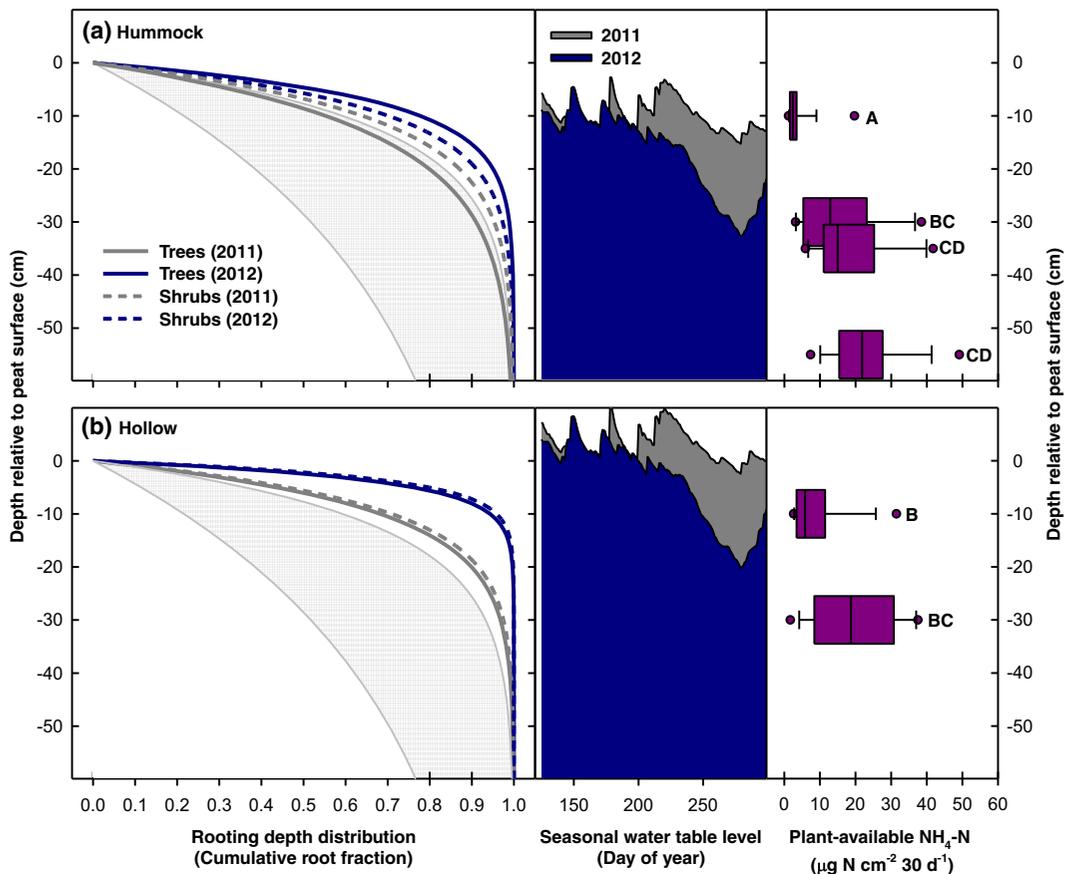
Fig. 5 Rooting depth distributions in the S1 bog were constrained to nutrient-poor peat by a shallow water table level in hummocks (**a**) and hollows (**b**). Fine-root growth data derived from minirhizotron observations in 2011 and 2012 have shallower depth coefficients (Online Resource 7) than in the hatched area, which encompasses the average rooting depth coefficients derived from biomes across the globe (Jackson et al. 1996). Note that depth values on the y-axis (cm) are expressed as depth from the peat surface rather than absolute depth in order to compare rooting depth, water table level, and nutrient availability. The surface of the hummocks was on average 13 cm greater than the hollows across minirhizotron locations and on average 25 cm greater than the hollows across all resin access tubes sampled in 2013. Water table level was only measured in the hollow, but is relativized by 13 cm in panel (a) to compare with rooting depth distribution in hummocks. Resin-available NH$_4$-N data are for a month-long period from June to July, 2013 from arrays of tubes installed across 16 SPRUCE experimental plots (see Online Resource 8 for additional data). Differing uppercase letters indicate significant differences in NH$_4$-N with depth across hummock and hollow microtopography

from a more limited array in hollows only in the south end of the bog (Online Resource 8) that NH$_4^+$ availability increased with peat depth, though the magnitude of the increase was strongest in hummock microtopography (depth × microtopography interaction; $P = 0.04$). PO$_4^{3-}$ availability also increased with peat depth across the hummocks and hollows ($P < 0.0001$), while NO$_3^-$ availability did not change significantly with microtopography or peat depth ($P > 0.48$). NH$_4^+$ was by far the most available N source in the bog, with NO$_3^-$ making up a negligible fraction of N (at or near detection limits); PO$_4^{3-}$ availability was intermediate (Online Resource 8).

The majority of resin-available nutrients were found deeper than the reach of most fine roots. In 2012, ~75% of tree and shrub fine roots were produced in the surface 10 cm of the hummocks and ~95% in the surface 10 cm of the hollows. However, hummock surface peat to 10 cm depth had only 6% of measured, resin-available NH$_4^+$ and PO$_4^{3-}$ and hollow surface peat to 10 cm depth had only one-third of measured, resin-available NH$_4^+$ and PO$_4^{3-}$ (Fig. 5; Online Resource 8).

Biological and environmental relationships

Tree basal area density Though we measured tree basal area density within a 5 m radius of minirhizotron pairs, fine-root production and peak standing length were most strongly correlated with the basal area density of nearby trees (within in a 1.5 m radius of each minirhizotron pair). The basal area density within 1.5 m of the minirhizotrons ranged from 0 to 25.9 cm^2/m^2, and differed widely across the bog (Table 1, Fig. 3).

The fine-root length production (km m^{-2} yr.$^{-1}$) of trees in the hummocks was linearly and positively related to nearby tree basal area in 2011 (Online Resource 3, linear regression Adj. R^2 = 0.54, P = 0.004), but not in 2012 (P = 0.79). Also, nearby tree basal area explained between 50 and 35% of the adjusted variation in tree fine-root peak standing length in the hummocks in 2011 and 2012, respectively (Fig. 3a). Patterns for tree roots were similar in hollows, though the relationships were weaker and not significant (P > 0.28).

Fine-root length production and peak standing length of shrubs in the hummocks were not significantly linearly related with nearby tree basal area in 2011 or 2012 (linear regression, $P \geq 0.08$); instead we observed a unimodal relationship where shrub fine-root length production and peak standing length were greatest at intermediate tree basal area density (Online Resource 3, Fig. 3b). We observed a similar pattern in the hollows (linear regression P > 0.24).

Shrub percent cover The percent cover of ericaceous shrubs near the paired minirhizotrons (including dominants *R. groenlandicum* and *C. calyculata* and as well as rarer *K. polifolia* and species in the genus *Vaccinium*) averaged ~50% (47 ± 9% SD, Table 1), and was negatively related with nearby tree basal area (Table 1; linear regression Adj. R^2 = 0.27, P = 0.05). However, the percent cover of shrubs was unrelated to tree or shrub fine-root production (linear regressions, P > 0.56 and 0.26, respectively) or tree or shrub peak fine-root standing length (P > 0.31 and 0.23, respectively).

Aboveground phenology Nearby tree basal area (cm^2) increased strongly between day of year ~160 to ~220 in 2011, and between day of year ~180 and ~212 in 2012 (Fig. 2, Online Resource 4). We fit a sigmoidal curve to the relationship between day of year and cumulative basal area increment calculated from the dendrobands, and used this function to estimate the cumulative

difference in basal area increment between days that the proportion of maximum fine-root length production was calculated. Two trees that did not show a positive growth rate in 2012 were excluded from the analysis. While it appears that the relative proportion of tree and shrub fine-root length production on a given date (i.e., phenology) may be negatively related to basal area accumulation (Fig. 2, Online Resource 4), we did not find this to be statistically detectable in 2011 or 2012 (linear regression, P > 0.29). *L. laricina* annual leaf out occurred before peak fine-root growth in both 2011 and 2012, while the pattern for *P. mariana* annual leaf out in relation to patterns of fine-root and wood growth was less clear (Fig. 2, Online Resource 4). Estimates of shrub leaf out from images taken in 2013 indicate that both shrub species would have leafed out prior to the first peak in shrub fine-root growth in 2011 and 2012.

Edaphic and environmental conditions In 2011, tree and shrub fine-root phenology were slightly positively related to PAR because the largest peaks in production were earlier in the growing season when PAR was greatest (Online Resource 4, adjusted R^2 = 0.14 and 0.12, respectively, P < 0.0001), but this relationship did not hold in 2012 (Fig. 2, P > 0.15). Tree and shrub fine-root phenology were unrelated to peat temperature in the surface of the hummocks in either year (Figs. 2, Online Resource 4, P > 0.20), with the exception of a very slight positive relationship between tree fine-root phenology and peat temperature in 2012 (Fig. 2, adjusted R^2 = 0.02, P = 0.04). There were statistically significant linear relationships among tree and shrub fine-root phenology and the depth to the water Table (P < 0.5 for trees in 2011 and 2012, and shrubs in 2012; for shrubs in 2011, P = 0.53). However, the adjusted R^2 values indicated that depth to water table during the growing season explained less than 5% of the variation in root phenology across functional types and years (Fig. 2, Online Resource 4).

Scaling Trends in fine-root biomass production (scaled from measurements of fine-root length and diameter in minirhizotrons) were similar to patterns in fine-root length production observed across gradients of tree density and hummock-hollow microtopography (Table 1), as well as peat depth (Online Resource 6).

Based on our measurements of the areal distribution of hummocks and hollows across the bog, the S1 bog was 62 ± 15% (SD) hummock (Online Resource 9). We used

Table 1 Fine-root biomass production of the dominant plant functional types on the S1 bog across gradients of microtopography and tree basal area density, extrapolated from minirhizotron observations of root length production and root diameter and relativized to the fractional coverage of hummocks and hollows

Minirhizotron no.	Tree BA within 1.5 m radius (cm^2/m^2)	Ericaceous shrub cover (%)	Micro-topography	Tree roots (g m^{-2} yr.$^{-1}$) 2011	2012	Shrub roots (g m^{-2} yr.$^{-1}$) 2011	2012	Sedge roots (g m^{-2} yr.$^{-1}$) 2011	2012
2	0.0	52	Hummock	61	216	107	39	0	0
1			Hollow	50	5	3	0	0	0
20	0.0	53	Hummock	89	4	22	1	0	0
19			Hollow	342	41	21	2	0	0
22	0.0	59	Hummock	114	53	31	18	0	0
21			Hollow	40	33	11	16	0	0
24	0.0	61	Hummock	106	19	11	6	0	0
23			Hollow	64	43	6	2	0	0
6	1.5	47	Hummock	341	30	35	17	9	81
5			Hollow	0	0	0	0	0	0
10	2.3	34	Hummock	103	20	9	3	0	0
9			Hollow	13	3	3	2	4	0
12	3.2	34	Hummock	114	46	24	0	0	0
11			Hollow	0	102	3	4	0	0
8	4.2	56	Hummock	775	19	35	3	0	0
7			Hollow	2	254	3	0	5	0
4	7.0	41	Hummock	44	12	142	8	0	0
3			Hollow	138	31	5	2	109	49
18	13.2	48	Hummock	631	22	141	10	0	0
17			Hollow	147	89	23	2	0	0
14	16.8	46	Hummock	392	96	79	6	0	0
13			Hollow	128	13	3	0	0	0
16	25.9	36	Hummock	374	105	80	10	0	0
15			Hollow	130	32	11	1	0	0
Average root growth			Hummock	262 ± 70	53 ± 17	60 ± 14	10 ± 3	1 ± 1	7 ± 7
			Hollow	88 ± 28	54 ± 20	8 ± 2	3 ± 1	10 ± 9	4 ± 4
			Relativized root growth	195 ± 41	54 ± 11	40 ± 9	7 ± 2	–	–
Average leaf + stem growth*				84 ± 82	66 ± 112	110 ± 44		–	
Root fraction				0.70	0.45	0.27	0.06	–	–

All error terms are standard error unless specified. Data are arranged from lower to higher surrounding tree basal area (BA) within 1.5 m of each minirhizotron pair. Tree basal area density was the summed basal area of all *P. mariana* trees taller than 1 m within a 1.5-m radius of the minirhizotrons (there were no *L. laricina* within a 1.5 m radius of minirhizotrons). *R. groenlandicum* was the dominant ericaceous shrub, ranging from 23 to 43% cover across all minirhizotron locations, while the ericaceous shrub *C. calyculata* ranged from 0 to 23%. Other ericaceous shrubs averaged less than 5% cover across all locations. We converted root length production observed in minirhizotrons to mass production using the relationship between root diameter (D, mm) and specific root length (SRL, m/g) derived in Online Resource 2 for trees and shrubs. We did not collect sedge voucher specimens, but developed a relationship between sedge root diameter and SRL for sedges collected from root ingrowth cores (SRL = 18.874 × D$^{-1.613}$, R^2 = 0.91). Relativized root growth takes into account to the relative fraction of hummocks relative to hollows

*Aboveground growth increments (SPRUCE project data, P. Hanson, *unpublished data*) +/− 1 SD (across 16 SPRUCE experimental plots) were calculated from tree allometry for trees in the plots in 2011 and 2012, and for current year leaf and twig increments for the ericaceous shrubs in harvested clip plots in 2012

the areal distribution of microtopography to calculate the relativized fine-root biomass production per unit ground area, and ultimately the fraction of net primary productivity allocated to fine roots (Table 1). Depending on the minirhizotron location and year, the relative contribution of fine roots to whole-plant NPP ranged from 16 to 85% for trees (averaging 70 and 45% in 2011 and 2012, respectively) and ranged from 1 to 47% for shrubs (averaging 27 and 6% in 2011 and 2012, respectively; Table 1).

Data availability

The data discussed throughout the Results section are available online (Data Citations: Iversen et al. 2017a; Iversen et al. 2017b; Iversen et al. 2017c; Iversen et al. 2017d; Ontl and Iversen 2017).

Discussion

Fine roots are an important component of ecosystem carbon, water and nutrient fluxes, especially in cold, nutrient-limited, northern peatlands (Megonigal et al. 2004). However, the distribution and dynamics of fine roots in waterlogged ecosystems with highly organic soils are poorly characterized, in part because it is difficult to do so. We adapted non-destructive minirhizotron methodology, which has rarely been used in peatland ecosystems, to better understand the distribution and dynamics of fine roots across a forested, ombrotrophic bog. We found that fine-root growth varied spatially across the bog, and tended to be seasonally dynamic, but living roots were shallowly distributed in a thin layer of nutrient-poor, aerobic peat above the average growing season water table level.

Spatial patterns in dynamic root growth

We hypothesized that fine-root standing crop and growth would vary spatially across the bog, with the greatest amount of standing crop and growth in areas with the greatest tree density or shrub cover and also in raised hummocks compared with depressed hollows. We found that fine-root peak standing crop and growth across the bog were highly variable across gradients of microtopography and tree density. In some cases, minirhizotron estimates of fine-root peak standing length just beneath the surface of the bog exceeded tens of kilometers of fine roots per m^2 ground area. In support of our hypothesis, fine-root peak standing length was generally greater in raised hummocks than in saturated hollow depressions (Fig. 3), and fine-root production tended to follow this pattern in many, but not all, cases (Table 1). This pattern is likely due to the more aerobic nature of raised hummock microtopography compared with depressed hollows (e.g., Lieffers and Rothwell 1987; Moore et al. 2002; Kajimoto et al. 2003; Sullivan et al. 2008; Murphy et al. 2009b), but could also be due to warmer growing season temperatures in hummocks compared with hollows (e.g., Kajimoto et al. 2003; Hanson et al. 2011).

Spatial patterning in the distribution and dynamics of fine roots across the undulating microtopography of many peatlands may be linked to patterns in aboveground biomass (Silvola et al. 1996; Murphy and Moore 2010). In partial support of our hypothesis, we found that nearby tree basal area explained a large proportion of the variation in tree fine-root peak standing length (Fig. 3a). This may be due to most roots being located within a few meters of the bole of the tree (e.g., Kajimoto et al. 2003), and indeed we observed the strongest relationship between fine-root peak standing length and tree basal area within 1.5 m of the minirhizotrons. In contrast, the unimodal relationship between nearby tree basal area and shrub fine-root peak standing length (Fig. 3b) could be related to shading of shrubs limiting C acquisition in areas of high tree density (e.g., Wieder et al. 2009), and we did find a negative relationship between nearby tree basal area and shrub percent cover. However, the percent cover of shrubs had no relationship with shrub fine-root growth or peak standing length, though shrub biomass has been found previously to predict shrub fine-root production in a drier, treeless bog (Murphy et al. 2009a).

We observed greater fine-root production in 2011 than in 2012 (Online Resource 3). Previous work has shown that the fine-root production of individual tree species can vary as much as 3-fold among years (McCormack et al. 2014), but it is also possible that there was a flush of root growth associated with soil disturbance and colonization after minirhizotron installation in summer, 2010 (e.g., Iversen et al. 2008). Furthermore, disturbance may have stimulated the growth of fine roots deeper into the waterlogged peat profile in 2011 (Fig. 5), which may have resulted in greater mortality. For example, in 2011, we observed ~2800 new fine roots (out of a total of ~3100 roots), but only 60% of these were alive at the end of the growing season. In

2012, we observed only ~500 new fine roots (out of a total of ~1100), but more than 80% of these were alive at the end of the growing season. The large difference in root production between years likely cannot be attributed to a larger volume of oxic peat in the acrotelm in 2011; the water table level was closer to the peat surface in 2011 than in 2012 (Fig. 5).

Our estimates of population turnover of fine roots newly-produced during the period of minirhizotron observations (0.52 and 0.81 yr.$^{-1}$ for shrubs and trees, respectively in 2012) fall within the range of expected fine-root turnover in boreal forests and wetlands (e.g., Finér and Laine 1998; Gill and Jackson 2000; Bhuiyan et al. 2016). Furthermore, because the root population turnover times in 2012 were on average less than 1.0 yr.$^{-1}$, we were able to calculate fine-root lifespan as the inverse of turnover (McCormack et al. 2014). In 2012, root population lifespan averaged 1.2 and 1.9 yr. for trees and shrubs, respectively, which is within the decadal realm of fine-root C ages determined from ^{14}C analysis in surface peat above the water table (Fig. 4; Online Resource 5). Estimates of fine-root C age are expected to be longer than minirhizotron estimates for a number of reasons related to the sampling biases of the different methodologies (e.g., Strand et al. 2008).

Interestingly, while minirhizotron measurements and ^{14}C methodology supported the fast turnover of living roots in surface peat, ^{14}C methodology also illuminated the extremely slow rates of fine-root detrital turnover in deeper, anaerobic peat, as would be expected in a saturated peatland (resulting in intact fine roots that were thousands of years old; Fig. 4). Thus, root detritus is an important component of peat formation, and the differential growth of roots into hummock microtopography could potentially contribute to the sustained differences in the height of hummocks compared with hollows (e.g., Eppinga et al. 2010).

The phenology of root growth

The timing of fine-root production throughout the year exerts important controls over peatland plant and soil processes (Silvola et al. 1996; Ström et al. 2012), but is rarely directly measured in any biome (reviewed in McCormack et al. 2014; Abramoff and Finzi 2015). To our knowledge, fewer than a handful of studies have quantified the timing of fine-root production in ecosystems underlain by organic soils (Iversen et al. 2012). Theory predicts that patterns of fine-root phenology can range from equally-distributed production throughout the year to unimodal and multimodal peaks of production, depending on resource availability and favorable environmental conditions (reviewed in McCormack et al. 2014). Focusing on the raised hummocks where the majority of fine-root peak standing length occurred, we found that the relative number of new fine roots produced was variable throughout the season, but peak fine-root growth occurred in multiple flushes (in what appeared to be a bimodal pattern) for both trees and shrubs (Fig. 2, Online Resource 4).

We hypothesized that fine-root phenology would be driven by edaphic and environmental conditions such as peat temperature and photosynthetically active radiation. In contrast, we found that fine-root phenology was generally unrelated to peat temperature in the hummock surface, PAR (which was greatest during a period of cool temperatures and a high water table level where a large amount of root growth would be unexpected), or water table depth throughout the growing season. However, peat temperature may have constrained the beginning or end of the root growing season (Fig. 2d, Online Resource 4). For example, fine-root growth of *Picea* species in other sites has been linked to a threshold in soil temperature (Vapaavuori et al. 1992; Ruess et al. 2003), and net C uptake in the spring across several deciduous forest FLUXNET sites began after soil temperature reached the threshold of mean annual air temperature (Baldocchi et al. 2005).

We further hypothesized that fine-root phenology would be offset from the growth of leaves and wood. Indeed, the availability of carbohydrate with respect to competing sinks within the plant may have played a more important role in the timing of fine-root growth than edaphic or environmental conditions. A first peak in root growth occurred early in the growing season before peak wood growth, and a second peak occurred later in the growing season, after peak wood growth was past (Fig. 2b, Online Resource 4). Our measurements span a patchwork of data that predicts similar or later root growth compared with leaves (Abramoff and Finzi 2015; Iversen et al. 2015), peak root growth prior to bud break and leaf expansion (McCormack et al. 2014; McCormack et al. 2015b), and alternating growth between shoots and fine roots (this study; Reich et al. 1980). McCormack et al. (2014, 2015b) also observed a somewhat bimodal trend in root growth for another conifer, *Pinus strobus*. While many studies focus on the relative timing of leaf and root growth, our data indicate

that the timing or magnitude of wood growth may also play an important role in mediating the allocation of C to fine roots (e.g., Vapaavuori et al. 1992; Malhi et al. 2011). An earlier increase in basal area growth in 2011 (Online Resource 4) may explain the differences in timing of peak root growth in 2011 and 2012, though the strong and early peak in fine-root growth in 2011 could also be related to the disturbance associated with minirhizotron installation (e.g., Joslin and Wolfe 1999). A great deal more work on the subject of root growth phenology is needed, especially in ecosystems underlain by organic soils. It will be necessary to use minirhizotron (or rhizotron) technology to observe these important patterns in root birth and growth throughout the year.

Rooting depth distribution

In peatlands, the thin layer of aerobic soil above the average summer water table depth exerts an important control over the distribution of fine roots throughout the soil profile (e.g., Murphy and Moore, 2010), especially for woody trees and shrubs that do not form aerenchymous roots. We hypothesized that newly-produced fine roots of the dominant woody plants would be shallowly distributed above the water table, limiting their access to nutrients available in deeper peat. In support of our hypothesis, we observed that more than 95% of newly-produced roots observed using minirhizotron technology in 2012 were confined to the aerobic zone above the deepest growing season water table level (Fig. 5). Furthermore, the calibrated C age of shrub roots sampled from surface peat was less than 10 years old (Fig. 4), highlighting the concentration of living, functioning roots in the shallowest peat layers. The importance of water table level in controlling the depth distribution of peatland fine roots was further illustrated by the fact that roots colonizing hummocks, which sit further above the water table, were more deeply distributed than roots colonizing hollow depressions (Fig. 5). Shallow rooting distributions for woody plant species have been observed in other systems underlain by organic soils (Lieffers and Rothwell 1987; Backéus 1990; Kajimoto et al. 2003; Kohzu et al. 2003; Bhuiyan et al. 2016), and the rooting depth coefficients (Online Resource 7) indicated that living tree and shrub roots in the S1 bog were on average even more shallowly distributed than roots in arctic tundra underlain by permafrost (Jackson et al. 1996). Ultimately, in saturated soils, minirhizotrons may provide a more accurate

estimate of rooting depth distribution than fine-root standing crop sampled from peat cores. Limited decomposition in anaerobic peat may confound estimates of living root biomass sampled from peat cores throughout the soil profile (e.g., Moore et al. 2002). For example, we found well-preserved (i.e., intact), but dead, shrub roots up to 5000 yr. old in peat samples as deep as 2-m (Fig. 4). These roots were close in age to the bulk peat from similar depth increments (McFarlane et al. submitted). Given the rooting depth distribution of living shrub roots appears to depend strongly on the position of the water table, we hypothesize that shrubs living many millennia ago potentially invested in deeper roots in response to drought conditions, and these roots were then inundated by water in subsequent growing seasons and preserved under anaerobic conditions.

Prior characterization of peat in the S1 bog indicates that dissolved organic carbon (DOC), even in peat as deep as 2 m, is of recent origin compared with the bulk peat (Tfaily et al. 2014), and may provide an important C source for priming of microbial decomposition of deep peat. Given the shallow rooting depth of the woody species in the bog, and the sparse cover of deeply-rooted sedges, if the young DOC in deeper peat is plant-derived it must be vertically transferred to deeper peat on relatively fast timescales at this site (e.g., Glaser et al. 2016). Future work should focus on comparing the timing of DOC production with the timing of fine-root growth and turnover throughout the soil profile.

We further hypothesized that the shallow rooting depth distribution woody plants would limit their access to nutrients available in deeper peat. In support of our hypothesis, we observed strong increases in nutrient availability with peat depth in the S1 bog (Fig. 5, Online Resource 8). Similar patterns have been observed in other peatland ecosystems (Kohzu et al. 2003; Finger et al. 2016), indicating that the shallow water table depth in peatlands constrains plant roots to the zone of peat where nutrient availability is least. Indeed, the large concentration of fine roots in surface peat may draw down the availability of nutrients, while nutrients may accumulate in deeper peat where fine roots are scarce. The discrepancy between the spatial distribution of nutrients and fine roots was exacerbated in the surface of hummocks where the overwhelming majority of fine roots were observed, and where, in contrast to other studies (e.g., Eppinga et al. 2010), we found that nutrient availability was less than in adjacent depressed hollows, though the total amount of nutrients

available to roots could be equal or greater, given deeper rooting distributions in hummocks.

Interactions among water table level, rooting depth distribution, and the distribution of nutrients throughout the peat profile likely contribute to the extreme nutrient limitation of peatland plants, especially those growing in ombrotrophic bogs that receive their limited nutrient inputs from precipitation. If a lowering of the water table resulting from drier conditions in response to warming (e.g., Shi et al. 2015) allows deeper root growth in aerobic peat, exploitation of greater nutrient availability at depth may allow increased plant production in this nutrient-limited bog, though the ability of ericaceous shrubs and trees to develop deeper rooting distributions may differ (e.g., LeBarron 1945; Gale and Grigal 1987; Lieffers and Rothwell 1987; Backéus 1990; Weltzin et al. 2000; Murphy et al. 2009a; Iwasaki et al. 2010; Murphy and Moore 2010).

Fine-root contribution to net primary production

Extrapolated estimates of annual fine-root biomass production from minirhizotron observations (Table 1) are of the same magnitude as estimates of root growth from other bogs obtained using destructive sampling techniques (Reader and Stewart 1972; Backéus 1990; Finér and Laine 1998; Weltzin et al. 2000; Bond-Lamberty et al. 2004; Murphy et al. 2009a; Wieder et al. 2009; Laiho et al. 2014). In the S1 bog, fine-root biomass production comprised between 45 and 70% of tree NPP, and between 6 and 27% of shrub NPP, after accounting for differences in the distribution of hummocks and hollows across the bog (Table 1). The lower estimates (45% and 6% for trees and shrubs, respectively) are from 2012, two years after minirhizotron installation, and are less likely to be affected by initial fine-root colonization of the tubes. These estimates are close to those observed in other bogs dominated by woody plants, where estimates of fine-root contribution to NPP ranged from 0 to 40% for trees (Bond-Lamberty et al. 2004; Wieder 2006), but they are somewhat less than estimates of ericaceous shrub fine-root NPP fraction, which ranged from 25 to 75% (Reader and Stewart 1972; Backéus 1990; Weltzin et al. 2000). Our lower estimates of shrub fine-root production could be related to the focus of minirhizotrons on narrow-diameter absorptive roots. For example, there was up to 20 km/m^2 of shrub fine-root length in some locations, but absorptive shrub roots have an extremely high specific root length (~750 m/g for first and second order roots, Online Resource 2), resulting in lower root biomass per unit root length.

Representing fine roots in peatland models

Our findings on the patterns of rooting distribution and dynamics in an ombrotrophic bog can help to inform the treatment of fine roots in ecosystem models projecting C, water, and nutrient fluxes in peatlands (e.g., Frolking et al. 2010; Riley et al. 2011; Shi et al. 2015). For example, we observed relationships between the basal area of nearby trees and fine-root peak standing length as well as patterns of relative biomass allocation that could be used to constrain fine-root biomass in models. We also observed dynamic patterns in fine-root phenology in comparison with leaf and wood phenology, indicating that dynamic allocation coefficients will be needed to predict patterns in C flux to different plant organs. In addition, we observed that most fine roots were shallowly distributed; thus, the average depth to the water table could be used to predict the maximum depth of living, woody fine roots and modeled plant-available nutrients should be constrained to shallower peat depths (e.g., Frolking et al. 2010). Lastly, the large specific root length of ericaceous shrubs indicates that root length, rather than root biomass, may be more useful for predicting the importance of these and other fine roots for resource acquisition throughout the shallow peat profile. Similarly, extramatrical hyphae may increase fine-root access to peat resources (Fernandez and Kennedy 2015).

Conclusions

As one of the few studies to adapt minirhizotron technology for use in waterlogged peatlands, we were able to provide a rare glimpse into the hidden patterns of fine-root distribution and dynamics in a forested, ombrotrophic bog, and the timing of fine-root growth throughout the year. As we hypothesized, we found that fine-root standing crop and growth varied spatially across the bog in relation to tree density and microtopography, and we observed tradeoffs in root growth with aboveground woody growth, rather than as a response to environmental variables such as peat temperature and PAR. Importantly for understanding the strong nutrient limitation of peatland plants, we found

that the water table constrains living fine roots to the aerobic zone, which is extremely poor in plant-available nutrients. Furthermore, we observed ancient, undecomposed, fine roots in peat below the water table, suggesting a significant contribution of roots to historical accumulated peat. We expect the biological, edaphic, and environmental controls over the distribution and dynamics of fine roots in this ombrotrophic bog to be sensitive to projected warming and drying in northern peatlands as well as increases in photosynthate associated with rising atmospheric $[CO_2]$. These changes could alter the balance of peatland C, water, and nutrient fluxes, and therefore peatland C storage.

References

Abramoff RZ, Finzi AC (2015) Are above- and below-ground phenology in sync? New Phytol 205:1054–1061

Backéus I (1990) Production and depth distribution of fine roots in a boreal open bog. Ann Bot Fenn 27:261–265

Baldocchi DD, Black TA, Curtis PS, Falge E, Fuentes JD, Granier A, Gu L, Knohl A, Pilegaard K, Schmid HP, Valentini R, Wilson K, Wofsy S, Xu L, Yamamoto S (2005) Predicting the onset of net carbon uptake by deciduous forests with soil temperature and climate data: a synthesis of FLUXNET data. Int J Biometerol 49:377–387

Bhuiyan R, Minkkinen K, Helmisaari H-S, Ojanen P, Penttilä T, Laiho R (2016) Estimating fine-root produciton by tree speceis and understory functional groups in two contrasting peatland forests. Plant Soil. doi:10.1007/s11104-016-3070-3

Bond-Lamberty B, Wang CK, Gower ST (2004) Net primary production and net ecosystem production of a boreal black

spruce wildfire chronosequence. Glob Chang Biol 10:473–487

Bridgham SD, Megonigal JP, Keller JK, Bliss NB, Trettin C (2006) The carbon balance of north American wetlands. Wetlands 26:889–916

Bridgham SD, Pastor J, Dewey B, Weltzin JF, Updegraff K (2008) Rapid carbon response of peatlands to climate change. Ecology 89:3041–3048

Chanton JP (2005) The effect of gas transport on the isotope signature of methane in wetlands. Org Geochem 36:753–768

Crow SE, Wieder RK (2005) Sources of CO_2 emission from a northern peatland: root respiration, exudation, and decomposition. Ecology 86:1825–1834

Denman KL, Brasseur G, Chidthaisong A, Ciais P, Cox PM, Dickinson RE, Hauglustaine D, Heinze C, Holland E, Jacob D, Lohmann U, Ramachandran S, da Silva Dias PL, Wofsy SC, Zhang X (2007) Couplings between changes in the climate system and biogeochemistry. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds) Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, New York, New York, USA, pp 501–581

Eppinga MB, Rietkerk M, Belyea LR, Nilsson MB, De Ruiter P, Wassen MJ (2010) Resource contrast in patterned peatlands increases along a climatic gradient. Ecology 91:2344–2355

Fernandez CW, Kennedy PG (2015) Revisiting the 'Gadgil effect': do interguild fungal interactions control carbon cycling in forest soils? New Phytol 209:1382–1394

Finér L, Laine J (1998) Root dynamics at drained peatland sites of different fertility in southern Finland. Plant Soil 201:27–36

Finger RA, Turetsky MR, Kielland K, Ruess RW, Mack MC, Euskirchen ES (2016) Effects of permafrost thaw on nitrogen availability and plant-soil interactions in a boreal Alaskan lowland. J Ecol. doi:10.1111/1365-2745.12639

Fitter A (1982) Morphometric analysis of root systems: application of the technique and influence of soil fertility on root system development in two herbaceous species. Plant Cell Environ 5:313–322

Frolking S, Roulet NT, Tuittila E, Bubier JL, Quillet A, Talbot J, Richard PJH (2010) A new model of Holocene peatland net primary production, decomposition, water balance, and peat accumulation. Earth Syst Dynam 1:1–21

Gale MR, Grigal DF (1987) Vertical root distributions of northern tree species in relation to successional status. Can J For Res 17:829–834

Gaudinski JB, Trumbore SE, Davidson EA, Cook AC, Markewitz D, Richter DD (2001) The age of fine-root carbon in three forests of the eastern United States measured by radiocarbon. Oecologia 129:420–429

Gill RA, Jackson RB (2000) Global patterns of root turnover for terrestrial ecosystems. New Phytol 147:13–31

Glaser PH, Siegel DI, Chanton JP, Reeve AS, Rosenberry DO, Corbett JE, Dasgupta S, Levy Z (2016) Climatic drivers for multidecadal shifts in solute transport and methane production zones within a large peat basin. Glob Biogeochem Cycles. doi:10.1002/2016GB005397

Gorham E (1991) Northern peatlands: role in the carbon cycle and probably responses to climatic warming. Ecol Appl 1:182–195

Griffiths NA, Sebestyen SD (2016) SPRUCE S1 bog porewater, groundwater, and stream chemistry data: 2011-2013. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. http://dx.doi.org/10.3334/CDIAC/spruce.018

Guo DL, Li H, Mitchell RJ, Han WX, Hendricks JJ, Fahey TJ, Hendrick RL (2008a) Fine root heterogeneity by branch order: exploring the discrepancy in root turnover estimates between minirhizotron and carbon isotopic methods. New Phytol 177:443–456

Guo DL, Xia MX, Wei X, Chang WJ, Liu Y, Wang ZQ (2008b) Anatomical traits associated with absorption and mycorrhizal colonization are linked to root branch order in twenty-three Chinese temperate tree species. New Phytol 180:673–683

Hanson PJ, Riggs JS, Dorrance C, Hook LA (2011) SPRUCE environmental monitoring data: 2010-2011. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. http://dx.doi.org/10.3334/CDIAC/spruce.001

Hanson PJ, Riggs JS, Hook LA, Nettles WR (2015) SPRUCE S1 bog phenology movies, 2010-2016. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. http://dx.doi.org/10.3334/CDIAC/spruce.011

Hollingsworth TN, Lloyd AH, Nossov DR, Ruess RW, Charlton BA, Kielland K (2010) Twenty-five years of vegetation change along a putative successional chronosequence on the Tanana River, Alaska. Can J For Res 40:1273–1287

Hua Q (2009) Radiocarbon: a chronological tool for the recent past. Quarternary Geochronology 4:378–390

Iversen CM (2014) Using root form to improve our understanding of root function. New Phytol 203:707–709

Iversen CM, Ledford J, Norby RJ (2008) CO_2 enrichment increases carbon and nitrogen input from fine roots in a deciduous forest. New Phytol 179:837–847

Iversen CM, Murphy MT, Allen MF, Childs J, Eissenstat DM, Lilleskov EA, Sarjala TM, Sloan VL, Sullivan PF (2012) Advancing the use of minirhizotrons in wetlands. Plant Soil 352:23–39

Iversen CM, Hanson PJ, Brice DJ, Phillips JR, McFarlane KJ, Hobbie EA, Kolka RK (2014) SPRUCE peat physical and chemical characteristics from experimental plot cores, 2012. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. http://dx.doi.org/10.3334/CDIAC/spruce.005

Iversen CM, Sloan VL, Sullivan PF, Euskirchen ES, McGuire AD, Norby RJ, Walker AP, Warren JM, Wullschleger SD (2015) The unseen iceberg: plant roots in arctic tundra. New Phytol 205:34–58

Iversen CM, Childs J, Norby RJ, Garrett A, Martin A, Spence J, Ontl TA, Burnham A, Latimer J (2017a) SPRUCE S1 bog fine-root production and standing crop assessed with minirhizotrons in the Southern and Northern ends of the S1 bog. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. http://dx.doi.org/10.3334/CDIAC/spruce.019

Iversen CM, Garrett A, Martin A, Turetsky MR, Norby RJ, Childs J, Ontl TA (2017b) SPRUCE S1 bog tree basal area and understory community composition assessed in the Southern and Northern ends of the S1 bog. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. http://dx.doi.org/10.3334/CDIAC/spruce.024

Iversen CM, Ontl TA, Brice DJ, Childs J (2017c) SPRUCE S1 bog plant-available nutrients assessed with ion-exchange resins from 2011-2012 in the Southern end of the S1 bog. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. http://dx.doi.org/10.3334/CDIAC/spruce.022

Iversen CM, Latimer J, Burnham A, Brice DJ, Childs J, Vander Stel HM (2017d) SPRUCE plant-available nutrients assessed with ion-exchange resins in experimental plots, beginning in 2013. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. http://dx.doi.org/10.3334/CDIAC/spruce.036

Iwasaki H, Saito H, Kuwao K, Maximov TC, Hasegawa S (2010) Forest decline caused by high soil water conditions in a permafrost region. Hydrol Earth Syst Sc 14:301–307

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED (1996) A global analysis of root distributions for terrestrial biomes. Oecologia 108:389–411

Johnson MG, Tingey DT, Phillips DL, Storm MJ (2001) Advancing fine root research with minirhizotrons. Environ Exp Bot 45:263–289

Joslin JD, Wolfe MH (1999) Disturbances during minirhizotron installation can affect root observation data. Soil Sci Soc Am J 63:218–221

Kajimoto T, Matsuura Y, Osawa A, Prokushkin AS, Sofronov MA, Abaimov AP (2003) Root system development of *Larix gmelinii* trees affected by micro-scale conditions of permafrost soils in central Siberia. Plant Soil 255:281–292

Kohzu A, Matsui K, Yamada T, Sugimoto A (2003) Significance of rooting depth in mire plants : evidence from natural 15 N abundance. Ecol Res 18:257–266

Kolka R, Sebestyen S, Verry ES, Brooks K (2011) Peatland biogeochemistry and watershed hydrology at the Marcell experimental Forest. CRC Press, Boca Raton

Kramer PJ (1969) Plant and soil water relationships: a modern synthesis. McGraw Hill, New York

Laanbroek HJ (2010) Methane emission from natural wetlands: interplay between emergent macrophytes and soil microbial processes. A mini-review. Ann Bot 105:141–153

Laiho R, Vasander H, Penttilä T, Laine J (2003) Dynamics of plant-mediated organic matter and nutrient cycling following water-level drawdown in boreal peatlands. Glob Biogeochem Cycles 17:1503

Laiho R, Bhuiyan R, Strakova P, Makiranta P, Badorek T, Penttila T (2014) Modified ingrowth core method plus infrared calibration models for estimating fine root production in peatlands. Plant Soil 385:311–327

LeBarron RK (1945) Adjustment of black spruce root systems to increasing depth of peat. Ecology 26:309–311

Lieffers VJ, Rothwell RL (1987) Rooting of peatland black spruce and tamarack in relation to depth of water table. Can J Bot 65:817–821

Malhi Y, Doughty C, Galbraith D (2011) The allocation of eco-system net primary productivity in tropical forests. Philos T Roy Soc B 366:3225–3245

Malhotra A, Roulet NT, Wilson P, Giroux-Bougard X, Harris LI (2016) Ecohydrological feedbacks in peatlands: an empirical test of the relationship among vegetation, microtopography, and water table. Ecohydrology 9:1346–1357

McCormack ML, Adams TS, Smithwick EAH, Eissenstat DM (2014) Variability in root production, phenology, and turnover rate among 12 temperate tree species. Ecology 95:2224–2235

McCormack ML, Dickie IA, Eissenstat DM, Fahey TJ, Fernandez CW, Guo DL, Helmisaari HS, Hobbie EA, Iversen CM, Jackson RB, Leppalammi-Kujansuu J, Norby RJ, Phillips RP, Pregitzer KS, Pritchard SG, Rewald B, Zadworny M (2015a) Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere process-es. New Phytol 207:505–518

McCormack ML, Gaines KP, Pastore M, Eissenstat DM (2015b) Early season root production in relation to leaf production among six diverse temperate tree species. Plant Soil 389: 121–129

McFarlane KJ, Iversen CM, Phillips JR, Brice DJ, Hanson PJ (Submitted) Temporal and spatial heterogeneity of carbon accumulation in an ombrotrophic bog in northern Minnesota over the Holocene. The Holocene

McGuire AD, Anderson LG, Christensen TR, Dallimore S, Guo LD, Hayes DJ, Heimann M, Lorenson TD, Macdonald RW, Roulet N (2009) Sensitivity of the carbon cycle in the Arctic to climate change. Ecol Monogr 79:523–555

Megonigal JP, Hines ME, Visscher PT (2004) Anaerobic metabo-lism: linkages to trace gases and aerobic processes. In: Schlesinger WH (ed) Biogeochemistry. El Sevier-Pergamon, Oxford, pp 317–424

Moore TR, Bubier JL, Frolking SE, Lafleur PM, Roulet NT (2002) Plant biomass and production and CO_2 exchange in an ombrotrophic bog. J Ecol 90:25–36

Murphy MT, Moore TR (2010) Linking root production to above-ground plant characteristics and water table in a temperate bog. Plant Soil 336:219–231

Murphy MT, Laiho R, Moore TR (2009a) Effects of water table drawdown on root production and aboveground biomass in a boreal bog. Ecosystems 12:1268–1282

Murphy MT, McKinley A, Moore TR (2009b) Variations in above- and below-ground vascular plant biomass and water table on a temperate ombrotrophic peatland. Botany 87:845–853

Norby RJ, Todd DE, Fults J, Johnson DW (2001) Allometric determination of tree growth in a CO_2-enriched sweetgum stand. New Phytol 150:477–487

Ontl TA, Iversen CM (2017) SPRUCE S1 bog areal coverage of hummock and hollow microtopography assessed along three transects in the S1 bog. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, U.S. Department of Energy, Oak Ridge, Tennessee, U.S.A. http://dx.doi.org/10.3334/CDIAC/spruce.023

Parsekian AD, Slater L, Ntarlagiannis D, Nolan J, Sebestyen SD, Kolka RK, Hanson PJ (2012) Uncertainty in peat volume and soil carbon estimated using ground-penetrating radar and probing. Soil Sci Soc Am J 76:1911–1918

Perala DA, Verry ES (2011) Forest management practices and silviculture. Peatland biogeochemistry and watershed hydrolo-gy at the Marcell experimental Forest. CRC Press, Boca Raton

Reader RJ, Stewart JM (1972) Relationship between net primary production and accumulation for a peatland in southeastern Manitoba. Ecology 53:1024–1037

Reich PB, Teskey RO, Johnson PS, Hinckley TM (1980) Periodic root and shoot growth in oak. For Sci 26:590–598

Riley WJ, Subin ZM, Lawrence DM, Swenson SC, Torn MS, Meng L, Mahowald NM, Hess P (2011) Barriers to predicting changes in global terrestrial methane fluxes: anal-yses using CLM4Me, a methane biogeochemistry model integrated in CESM. Biogeosciences 8:1925–1953

Ruess RW, Hendrick RL, Burton AJ, Pregitzer KS, Sveinbjornsson B, Allen ME, Maurer GE (2003) Coupling fine root dynamics with ecosystem carbon cycling in black spruce forests of interior Alaska. Ecol Monogr 73:643–662

Sebestyen SD, Dorrance C, Olson DM, Verry ES, Kolka RK, Elling AE, Kyllander R (2011) Long-term monitoring sites and trends at the Marcell experimental Forest. In: Kolka RK, Sebestyen SD, Verry ES, Brooks KN (eds) Peatland biogeo-chemistry and watershed hydrology at the Marcell experi-mental Forest. CRC Press, Inc., New York, pp 15–72

Shi X, Thornton PE, Ricciuto DM, Hanson PJ, Mao J, Sebestyen SD, Griffiths NA, Bisht G (2015) Representing northern peatland microtopography and hydrology within the commu-nity land model. Biogeosciences 12:6463–6477

Silvola J, Alm J, Ahlholm U, Nykanen H, Martikainen PJ (1996) The contribution of plant roots to CO_2 fluxes from organic soils. Biol Fert Soils 23:126–131

Spalding KL, Buchholz BA, Bergman L-E, Druid H, Frisén J (2005) Age written in teeth by nuclear tests: a legacy from above-ground testing provides a precise indicator of the year in which a person was born. Nature 437:333–334

Strand AE, Pritchard SG, McCormack ML, Davis MA, Oren R (2008) Irreconcilable differences: fine-root life spans and soil carbon persistence. Science 319:456–458

Ström L, Mastepanov M, Christensen TR (2005) Species-specific effects of vascular plants on carbon turnover and methane emissions from wetlands. Biogeochemistry 75:65–82

Ström L, Tagesson T, Mastepanov M, Christensen TR (2012) Presence of Eriophorum scheuchzeri enhances substrate availability and methane emission in an Arctic wetland. Soil Biol Biochem 45:61–70

Sullivan PF, Arens SJT, Chimner RA, Welker JM (2008) Temperature and microtopography interact to control carbon cycling in a high arctic fen. Ecosystems 11:61–76

Tfaily MM, Cooper WT, Kostka JE, Chanton PR, Schadt CW, Hanson PJ, Iversen CM, Chanton JP (2014) Organic matter transformation in the peat column at Marcell experimental Forest: Humification and vertical stratification. J Geophys Res–Biogeo 119:661–675

Vapaavuori EM, Rikala R, Ryyppo A (1992) Effects of root temperature on growth and photosynthesis in conifer seed-lings during shoot elongation. Tree Physiol 10:217–230

Verry ES, Brooks KN, Barten PK (1988) Streamflow response from an ombrotrophic mire. In: Proceedings of the interna-tional symposium on the hydrology of wetlands in temperate and cold regions. International Peat Society/The Academy of Finland, Helsinki, Finland, pp 52–59

Vogel JS, Southon JR, Nelson DE, Brown TA (1984) Performance of catalytically condensed carbon for use in accelerator mass-spectrometry. Nucl Instrum Meth B 5:289–293

Vogt KA, Vogt DJ, Blomfield J (1998) Analysis of some direct and indirect methods for estimating root biomass and production of forests at an ecosystem level. Plant Soil 200:71–89

Walker TN, Garnett MH, Ward SE, Oakley S, Bardgett RD, Ostle NJ (2016) Vascular plants promote ancient peatland carbon loss with climate warming. Glob Chang Biol 22:1880–1889

Wang CK, Bond-Lamberty B, Gower ST (2003) Carbon distribution of a well- and poorly-drained black spruce fire chronosequence. Glob Chang Biol 9:1066–1079

Wania R, Ross I, Prentice IC (2010) Implementation and evaluation of a new methane model within a dynamic global vegetation model: LPJ-WHyMe v1.3.1. Geosci Model Dev 3: 565–584

Weltzin JF, Pastor J, Harth C, Bridgham SD, Updegraff K, Chapin CT (2000) Response of bog and fen plant communities to warming and water-table manipulations. Ecology 81:3464–3478

Wieder RK (2006) Primary production in boreal peatlands. In: Weider RK, Vitt DH (eds) Boreal peatland ecosystems. Springer-Verlag, Berlin, pp 145–164

Wieder RK, Scott KD, Kamminga K, Vile MA, Vitt DH, Bone T, Xu B, Benscoter BW, Bhatti JS (2009) Postfire carbon balance in boreal bogs of Alberta, Canada. Glob Chang Biol 15:63–81

Yu Z, Loisel J, Brosseau DP, Beilman DW, Hunt SJ (2010) Global peatland dynamics since the last glacial maximum. Geophys Res Lett 37:L13402