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Effects of Permafrost Degradation on Woody Vegetation at Arctic Treeline on the Seward Peninsula, Alaska

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ABSTRACT

Permafrost degradation leads to substantial changes in soil thermal and hydrologic characteristics. We investigated the effects of changes in active layer thickness and soil drainage on vegetation distribution near the arctic treeline on the Seward Peninsula, Alaska. We measured active layer thickness, soil moisture, density of tall shrub species, cover of low shrub species, and reconstructed white spruce establishment history along transects across the banks of a network of thaw ponds. We found that active layer thickness did not vary along our transects, but soils on thaw pond banks were significantly drier than those on level tundra or in thaw-pond channels. Thaw-pond banks were the only sites in which trees successfully established, and shrub communities on thaw-pond banks were taller and more dominated by tall shrub species like willow and shrub birch. The data suggest that the establishment of tree and tall shrub species at the arctic treeline can be limited by the availability of well-drained microsites, and the response of these species to regional climatic changes will be constrained by the availability of such microsites and thus contingent upon further degradation of the permafrost. Copyright © 2003 John Wiley & Sons, Ltd.

KEY WORDS: arctic treeline; palsa; permafrost; thaw pond; thermokarst

INTRODUCTION

Large areas of the northern hemisphere, up to 18% of the exposed land surface, are underlain by permafrost (Brown et al., 1997; Zhang et al., 2000). Future increases in regional temperature are expected to lead to widespread degradation of permafrost, particularly in the zone of discontinuous permafrost where ground temperatures are close to the freezing point. Woo et al. (1992), for example, estimated that a warming of 4–5°C could lead to a 50% reduction in the area underlain by discontinuous permafrost in arctic and subarctic Canada, and similar reductions are expected for Alaska (Anisimov and Nelson, 1997). In Alaska, significant increases in ground temperatures have already occurred in many locations (Lachenbruch and Marshall, 1986; Osterkamp and Romanovsky, 1999) and permafrost degradation has accelerated in interior Alaska in recent decades (Jorgenson et al., 2001).

Permafrost warming and degradation have the potential to significantly affect plant communities and ecosystem processes in arctic and subarctic regions. Permafrost warming and degradation are associated with dramatic changes in below-ground conditions for plant growth. Rising ground temperatures may increase N mineralization rates (e.g., Waelbroeck et al., 1997), and permafrost degradation can create areas of improved drainage as a result of improved vertical movement of water through the soil (Woo

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et al., 1992) as well as the creation of well-drained microtopographic features (e.g., thaw-pond banks; Worsley et al., 1995). Plant communities that are unable to successfully colonize cold, poorly drained soils underlain by permafrost would be expected to expand as permafrost degrades. Communities dominated by tall woody vegetation (shrub-tundra or forest-tundra) may be particularly likely to expand as a result of degrading permafrost (Kershaw and Gill, 1979; Worsley et al., 1995; Allard et al., 1996; Nicholas and Hinkel, 1996; Rovansek et al., 1996). Vegetation changes, especially the expansion of tall woody vegetation, may, in turn, influence permafrost. Studies of cycles of palsas development, for example, have suggested that the colonization of palsas by tall woody vegetation may lead to increased snowpack, greater insulation of the ground, and thus an acceleration in the rate of permafrost degradation (Laberge and Payette, 1995; Worsley et al., 1995).

Widespread degradation of permafrost, and the concomitant expansion of thermokarst-related landforms, might therefore be associated with changes in the distribution and extent of plant communities in the arctic and subarctic. Furthermore, in some situations it appears that ecosystem responses to future warming may be contingent on permafrost thawing (e.g., Waelbroeck et al., 1997). At the arctic treeline in northwestern Alaska white spruce commonly occupy upland hills and well-drained floodplains of larger stream channels, but they are largely absent from level tundra areas away from stream channels. Rising air temperatures during the 20th century (Chapman and Walsh, 1996; Serreze et al., 2000) were associated on the Seward Peninsula with an advance of the distributional limit of spruce of more than 10 km in upland locations. In both the Seward Peninsula and the Noatak River valley, however, spruce failed to move off well-drained river floodplains into adjacent level tundra areas, except in areas affected by thermokarst (Suarez et al., 1999; Lloyd et al., 2003). The two expressions of arctic treeline, upland treelines and those associated with the edge of stream channels, therefore exhibited different responses to climate warming, and it appears that response to climate warming in the latter situation is contingent upon thawing of permafrost.

This study examines the relationship between vegetation and soil characteristics in an active thaw pond complex on Seward Peninsula in order to determine the mechanistic relationship between thermokarst formation and vegetation change at the forest-tundra boundary. In particular, we address two questions. (1) What is the relationship between active-layer thickness, soil drainage, and vegetation? (2) What are the temporal dynamics of tree colonization and mortality in this thaw pond complex?

**METHODS**

**Description of Study Site**

The study site is located on the Seward Peninsula in western Alaska (64°50.6'N, 163°42.3'W) at an elevation of approximately 42 m a.s.l. (Figure 1). The site encompasses a potential thermokarst depression with relatively shallow soils underlain by low permeability bedrock soils and underlain by permafrost. These low permeability bedrock soils are typically associated with steep slopes, high relief, and large thaw-lokken. The entire area is covered by tussocks of Eriophorum vaginatum and Salix glaucophylla (approximately 25% Salix glaucophylla and 25% Eriophorum vaginatum (approximatetly 25% Salix glaucophylla and 25% Eriophorum vaginatum). We selected a substantially undisturbed study site that was approximately 600 m long and 100 m wide.

**Figure 1.** Aerial photograph of study site near Council, Alaska. The thaw ponds are the very dark areas on the left and right sides of the photograph, and the area referred to as the ‘thaw-pond channel’ is the light grey network of channels in the centre of the photograph. Transect locations are indicated by white lines. Transects 1–5 are located in areas with trees; transects 6–10 are located in areas without trees. Dead trees were sampled in the area labelled ‘palsas’.

**Soil Profiles**

We measured the thickness of the active layer, the depths of the permafrost table, the thaw depths, and the drainage on each of the five transects. Active-layer thickness and permafrost table were measured using a 1 m long and 25 mm diameter metal rod along with a 1 m long steel tape. Eriophorum vaginatum tussocks were detected by inserting the metal rod 1.5 m into the ground. Eriophorum vaginatum tussocks were located by the use of a 1 m long and 15 mm diameter metal rod inserted 1.5 m into the ground.
The area encompasses a network of thaw ponds, some partially or fully drained. There are two discrete ponds with relatively deep standing water, and a network of low-lying depressions between them in which soils are saturated and standing water is common. These low-lying areas, which we will refer to as the thaw-pond channels, support a wet sedge meadow community. The edge of the thaw-pond complex is a steep scarp approximately 2 m in elevation, supporting shrub tundra (Betula nana and Salix glauca) and open white spruce (Picea glauca) woodlands. The entire area is surrounded by a level plain dominated by tussock tundra vegetation, including Eriophorum vaginatum and low shrubs (Betula nana, Empetrum nigrum, Arctostaphylos spp., Rubus chamaemorus, Salix arctica, Vaccinium spp.). The entire site is substantially below the elevation of alpine treeline (approximately 100 m a.s.l.) and could thus support trees if below-ground conditions were appropriate.

**Sampling Methods**

We sampled vegetation and soil properties along transects that extended from the channel of the thaw pond (where there was standing water in most locations) up the thaw-pond banks into the surrounding tundra flats. Transect positions will be referred to as channel (low-lying depressions at the elevation of the thaw ponds), banks (the scarp at the edge of the thaw ponds and low-lying depressions), and flats (the level terrain at the top of the banks). In order to separate the effects of vegetation and topography on soil characteristics, we established five transects in each of two vegetation types: areas where spruce were present in some part of the transect (tree transects) and areas that were entirely treeless (shrub transects). Tree transects were established and sampled in 2001, and shrub transects were sampled in 2002. All shrub transects were at least 10 m from any mature spruce tree.

**Soil Properties**

We measured thaw depth and soil moisture in 2001 on thaw-pond banks and in tundra along one of the five tree transects, and then repeated those measurements in 2002 along all of the transects along which vegetation sampling was conducted. Environmental measurements began in the centre of the thaw-pond channel, and extended up the thaw-pond banks and onto level tundra. Active layer was measured in late August using a thaw depth probe, inserted into the ground at approximately 1.5 m intervals along each of the 10 vegetation transects. Thaw depth measurements in late August are a close approximation of maximum thaw depth. Soil moisture was measured as volumetric soil water content in the same locations using a dielectric constant measuring device (CS 620 probe, Campbell Scientific, Inc.). The probes were inserted into the soil at a 45° angle without any compression to represent the top 10 cm of organic soil (surface soil moisture) and the top 10 cm of mineral soils (subsurface soil moisture). Distance and elevation were measured along each transect using a laser-equipped total station (Topcon GTS-313).

**Woody Plant Abundance**

In tree transects, trees were sampled in at least three 5 x 10 m plots, oriented with long axis parallel to the thaw-pond banks. In shrub transects, plot size was 5 x 2 m, with the short axis parallel to the thaw-pond banks. We surveyed the thaw-pond channels and determined that live woody plants were absent from the thaw-pond channels, so we sampled woody vegetation on transects beginning at the banks and running out into the flats. Bank plots were located on the face of the bank. Plots in the surrounding flats were located beginning 5 m from the upper edge of the bank plot, and continued at 5 m intervals until we reached plots that were lacking spruce. At least one corner of each plot was permanently marked with a 1 m metal post.

In plots along the tree transects, we counted and permanently tagged each spruce tree within each plot. To estimate tree ages, we obtained at least one increment core, extending through the pith, from the base of each spruce with a basal diameter greater than 5 cm. Ages of smaller trees were estimated from counts of annual stem internodes. We obtained cores or basal cross sections from all dead trees in each plot. In addition to sampling trees within our study plots, we obtained cross sections from dead trees that were found within the thaw-pond channels, in which live spruce are currently absent. Such trees were primarily found in the area labelled ‘palsa’ in Figure 1.

In plots along shrub transects, we estimated the density (number of stems) of each species of tall shrub (Betula nana and Salix glauca). Abundance of all other shrub species was estimated by a visual estimate of per cent cover. The height of the shrub canopy was estimated by measuring the height of the tallest shrub stem at 1 m intervals along the long edges of each plot (n =12 points per plot). From these measurements, we calculated the mean height of each species as well as the overall height of the shrub canopy. Height measurements were taken vertically from the upper surface of the ground or moss cover.
Dendrochronological Analyses

Tree cores were mounted in wooden strips and sanded with progressively finer grits of sandpaper (up to 400 grit) until annual rings were clearly visible. Rings were measured using a linear encoder measuring bench with a precision of 0.001 mm (Velmax, Inc.). Rings were crossdated using the computer program COFECHA (Holmes, 2000) and crossdating was visually verified using standard procedures (Stokes and Smiley, 1968). To analyse the growth of dead trees within the current thaw-pond channel, we calculated the mean ring-width in each year of all crossdated trees in the thaw-pond channel (n = 10 trees). We constructed a similar chronology from a group of same-aged trees growing on thaw-pond banks (n = 22 trees). Both chronologies were constructed from unstandardized ring-widths, so both may be affected by age-related growth trends (e.g., an expected decline in ring-width as a tree increases in size). Because the age of trees did not differ between the two sites this should not affect the relative differences in growth.

Statistical Analyses

We used one-way analysis of variance to compare the abundance of common shrub species among the three slope positions (channel, bank, flats). Differences between pairs of means were tested using Tukey's HSD, which controls the experiment-wise error rate. Because shrubs were absent from the channel plots, we used an independent samples t-test to compare shrub height (overall canopy height and height of Betula nana and Salix glauca) between plots on banks and in the flats. We used a one-way analysis of variance to analyse differences in active layer thickness, surface soil moisture, and subsurface soil moisture in 2001. Pairwise comparisons between slope positions were tested using Tukey’s HSD. We tested the effects of vegetation on soil properties by comparing contrasting vegetation types (tall shrub tundra versus spruce woodland) within a particular slope position using an independent samples t-test. We used an independent samples t-test to compare differences in active-layer thickness and soil moisture between thaw-pond banks and tundra in 2000.

RESULTS

Soil Properties

The depth of the active layer at the end of summer (August) was significantly greater in channel plots than on thaw-pond banks in 2001 (F = 12.839, P = 0.001, df = 2; Figure 2a), but it did not differ significantly among slope positions in 2002 (F = 0.311, P = 0.733, df = 2; Figure 2a).

Soil moisture on thaw-pond banks tended to be lower than in plots on the surrounding flats (Figure 2b-c). In 2001, surface soil moisture was significantly drier on banks than in plots on the flats (t = -2.59, P = 0.036, df = 7; Figure 2b). In 2002, surface soil moisture varied significantly with slope position (F = 182.065, P < 0.0001, df = 2; Figure 2b). Surface soil moisture was significantly greater in channel plots than in plots on banks (P < 0.0001) or in the flats (P < 0.0001), but did not differ between bank plots and those on the flats (P = 0.533).

Subsurface soil moisture was lower on the thaw-pond banks than in the surrounding flats in 2001, but the difference was not significant (t = -2.313, P = 0.06, df = 6; Figure 2c). Subsurface soil moisture in 2002 varied significantly with slope position (F = 63.095, P < 0.0001, df = 2; Figure 2c), and differed significantly between all pairs of slope positions (P < 0.0001).

Surface soil moisture was greater in the channel plots (16.93 ± 1.68, n = 12) than in spruce woodland (11.06 ± 1.82, n = 12) (F = 53.02, P < 0.0001; df = 2), but did not differ significantly from tundra flats (11.81 ± 1.22, n = 12) (F = 1.30, P = 0.27; df = 2).

Woody Vegetation

Shrubs were abundant in each of the substrates with an average density of shrubs at the channel plots of 36 stems/plot. The abundance of the shrub species, Betula nana and Salix glauca, contributed to slope position, and in particular channel plots was significantly different from the other two sites (F = 20.92, P < 0.0001). The abundance of shrubs was the highest in the channel plots of the shrub tundra.

![Graph showing active layer thickness](image)

![Graph showing surface soil moisture](image)

![Graph showing subsurface soil moisture](image)

**Figure 2** Patterns of (a) thaw depth and (b,c) soil moisture along transects from thaw-pond channels to surrounding tundra flats. Values are mean ± 1 s.e.

**Table 1** Mean values for different vegetation types. Overall, the mean shrub height was significantly greater in channel plots with an average of 76 cm, compared to 62 cm in spruce woodland and 64 cm in tundra flats. Species were sampled in 2001.

<table>
<thead>
<tr>
<th>Species</th>
<th>Channel</th>
<th>Bank</th>
<th>Flats</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Betula nana</strong></td>
<td>76 cm</td>
<td>62 cm</td>
<td>64 cm</td>
</tr>
<tr>
<td><strong>Salix glauca</strong></td>
<td>78 cm</td>
<td>64 cm</td>
<td>58 cm</td>
</tr>
<tr>
<td><strong>Ledum groenlandicum</strong></td>
<td>59 cm</td>
<td>56 cm</td>
<td>49 cm</td>
</tr>
<tr>
<td><strong>Vaccinium</strong></td>
<td>56 cm</td>
<td>54 cm</td>
<td>48 cm</td>
</tr>
</tbody>
</table>

Surface soil moisture on the banks was significantly greater in plots supporting shrub-tundra vegetation (16.93 ± 10.79%) than in those supporting spruce woodlands (11.26 ± 4.93%; t = -2.52, P = 0.016, df = 53). Subsurface soil moisture and thaw depth did not differ significantly between vegetation types.

**Woody Plant Abundance**

Shrubs were absent from channels. The majority of shrub species occurred at similar cover values at the other slope positions (banks and flats). The abundance of the two most common shrub species, however, differed significantly according to slope position (Figure 3). *Betula nana* density was significantly higher on banks than in the flats (F = 20.264, P < 0.0001, df = 2). *Salix glauca* was most abundant on banks, and was virtually absent from flats (F = 39.284, P < 0.0001).

The mean height of the shrub canopy differed between banks and flats (Table 1). The overall height of the shrub canopy was significantly greater on banks than in the flats (t = 7.636, P < 0.0001). This pattern was repeated for all species with an adequate sample size to test: *Betula nana*, *Ledum groenlandicum*, *Salix arctica*, and *Vaccinium uliginosum* (Table 1).

Spruce density varied according to slope position (F = 7.891, P = 0.004, df = 2). Live spruce were absent from channels, and spruce were significantly more abundant on banks, where mean (+/− s.e) tree density (including seedlings) was 1866.6 ± 417 trees/ha, than on the flats, where density was 125 ± 79.8 trees/ha. Differences between all pairs of slope positions were significant (P < 0.05).

**Dendrochronology**

Spruce have established continuously on banks since at least the mid-1800s, and high rates of establishment continue through present on those sites (Figure 4a). Spruce establishment on the flats is much more recent in origin. In plots within 10 m of the banks, there are very scattered spruce >100 years old, and the bulk of the population comprises small, stunted seedlings and saplings that have established since 1950 (Figure 4b). Plots on the flats that are located 15 m from the banks (which were the most distant ones with spruce), contained scattered spruce <40 years old (Figure 4c).

Although no live spruce were present within the channel itself, there were several dead spruce rooted in the thaw-pond channel. These trees established in the early 1800s, approximately synchronous with the establishment of the oldest trees on the thaw-pond banks, and died within the last 50 years (Figure 5).

**DISCUSSION**

**Patterns of Vegetation Distribution and Soil Characteristics**

Our data confirm previous studies that have found that well-drained soils on steep banks support

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**Table 1** Height of the shrub canopy. Values are mean ± s.e; bank is the mean in plots on the banks and flats is the mean of plots on the flats. Shrubs were absent from channels, so no height data are shown for channel plots. Overall height is the mean height of the shrub canopy across species. Individual species comparisons were made for all species with an adequate sample size. Heights of three additional species (*Emetrum nigrum*, *Rubus chamaemorus*, *Salix glauca*) were sampled, but sample sizes were too low to allow statistical comparison.

<table>
<thead>
<tr>
<th>Species</th>
<th>Ht on bank (cm)</th>
<th>Ht on flats (cm)</th>
<th>t</th>
<th>P</th>
<th>df</th>
</tr>
</thead>
<tbody>
<tr>
<td>Overall</td>
<td>53.8 ± 3.52</td>
<td>30.31 ± 1.28</td>
<td>7.636</td>
<td>&lt;0.0001</td>
<td>178</td>
</tr>
<tr>
<td><em>Betula nana</em></td>
<td>58.2 ± 3.9</td>
<td>37.3 ± 1.61</td>
<td>5.652</td>
<td>&lt;0.0001</td>
<td>107</td>
</tr>
<tr>
<td><em>Ledum groenlandicum</em></td>
<td>34.5 ± 7.5</td>
<td>23.11 ± 1.64</td>
<td>2.493</td>
<td>0.034</td>
<td>9</td>
</tr>
<tr>
<td><em>Salix arctica</em></td>
<td>21 ± 1</td>
<td>17.25 ± 0.5</td>
<td>3.974</td>
<td>0.016</td>
<td>4</td>
</tr>
<tr>
<td><em>Vaccinium uliginosum</em></td>
<td>35.71 ± 2.8</td>
<td>23.9 ± 1.6</td>
<td>3.378</td>
<td>0.002</td>
<td>32</td>
</tr>
</tbody>
</table>

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insulating effect of the snow may result in a case where the snow and the tundra soils are warmer than the air, regardless of temperature. However, significant differences were found between sites with and without tundra. The tundra sites had significantly lower winter temperatures than the adjacent forested areas. These differences may result in a feedback effect, where the snow and tundra are warmer than the air, which in turn results in a higher temperature in the tundra. This leads to the idea of a potential for a new plant community, which is referred to as a "shrub tundra". The shrub tundra is characterized by a greater abundance of shrubs and a thinner layer of snow. The shrubs are able to grow in this environment due to the warmer temperatures and increased water availability. It is important to note that the specific species of shrubs that are able to grow in this environment are not yet fully understood.

Figure 4  Density of spruce trees recruiting per decade from 1800 to present on (a) bank and (b,c) flats. Year shown is the last year of the decade (e.g., 1890 is the decade from 1889-1890). The height of the bar indicates the density of spruce trees/ha that successfully established during a particular decade. Values are the mean of five transects.

Figure 5  Establishment dates (hatched bars) and outer ring dates (black bars) of dead trees within the thaw-pond channels. Outer ring dates are estimates of death date, but are not corrected for the possible loss of small amounts of wood from the outer surface. The year shown on the x-axis is the last year of the decade (e.g., 1890 is the decade from 1889-90).

plant communities distinct from those found on surrounding level tundra (e.g., Kershaw and Gill, 1979; Worsley et al., 1995; Rovansek et al., 1996). We found that thaw pond banks supported a significantly higher density of trees and large shrub species (Betula nana and Salix glauca), and that shrubs were significantly taller on banks than elsewhere. Thaw-pond banks appear to provide a microsite that favours tall woody vegetation (open spruce forest and tall shrubs) over the tussock tundra that dominates more level terrain.

These data provide further evidence that the establishment of shrubs and trees in the Arctic is likely to be limited by a suite of environmental factors that include both above ground (e.g., air temperature) and below ground conditions (e.g., Hobbie and Chapin, 1998). In our sites, the increased abundance of trees and tall shrubs on thaw-pond banks is best explained by improved soil drainage rather than soil thermal characteristics. Although tall woody vegetation is thus associated with soils that have a relatively shallow active layer but good drainage.

Two alternative explanations exist to explain this association between tall woody vegetation and drier soils. First, improvements in soil drainage may occur because of topographic changes that follow permafrost degradation, and those drier microsites may then provide favourable colonization sites for trees and tall shrubs. The mechanism for the dependence of tall woody plants on well-drained sites is not known. Hobbie and Chapin (1998) demonstrated that the growth and survivorship of tree and shrub species in tundra were limited by low nutrient availability, and it is thus possible that the response to well-drained soils may be an indirect response mediated by a factor like nutrient availability.

Second, the causal relationship between dryness and tall woody vegetation may be the reverse: tall woody plants may occur on thaw-pond banks for other reasons (greater protection from winter winds, or warmer surface soils associated with greater

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insolation on an inclined surface) and drier soils may result from the presence of vegetation with a comparatively large leaf area index. Although soils on thaw-pond banks were significantly drier regardless of vegetation type, vegetation did have a significant effect on soil moisture on banks. Bank sites supporting open spruce forests had significantly lower surface soil moisture than bank sites supporting tall shrubs. The relationship between vegetation type and soil moisture is likely to be complex in these areas. Despite greater leaf area, tall woody vegetation may not be associated with greater fluxes of water out of soil. Evaporation rates and latent heat fluxes are typically lower in shrub and forest-tundra than in tussock-tundra (McFadden et al., 1998, Chapin et al., 2000), and improved trapping of snow in winter can lead to greater spring runoff in areas dominated by tall woody vegetation (Liston et al., 2002). The causal relationship between vegetation and soil moisture (i.e., trees and shrubs occur in driest sites or trees and shrubs cause enhanced drying of soils) thus remains unknown, and warrants further exploration.

Finally, it is also possible that the enhanced abundance of tall woody plants on the banks reflects constraints at very early life stages (e.g., seed germination). Lloyd et al. (2003) documented that white spruce at an adjacent treeline site established in tussock-tundra communities only in sites where soils had been extensively disturbed. The generally poor competitive ability of white spruce and other tall woody species as very young seedlings has been established in other studies as well (e.g., Zasada et al., 1992; Hobbie and Chapin, 1998), and a dependence on small-scale disturbance for reproduction by seed seems to be a common trait of arctic species (Gartner et al., 1986). Bank environments may, by virtue of their topographic setting, provide a higher frequency of small-scale disturbances and thus promote regeneration and establishment of tall woody plants.

**Temporal Dynamics of Spruce Establishment and Thaw Pond Formation**

Live spruce are currently restricted, in this site, to thaw-pond banks. The relatively old age of the bank populations (150–180 years) suggests that the banks have been a stable environment for at least that long. This stability suggests that feedbacks between forest vegetation and permafrost that are likely to enhance permafrost degradation (e.g., enhanced snow trapping) are either weak or absent from these sites. Recruitment continues to occur at relatively high densities to present, indicating that conditions for spruce remain favourable. The relatively young populations in the flat areas surrounding the thaw ponds are characterized by low populations densities and high rates of mortality (as evidenced by the abundance of dead seedlings), and thus probably represent opportunistic establishment in sites that cannot support adult trees rather than an advance of spruce into the level tussock-dominated areas around the thaw ponds.

Despite the absence of life spruce from the low-lying depressions between the thaw ponds, large, upright dead spruce are rooted, in the centre of the thaw-pond channels where soils are currently saturated. These dead spruce established in the early 1800s, at approximately the same time that spruce began establishing on thaw-pond banks. The most likely explanation for the occurrence of isolated spruce within the channel of the thaw pond, far from the favourable habitat of the thaw-pond banks, is that they developed on palsas, which can provide similarly well-drained habitats (e.g., Laberge and Payette, 1995; Worsley et al., 1995). Palsas may have developed at that time as a result of regional climatic changes (e.g., the Little Ice Age) or autogenic processes associated with the development of deep, insulating moss layers within the thaw-pond channels (e.g., Worsley et al., 1995).

**Implications for Vegetation Response to Changing Climate**

Our results suggest, therefore, that tall woody vegetation (open spruce woodlands and tall shrubs) is dependent on well-drained soils in order to successfully establish in level terrain underlain by permafrost. The response of vegetation to climate warming may thus be contingent upon the creation of well-drained microsites. Such sites are likely to be relatively restricted in extent (e.g., to thaw-pond banks and well-drained hummocks), at least during the initial stages of permafrost degradation, and thus the expansion of spruce woodlands and tall shrubs is likely to be limited.

The expansion of tree and shrub-dominated vegetation types (e.g., spruce woodlands, tall shrub tundra) is expected to feed back on climate (Chapin et al., 2000), and our results suggest that decadal-scale vegetation responses to climate cannot be adequately predicted without considering the coupling of vegetation change on permafrost. For example, rates of vegetation change at these types of sites are likely to experience substantial lags following the onset of warming as a result of their dependence on permafrost degradation. Lloyd et al. (2003), for example, found that the spatial displacement of treeline during the 20th century at permafrost-affected sites was <5% of
that observed at upland sites where permafrost was not an important control over vegetation distribution.

Further non-linearities in the temporal dynamics of these systems are expected because of the feedbacks of vegetation on permafrost. For example, the expansion of tall woody vegetation may initiate a positive feedback on permafrost degradation as a result of increased snow trapping (Liston et al., 2002) and thus warmer winter temperatures (Laberge and Payette, 1995; Worsley et al., 1995). Alternatively, greater shading of the ground surface by tall woody vegetation (e.g., Chapin et al., 2000) may decrease ground temperatures in summer and lead to negative feedbacks on permafrost degradation. The coupling between vegetation and permafrost at high permafrost-affected sites near arctic treeline is thus likely to be an important control over ecosystem responses to warming, and non-linear responses to warming seem likely.

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REFERENCES


Worsley P, Gurney SD, Collins PE. 1995. Late Holocene 'mineral palsas' and associated vegetation patterns: a case study from Lac Hendry, northern Quebec, Canada and significance for European Pleistocene thermokarst. *Quaternary Science Reviews* 14: 179–192.
