

RESEARCH ARTICLE

Fine-scale influences on thaw depth in a forested peat plateau landscape in the Northwest Territories, Canada: Vegetation trumps microtopography

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Abstract

The influence of vegetation and microtopography on fine-scale variability of thaw depth is largely unknown but potentially important for improving modeling of ecosystem–permafrost interactions. To elucidate their influence, we measured tree density, shrub cover and cryptogam presence (lichen and bryophyte) on forested permafrost peat plateaus in the discontinuous permafrost zone in the southern Northwest Territories, Canada. Greater tree density was associated with shallower thaw depth (approximately one quarter of the variance), whereas shrub cover had a negligible influence on thaw depth. Cryptogam species influenced thaw depth, with greater thaw depth associated with *Sphagnum* than with *Cladonia* (a difference on the order of 10%). Greater thaw depth occurred beneath hummocks than beneath hollows (a difference also on the order of 10%). Together, canopy cover, cryptogam species and microforms contribute to a variation of roughly half the variance in thaw depth in the peat plateau landscape.

KEYWORDS

boreal forest, microtopography, permafrost, plants, species, vegetation ecology

1 | INTRODUCTION

While climate is the primary factor determining permafrost presence¹, biotic and abiotic factors—including hydrology, snow cover, topography, soil properties, organic matter accumulation and vegetation—have been considered of equal importance.² Rising air temperature due to climate change is not only contributing directly to permafrost degradation through warming, but some factors affecting permafrost are also changing in response to current environmental change, including vegetation.³ Thus, understanding high-latitude permafrost dynamics and distribution in the face of climate change must encompass biotic factors such as vegetation.

The influence of vegetation on thaw depth has been demonstrated for associations of species at the community level^{4,5} and for tree, shrub and bryophyte cover. When vegetation and organic material are removed, the depth of thaw may be meters greater than at similar intact vegetated sites.⁶ Greater vegetation cover as indicated by greater optically measured leaf area index (LAI) can be associated with shallower thaw depth.⁷ Shrub cover has been linked both to greater thaw depth attributed to greater snow accumulation⁸ and to shallower

thaw depth associated with increased shading.⁹ On the ground, greater bryophyte thickness has led to a decrease in thaw depth as seen through experimental manipulation of mat thickness¹⁰ and observational measurements⁷, while complete bryophyte removal has led to increased ground heat flux.¹¹ Together, these studies show that the effects of vegetative cover on permafrost differ by type. However, none of these studies has distinguished the effects by vegetative stratum (vertical layering) separately nor among different species in each plant functional type, differences which may occur due to different physical properties regulating soil temperature and moisture regimes of particular species.

In addition to vegetation, fine-scale (< 1 m²) variations in thaw depth are influenced by microtopography. This involves small differences in elevation and microform types, such as hummocks (generally small mounds of organic soil on the order of 10–30 cm high and 30–50 cm across) and hollows (spaces between hummocks). Soil temperature can be greater and the active layer deeper in hummocks compared to nearby hollows, while the overriding trend is that the frost table is parallel to the surface.^{5,12} However, the reverse trend can be observed. For example, Wright et al.¹³ recorded the greatest thaw depths in the two most

pronounced hollows in their dataset in peat plateaus. Many site-specific conditions could be responsible for the observed differences, such as hummock size, hydrology and vegetative cover.

This field study aims to understand the influence of vegetation and microtopography on fine-scale variations in thaw depth on forested permafrost peat plateaus. By observing fine-scale differences, it is possible to isolate controlling factors and understand the influence of each vegetation stratum (vertical layer). This detailed approach may shed light on the key vegetative and microtopographic factors driving broader scale differences in thaw depth, which is an important prerequisite for improving land surface scheme and ecosystem model performance at high latitudes (eg, Porada et al.¹⁴).

Our objectives are (i) to quantify the effect of vegetation strata on thaw depth and (ii) to evaluate the link between microtopography and thaw depth. Accordingly, we addressed three questions. First, what are the relative influences of tree and shrub cover on thaw depth? Based on the findings of Camill¹⁵, who found permafrost formation near trees, and Williams et al.¹⁶, who noted permafrost disappearance with the loss of trees, we hypothesize that greater tree cover will lead to shallower thaw depth. Conversely, greater shrub cover will result in more snow accumulation, leading to greater thaw depth, as observed by Pelletier.⁸ Second, does thaw depth vary depending on bryophyte and lichen cover at the species level? As found by Wright et al.¹³, we anticipate finding shallower thaw depth below lichens than below bryophytes. In addition, we expect to find differences among species given that factors, such as moisture retention capacity and albedo, vary by species.^{17,18} Third, do microforms and relative elevation influence thaw depth? We anticipate that hummocks and higher relative elevations will be associated with greater thaw depth, as observed in most previous studies (eg, Minke et al.⁵, Sullivan et al.¹²).

2 | MATERIALS AND METHODS

2.1 | Study area and sampling design

The research was conducted at the southern limit of the discontinuous permafrost zone in the southern Northwest Territories (NWT), 50 km south of Fort Simpson (61°18'N, 121°18'W) (Figure 1A). The region around Fort Simpson is characterized by a dry (388 mm mean annual precipitation, 48% as snowfall), cold continental climate (mean annual air temperature of -4.8°C) (Environment Canada²¹ for 1981–2010). The study area (1.4 × 1 km), in the southern portion of the Scotty Creek watershed (~ 152 km²), is composed of forested dry peat plateaus (~ 40%), channel fens (~ 25%), open collapse bogs (~ 25%) and lakes (~ 10%), with permafrost only beneath the peat plateaus (data from Chasmer et al.²⁰, percentages apply to specific study area). Organic soil up to 8 m in the peat plateaus overlies a sandy mineral soil layer.²²

We established 78 sites (Figure 1B) on the peat plateaus, their coordinates randomly selected using the random number generator (function *rand*) in Excel 2007 (Microsoft, Redmond, WA) from a cyclic grid of points with 10–15–25 m spacing. All sites were at least 5 m from plateau edges (pre-determined positions were moved away from the edge if closer than 5 m to an edge) to avoid edge effects on thaw depth.^{13,23} The sites were navigated to with a handheld GPS (accuracy 7–8 m) in the field (Garmin ETREX 530, GARMIN International Inc., Olathe, KS). Of the 78 sites, six were excluded from subsequent analyses: three were considered outliers due to the dominance of species present there that were not found in other sites and three others due to extreme thaw depths observed (more than double those of the other sites). Each site had six plots, with four plots arranged on the corners of a 2 × 2 m square and two plots on one

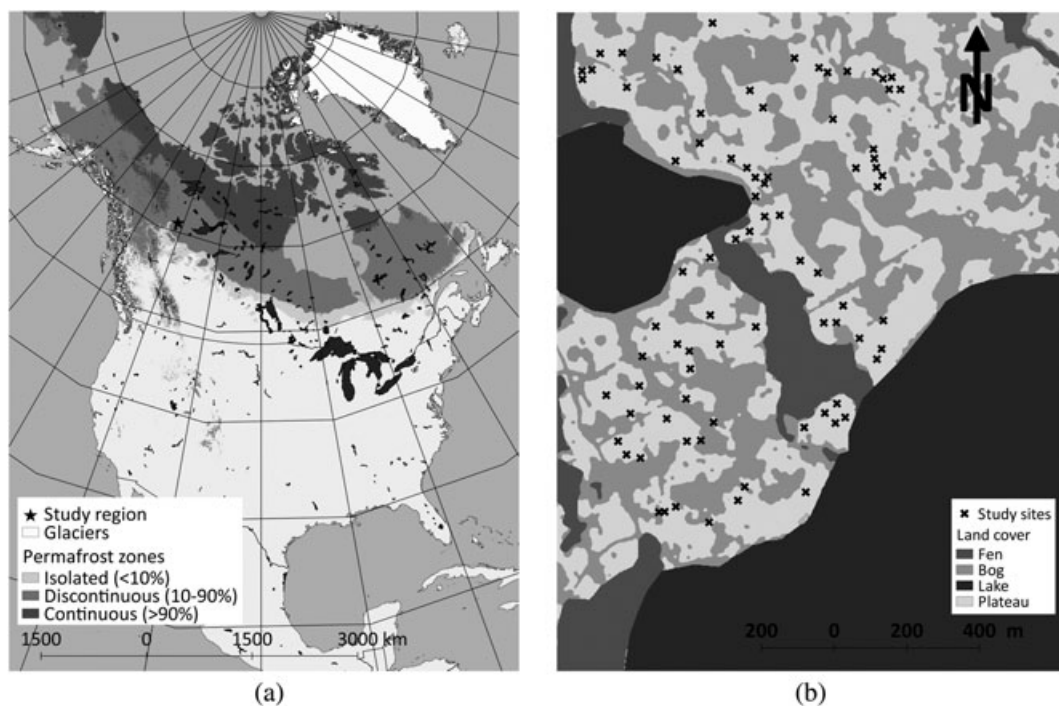


FIGURE 1 (a) location map of study area and (b) plan of 78 sites. Permafrost distribution in A is based on Gruber.¹⁹ Land cover classification in B from Chasmer et al.²⁰ (map projection NAD 1983 UTM zone 10)

randomly chosen hummock and one hollow within a 3 m radius of the center of each site (Figure 2A).

2.2 | Field methods

At the center of all six plots at each site, we measured thaw depth and water-table position below the ground surface over a 2-week period in August 2013 (Figure 2B). We measured thaw depth with a graduated steel rod inserted into the ground until resistance was met, which we could safely judge as the frost table as large roots and rocks were absent in this landscape. We ascertained that we had not reached a layer of partially frozen material or other minor obstructions by an additional push on the frost probe and listening for a “clunking sound.” The ground surface was defined as the bottom of the living layer of cryptogams as judged by the transition from “green” to “brown” (for bryophytes) or “white” to “black” (for lichens).

We used the point-centered quarter method to estimate tree density around each plot.²⁴ We split a 3-m-radius circle around each plot center into four quarter-circle quadrants (Figure 2B). We measured the distance from plot center to the nearest tree greater than or equal to 1.3 m in height in each quadrant²⁴ and noted diameter at breast height (DBH), ie, 1.3 m, and species. In summer 2014, at half of the plots with trees further than 3 m away from the plot center ($n = 37$), we returned to measure the distance to the nearest tree beyond 3 m. In calculating the average distance for those plots with a tree greater than 3 m away for which the exact distance remained unmeasured, we substituted 4 m (the average measured distance of trees beyond 3 m) as the value for the distance-to-trees and we used 3.5 cm for DBH (average DBH for trees in the study area).

Over a 25×25 cm quadrat centered on each plot center, we visually estimated vegetation cover including tree branches to species level (below 1.3 m in height) (Figure 2B). We also noted cryptogam species at plot center and cryptogam layer thickness (the depth from the living surface to the bottom of the living layer). Common cryptogam species (more than two occurrences) were identified to morphotype in the field and later identified to species.

For uncommon species where reliable field identification was not possible, the following taxonomic categories were used instead of species: *Salix* spp., *Polytrichum* spp., acrocarp moss and unidentified lichen (these represented <1% of cover). Vascular plant identification methodology is described in Garon-Labrecque et al.²⁵ Cryptogam identification was based on Ireland,²⁶ Faubert^{27–29} and Brodo et al.³⁰ Plant nomenclature followed Brouillet et al.³¹ for vascular plants, Faubert^{27–29} for bryophytes and Esslinger³² for lichens. Vouchers were deposited in the National Herbarium of Canada bryophyte (CANM) and lichen (CANL) collections at the Canadian Museum of Nature.

To characterize microtopography, a microform category was attributed to each plot and relative elevation was measured at plot center. Each plot was classified as either hummock, hummock side, hollow or flat, where “flat” referred to areas without a pronounced curvature over at least 1×1 m. Hummocks and hollows were further subdivided into “well-rounded” and “irregularly shaped” categories based on their size and shape, where well-rounded hummocks were distinct rounded protrusions in the landscape around 20 cm in height³³ and irregularly shaped hummocks were larger than 20 cm with flatter or uneven tops. Relative elevation was determined by measuring the distance between the ground surface at the center of each plot and a fixed arbitrary height at each site at which a string was suspended and leveled between two metal rods. Relative elevation was calculated by determining the height above the lowest point among the six plots in each site. For hummock sides, we also measured slope angle and aspect with a compass and integrated inclinometer.

We also collected conventional physical measures related to thaw depth, which are described in detail in the Supporting Information, Appendix S1. Briefly, LAI was measured optically with an LAI-2200 plant canopy analyzer (LI-COR Biosciences, Lincoln, NB) at each plot as a complementary method to characterize vegetative cover. Soil temperature at 15 cm depth was recorded continuously over a year with HOBO Pendant temperature sensors (Onset, Bourne, MA) at 14 sites as another metric for the soil thermal regime. Volumetric soil moisture content was measured at each plot

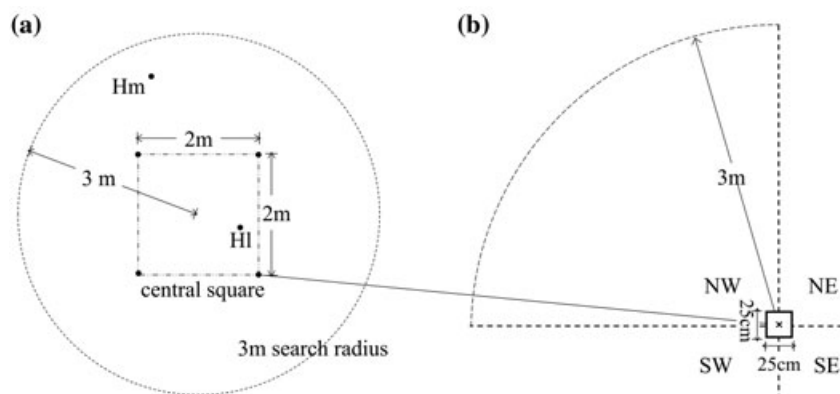


FIGURE 2 Design layout of field experiment. (a) site layout of six plots. Four fixed plots (●) were located at the corners of a 2×2 m central square. Two plots (Hm = hummock, Hl = hollow) were located randomly within a 3 m search radius of site center. (b) detailed layout of a plot with one of four tree quarter circle quadrants with 3 m radius illustrated, including 25×25 cm quadrat (□) around plot center. The quadrants were used to select trees for distance-to-trees and DBH (diameter at 1.3 m height) measurements. The plots were used for the vegetation percent cover estimations and categorization of the microtopography. Thaw depth, water-table depth, cryptogam thickness, relative elevation, slope, aspect and cryptogam species measured at plot center

using a portable soil moisture probe (Hydrosense II, Campbell Scientific, Logan, UT) to capture an aspect of thermal conductivity in the soil column. We also conducted snow surveys at 15 sites in the winter as thick snow cover insulates the ground against low winter temperatures.

2.3 | Data analysis

All statistical analyses were performed in R 3.1.0³⁴ using the following packages: *vegan* 2.0–10,³⁵ *party* 1.0–25,³⁶ *gvlma*³⁷ and *gplots* 2.14.2.³⁸

2.3.1 | Plant communities

We performed a correspondence analysis using the chi-square dissimilarity measure with species percent cover as inputs to visualize the similarity among sites ($n = 72$). The percent cover values used were the site-level averages of the six plots for those species that occurred in at least two sites. In addition, we used a K-means clustering approach³⁹ to divide the sites into three distinct plant communities with the function *cascadeKM()* from the *vegan* package.³⁵ To give equal weight to actual percent cover, we used raw data without transformations and the Euclidean distance measure.

We used an unbalanced one-way ANOVA to test for differences in thaw depth at the site level ($n = 72$) by plant community and chose the number of groups (plant communities) according to the maximum number that maintained statistically significant differences in thaw depth among groups with Holm's correction for multiple tests.³⁹

2.3.2 | Vegetation and microtopography contributions to thaw depth

We built a conditional inference tree at the plot level ($n = 432$ plots), with thaw depth as the response variable and distance-to-trees, DBH, shrub cover (which included occasional tree branch cover), relative elevation, four cryptogam categories, cryptogam layer thickness and six microform types as the input variables. The four cryptogam categories were *Sphagnum* (all species), *Cladonia* (all species), other bryophytes and absence of cryptogams (litter). We used the *ctree()* algorithm in the *party* package to construct the conditional inference tree. The *ctree()* algorithm recursively selects input variables with the strongest association with the response variable until the null hypothesis of independence between the remaining input variables and the response variable cannot be rejected at $P < 0.05$.³⁶ To validate the results of the decision tree (which are known to be unstable), random forest analysis (ie, multiple decision trees) was run with the function *cforest()* and variable importance computed for each input variable. The conditional inference tree approach is suited to cases with mixed variable types and also to modeling nonlinear and nonadditive relationships.⁴⁰

The relationship between the quantitative input variables retained in the decision tree and thaw depth was further examined through site-level simple linear regression analyses. Appropriate transformations of data were performed before regression to meet the assumptions of normality (skewness and kurtosis) and

homoscedasticity required for linear regression analysis. The validity of those assumptions was verified with the function *gvlma()* from the package *gvlma*.

2.3.3 | Cryptogam and microtopography analyses

For the analysis of the cryptogam at plot center data at the species level, we performed an unbalanced one-way ANOVA by plant community, comparing the thaw depth for those cryptogam species that occurred in more than three plots as well as litter occurrences. For the ANOVAs, instead of comparing cryptogam species to raw thaw depth values, we used the residuals of simple linear regression analyses of thaw depth against vascular vegetation. The use of residuals excludes the effect of vascular vegetative cover (given the preference of each species for various degrees of shading) and isolates the influence of the cryptogam cover in the analysis.

To determine the influence of vegetation and microform on thaw depth, we used an unbalanced two-way ANOVA and the associated pair-wise analyses with microforms and cryptogams. We also analyzed microtopography at a finer scale for hummock sides. We included slope (degrees), aspect in northness (north–south) and aspect in eastness (east–west) (calculated through trigonometric transformations⁴¹) in addition to relative elevation in a multilinear regression analysis. An additional simple linear regression analysis was conducted between thaw depth and relative elevation for all microforms within each dominant genus.

3 | RESULTS

3.1 | Vegetation

The peat plateaus in the study area are black spruce woodlands where Labrador tea (*Rhododendron groenlandicum*) is the dominant shrub. These trees were small (average canopy height between 3 and 8 m), sparse and characterized by short stunted branches (usually 30–50 cm, sometimes up to 200 cm long) along a central upright or leaning trunk. The shrubs (around 50 cm tall with an average cover of 42%) were mostly ericaceous species, with Labrador tea present in all sites. Herbaceous cover was minor, representing less than 1% of total cover. For a more exhaustive list of vascular plant species present in the area, refer to Garon-Labrecque et al.²⁵ The ground was almost entirely covered by cryptogams (average cover around 80%). In contrast to the nearby saturated bogs and fens, the peat plateaus were very dry, with less than 2 cm of water noted above the August frost table. Most of the study area was characterized by a pronounced microtopography of hummocks and hollows (10–30 cm height difference) spaced 50–100 cm apart.

3.2 | Plant communities

The correspondence analysis of species percent cover data of shrubs ($n = 9$), herbs ($n = 3$) and cryptogams ($n = 15$) illustrates the differences among sites (Figure 3). The total inertia was 1.281, and the first and second axis explained 20% and 9% of the variance respectively. In addition, a K-means partitioning was used to group the sites into three plant communities. As the dominant vascular

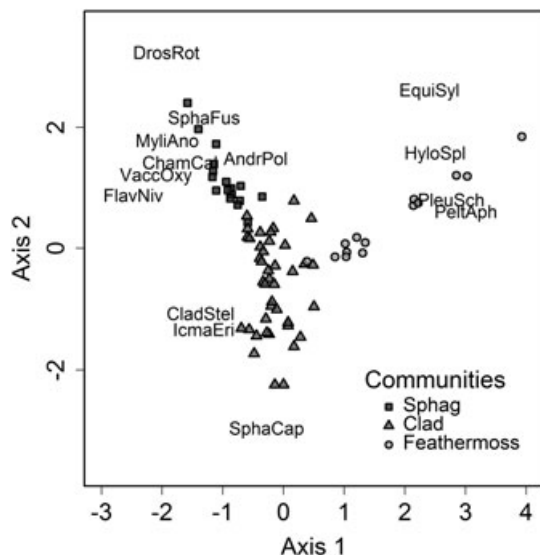


FIGURE 3 Correspondence analysis of vegetation composition using the chi-square dissimilarity measure among sites based on raw species percent cover. Shapes indicate K-means group. Labels show indicator species for each group. (VaccOxy = *Vaccinium oxycoccos*, ChamCal = *Chamaedaphne calyculata*, AndrPol = *Andromeda polifolia*, DrosRot = *Drosera rotundifolia*, EquiSyl = *Equisetum sylvaticum*, SphaFus = *Sphagnum fuscum*, HyloSpl = *Hylocomium splendens*, MyliAno = *Leiomylia anomala*, FlavNiv = *Flavocetraria nivalis*; SphaCap = *Sphagnum capillifolium*; CladStel = *Cladonia stellaris*; IcmaEri = *Icmadophila ericetorum*; PleuSch = *Pleurozium schreberi*, PeltAph = *Peltigera aphthosa*)

vegetation was similar in all groups (tree canopy of black spruce and shrub layer of Labrador tea), the three groups were best differentiated by the dominant cryptogam cover and were given the following names: *Sphagnum fuscum* (Sphag), *Cladonia* (Clad) and feathermoss (Figure 3). The correspondence analysis demonstrated that the sites in the feathermoss community were clearly different from the Sphag and the Clad sites along the first axis, while the Sphag and the Clad sites were dispersed along the second axis, following a gradient with overlap between K-groups (Figure 3). In addition to the striking differences in cryptogam species cover, the plant communities had somewhat different tree canopy structure and the feathermoss communities lacked a distinct microtopography. The trees in the feathermoss sites were relatively large (DBH = 4 cm vs. DBH = 3 cm in the other two communities), tall (average height = 8 m compared to 3 m elsewhere; data from Chasmer et al.²⁰) with relatively long branches (100–200 cm compared to 30–50 cm elsewhere). Also, tree cover was less dense in the Sphag sites (4400 trees/ha or distance-to-trees 1.2 ± 0.045 m, mean \pm SE) compared to the Clad sites (6900 trees/ha or distance-to-trees 1.5 ± 0.095 m, mean \pm SE). For a full list of species present with percent cover by plant community, see Table 1.

Significant differences in thaw depth were found among the three plant communities identified by the K-means clustering approach ($P < 0.001$; ANOVA). The feathermoss group (14 sites) had the shallowest thaw depth (43 ± 1.0 cm, mean \pm SE) followed by the Clad group (41 sites) at 47 ± 0.7 cm and the Sphag group (17 sites) at 53 ± 1.8 cm.

3.3 | Vegetation and microtopography contributions to thaw depth

The average thaw depth recorded was 47.7 ± 0.7 cm (mean \pm SE). The average thaw depth range within sites (ie, between the plot with the greatest thaw depth and that with the shallowest within each site) was 28 cm, whereas the range between the site with the shallowest thaw depth (at 37 cm) and the site with the greatest thaw depth (at 67 cm) was only slightly more. Thus, the high intrasite variability allowed us to consider all plots as sufficiently independent samples within each plant community for the analyses.

In the conditional inference tree analysis at the plot level that included distance-to-trees, DBH, shrub cover, relative elevation, cryptogam categories, cryptogam layer thickness and microforms, the selected input variables were distance-to-trees, cryptogam categories and microforms. The random forest analysis confirmed that those three were the most important variables and suggested that the influence of cryptogam thickness was comparable to the influence of microforms (Table 2). At the site level, distance-to-trees explained 17% of the variation in thaw depth ($r^2 = 0.17$; $P = 0.0002$; simple linear regression; Figure 4). Albeit with a weaker relationship, thaw depth also decreased with increasing LAI ($r^2 = 0.07$; $P = 0.025$; simple linear regression); see Appendix S1 for details on methodology. The contributions of cryptogam categories and microforms to the variation in thaw depth are explored in detail below.

3.4 | Cryptogam and microtopography analyses

To analyze the influence of the cryptogam species present at plot center on thaw depth, we compared the data among the Sphag and the Clad sites together and the data for the feathermoss community on its own because the Sphag and Clad communities shared sufficiently similar vegetation canopy characteristics (tree size and shape) with similar microtopography (see section 4.1). In the Sphag and Clad sites, there were significant differences among thaw depths associated with species ($P < 0.0001$; one-way ANOVA; $n = 347$; Figure 5A). In addition to significant differences in thaw depths between *Sphagnum* and *Cladonia* species, *Sphagnum fuscum* was significantly different from *Ptilidium ciliare* and from points lacking cryptogam presence (ie, only litter) ($P = 0.05$; Tukey honest significant difference [HSD]). In the feathermoss community, we found that the thaw depth associated with each species was not significantly different from each other ($P = 0.50$; one-way ANOVA; $n = 84$; Figure 5B). Given that the feathermoss sites were dominated by the two feathermoss species, with few occurrences of other species ($n < 35$), the sample size was too small to draw any definite conclusions comparing the feathermoss species to other species, although it appears thaw depth is shallower below feathermoss species compared to *Sphagnum* species within a given plant community.

Analyses of microtopography influence (microforms and relative elevation) on thaw depth were limited to the Sphag and Clad sites as the ground surface was relatively flat in the feathermoss sites. In a two-way ANOVA with microform and cryptogam, both were significant but not their interaction (cryptogam: $P < 0.0001$, microform: $P = 0.03$; two-way ANOVA). In the pair-wise analyses, while *Sphagnum*

TABLE 1 Tree variables (diameter at breast height [DBH] [diameter at 1.3 m height], distance-to-trees) and average percent cover by species over 25 × 25 cm quadrat for each plant community determined by K-means partitioning of raw species cover split by functional groups. Average cover per species presented here was calculated based on the 72 sites retained in the analyses

	Authority	Occurrences (of 72 sites)	Plant community		
			Sphag (n = 17 sites)	Clad (n = 41 sites)	Feathermoss (n = 14 sites)
Total area (m ²)			6.4	15.4	5.3
DBH (cm)			3.1	3.4	4.1
Tree density (trees/ha)			4400	6900	5100
Litter (%)			16.0	22.7	36.4
Vascular vegetation					
Trees (%)					
<i>Betula occidentalis</i>	Hooker	1	–	–	0.7
<i>Larix laricina</i>	(Du Roi) K. Koch	1	–	–	0.3
<i>Picea mariana</i>	(Mill.) Britton, Sterns & Poggenb	67	6.9	10.1	10.0
Shrubs (%)			36.3	46.8	33.6
<i>Andromeda polifolia</i>	L.	11	0.3	0.1	–
<i>Betula glandulosa</i>	Michx.	3	0.2	< 0.1	0.2
<i>Chamaedaphne calyculata</i>	(L.) Moench	31	2.2	0.5	0.5
<i>Empetrum nigrum</i> subsp. <i>hermaphroditum</i>	(Lange ex Hagerup) Böcher	4	–	0.2	< 0.1
<i>Rhododendron groenlandicum</i>	(Oeder) Kron & Judd	72	20.8	32.1	25.1
<i>Rhododendron tomentosum</i>	Harmaja	14	1.0	0.4	–
<i>Rubus chamaemorus</i>	L.	54	4.5	4.4	0.6
<i>Vaccinium oxycoccus</i>	L.	39	0.9	0.3	–
<i>Vaccinium uliginosum</i>	L.	2	–	< 0.1	–
<i>Vaccinium vitis-Idaea</i>	L.	71	6.8	8.7	7.0
<i>Salix</i> spp.	NA	1	–	–	0.3
Herbaceous plants (%)			0.3	0.3	0.9
<i>Drosera rotundifolia</i>	L.	9	0.2	< 0.1	–
<i>Equisetum sylvaticum</i>	L.	3	< 0.1	–	0.4
<i>Geocalium lividum</i>	(Richardson) Fernald	16	0.1	0.25	0.3
<i>Maianthemum trifolia</i>	(L.) Sloboda	1	–	< 0.1	–
<i>Poaceae</i> spp	NA	1	–	–	0.1
<i>Pyrola asarifolia</i> subsp <i>asarifolia</i>	Michx.	1	–	–	< 0.1
Bryophytes (%)			61.4	33.8	51.0
<i>Dicranum undulatum</i>	Schrad. ex Brid	20	0.8	0.7	0.2
<i>Hylocomium splendens</i>	(Hedw.) Schimp	28	–	1.6	25.4
<i>Leomylia anomala</i>	J. J. Engel & Braggins	41	4.2	1.0	0.5
<i>Pleurozium scheberi</i>	(Willd. ex Brid.) mitt	29	1.1	3.0	16.8
<i>Polytrichum</i> spp.	NA	1	–	0.2	–
<i>Ptilidium ciliare</i>	(L.) Hampe	37	1.2	2.7	6.6
<i>Sphagnum capillifolium</i>	(Ehrh.) Hedw	25	0.9	12.1	0.8
<i>Sphagnum fuscum</i>	(Schimp.) H. Klinggr	48	53.2	12.4	–
Acrocarp moss	NA	7	< 0.1	0.2	0.7
Lichens (%)			30.0	44.5	14.5
<i>Cladonia amaurocraea</i>	(Flörke) Schaerer	3	0.3	0.2	–
<i>Cladonia arbuscula</i> subsp. <i>mitis</i> (= <i>Cladonia mitis</i>)	(Sandst.) Ruoss	60	10.5	17.1	5.5
<i>Cladonia stellaris</i>	(Opiz) Pouzar & Vězda	34	2.4	7.4	0.7
<i>Cladonia stygia</i>	(Fr.) Ruoss	64	14.9	17.3	5.5
<i>Cladonia uncialis</i>	(L.) weber ex F. H. Wigg.	14	0.7	1.1	–
<i>Flavocetraria nivalis</i>	(L.) Kärnefelt & A. Thell	5	1.0	0.1	–

(Continues)

TABLE 1 (Continued)

	Authority	Occurrences (of 72 sites)	Plant community		
			Sphag (n = 17 sites)	Clad (n = 41 sites)	Feathermoss (n = 14 sites)
<i>Icmadophila ericetorum</i>	(L.) Zahlbr.	3	0.2	0.3	–
<i>Peltigera aphthosa</i>	(L.) Willd.	15	–	0.4	2.3
<i>Peltigera neopolydactyla</i>	(Gyel.) Gyel.	1	–	< 0.1	–
Unidentified lichens	NA	13	< 0.1	0.5	0.6

TABLE 2 Ranked variable importance as determined by the random forest analysis

Variable	Variable importance
Cryptogam	26.7
Distance-to-trees	12.1
Microform	10.9
Cryptogam thickness	9.1
Shrub cover	3.6
Relative elevation	1.1
DBH (diameter at 1.3 m)	–0.4

and *Cladonia* were significantly different ($P < 0.0001$; Tukey HSD), none of the microform categories were significantly different from each other ($P > 0.05$; Tukey HSD), with the greatest difference between well-rounded hollows and well-rounded hummocks ($P = 0.096$; Tukey HSD). Comparing extremes, the difference between *Cladonia* in a hollow (40.8 ± 1.2 cm) and *Sphagnum* at the top of a hummock (57.0 ± 1.2 cm) was approximately 16 cm (Figure 6). Within *Sphagnum* and within *Cladonia* side of hummocks, relative elevation, slope and aspect had no influence on thaw depth ($R^2 = 0.009$; $P = 0.96$; multilinear regression). In addition, isolating relative elevation to confirm the results of the conditional inference tree analysis, a simple linear regression between thaw depth and relative elevation for all

microforms within each dominant genus revealed a lack of relationship for both genera: *Sphagnum* ($r_s^2 = 0.003$; $P_s = 0.55$; simple linear regression) and *Cladonia* ($r_c^2 = 0.011$; $P_c = 0.16$).

The relationships between the conventional physical measurements with thaw depth were generally weak (Appendix S1). No evident relationship using a simple linear regression was found between thaw depth and annual soil temperature (T_s) at 15 cm depth ($r^2 = 0.03$; $P = 0.53$). Comparing the cryptogam genera, *Sphagnum* had the highest thawing degree days (1320 thaw degree days [TDD]; $n = 4$) relative to *Cladonia* (820 TDD; $n = 6$), while mean winter temperatures indicated the reverse. In a two-way ANOVA with microform and cryptogam related to soil moisture, soil moisture was significantly different depending on both microform and cryptogam at 5 cm depth (cryptogam: $P < 0.0001$, microform: $P = 0.002$; two-way ANOVA; Figure S2), whereas only microform led to a significant difference at 15 cm depth (cryptogam: $P = 0.975$, microform: $P < 0.0001$; two-way ANOVA). Soil moisture increased somewhat away from trees for areas covered by *Sphagnum* (Table S1). We found no correlation between thaw depth and snow depth (simple linear regression; $r^2 = 0.014$; $P = 0.83$; Figure S3). Furthermore, none of the vegetation characteristics, including plant community at the site level, influenced snow depth.

4 | DISCUSSION

4.1 | Drivers of thaw depth differences among vegetation communities

Our fine-scale analyses of each vegetative stratum and microtopography provide insight into the strata driving the observed differences in average thaw depth among the three plant communities: feathermoss (41 cm), *Cladonia* (Clad) (47 cm) and *Sphagnum fuscum* (Sphag) (53 cm). First, greater tree density was associated with shallower thaw depth (Figure 4). Thus, the smaller average distance-to-trees in Clad community sites (1.2 m) compared to Sphag community sites (1.5 m) and the bigger trees observed in the feathermoss communities may be one of the factors leading to differences in thaw depths. Second, the differences in thaw depths among communities is unlikely to be attributable to observed differences in total shrub cover among plant communities (feathermoss community: 33%, Clad community: 48%, Sphag community: 34%) as our plot-level results indicate that, in this landscape, shrub cover did not influence thaw depth. Third, within the Sphag and the Clad sites, we were able to attribute a large difference in thaw depth to the type of cryptogam (*Sphagnum* spp., *Cladonia* spp. and *Ptidium*

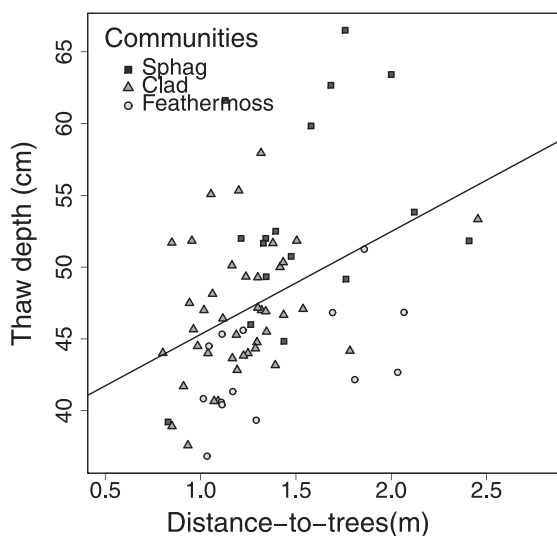


FIGURE 4 Relationship between thaw depth and distance-to-trees at the site level. Thaw depth increased with distance-to-trees ($r^2 = 0.17$; $P = 0.0002$; $n = 72$). Symbols indicate plant communities

FIGURE 5 Mean thaw depth (residual plus mean) for cryptogam species and thaw depth at plot center. (a) Sphag and Clad communities ($n = 347$ plots) and (b) feathermoss communities ($n = 84$ plots). Error bars are 95% confidence intervals around the mean. Bars with different letters are significantly different ($P \leq 0.05$; Tukey HSD). SF = *Sphagnum fuscum*; SC = *Sphagnum capillifolium*; LI = litter; PS = *Pleurozium schreberi*; CSe = *Cladonia stellaris*; CM = *Cladonia mitis*; CSy = *Cladonia stygia*; PC = *Ptilidium ciliare*; HS = *Hylocomium splendens*

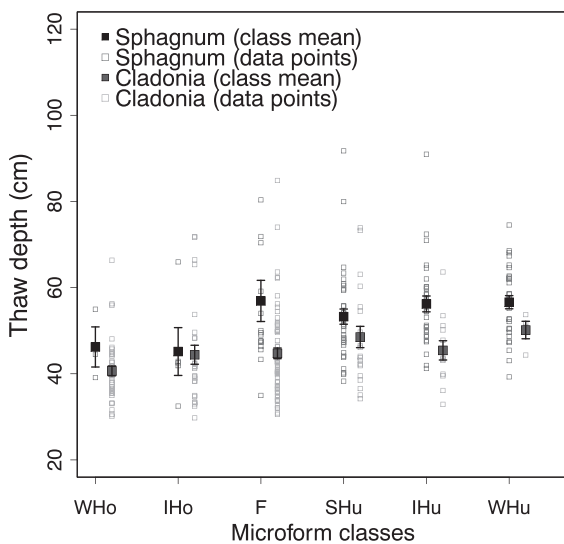
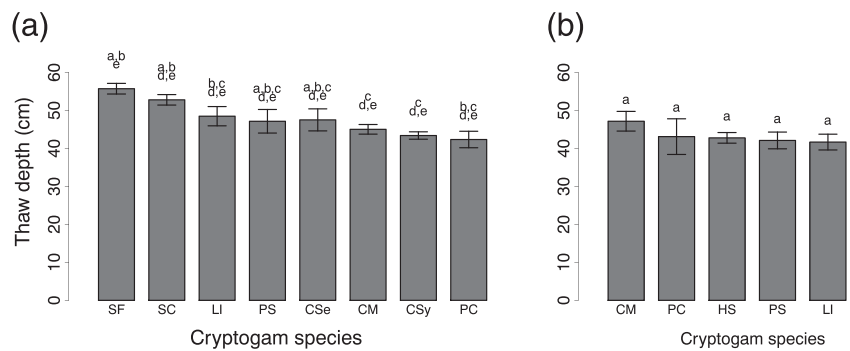


FIGURE 6 Thaw depth by microform class for the two dominant genera (*Sphagnum* and *Cladonia*). Error bars are 95% confidence intervals around the mean class values. WWho = Well-rounded hollow; IHo = Irregularly-shaped hollow; F = Flat region; SHu = Side hummock; IHu = Irregularly-shaped hummock; WHu = Well-rounded hummock

ciliare in order of decreasing thaw depth) present at the thaw depth sample points, while no conclusions could be drawn about the feathermoss species. Lastly, even though more convex microforms (hummocks) were associated with greater thaw depth than concave microforms (hollows), no particular conclusions at the community level could be drawn about microforms as no microform type dominates a plant community. Thus, the detailed analyses allowed a more complete understanding of how each vegetative stratum influences thaw depth at a larger scale depending mostly on tree density and cryptogam cover as well as perhaps microtopography.

Complementary analyses conducted to distinguish between the effect of communities, distance-to-trees and cryptogam species indicated that once thaw depth measurements for each cryptogam taxon were adjusted for distance-to-trees, there were no differences between Sphag and Clad communities. For example, thaw depths adjusted for distance-to-trees were similar between Sphag and Clad communities, with *Sphagnum fuscum* present at the plot center (t test; $P = 0.27$).

While greater vegetation cover in the tree canopy led to shallower thaw depths, shrub cover in this landscape did not

influence thaw depth. Shading provided by the tree canopy in summer reduces ground surface temperatures, probably leading to shallower thaw depths. Snow interception by tree branches played a negligible role as snow depth did not vary with tree cover at the site level (see Appendix S1). In addition, transpiration from the vegetation canopy may reduce soil moisture,⁴² which in turn lowers thermal conductivity, thus potentially reducing thaw depth. While we detected a weak relationship between volumetric soil moisture content and distance-to-trees (see Appendix S1), black spruce sap flux measurements in this study area indicated that the trees on the peat plateau had a minor contribution (< 1%) to overall evapotranspiration rates at the landscape level (field measurements). Below the trees, shading provided by the shrub canopy did not lead to shallower thaw depths, contrary to results of previous studies (eg, Nauta et al.⁹). It is possible that greater snow accumulation within shrub branches, as seen by Pelletier,⁸ canceled out the shading effect in this landscape. In addition to being fairly short (50 cm) and close to the snow level (55 cm), the ericaceous shrubs in this landscape were mostly evergreen and did not exhibit a clumped distribution in the landscape as observed elsewhere.^{8,9}

4.2 | Potential mechanisms driving differences among cryptogams regarding thaw depth

The mechanisms behind the thaw depth differences among cryptogams are complex, probably related in part to radiative and conductive heat transfer. We attribute the greater thaw depths observed below *Sphagnum* compared to *Cladonia* to the lower albedo and higher moisture retention capacity of the former.

First, both *Sphagnum fuscum* and *S. capillifolium* are darker than the lichens *Cladonia stygia*, *C. mitis* and *C. stellaris* and this visual observation is supported by known spectral reflectance characteristics for some species of *Sphagnum* and *Cladonia* (eg, Bubier et al.⁴³). With a lower albedo in *Sphagnum*, the darker surface absorbs more radiative energy, which increases the ground surface temperature. Previous observational and experimental studies on lichens have found that darker species are 2–20°C warmer at the surface under conditions of direct sunlight than lighter species with similar morphological structure and physical properties.^{44,45}

Second, higher moisture retention capacity (volumetric soil moisture content a given period after saturation) in *Sphagnum* compared to *Cladonia* would increase thermal conductivity, increasing the soil

temperature and depth of thaw. Soil temperature recordings at 15 cm depth suggest that *Sphagnum* does have greater thermal conductivity compared to *Cladonia* as the annual temperature amplitude was greater in the former (see Appendix S1, Figure S1). Thermal conductivity is directly related to moisture content in bryophytes,¹⁸ although it has not been demonstrated in lichens to our knowledge. *Cladonia* is known to dry within hours⁴⁶ and studies have found that *Sphagnum* remains wet considerably longer (days to weeks) than any other bryophyte.⁴⁷ Soil moisture measurements taken between cryptogam surface and 5 cm below the surface show that soil moisture levels were higher for *Sphagnum* than for *Cladonia* (see Appendix S2, Figure S2). Combined with albedo, moisture retention capacity may be responsible for the observed differences in thaw depth among different cryptogams.

4.3 | Cryptogams confound microtopography results

Had the microtopography and thaw depth data been analyzed without considering cryptogamic information, double the difference in thaw depth would have been attributed to microform. Furthermore, a false relationship (albeit small) between relative elevation and thaw depth would have showed up in the data analysis had all data been pooled ($R^2 = 0.05$; $P = 0.00002$; simple linear regression), which disappears once the analysis is split by genus (section 3.4). The importance of separating cryptogam and microform data is due to the predominance of *Sphagnum* on hummocks and *Cladonia* in hollows (see Appendix S2 for more details on microforms and cryptogam species). *Sphagnum* hummocks are higher on average (27 cm) than *Cladonia* hummocks (18 cm). The importance of vegetation could explain the varying reports on the influence of microtopography.^{5,12,13} In addition, other subsurface properties and processes that were not measured in the present study (eg, organic matter accumulation, type of peat material and hydrology) could also play a role in the differences in thaw depth measured between hummocks and hollows. These results underline the importance of noting vegetation information to correctly attribute differences in thaw depth.

4.4 | Implications for high-latitude ecosystem models and land surface schemes

The relationships between vegetation and thaw depth are important to incorporate into process-based ecosystem models and land surface schemes of permafrost dynamics (eg, Porada et al.¹⁴, Beringer et al.⁴⁸). However, these models have few empirical results to parameterize permafrost-vegetation interactions. For example, the Northern Ecosystem Soil Temperature model⁴⁹ incorporates LAI as a structural vegetation parameter to calculate available energy for ground heat flux to, in turn, predict thaw depth. Yet, we found that tree density had a tighter relationship with thaw depth than LAI and thus better captured the relationship between the vegetation canopy and energy entering the ground (see Appendix S1).

Ecosystem models and land surface schemes tend to group vegetation into broadly defined plant functional types together without finer characteristics included (eg, Porada et al.¹⁴, Wissler et al.⁵⁰). For example, shrubs tend to be treated in models as a single

functional group (eg, Lawrence and Swenson⁵¹), even though opposite effects of shrub cover on thaw depth have been observed: sometimes shallower thaw depth below shrubs,⁹ sometimes deeper⁸ and in this study we found no differences due to shrub cover. Most modeling efforts focus on the cooling effect of mosses (eg, Beringer et al.⁴⁸) or aggregate lichens and bryophytes.¹⁴ However, our results suggest that lichens may be more effective insulators than bryophytes and should not be neglected (Figure 5). Cryptogams should be split into at least three subgroups (*Sphagnum*, green mosses and *Cladonia*), if not more (eg, subdividing green mosses into feathermosses, brown fen mosses, acrocarp mosses and others). Upscaling these results between ecosystem types requires caution, because soil properties, hydrological regimes and other factors tied to different vegetation associations may have a stronger influence on thaw depth⁵² than the relationships described here (eg, mineral soil underlying lichens could lead to deeper thaw depth than *Sphagnum* overlying peat). Thus, more detailed vegetation information is needed for such models considering that neither a single vegetation parameter such as LAI nor a single functional group encompassing all shrub species adequately captures the range of spectral, physical, thermal and other properties among plant species to accurately solve the energy balance for thaw depth predictions.

5 | CONCLUSIONS

Our results show that trees and cryptogams had a significant influence on the variance of thaw depth on peat plateaus in the southern NWT, whereas shrub cover had no measurable effect. Although each factor led to a minor difference in thaw depth on its own (13 cm range due to trees and 16 cm difference depending on cryptogam species and microform), the cumulative effect of all these factors was 29 cm, which is over 50% of the average thaw depth. By including every stratum in our surveys, we were able to separate and quantify the influence of each one in a landscape where canopy cover, microtopography and cryptogam species are linked. For example, cryptogam species have particular habitat preferences that are related to microtopography and to availability of light that is determined by canopy cover. Ignoring cryptogam information led to falsely attributing to microform (hummocks and hollows) double the measured influence on thaw depth compared to including cryptogam information in the analyses. The key vegetative factors (trees, cryptogams and microforms) driving differences in thaw depth provide valuable quantitative relationships between vegetation strata and thaw depth for model parameterization as well as provide a broader basis for abiotic and biotic measures to include in field surveys.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

Appendix S1. Thaw depth is compared to conventional physical measures: leaf area index (LAI), soil temperature at 15 cm, soil moisture at 5 and 15 cm, and snow depth.

Appendix S2. Detailed cryptogam and microtopography information detailing basic statistics on occurrences.

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