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Abstract

Key message:

We demonstrate the negative impacts of ground thaw on sap flow in black spruce. Climate warming is accelerating permafrost thaw; our study may inform observed warming-related productivity declines in subarctic forests.

Abstract:

Many of Canada's northern boreal peatlands are situated on discontinuous permafrost. Here, permafrost provides the physical foundation on which forests persist. However, climate warming is leading to increased rates of permafrost thaw resulting in both increased active layer thickness (ALT) as well as shrinkage of the area underlain by permafrost due to lateral thaw at plateau margins. Such changes to the substrate likely impact growth and physiological processes of the trees. Despite this, little is known about the role of active layer development, and changes to it, including thaw of the underlying permafrost on tree water relations. Here, we measured sap flow in black spruce from a peatland experiencing rapid permafrost thaw and quantified drivers of changes in sap flow. Time series analyses revealed that of the environmental drivers examined, vapour pressure deficit was the strongest predictor of diurnal sap flow, while seasonal patterns were driven largely by energy inputs; however, the environmental drivers of importance did not change as a function of ground thaw conditions. To understand the implications of changing permafrost and active layer conditions, we quantified differences in sap flow between trees in interior positions of permafrost plateaus and trees on degrading plateau edges. We found >65 % reductions in sap flow in edge trees, attributable to reduced root function at waterlogged edges. Seasonal thaw processes also influenced sap flow. Paired measures of ALT indicated a negative linear relationship with sap flow that was stronger for interior trees. Greater ALT, which corresponds with deeper frost and water tables reduced sap flow by up to 60 % and is likely attributable to drying in surface soil layers where rooting occurs. Climate warming will accelerate permafrost thaw, which our data suggests will drive decreases in the productivity of black spruce-dominated subarctic forests and may thus enhance our understanding of widespread reductions in productivity in boreal forests in northwestern North America.

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Electronic supplementary material	Below is the link to the electronic supplementary material. Supplementary material 1 (DOCX 56 kb)

1

2 Sap flow responses to seasonal thaw and permafrost degradation
3 in a subarctic boreal peatland

4 **Rajit Patankar · William L. Quinton ·**
5 **Masaki Hayashi · Jennifer L. Baltzer**

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49 in boreal forests in northwestern North America.

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Introduction

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56 Much of Canada's boreal forest occurs on permafrost (i.e.
57 perennially cryotic ground) and much of this lies in the
58 zone of discontinuous permafrost (10–90 % permafrost by

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areal extent); boreal peatlands comprise a significant part of this landscape (Tarnocai 2006). Here, the volumetric expansion of the moisture fraction of saturated soil as it freezes results in the formation of permafrost plateaus that are elevated above the surrounding wetlands (bogs and fens). These permafrost plateaus provide the rooting foundation on which conifer-dominated forests establish and often represent the local physical limits of forest extent (Camill et al. 2010; Baltzer et al. 2014). However, recent evidence has shown that climate warming is leading both to deeper end of season thaw and lateral thaw of permafrost resulting in the widespread conversion of permafrost plateaus to wetlands (Quinton et al. 2011) and subsequent degradation and loss of forests due to permafrost thaw-induced ground surface subsidence (Beilman and Robinson 2003; Camill 2005; Baltzer et al. 2014).

While much is known about landscape and regional consequences of permafrost thaw in subarctic peatlands, less is known about the impacts of these processes on the physiological function of individual trees or how changes in tree function may feed back on thaw processes. Sap flow (the flow of water and minerals through conducting tissue) from individual trees can be used to examine whole tree physiological responses to environmental changes, and to estimate stand-level processes such as canopy transpiration. Previous studies quantifying sap flow in larch (*Larix cajanderi* Mayr.) growing on continuous permafrost in Eastern Siberia found marked decreases in sap flow in response to high soil moisture resulting from vertical permafrost thaw (i.e. active layer thickening). In this instance, waterlogging resulted in decreased transpiration rates and the browning and suppression of larch foliage (Iijima et al. 2013). Given the areal extent of boreal forests globally ($\sim$14 million km^2), understanding changes in water fluxes and productivity in these systems in response to changing permafrost conditions is of global significance.

How changing permafrost conditions influence root function and sap flow rates depends on the impacts of these changing conditions on the rooting environment. As described above, discontinuous permafrost thaws concurrently from above (i.e. vertical thaw) and from its sides (i.e. lateral thaw). Permafrost thaw leads to the subsidence of the plateau ground surface, which at plateau edges leads to subsidence into adjacent wetlands and waterlogging of the soil (Quinton et al. 2009, 2011; Baltzer et al. 2014). Measured rates of lateral permafrost thaw are as great as 1 m year^{-1} (Quinton et al. 2011) and this can lead both to the destabilisation of the physical foundation on which the trees are growing (i.e. "drunken trees") and/or the loss of root function due to waterlogging. Hypoxic and anoxic conditions can lead to reduced water uptake mediated by the gating of water channel proteins (aquaporins) in roots in response to the build-up of toxic by-products of

anaerobic respiration (Tournaire-Roux et al. 2003). Hence, individual trees situated on the margins of degrading permafrost plateaus appear to confront multiple stressors including the physical lean of aboveground stems and partially waterlogged rooting systems at the wetland–plateau interface. As such, we expect lateral permafrost thaw to have negative consequences for rates of sap flow and by extension, whole tree productivity. Indeed recent evidence from Northwestern Canada indicates that root function and radial growth of *Picea mariana* are reduced when in close proximity to a plateau edge (Baltzer et al. 2014). In contrast, vertical ground thaw in the interior portions of permafrost plateaus results in a deeper and warmer end of season active layer (Quinton et al. 2011; Quinton and Baltzer 2013), which in theory could enhance growing season root function and whole tree sap flow and productivity. Warmer soils could enhance root function and microbial activity thereby providing greater access to soil water and nutrients and supporting enhanced physiological function in the tree (Rustad et al. 2001; Aerts 2006). An alternative possibility is that vertical thaw will result in drought stress. Because permafrost and the overlying frozen portion of the active layer are impermeable, the water table perches on the frost table (Quinton and Baltzer 2013), meaning that as the frost table lowers with ground thaw, plant access to the thawed, saturated layer between the water table and frost table may be impeded if roots are not evenly distributed throughout the depth of the active layer.

Sap flow is also highly responsive to atmospheric conditions. Both vapour pressure deficit (D) and radiation are important drivers of stomatal conductance and transpiration and these parameters form the basis of commonly used models of potential evapotranspiration (reviewed in Fisher et al. 2011). D is a critical determinant of sap flow as a consequence of its role in determining the soil–plant–atmosphere water potential gradient; higher D results in greater sap flow when soil conditions are favourable (Bovard et al. 2005). Energy drives the liquid–vapour phase change in water, thus increased energy inputs will mean increased transpiration and sap flow. However, there is an evidence that soil conditions, in particular soil moisture may alter canopy response to local atmospheric conditions such as air temperature, radiation, and D (Bovard et al. 2005). Changes in the soil moisture conditions attributable to permafrost thaw may thus be expected to alter the response of individuals to these variables and lead to a more complex stand-level response to microenvironmental conditions (Lopez et al. 2007).

To enhance our understanding of the physiological responses of trees to vertical and lateral ground thaw processes, we examine diurnal and seasonal patterns of stem sap flow in *Picea mariana*, a common, widespread boreal conifer growing on discontinuous permafrost
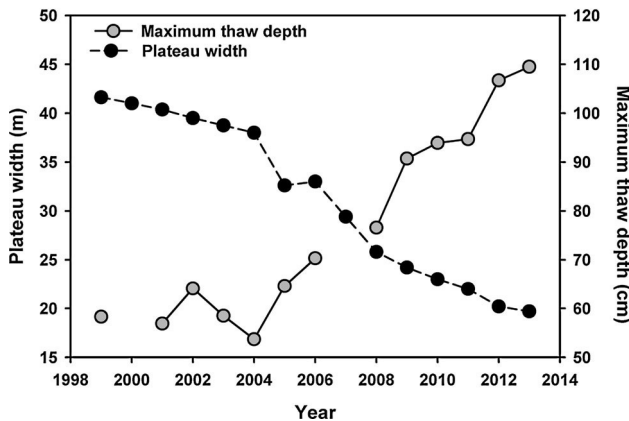
Fig. 1 *Top panel* aerial image of an intensively measured permafrost plateau at Scotty Creek, NWT. In this image, the treed portion of the image is underlain by permafrost while the treeless portions are permafrost-free wetlands. The *white dashed line* across the plateau indicates the location of the frost table transect reported in the *bottom panel*. *Bottom panel* permafrost plateau width (*black symbols*) and depth to permafrost or active layer thickness (*grey symbols*) measured repeatedly from 1999 to present along a transect traversing the plateau depicted in the *top panel*. Both plateau width and depth to permafrost were measured by depth to refusal of a steel rod. Updated from Quinton et al. (2011)

165 where rates of both lateral and vertical thaw have been
166 high in recent years (Quinton et al. 2011; Fig. 1). Spe-
167 cifically, we compare sap flow processes between trees
168 on the edges of permafrost plateaus that are experiencing
169 rapid lateral thaw and those on the plateau interior where
170 we use seasonal ground thaw as a proxy for vertical
171 permafrost thaw (i.e. we examine the response of sap
172 flow to increasing active layer thickness through the
173 growing season). Our research objectives are threefold:
174 (1) quantify the impact of lateral permafrost thaw and
175 associated soil conditions (moisture and temperature) on
176 diurnal and seasonal patterns of sap flow and cumulative
177 sap fluxes; (2) quantify sap flow in response to seasonal
178 active layer development with a view to understanding
179 responses of sap flow to active layer thickening; (3)
180 quantify response of sap flow to microenvironmental
181 predictors including incoming radiation, air and soil
182 temperatures, vapour pressure deficit, and rainfall and
183 assess whether these responses vary as a function of
184 ground thaw conditions.

Methods

Study site

Scotty Creek (61°18′N, 121°18′W) is located approxi-
mately 50 km south of Fort Simpson, Northwest Territo-
ries, Canada, in the zone of extensive discontinuous
permafrost. This region is characterised by peatland com-
plexes comprised of permafrost plateaus, ombrotrophic flat
bogs and fens (Quinton et al. 2009) typical of the southern
fringe region of permafrost described by Kwong and Gan
(1994). The wetlands (bogs and fens) are permafrost-free
and largely treeless. Permafrost underlying the plateaus is
moderately ice-rich, resulting in a ground surface that is
elevated 0.5–1.5 m above surrounding wetlands [estimated
from Light Detection and Ranging (LiDAR) at Scotty
Creek in 2010]. Consequently, a hydraulic gradient exists
between the forested areas and the surrounding wetlands
such that the plateaus are relatively well drained and
contribute runoff to their adjacent bogs and fens (Quinton
et al. 2009). Permafrost thaw results in ground surface
subsidence and waterlogging (Baltzer et al. 2014). *Picea
mariana*-dominated forests with a canopy height of 8–10 m
occur on permafrost plateaus, and the distribution of these
forests corresponds very closely with the distribution of
permafrost (Quinton et al. 2011). This site is undergoing
rapid vertical and horizontal ground thaw (Fig. 1) leading
to the loss of permafrost plateaus and associated *P. mari-
ana* forests (Quinton et al. 2011; Baltzer et al. 2014).

Sap flow measurements

We installed Heat Ratio Method (HRM) sap flow sensors
(SFM1 Sap Flow Meters ICT International, Armidale,
Australia) on 12 mature *P. mariana* trees. Each metre
consists of a sensor attached to two temperature probes that
are inserted into xylem tissue and that measure a temper-
ature pulse from a heat pulse needle inserted between the
lower (upstream) and upper (downstream) probes. The
needle pulses heat at a predetermined frequency, and the
sensor measures the ratio of increase in temperature
between the probes. Heat pulse sap flow velocity ($m^3\ h^{-1}$)
is then calculated as:

$$V_h = \frac{k}{n}\ln\left(\frac{v_1}{v_2}\right) \qquad (1)$$

where k is the thermal diffusivity ($m^2\ s^{-1}$) of wood, n is the
distance between heat pulse needle and temperature probes,
v_1 and v_2 are temperature increases at equidistant points
from the heater, proximal and distal to the tree crown,
respectively. For a more detailed explanation of the heat
ratio method refer to Burgess et al. (2001). Six individuals
occurring on degrading plateau edges (hereafter "edge

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trees") and six on stable, interior plateau locations (hereafter, "interior trees"; we considered interior locations to be at least 15 m from a plateau edge to avoid edge effects; Baltzer et al. 2014) were selected and sap flow sensors installed on a major root and at the sub-crown level (immediately below the first live branch) of each tree on the bog-facing side of the tree, which in this case was east-facing. Only one sensor was installed in each individual at each sampling height as circumferential variability in sap flow is considered low for small diameter trees such as those measured in the present study (Cermak et al. 2004). Trees were selected from a single stand approximately 1 ha in area to reduce variability attributable to environmental variability among stands. All trees were similar size (6.9–7.9 cm diameter at breast height; 4.6–8.0 m height with live crown ratios greater than 50 %) thereby avoiding size-related biases in sapwood area and sap flow estimates, with the majority of the canopy having healthy foliage. Sapwood area was measured on tree cores from similarly sized individuals at the site, and these values were used in the conversion of sap flux density to whole tree sap flow using Sap Flow Tool software (ICT International, Armidale, Australia). Trees with any apparent damage to the stem were avoided. Sensors were installed during 1–3 June 2012. Sap flow measurements were made continuously from installation to 2 August 2012, thus providing sap flow for the majority of the growing season, including the seasonal thaw of the portion of the active layer in which the trees are rooted (J. Baltzer, personal observation).

Environmental measurements

Measurements of air temperature, relative humidity (RH), vertical soil temperature profiles (0, 5, 10, 20 and 40 cm), shortwave radiation, and below canopy rainfall were made continuously at 30-min intervals from a monitoring station (CR10X Campbell Scientific) on a nearby plateau with comparable vegetation conditions. Vapour pressure deficit (D) was calculated using RH and air temperature by first calculating saturated vapour pressure (SVP), and then determining D from RH and SVP.

Responses of soil conditions to ground thaw

Seasonal thaw depth (cm) was measured weekly during the growing season by probing (depth to refusal) with a 2-m frost probe adjacent to each sample tree. At the same location, water table was measured by inserting a perforated PVC tube (1″ diameter) into the soil and determining the depth below the ground surface at which water was present using the bubbling method. Where no water table was detectable, water table was recorded as being equal to the frost table.

To assess plant available soil moisture as active layer development progressed through the growing season, soil moisture measurements were made at the monitoring station described above during the 2011–2012 period. Unfrozen volumetric water content (VWC) was measured with capacitance sensors (Model CS 615, nominal accuracy ±3 %, Campbell Scientific) installed at 10-, 20-, 30-, and 40-cm depths. Capacitance sensors were calibrated against the water content of 17 peat samples collected from the face of the soil pit during installation. After the sensors were installed (sensor installation occurred in 2001 and measurement has been continuous since), the pits were backfilled with the excavated material preserving the original layering and groundcover as best as possible.

Statistical analyses

We were interested in assessing whether the responses of P. mariana to microenvironmental predictors vary as a function of ground thaw conditions. To address this question, we employed a time series approach to quantify the influence of measured environmental variables on diurnal and seasonal sap flow patterns in trees following Ford et al. (2005). This was done to account for the serial dependence inherent in sap flow data at these (diurnal and seasonal) time scales (i.e. sap flow at time t is highly correlated to sap flow at $t - 1$ for a given individual) that results in a lack of independence between observations, thereby violating assumptions of traditional regression analyses. Specifically, we used autoregressive integrated moving average (hereafter ARIMA) models that comprise of three terms: an autoregressive term (AR), a differencing term (I), and a moving average term (MA). Briefly, ARIMA models are able to account for serial dependence in data via the use of the AR and MA terms, and in addition are capable of using time series from independent variables (such as 30-min air temperature) to describe the influence of outside factors (for a more general explanation of ARIMA models see Box and Jenkins 1976; Brockwell and Davis 2002). We constructed several models using all possible combinations of the environmental variables for edge and interior trees separately. Predictor variables included: shortwave radiation (Sw), air temperature, vapour pressure deficit (D), rainfall, and soil temperature at 20 cm. We selected the 20-cm depth because of the observed surficial distribution of roots in P. mariana (J. Baltzer, personal obs.; Gale and Grigal 1987; Lieffers and Rothwell 1987), but this decision is unlikely to impact the model given the strong correlation in seasonal patterns of soil temperature across depths (Fig. 2). Air temperature and D were found to be highly correlated at the diurnal scale, and thus air temperature was removed from the diurnal ARIMA models to avoid multicollinearity. Because several edge trees showed little or

Fig. 2 Mean daily **a** shortwave radiation, **b** air temperature (°C), **c** soil temperatures at 0, 20, and 40 cm below the ground surface on a permafrost plateau, **d** vapour pressure deficit (*D*, in kPa), **e** daily rainfall (mm), and **f** daily cumulative sap flow (cm³) for edge and interior trees. Edge trees were those occurring on the degrading edges of permafrost plateaus, while interior trees are those located on interior positions of a plateau, away from any degrading edges. Period of measurement is from 3 June 2012 to 2 August 2012
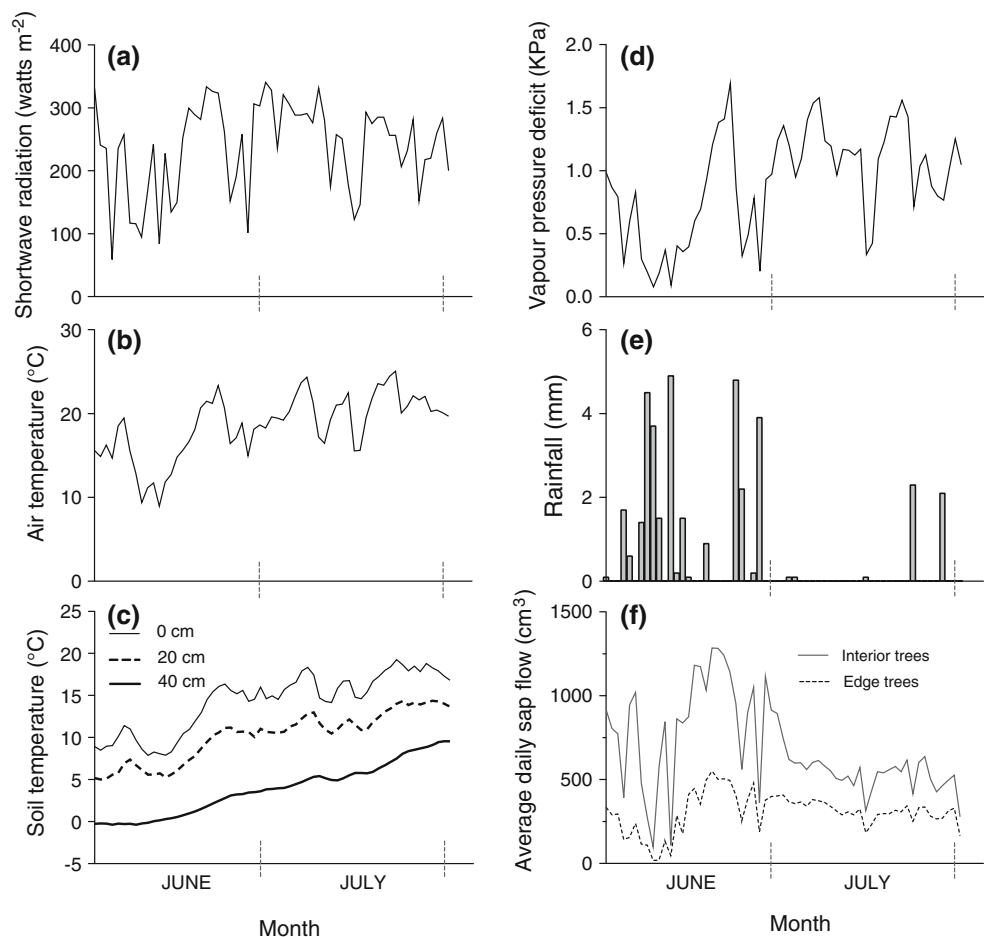
332 no sap flow, for the diurnal analyses, we used ARIMA
333 models on the edge and interior trees (*n* = 2 trees per
334 location) with the fastest flow rates where diurnal patterns
335 were evident in both edge and interior trees. For the sea-
336 sonal analyses, we used the averaged data from interior and
337 edge trees (*n* = 2 trees per location) that had complete
338 seasonal data (due to occasional sensor malfunction, sev-
339 eral trees had incomplete seasonal data). In each case, only
340 two of the six individuals were used for the ARIMA
341 models because ARIMA depends on equally spaced
342 intervals thus only those individuals with 100 % of mea-
343 surements through the season (seasonal ARIMA) or 3-day
344 period (diurnal ARIMA) could be included. We then
345 computed Akaike's Information Criterion (AIC) for each
346 model. AIC is a test statistic employed to examine the
347 goodness of fit of various models that consider both model
348 fit and complexity; models with smaller AIC values are
349 better fitting models than models with larger AIC values.
350 Corrected AIC values (AICc) impose a greater penalty for
351 extra parameters in the model. We based model selection
352 on the model that had an AICc that was at least two units
353 smaller than the next best model (Burnham and Anderson
354 1998). All time series analyses were carried out using the

355 'xts' package in R (v 2.13.1; R Development Core Team,
356 2011).
357 We used a one-way ANOVA to compare the average
358 end of season cumulative output (i.e. 60-day cumulative
359 output per tree) between edge and interior trees (*n* = 4 per
360 location). A nonparametric Mann–Whitney *U* test was used
361 to compare seasonal sap flow rates between edge and
362 interior trees across the season used in the seasonal AR-
363 IMA models. We also ran a linear mixed effects model
364 using the lme function in the nlme package for both sub-
365 crown and root sensor positions to quantify the response of
366 sap flow to location (edge vs. interior) across three time
367 periods during the measurement period (early, mid, late)
368 during which we had complete sap flow data for four trees
369 per location. Fixed terms included location, time period
370 and their interaction and individual was included as a
371 random term. Visual inspection of residuals did not reveal
372 any obvious deviations from homoscedasticity or normal-
373 ity. *P* values were obtained using likelihood ratio tests of
374 the full model containing the effect in question against the
375 model without the effect in question. Because there was a
376 significant interaction term in both the sub-canopy and root
377 models, we further assessed differences between edge and

interior locations during each time period to test for the main effect of location. We were interested in comparing the strength of the relationship between seasonal sap flow and frost table depth for interior and edge trees, thus we fit a linear mixed effects model using the lme function in the nlme package. Fixed effects included frost table depth (measured adjacent to sampled trees weekly through the season), location (edge vs. interior) and their interaction. We included a random effect for individual. Visual inspection of residuals did not reveal any obvious deviations from homoscedasticity or normality. P values were obtained using likelihood ratio tests of the full model containing the effect in question against the model without the effect in question. We quantified potential differences in the slope and elevation of the relationships between water table and frost table depth between edge and interior locations using SMA regression in the smatr package. All tests were conducted using R (v 2.13.1; R Development Core Team, 2011).

Results

Mean daily air and soil temperatures steadily increased during the course of the study period (Fig. 2). Further, there were frequent rainfall events during the early part of the summer with a total of 20 of the 60 sampling days experiencing rainfall (range 0.1–4.9 mm/day).

Sap flow responses to lateral permafrost thaw

Interior and edge *P. mariana* trees showed clear diurnal patterns in stem sap flow during the early (3–5 June 2012) and late (30 July–1 August 2012) summer periods, with peaks around midday and lulls at night (Fig. 3). Because of the very long summer photoperiod at this site, trees maintained sap flow for ~ 22 h per day at the start and ~ 18 h per day at the end of the measurement period (Fig. 3). The only exception to these diurnal patterns was seen in the 'slow' edge tree during the early season (Fig. 3b), wherein sap flow rates were minimal (i.e. just above zero flow). In all cases, peak diurnal sap flow rates were markedly higher in interior trees compared to edge trees (Fig. 3). Peak midday sap flow rates in the interior tree with the highest flow rate averaged across the 72-h measurement periods were ~ 146 and 138 cm^3 h^{-1} (Fig. 3a, c) during the early and late season respectively; the corresponding peak midday values in the edge tree with the highest flow rate were ~ 70 (early) and 60 (late) cm^3 h^{-1} (Fig. 3a, c) during these time periods. In short, trees exposed to lateral ground thaw had sap flow rates that were less than half those of the interior trees. These diurnal patterns were mirrored in the seasonal patterns of sap flow. Interior trees had consistently higher daily sap flow rates compared to edge trees across the summer (Fig. 2f). As a result of daily rates being higher (Fig. 2f), the total end of season sap flow (from all trees combined per habitat) and the average cumulative sap flow (i.e. total sap flow per tree over the entire season) was significantly higher in interior (mean 12.1 L, SE 1.4) compared to edge (mean 4.3 L, SE 0.3) trees (unpaired t test: $t_{1,5} = 4.338$, $P = 0.0226$).

Sap flow responses to seasonal thaw

A Mann–Whitney U test examining differences in daily flow rates between the interior and edge trees with the fastest rates of sap flow showed that across the summer, the interior tree experienced significant declines (Mann–Whitney $U = 160$, $P < 0.001$) while the edge tree did not (Fig. 2f). This is a conservative result, the same analysis comparing average sap flow from the average of the trees with fastest and slowest rates from each location exacerbated the location-dependent differences in sap flow reductions through the growing season (Mann–Whitney $U = 4,774$, $P < 0.0001$). Linear mixed effects models of sap flow as a function of location (edge vs. interior) and time (early, mid, late season) also indicated interaction terms between location and time that were significant for the sub-crown position ($P = 0.01763$) and marginally significant for the root position ($P = 0.07318$) providing further evidence that as the season progresses, interior trees reduce sap flow while edge trees do not (Fig. 4). Indeed, at the start of the growing season interior trees had significantly greater sap flow than edge trees at the sub-crown and root positions ($P = 0.006$ and 0.01, respectively). At the July 13–15 period, this difference was still apparent but had weakened ($P = 0.049$ and 0.09, respectively; Fig. 4). By early August, there was no difference in sap flow between edge and interior locations for either sub-crown or root positions ($P = 0.133$ and 0.22, respectively).

Of the measured environmental predictors, only soil temperature showed a consistent seasonal trend, increasing as one might expect as the summer progressed. We were thus interested in examining relationships between sap flow rates and thaw conditions measured adjacent to individual trees. Daily sap flow rates from the four edge and four interior trees that had sufficient paired sap flow–frost table data showed decreases in sap flow with increasing frost table depths, but the slope of these relationships was significantly greater in interior trees as evidenced by a significant interaction term in the linear mixed model ($P = 0.0192$). Because of the difference in the slope of the relationship, the reductions in sap flow in response to active layer development were greater in interior trees where 50–60 % reductions in sap flow were observed as a
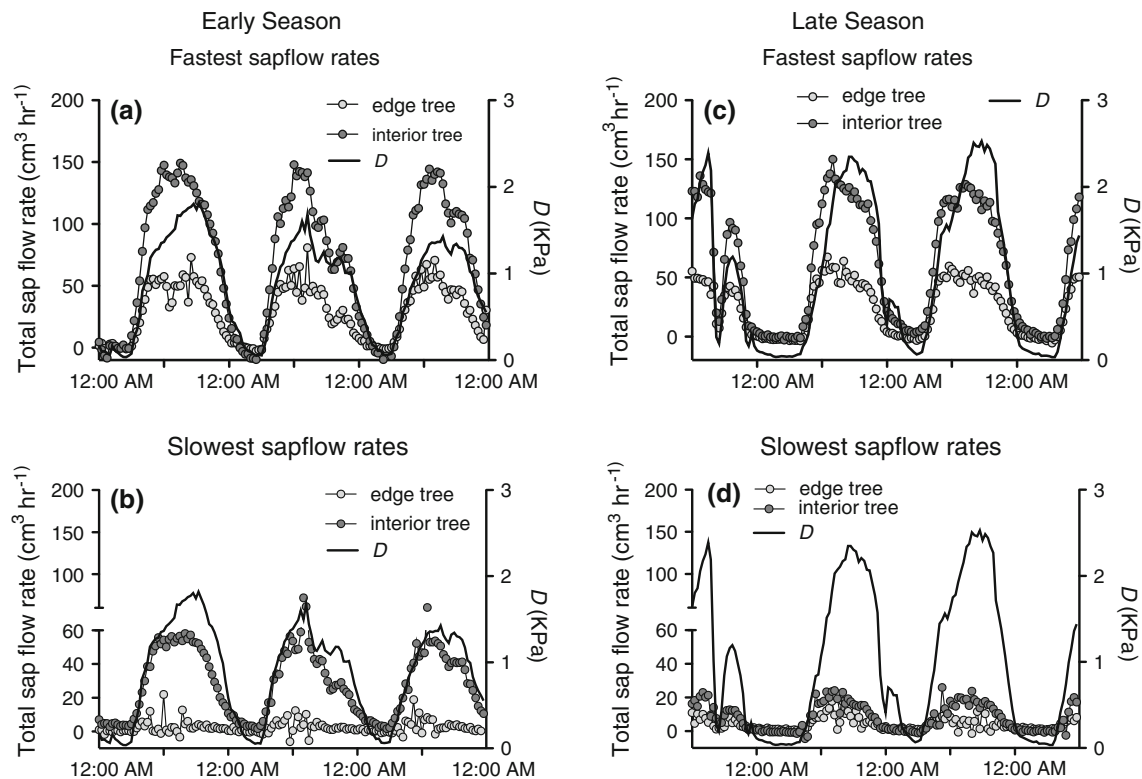
Fig. 3 Diurnal patterns in sap flow during early and late summer 2012 from interior and edge *P. mariana* trees (*n* = 2 per habitat) growing on permafrost plateaus in Scotty Creek. Early season measurement was from 3 to 5 June (**a**, **b**); late season measurement was from 30 July–2 August 2012 (**c**, **d**). Times shown are Mountain

Daylight Time (MDT). Solar noon occurs at approximately 14:00 MDT for both periods. Sap flow rates for the fastest (**a**, **c**) and slowest (**b**, **d**) edge and interior trees are shown separately for the two time periods. Vapour pressure deficit (kPa) is represented by *solid black line* scaled on the right *y* axis

477 function of increasing active layer thickness (Fig. 5). In
478 contrast, the relationships between sap flow and active
479 layer thickness were much noisier in edge trees and while
480 the relationships were negative, reductions were dampened
481 with little apparent change in sap flow through the growing
482 season (Fig. 5).

483 Are environmental predictors of sap flow mediated
484 by permafrost conditions?

485 Individual ARIMA models of diurnal sap flow over a 72-h
486 period revealed that flow rates in both interior and edge
487 **AQ2** trees were most responsive to changes in vapour pressure
488 deficit (Table 1; Figs. 3, 6). The 'looping' pattern seen in
489 the relationships between sap flow and *D* (Fig. 6) repre-
490 sents hysteresis and indicates rate-dependent differences in
491 sap flow during the ramp up (morning) and ramp down
492 (afternoon) phases from the peak sap flow periods (mid-
493 day). Model selection based on corrected AIC values
494 revealed that the model with *D* alone best described diurnal
495 variance in sap flow rates for both edge and interior trees.
496 There were no close, competing best-fit models (Table 1).
497 The diurnal time series model using *D* for interior and edge

trees were (2, 0, 2: AR, I, MA components, respectively) 498
and (1, 0, 2) models, that explained 89 and 78 % of vari- 499
ance in diurnal sap flow rates for interior and edge trees, 500
respectively. 501

In both edge and interior trees, the strongest predictor of 502
seasonal rates of sap flow was shortwave radiation (Sw). 503
All models including Sw had strong explanatory power and 504
varied little in their AIC$_c$ values, suggesting that variables 505
other than Sw contributed little to seasonal changes in daily **AQ3** 506
cumulative sap flow (Table 2). When Sw was removed 507
from the models, AIC$_c$ increased substantially and r^2 val- 508
ues decreased, again supporting the importance of Sw in 509
determining seasonal patterns in sap flow. The minimum 510
AIC selected averaged seasonal time series model for both 511
edge and interior trees included Sw, *D* and air temperature 512
and was a (0, 1, 1) model and (1, 1, 1) model explaining 513
57 and 61 % of variance, respectively (Table 2). 514

Responses of soil conditions to seasonal and permafrost 515
thaw 516

Volumetric water content peaked near the start of May 517
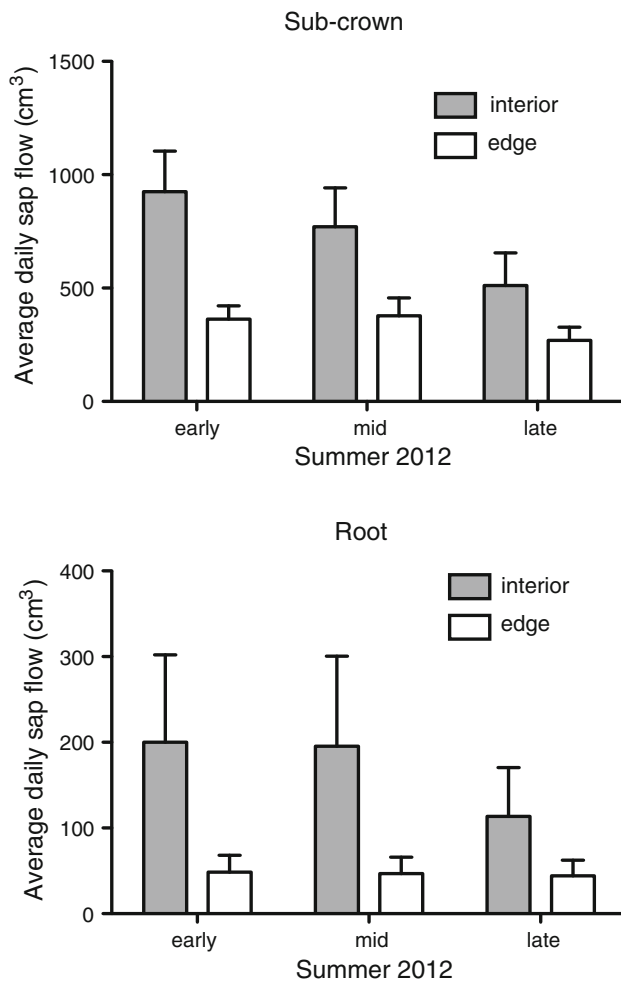following completion of snowmelt and rapidly declined in 518

Fig. 4 Average (±SEM) daily sap flow (cm³) at sub-crown and root positions on interior and edge *P. mariana* trees (*n* = 4 per habitat) at three periods during the measurement period in 2012: early (3–5 June), mid (13–15 July), and late (30 July–2 August). Linear mixed effects models indicated a significant (*P* = 0.0176) and marginally significant (*P* = 0.0732) interaction between location and time period; early in the season there are large differences between edge and interior sap flow rates, while these differences diminish as the season progresses
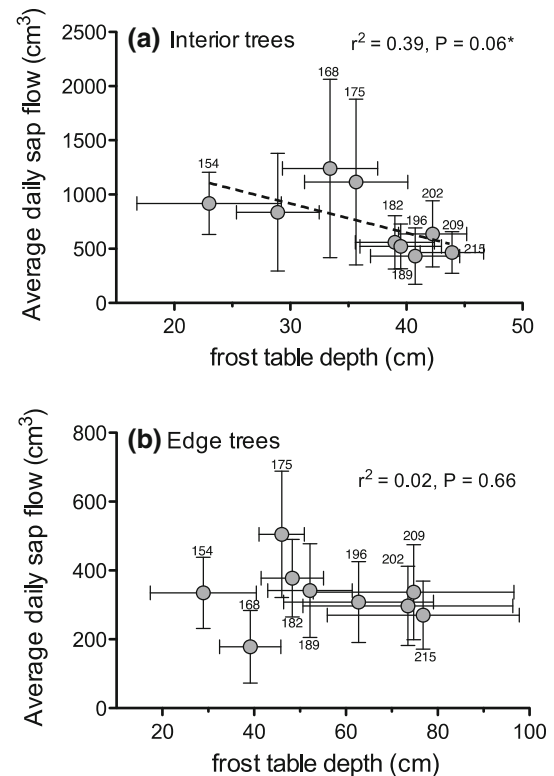

Fig. 5 Simple linear regression relationships between paired measurements of average daily sap flow rates and frost table depth averaged across four *P. mariana* individuals in each location. *Bidirectional error bars* correspond with 1 SEM. Frost table depth (cm) was measured by probing next to individual trees approximately every week from early June to early August 2012. *Numbers above the symbols* correspond with the day of year on which frost depth was measured. Linear mixed effects models indicated a significant interaction term in the frost table–sap flow relationship as a function of location (*P* = 0.0192) with interior trees having a much more negative response to thickening active layer

519 the 0–10 and 10–20 cm soil layers (Fig. 7) where the
520 majority of black spruce roots are found. By the start of
521 July, volumetric water content was reduced to ∼30 and
522 ∼50 % at 10- and 20-cm depths, respectively (Fig. 7).
523 This is in contrast to peak VWC in May and June of
524 75–80 % (Fig. 7). Paired measurements of frost table and
525 water table depths adjacent to our sample trees indicated a
526 significant difference in the relationship between water
527 table and frost table between edge and interior locations.
528 Both interior and edge locations had significant positive
529 relationships between frost and water table depths with
530 both frost and water table deepening through the season
531 (Table S1). However, the slope of this relationship was
532 much steeper in interior locations compared with edge

533 locations (slope and confidence intervals for interior trees:
534 1.42 [1.22, 1.79] and edge trees: 0.19 [0.15, 0.24]; SMA
535 test for common slope: *P* < 0.0001).

Discussion 536

537 Here, we demonstrate three key drivers of sap flow rates in
538 a boreal peatland that differentially impact the pattern and
539 magnitude of sap flow in *P. mariana* occurring in a rapidly
540 thawing permafrost landscape. First and foremost, micro-
541 environmental conditions particularly vapour pressure
542 deficit (*D*) and shortwave radiation (*Sw*) drove daily and
543 seasonal patterns of sap flow, respectively, and this was
544 largely insensitive to the ground thaw conditions experi-
545 enced by individual trees. In fine-scale variation that occurs
546 diurnally, *D* explained between 78 and 89 % of variation in
547 the half hourly stem sap flow (Fig. 2; Table 1). In contrast,
548 daily cumulative sap flow was largely a function of *Sw*

Table 1 Linear model regression statistics and AIC values from the individual ARIMA models examining the influence of various environmental variables on diurnal sap flow rates in *Picea mariana* trees growing on edge and interior locations on permafrost plateaus in Scotty Creek, Northwest Territories, Canada for the period of June 1–3, 2012 ($n = 2$ individuals per location)

Model	AIC	AICc	r^2	F	P
Edge trees					
D	978.7	979.2	0.78	503.0	<0.001
Sw	986.16	986.33	0.77	462.7	<0.001
Sw + D	986.09	986.26	0.86	444.8	<0.001
Sw + soil temp	986.17	986.34	0.77	229.7	<0.001
Sw + D + soil temp	986.11	986.28	0.89	358.4	<0.001
D + soil temp	990.4	991.5	0.88	530.7	<0.001
Soil temp	1,011.6	1,012.4	0.55	171.0	<0.001
Interior trees					
D	929.4	930.2	0.89	1,199.0	<0.001
D + soil temp	955.4	956.0	0.96	1,837.0	<0.001
Sw	968.8	969.07	0.80	548.8	<0.001
Sw + D	968.8	969.05	0.95	1,323	<0.001
Sw + soil temp	968.8	969.07	0.80	277.6	<0.001
Sw + D + soil temp	968.8	696.05	0.96	1,259	<0.001
Soil temp	978.1	978.9	0.52	155.3	<0.001

Models were based on 30-min intervals. Environmental variables included vapour pressure deficit (*D*; kPa), short wave radiation (Sw, W m^{-2}), and soil temperature at 20 cm (soil temp; °C). Sap flow values correspond to the cumulative 30-min sap flow per individual (cm^3). Rainfall was not included in this model as there was no rainfall during the 3-day period being modelled here. Grey shading corresponds to the minimum AIC$_c$ model
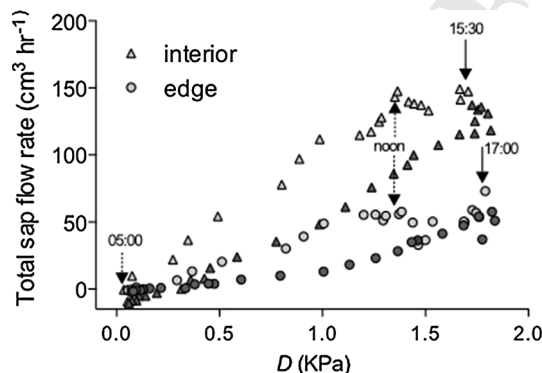

Fig. 6 Diurnal sap flow rates in edge and interior *P. mariana* trees (average of four individuals per location) in relation to **a** vapour pressure deficit (kPa) and **b** air temperature (°C) from Scotty Creek. The *looping patterns* seen here represent hysteresis and indicate a rate-dependent change during the diurnal time course of sap flow production. In this case, for both interior and edge *P. mariana* trees, the higher and lower sap flow rates seen are during the ramp up (morning; *light shading*) and ramp down (evening; *dark shading*) phase following peak sap flow rates during the day

inputs with models including Sw explaining between 60 and 80 % of variation. While *D* and Sw drove sap flow patterns, the rates themselves were driven largely by the ground conditions that the individual was experiencing. Lateral permafrost thaw and associated soil waterlogging (Baltzer et al. 2014) led to dramatic reductions in sap flow with edge trees having sap flow rates that were at least two-thirds less than those of the interior trees (Figs. 2, 3, 4). Similarly, seasonal thaw and active layer development drove seasonal reductions in sap flow, particularly in interior trees (Figs. 2, 3, 4, 5). This pattern is suggestive of a role for soil water limitations due to the coupled deepening of the water table and the frost table (Fig. 7; Table S1); however, further ecophysiological investigations of seasonal drought stress are warranted to verify this possibility. Thus, while microenvironmental variables serve as good predictors of diurnal and seasonal sap flow patterns, the quantity of water moving through the trees was largely determined by soil conditions, which in this system are tightly coupled with ground thaw processes.

Impacts of lateral permafrost thaw on sap flow in *P. mariana*

There were clear differences in diurnal, seasonal, and cumulative flow rates attributable to proximity to permafrost plateau edge (Figs. 2, 3, 4, 5). Edge trees showed marked declines in daily total sap flow rates compared to interior trees (Fig. 2) resulting in large cumulative differences in crown sap flow ($P = 0.0226$). In no instance (early vs. late season or fast- vs. slow-flow trees) diurnal sap flow rates higher were in edge than interior trees. The decrease in diurnal rates on edge sites was uniform (Figs. 3, 4) and suggests that lateral permafrost thaw and corresponding ground surface subsidence and soil waterlogging directly impact the root function and consequently stem sap flow in trees at the plateau–wetland margins. We found that the roots of *P. mariana* showed a similarly strong reduction in sap flow (Fig. 4), which appears to be driven by the adjacent bog conditions. Indeed, we measured sap flow on the roots of a single-edge tree on the bog and plateau sides of the tree for a 3-day period and found that the plateau side root was functioning normally while sap flow in the bog edge side root was 100-fold lower (data not shown) supporting the idea that reduced sap flow in edge trees is a function of the waterlogged bog conditions. Although *P. mariana* frequently occurs in sites that have relatively high water tables and poor soil aeration (Campbell 1980; Larsen 1982), the species has been shown to have a limited physiological capacity to cope with waterlogging (Islam et al. 2003; Islam and Macdonald 2004). Specifically, root hydraulic conductance in *P. mariana* has been shown to decrease when subjected to waterlogging (Islam and Macdonald 2004).

Table 2 Linear model regression statistics and AIC values from individual ARIMA models examining the influence of environmental variables on seasonal sap flow in edge and interior *P. mariana* trees during summer 2012 ($n = 2$ individuals per location)

Model	AIC	AIC_c	r^2	F	P
Edge trees					
Sw + D + air temp	*637.53*	*637.96*	*0.57*	*25.39*	*<0.001*
Sw + air temp	*637.65*	*638.08*	*0.57*	*37.63*	*<0.001*
Sw + D + air temp + soil temp	*637.77*	*638.2*	*0.62*	*23.21*	*<0.001*
Sw + Air temp + soil temp	*637.89*	*638.32*	*0.62*	*31.06*	*<0.001*
Sw + D + air temp + rainfall	*638.07*	*638.8*	*0.59*	*20.03*	*<0.001*
Sw + D + air temp + rainfall + soil temp	*638.44*	*638.87*	*0.64*	*19.17*	*<0.001*
Sw + D	*638.15*	*638.88*	*0.56*	*36.45*	*<0.001*
Sw + air temp + rainfall	*638.17*	*638.9*	*0.58*	*26.7*	*<0.001*
Sw	*638.26*	*638.99*	*0.56*	*73.9*	*<0.001*
Sw + air temp + rainfall + soil temp	*638.57*	*638.99*	*0.63*	*24.2*	*<0.001*
Sw + D + soil temp	*638.6*	*639.33*	*0.62*	*31.26*	*<0.001*
Sw + D + rainfall	*638.68*	*639.41*	*0.57*	*25.49*	*<0.001*
Sw + soil temp	*638.71*	*639.44*	*0.61*	*44.55*	*<0.001*
Sw + rainfall	*638.79*	*639.52*	*0.57*	*38.3*	*<0.001*
Sw + D + rainfall + soil temp	*639.14*	*639.87*	*0.63*	*24.26*	*<0.001*
Sw + rainfall + soil temp	*639.26*	*639.98*	*0.63*	*31.68*	*<0.001*
D	648.1	648.5	0.32	27.31	<0.001
Rainfall	664.3	664.8	0.28	22.41	<0.001
Interior trees					
Sw + D + air temp	*783.66*	*784.38*	*0.61*	*29.36*	*0.001*
Sw + air temp	*783.77*	*784.5*	*0.60*	*43.65*	*0.001*
Sw + D + air temp + soil temp	*783.92*	*784.65*	*0.78*	*50.49*	*0.001*
Sw + air temp + soil temp	*784.04*	*784.76*	*0.77*	*62.38*	*0.001*
Sw + D + air temp + rainfall	*784.93*	*785.66*	*0.65*	*25.79*	*0.001*
Sw + air temp + rainfall	*785.05*	*785.78*	*0.64*	*33.29*	*0.001*
Sw + D + air temp + rainfall + soil temp	*785.21*	*785.94*	*0.81*	*46.8*	*0.001*
Sw + air temp + rainfall + soil temp	*785.33*	*786.06*	*0.79*	*51.59*	*0.001*
Sw + D	*785.37*	*786.1*	*0.61*	*44.8*	*0.001*
Sw	*785.5*	*786.23*	*0.59*	*85.04*	*<0.001*
Sw + D + soil temp	*785.61*	*786.34*	*0.71*	*47.28*	*0.001*
Sw + soil temp	785.7	786.5	0.71	69.41	0.001
Sw + D + rainfall	786.66	787.38	0.65	34.99	0.001
Sw + rainfall	786.79	787.52	0.62	46.56	0.001
Sw + D + rainfall + soil temp	786.91	787.64	0.75	41.21	0.001
Sw + rainfall + soil temp	787.21	787.93	0.75	55.45	0.001
Rainfall	817.6	818.0	0.33	29.26	<0.001
D	817.3	818.1	0.27	21.63	<0.001

Environmental variables included shortwave radiation (Sw; W m^{-2}), vapour pressure deficit (*D*; kPa), daily rainfall (rainfall; mm), air temperature (air temp; °C), and soil temperature at 20 cm (soil temp; °C). Average cumulative daily sap flow (cm^3) was the dependent variable. Models excluding Sw were weaker; we include only the top models excluding Sw to demonstrate this. Italicized rows correspond to best-fit models

Reductions in sap flow attributable to lateral thaw ranged from 60 % to nearly 100 % in the edge trees suggesting an important role of the spatial distribution of the root system in relation to the degrading edge. An outstanding issue is how close to the edge of plateau a tree has to be to begin to experience a decline in water uptake and consequently canopy productivity. The rooting systems of black spruce extend laterally several metres from the stem (J. Baltzer, personal observation; and see Kajimoto et al. 2003 for *Larix gmelinii* on permafrost), and thus there is the potential for substantial edge effects with respect to whole tree physiological function and canopy water fluxes. This will become increasingly important as permafrost plateaus become more fragmented decreasing the plateau interior conditions (Baltzer et al. 2014). Although our sampling was restricted to a 1 ha region, tree ring studies from across the Scotty Creek basin have shown there to be strong radial growth reductions in *P. mariana* in response to permafrost thaw where growth was reduced by 50 % in trees occurring on plateau edges (Baltzer et al. 2014), suggesting a more general importance of the physiological processes documented here.
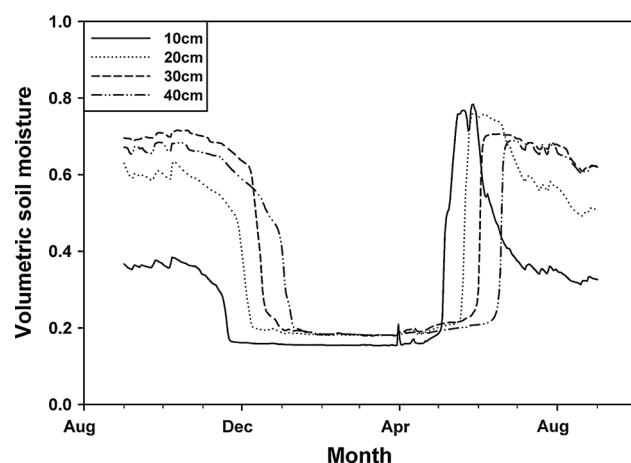
Fig. 7 Soil volumetric water content at 10-, 20-, 30-, and 40-cm depths in an adjacent permafrost plateau

622 Impacts of seasonal thaw on sap flow in *P. mariana*

623 At the measured plateau in Scotty Creek, active layer has
624 been thickening rapidly with average end of summer thaw
625 depth increasing from 60 to 110 cm over a 15-year period
626 of measurement on a single, degrading plateau (Fig. 1).
627 Thickening active layer is a common trend in high latitude
628 locations as air temperatures have warmed leading to
629 increased energy inputs into the soils (reviewed in Jor-
630 genson et al. 2010). Here, we use seasonal thaw processes
631 to assess the potential implications of this change from the
632 perspective of tree function. While all trees showed a
633 decline in sap flow in response to active layer thaw
634 (Fig. 5), frost table depth had a much more dramatic neg-
635 ative impact on trees occurring in the interior of the per-
636 mafrost plateaus as evidenced by a significant interaction
637 between plateau location and frost table depth (interaction
638 term in linear mixed model: $P = 0.0192$). While we did
639 not quantify the water status of the trees through the sea-
640 son, a reasonable explanation for the observed pattern is
641 reduced soil moisture availability. Early in the growing
642 season, the frost table is near the ground surface, the water
643 table is perched on the frost table, and soil moisture content
644 is high (Fig. 7; Quinton and Baltzer 2013). As the season
645 progresses, soil moisture is reduced as water is shed from
646 the plateaus into surrounding wetlands and in response to
647 the coupled deepening of frost table and water table
648 (Fig. 7; Table S1; Quinton and Baltzer 2013). The negative
649 response of sap flow rates in interior trees is thus likely a
650 function of the drying down of the upper soil layers in
651 which they are predominantly rooted (>95 % of *P. mari-
652 ana* roots in top 20 cm; Gale and Grigal 1987; Lieffers and
653 Rothwell 1987) though direct measures of drought stress
654 through the growing season are required to verify this idea.
655 Indeed, VWC in July and August was dramatically reduced
656 in the upper soil layers compared to May and June water

657 contents (Fig. 7). Similarly, the water table adjacent to the
658 sample trees deepened substantially through the summer, AQ4
659 particularly so in the plateau interiors (Table S1). In con-
660 trast, while some edge trees respond negatively to seasonal
661 thaw, this response is much weaker compared with interior
662 trees (Fig. 4; $P = 0.0192$ for interaction term between frost
663 table depth and location). This is likely because only a
664 portion of the roots of edge trees is experiencing interior
665 conditions (Fig. 8b), and rates of sap flow in edge trees are
666 already greatly reduced due to waterlogging of roots
667 extending past the plateau edge (Fig. 8b). While our
668 measured responses to seasonal thaw correspond with sap
669 flow reductions in Siberian *Larix* in response to vertical
670 permafrost thaw, the potential mechanism differs. Specifi-
671 cally, the Siberian study attributed reduced sap flow to
672 vertical thaw-induced soil waterlogging (Iijima et al. 2013)
673 as opposed to our proposed drying mechanism. These
674 differences may be attributable to the permafrost condi-
675 tions as the Siberian study site was on continuous perma-
676 frost where vertical thaw may simply lead to local
677 depressions of the ground surface and pooling of water
678 released from thawing permafrost. At Scotty Creek, the
679 hydraulic gradient from the elevated permafrost plateau to
680 the adjacent wetlands means that excess water drains from
681 the plateau (Quinton and Baltzer 2013). Whether system-
682 atic differences exist in the response of forests on different
683 types of permafrost (continuous vs. discontinuous) to ver-
684 tical permafrost thaw should be investigated. There has
685 been widespread documentation of reduced radial growth
686 or "browning" in high latitude boreal forests globally that
687 has been attributed to recent warming (e.g. Lloyd and Bunn
688 2007). The present evidence of reduced physiological
689 function in response to active layer depth is relevant in our
690 mechanistic interpretation of these trends.

Microenvironmental drivers of sap flow in *P. mariana* 691

692 Both vapour pressure deficit (D) and radiation (Sw) were
693 identified as important determinants of sap flow, which is
694 not unexpected, as it is well known that stomatal conduc-
695 tance and transpiration respond strongly to both of these
696 variables and indeed form the basis of commonly used
697 models of potential evapotranspiration (reviewed in Fisher
698 et al. 2011). Diurnal sap flow patterns seen here persisted
699 across the growing season, with similar patterns seen dur-
700 ing early (3–5 June) and late (July 30–1 Aug) summer in
701 the edge and interior trees. The similarity in flow patterns
702 between early and late periods in both locations suggests
703 that diurnal sap flow is linked with proximate environ-
704 mental factors at a finer scale, and are less dependent on
705 seasonal processes such as active layer thaw as compared
706 with the magnitudes of sap flow, which have clear corre-
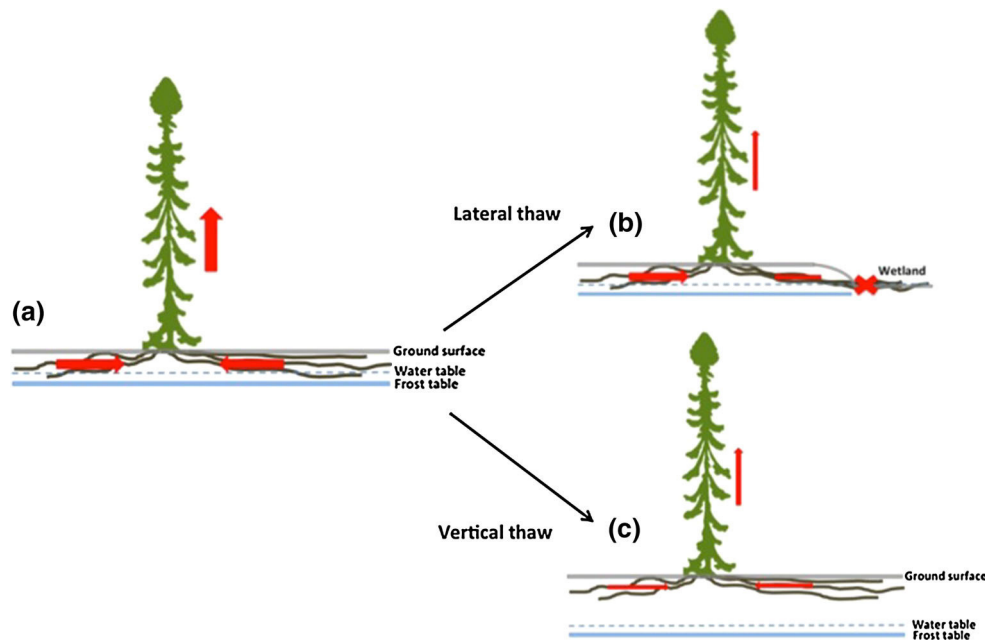707 spondence with permafrost and seasonal thaw conditions.

Fig. 8 Conceptual diagram of sap flow responses of *P. mariana* to lateral and vertical permafrost thaw processes in a boreal peatland. Rates of sap flow are depicted by *red arrows* and the size of the *arrow* denotes the rates of flow. **a** Shallow roots have access to sufficient soil moisture due to shallow active layer. **b** Lateral thaw leads to ground surface subsidence and soil waterlogging reducing the functionality of a portion of the rooting systems and as a consequence whole tree sap flow. **c** Vertical thaw leads to a deeper frost table, which reduces soil moisture available for shallow roots due to the correspondingly deeper water table and thereby reduces water uptake

708 For diurnal sap flow patterns, the model containing D was
709 the single best model (Table 1). The strong association
710 between half hourly rates of sap flow and D at the diurnal
711 scale is consistent with previous findings in boreal systems
712 (e.g. Blanken et al. 1997; Hogg et al. 1997) and other
713 coniferous species (e.g. Ford et al. 2007). Being a high
714 latitude system, during the growing season days are very
715 long (18–22 h) and the entire period of peak sap flow
716 during the day occurs when solar radiation is not limiting.
717 Despite this, we see reductions in sap flow as D approaches
718 its maximum (Fig. 3); sap flow increases approximately
719 linearly with D to between 1 and 1.5 kPa after which it
720 levels off or decreases slightly with further increases in
721 D (Fig. 3). This is consistent with studies from tropical,
722 temperate and boreal systems and suggests gradual closure
723 of stomata as the D of ambient air increases (reviewed in
724 Hogg et al. 1997), likely as a mechanism for maintaining
725 the hydraulic integrity of the system by minimising water
726 loss from the system during periods of high D (Zeiger
727 1983). Stem sap flow essentially lags canopy transpiration,
728 which in turn is modelled as a function of D (Whitehead
729 and Jarvis 1981). At the diurnal scale, D explained 78 and
730 89 % of variation in sap flow in edge and interior trees,
731 respectively (Table 1) and these tight relationships are
732 visible in Figs. 3 and 4. Ford et al. (2005) similarly found
733 that diurnal patterns of sap flow in loblolly pine (*Pinus*
734 *taeda* L.) trees closely followed D during the growing
735 season in a plantation site from the Southeastern USA and

736 that photosynthetically active radiation (PAR) was a
737 weaker predictor of sap flow than D.
738 In contrast, across the 2-month measurement period, Sw
739 was a much better predictor of cumulative daily sap flow
740 than was D; in fact, when Sw was removed from the
741 models, the predictive capacity of model was roughly
742 halved (Table 2). The important role of energy in driving
743 transpiration processes is clear; under most conditions,
744 increased energy inputs mean increased potential evapo-
745 transpiration (reviewed in Fisher et al. 2011) as energy
746 drives the conversion of liquid water to vapour. In the
747 2-month measurement period, there was no clear trend in
748 Sw through the season; however, frequent precipitation and
749 associated cloudiness led to substantial variability in Sw
750 and correspondingly large reductions in cumulative daily
751 sap flow (Fig. 2; Table 2). This was particularly evident
752 during June where precipitation events were frequent. It is
753 notable; however, that while sap flow decreases dramati-
754 cally at the start of July there was no corresponding
755 decrease in Sw (Fig. 2).

756 Plant–soil feedbacks in thawing landscapes

757 Transpiration is a fundamental part of the hydrological
758 cycle and as such changes in transpirational water fluxes
759 control, in part, the moisture content of the soil. In this
760 case, ground thaw-driven changes in soil moisture (either
761 water limitation or excess) reduce sap flow, with the

potential to feed back on soil moisture. In the case of lateral permafrost thaw, ground surface subsidence combined with water released from thawing permafrost results in high soil moisture at the edges of plateaus (Baltzer et al. 2014), reducing root function in *P. mariana* (Fig. 4), which in turn limits sap flow in the tree (Fig. 8). This should result in a positive plant–soil feedback (permafrost thaw/subsidence →↑ soil moisture →↓ transpiration →↑ soil moisture →↑ permafrost thaw). This is driven by the large differences (3 orders of magnitude) between air and water in thermal conductivity, which leads to wet soils having higher thaw rates than drier soils (Wright et al. 2009). Whether sap flow responses to seasonal thaw emulate the longer-term process of vertical thaw is outstanding but presumably, a thicker thawed layer earlier in the season will have important consequences on tree function and hydrological cycling in this system. Assuming responses of trees to seasonal thaw and vertical permafrost thaw are comparable, surface soil drying associated with active layer thickening can be expected to drive reductions in sap flow (Figs. 2, 4, 5, 8). The potential feedbacks here are less clear but given the lower sap flow rates later in the season, we may expect positive feedbacks on soil moisture at the frost table with implications for permafrost thaw (permafrost thaw → deeper active layer → deeper water table → dry surface soils →↓ transpiration →↓ water uptake →↑ soil moisture at the frost table →↑ permafrost thaw). Alternatively, trees may respond plastically through time to increasing active layer thickness by altering root distribution through the soil profile thereby maintaining function despite changing active layer depth (Lieffers and Rothwell 1987). Understanding the plant–soil feedbacks will facilitate improved prediction of the hydrological and productivity responses of high latitude systems to continued warming and associated permafrost thaw.

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