

RESEARCH ARTICLE

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Key Points:

- Black spruce at Scotty Creek NT have demonstrated widespread declines in annual growth since the mid-1900s
- Tree growth shows a shift from predominantly positive responses to temperature to predominantly negative temperature responses post-1970
- Black spruce growth trends may be related to the changing permafrost conditions as a result of warming

Supporting Information:

- Supporting Information S1
- Data Set S1

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Growth dynamics of black spruce (*Picea mariana*) in a rapidly thawing discontinuous permafrost peatland

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Abstract High-latitude warming has led to radical changes in abiotic conditions influencing forest growth. In the North American boreal forest, widespread declines in forest productivity (particularly in western regions) and changing climate-growth relationships have been documented. Previous studies have proposed that this decline can be attributed to drought stress as increasing temperatures may cause evapotranspirative demand to exceed available moisture. We used tree ring studies to document growth dynamics of black spruce, one of the most dominant boreal tree species, in a boreal peatland experiencing rapid permafrost thaw. We specifically look at how changing permafrost conditions influence growth. Growth of black spruce at this site has declined steadily since the mid-1900s and exhibited a shift from positive responses to temperature pre-1970 to predominantly negative responses in recent decades, despite precipitation increasing over time at this site. Our results show that there is no apparent effect of landscape position or rate of lateral permafrost thaw on growth trends of black spruce, despite gradients in soil moisture and active layer thickness across the mosaic of wetlands and drier permafrost plateaus at this site. However, this does not imply no effect of permafrost thaw on growth; our results support growing evidence that vertical permafrost thaw (i.e., active layer thickening) is causing drought stress in these slow-growing, shallow-rooted trees. To our knowledge, this study is the first to investigate permafrost as a driver of within-site variability in growth-climate responses, and we provide insight into the widespread growth declines and divergence of climate-growth relationships in high-latitude forests.

1. Introduction

High-latitude forests are facing radical changes to their growing conditions attributable to amplified warming in the north [Chapin *et al.*, 2005]. Many studies have suggested that as temperatures and atmospheric carbon dioxide (CO₂) concentrations rise, widespread increases in tree growth and northward expansion of boreal forests would be expected as a result of more favorable growing temperatures, CO₂ fertilization, and warming soils leading to increased microbial activity and release of stored nutrients from permafrost [e.g., Bonan and Shugart, 1989; Keeling *et al.*, 1996; Myneni *et al.*, 1997; Schuur *et al.*, 2007]. However, evidence from tree ring studies refutes this idea with many boreal forests showing a negative growth response to the changing climate, particularly warming (e.g., Lloyd and Bunn [2007] and Wilmking and Myers-Smith [2008] but see Wilmking *et al.* [2004] and Beck *et al.* [2011] for examples of some positive growth responses).

In tree ring studies, negative growth responses to warming have been widely attributed to higher incidences of drought stress as temperatures rise; without a corresponding increase in precipitation, higher evapotranspirative demands could drive declines in forest productivity and alter climate-growth relationships [e.g., Lloyd and Fastie, 2002; Driscoll *et al.*, 2005; Wilmking *et al.*, 2005; Walker and Johnstone, 2014]. However, tree ring studies have demonstrated substantial variability in these growth response patterns. Forest stands have often exhibited mixed responses to climate variables (primarily temperature) with some stands responding positively and others negatively [e.g., Lloyd and Bunn, 2007; Beck *et al.*, 2011; Porter and Pisaric, 2011]. Within stands, individual trees have similarly shown contrasting growth responses to climate conditions [Wilmking *et al.*, 2004; Pisaric *et al.*, 2007; Walker and Johnstone, 2014].

One possible driver for increasingly negative growth responses or variable within-stand responses is changing permafrost conditions. Permafrost (ground that has remained below 0°C for two or more consecutive years [Muller, 1947]) underlies much of the boreal forest. On discontinuous permafrost (30 to 80% areal extent

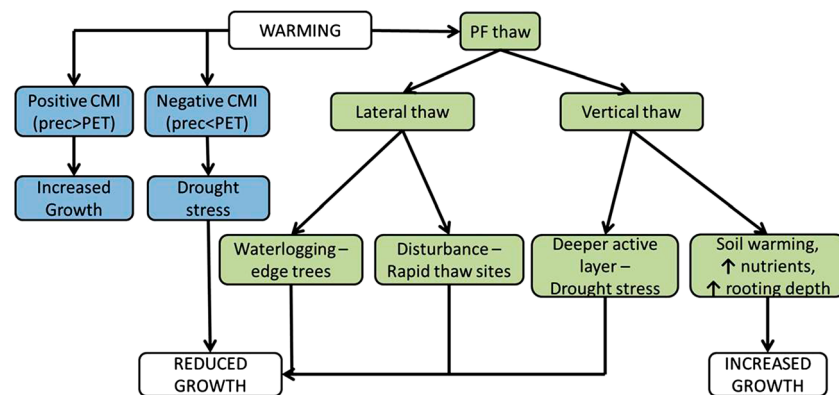


Figure 1. Predictions for possible effects of climate warming on black spruce growth dynamics, through both direct effects of warming and indirectly through permafrost thaw. Atmospheric processes are shown in blue boxes, while soil-driven processes are in green boxes. Abbreviations: CMI, Climate Moisture Index (measure of drought stress in a system); prec, precipitation; PET, potential evapotranspiration; PF, permafrost.

[Heginbottom, 2002]), which underlies much of the boreal forest [Tarnocai, 2006; Brandt, 2009], an in-depth examination of the potential role of changing permafrost conditions on tree growth responses has not been performed despite the dramatic changes associated with rapid permafrost thaw in discontinuous permafrost landscapes [e.g., Camill, 1999; Christensen et al., 2004; Quinton et al., 2011]. In the lowland boreal forest of Alaska, thaw has led to the transition of birch forests to black spruce (*Picea mariana*) forest cover [Lara et al., 2016]. In Northwestern Canada, the most notable of these land cover changes has been the transition of black spruce-dominated permafrost plateaus to treeless bogs and fens in boreal peatlands [e.g., Thie, 1974; Camill, 1999; Quinton et al., 2011; Baltzer et al., 2014]. In these boreal peatlands, permafrost thaw drives ground subsidence, which destabilizes the solid foundation upon which the black spruce-dominated forest is established [Quinton et al., 2011]. Furthermore, the encroaching wetlands cause waterlogging and tree death [Camill and Clark, 1998; Osterkamp et al., 2000; Camill, 2005]. Thus, permafrost thaw could be an important contributor to the spatial variability in individual and stand responses.

Boreal peatlands in the discontinuous permafrost zone consequently present a unique opportunity to test the drought stress hypothesis proposed in many of the studies of declining productivity in high-latitude forests, and to investigate the role of ground thaw processes as potential drivers of widespread boreal browning. The ample moisture available within this system, particularly where lateral thaw has occurred, could balance increasing evapotranspirative demands in trees as the climate warms. Our predictions are outlined in the schematic in Figure 1.

We predict that growth response to warming will be mediated by access to moisture. Specifically, if precipitation is increasing at a similar rate as temperature, we should see positive growth responses—assuming that moisture availability at the site meets evapotranspirative demands of the trees. However, moisture availability is not purely determined by atmospherically driven water shortages (i.e., potential evapotranspiration (PET) > precipitation); trees are also affected by soil processes including soil water holding capacity and root access to the water table.

In boreal peatlands, local variation in soil moisture associated with differential permafrost thaw may be important in dictating growth responses. Specifically, lateral thaw of permafrost reduces tree growth within the transition zone between permafrost plateaus and wetlands due to waterlogging of root systems [Baltzer et al., 2014; Patankar et al., 2015]. Vertical thaw is also occurring in the system and can affect the growth of black spruce. A deeper active (seasonally thawed) layer could promote growth due to the warmer soils, increased nutrient availability, and greater rooting depth [Bonan and Shugart, 1989] if the trees are able to respond and take advantage of these changing conditions. Alternatively, vertical thaw may negatively impact growth through the drying of surface soils. Specifically, the water table is perched on the frost table; thus, vertical thaw results in the lowering of the water table and drying of upper soil layers [Quinton and Baltzer, 2013; Patankar et al., 2015]. The effect of disturbance from permafrost thaw may also influence growth-climate responses of these forests; extensive permafrost degradation results in an unstable foundation upon which

trees have established. Increased negative growth responses may thus be expected at stands with high thaw rates for both physiological and physical reasons.

In this study, we used tree ring analysis to address two main questions pertaining to growth dynamics of black spruce in discontinuous permafrost peatland landscapes: (1) Do trees demonstrate consistent growth patterns over time, and what climatic variables underlie these patterns? (2) How does landscape position of a tree in relation to permafrost distribution and rate of lateral permafrost thaw within a stand influence the growth of black spruce?

This study provides an in-depth analysis of black spruce growth dynamics in a highly sensitive and rapidly changing peatland on discontinuous permafrost. We investigated possible mechanisms (outlined in Figure 1) driving widespread growth declines in the boreal region, within-site variability in growth responses, and divergence of climate-growth relationships that have been documented in high-latitude forests. In particular, we provided a novel focus on the role of permafrost in the growth patterns observed in this landscape. As peatlands comprise 24% of the circumpolar boreal forest [Wieder *et al.*, 2006], identifying the drivers of growth patterns, particularly with respect to the rapidly changing permafrost conditions in this region, is crucial to understanding variation in the long-term growth dynamics of boreal forests globally.

2. Methods

2.1. Study Location

This study was conducted at Scotty Creek, in the lower Liard River Valley of the Northwest Territories (61°18'N, 121°18'W). Scotty Creek's landscape is characterized by discontinuous permafrost. Areas underlain by permafrost (permafrost plateaus) form elevational relief of 0.5 to 1.5 m (Figure 2a) [Baltzer *et al.*, 2014] due to the volumetric expansion of water in the soil as it freezes. These plateaus provide a solid, drained foundation, where black spruce-dominated forests establish. In addition, permafrost-free areas take the form of bogs and fens in which forests cannot establish (Figure 2). Annual air temperature (1981 to 2010 climate normal) in neighboring Fort Simpson is -2.8°C , while precipitation, of which nearly half falls in the form of snow [Quinton *et al.*, 2009], averages an annual total of 387.6 mm from 1981 to 2010 [Environment Canada]. Scotty Creek has experienced extensive permafrost degradation since the mid-1900s [Quinton *et al.*, 2011]. At one intensively studied permafrost plateau, vertical thaw (active layer thickening) has been 0.36 m between 1999 to 2010, and lateral thaw totaling 18.6 m over the same time [Quinton and Baltzer, 2013].

2.2. Field and Laboratory Methods

A total of seven forest stands within 2 km² were sampled in August 2012 and August 2013. These stands ranged in area, the ratio of edge to interior (quantified using remotely sensed imagery), and rate of lateral thaw (see Table S1 and Figure S1 in the supporting information). Five of the stands had high edge to interior ratios, and the edges of the stands were generally well defined by the extent of the plateau (Figure 2). In these five stands, a core sample was taken at breast height (1.3 m) from all living and dead trees with a diameter at breast height (DBH) greater than or equal to 7 cm—the smallest DBH that we were able to core effectively. Due to the sensitivity of this system to disturbance, we did not take disk samples of smaller trees, as this would cause unnecessary disturbance to a highly sensitive landscape. The fairly uniform size distribution of the forests at the site permitted sampling of trees 7 cm DBH and greater without obvious bias toward dominant individuals (see Figure S2). We also recorded the coordinates of each tree to facilitate mapping of individuals for analysis of landscape position (edge versus interior of plateau) on growth dynamics. Two of the stands had low edge to interior ratios and were without well-defined edges delineating the stand. In these two low-edge stands, cores were taken from a >7 cm DBH tree nearest to every 20 m interval in a 100 × 100 m grid, totaling 36 trees per stand. Since these two low-edge stands did not have natural forest boundaries created by adjacent wetlands that we could use to delineate our sampling efforts, we required a different sampling strategy than at the high-edge stands. These low-edge trees were still treated the same way as trees from other stands in further analyses.

This sampling protocol resulted in a total of 445 trees (ranging from 22 to 171 trees per stand) that were successfully cross-dated and used in further analyses of this study. The core samples were mounted to boards and sanded with up to 800 grit sandpaper. Ring widths were measured in Coorecorder and cross-dated visually and statistically by using CDendro (Version 7.6, Cybis Elektronik & Data, Saltsjöbaden, Sweden) and

Note that these cores are not from within the plot but the samples stands were very close to the western side of the plot.

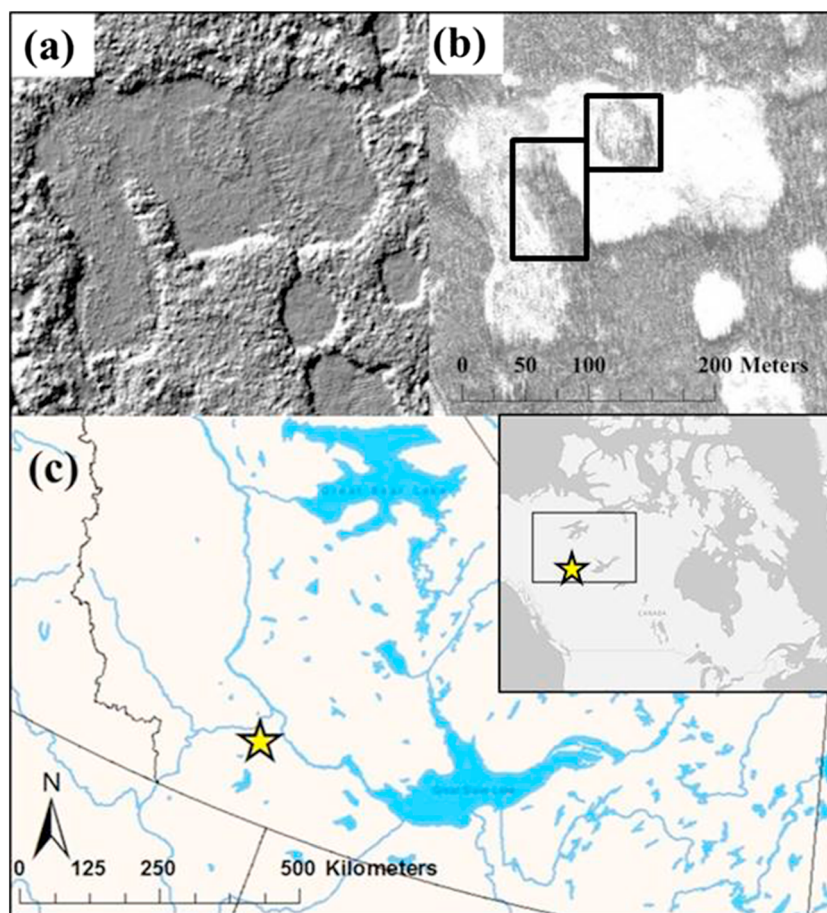


Figure 2. (a) Lidar-based shaded relief digital elevation model showing permafrost extent across the landscape (derived by Dr. C. Hopkinson) and (b) Worldview2 (© Digital Globe Corp, All Rights Reserved—acquired by Dr. W. Quinton) imagery showing the heterogeneous landscape of forests and bogs at Scotty Creek, NT (light/white areas are bogs), for the same area. In Figure 2a, the gradient in elevation extends 102 cm, where black is the lowest elevation and white is the highest. As seen in these images, the forest extent is closely related to the extent of permafrost. The two boxes in Figure 2b indicate examples of stands sampled, where the stand is defined by the edge of the plateau. The scale on Figure 2b applies to Figure 2a as well. (c) A map of the southern part of the Northwest Territories, Canada, shows the location of the study site, depicted by a star. The color base map from Figure 2c used with permission from NWT Centre for Geomatics, ENR-ITI Shared Services, Government of the Northwest Territories, 2015–2016. Map inset acquired on ArcMap 10.3, ESRI, HERE, DeLorme, MapmyIndia, © OpenStreetMap contributors and the GIS user community.

Cofecha [Holmes, 2000], respectively. Metadata on all individuals are provided in Data Set S1 in supporting information.

2.3. Characterization of Permafrost Conditions

Permafrost presence is tightly linked with forest cover at our study site (Figure 2) [Quinton *et al.*, 2011; Baltzer *et al.*, 2014]. Because of this close relationship, we were able to use remotely sensed imagery to determine the extent of permafrost in our seven stands for two time points with available imagery (1977 and 2010). The extent of permafrost at each stand was digitized in ArcMap10 using Worldview2 imagery (Digital Globe Corp.; taken 31 August 2010 at 1.4 m pixel resolution) and two VIS panchromatic aerial photographs (taken on 30 April 1977 and 12 June 1977 at 0.53 m pixel resolution [Chasmer *et al.*, 2010]). These techniques have been shown to be highly robust, which in addition to the error associated with these approaches is described in detail by Chasmer *et al.* [2010]. We were then able to calculate the rate of lateral thaw of each stand (herein referred to as “thaw rate”) using the percent areal reduction in forest cover (forest die-off occurs as permafrost is entirely lost below the trees due to ground surface subsidence and waterlogging [Quinton *et al.*, 2011]) between the 1977 and 2010 imagery described above (Figure S3).

This imagery and the strong association between permafrost presence and forest cover gave us the ability to designate trees as being “edge” or “interior” within the permafrost plateau. Edge trees were within the 10 m transition zone moving across the landscape between a plateau and wetland (e.g., soil moisture and active layer thickness differences associated with the proximity to edge penetrate approximately 10 m at this site [Baltzer *et al.*, 2014]), while interior trees were greater than 10 m from a wetland boundary. These groups were formed by mapping the coordinates of each tree onto the 2010 site imagery (where permafrost edges were digitized), and applying a buffer using ArcMap10 to determine which trees were within the 10 m transition zone.

2.4. Analysis

All analyses described below were performed in the R statistical programming environment, and unless otherwise noted, analysis was performed in the R base package [R Core Team, 2014].

2.4.1. Growth Patterns and Climate-Growth Relationships of Black Spruce

To characterize the growth trends of black spruce over time, we calculated annual basal area increments (BAI) of each tree. Under ideal, nonfluctuating conditions, the annual radial growth increments of a tree steadily decline as it ages; mathematically, this trend is produced as a trivial result of a constant volume of wood being added to the girth of an ever-growing cylinder. The conversion of ring widths to annual BAI removes this mathematical artifact and provides a robust means of representing growth changes over time [Biondi and Qeadan, 2008]. BAI was then converted to indexed measures using the C-method [see Biondi and Qeadan, 2008] with the package dplR [Bunn *et al.*, 2016]. The C-method of standardization maintains the biological growth trend of the individual series, and using area-based measurements provides a better representation of tree growth than ring width-based standardization methods [Biondi and Qeadan, 2008]. Thus, we found it to be the most appropriate method to represent growth patterns over time.

While processing our individual tree ring data, we noticed that there was variability in the growth trends of individuals over time—especially in the late twentieth century growth patterns, which is contemporaneous with documentation of diverging growth-climate and/or growth patterns in several studies [e.g., Driscoll *et al.*, 2005; D'Arrigo *et al.*, 2007; Pisaric *et al.*, 2007]. We grouped individual trees into one of three categories through fitting linear models to their C-BAI growth curve from 1970 to present. Trees with a significant positive slope over this time were categorized as increasing BAI trees, while those with a significant negative slope were designated as decreasing BAI trees. In addition, trees that did not exhibit a significant trend were designated as neutral trees.

Average annual temperature data were retrieved online from Environment Canada's Historical Climate Data archives (Environment Canada— www.climate.weather.gc.ca), and precipitation records (total annual precipitation and total annual snowfall) were acquired from Environment Canada's Second Generation Adjusted Precipitation Data [Mekis and Vincent, 2011] for the Fort Simpson, NT, weather station (~50 km north of Scotty Creek). Missing climate data were infilled as described in Text S1 in the supporting information. In addition to retrieving the average annual temperature, total annual precipitation, and total annual snowfall for the site, we calculated an annual climate-moisture index (CMI) [after Hogg, 1997] (Text S2). CMI is calculated by subtracting potential evapotranspiration from total precipitation, resulting in negative values of CMI when a system is moisture-limited and positive values of CMI when there is ample or excess moisture in the system. Trends in annual average temperature, total annual precipitation, total annual snowfall, and annual CMI are shown in Figure 3.

For the purposes of climate-growth analyses, all nonclimatic growth trends were removed from individual tree growth series by detrending with a smoothing spline with a frequency of 0.5 and wavelength of $0.67 \times n$ years. We used the package “gtools” [Warnes *et al.*, 2015a] to calculate the correlation coefficient for each individual series to our four climate variables (annual average temperature, total annual precipitation, total annual snowfall, annual CMI) in an early (1930 to 1970) and late (1971 to 2011) time period. We also performed climate-growth analyses with monthly climate variables; however, we found no results that had different implications than our annual analyses. These results are shown in Figure S4 in the supporting information. Each period corresponds to half of the time series of continuous climate data available near our site and is temporally consistent with when temperature and precipitation trends began to rise rapidly (Figure 3). We compared the proportions of trees responding positively,

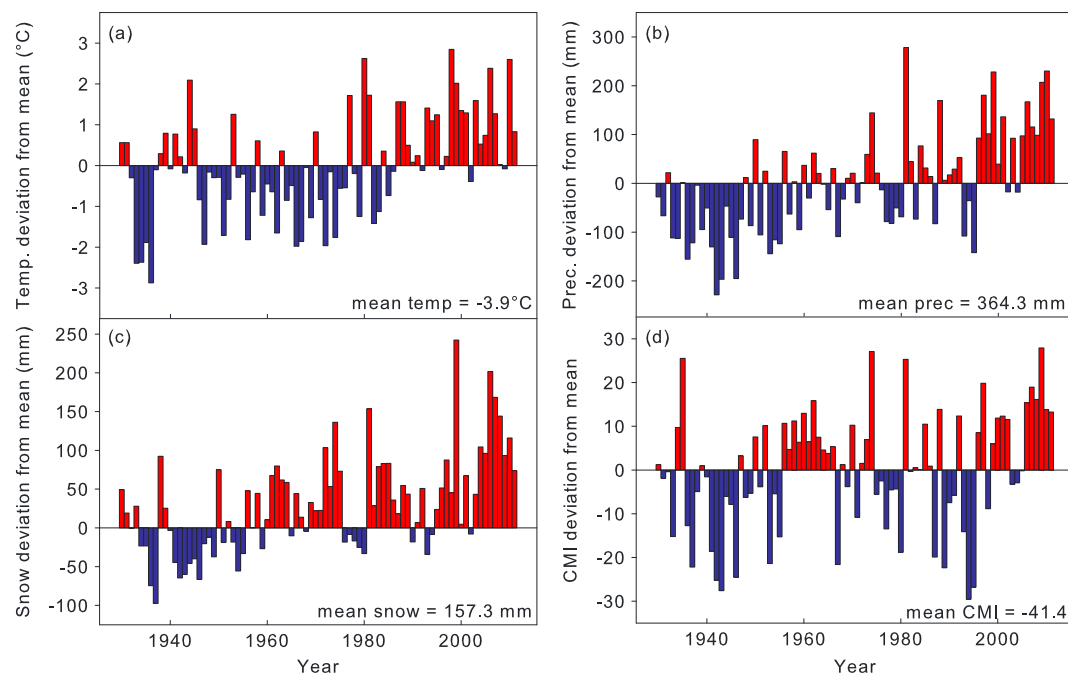


Figure 3. Trends in (a) average annual temperature (Temp), (b) total annual precipitation (Prec), (c) total annual snowfall (Snow), and (d) annual climate-moisture index (CMI). The annual deviations from mean values over the early (1930 to 1970) time period are shown in each panel, where positive values indicate higher-than-mean conditions.

negatively, and demonstrating no response to these variables using a chi-square test in the package “gmodels” [Warnes *et al.*, 2015b]. This comparison allowed us to determine whether individual responses to climate variables have stayed consistent over time or if there has been a shift in the directionality of climate responses that may be driving widespread growth declines. Post hoc testing of significant differences between groups in our chi-square analyses was performed by using the false discovery rate method in the package “fifer” [Fife, 2014]. We employed contingency table analyses using Fisher’s exact test in the package gmodels [Warnes *et al.*, 2015b] to compare the proportion of positive and negative growth responses to the four climate variables between trees exhibiting increasing BAI and decreasing BAI trends during the late (1971–2011) period. We confirmed that there was no stand-level variability introduced by pooling trees from different stands through creating semivariograms in the package “geoR” [Ribeiro and Diggle, 2016], which show that there is no increased autocorrelation between trees within a stand than between stands (Figure S5).

2.4.2. Influence of Permafrost Change on Growth Dynamics

In order to determine the effects of lateral permafrost thaw (and consequently root waterlogging) on tree productivity, we compared two characteristics of growth dynamics between edge and interior trees. First, we investigated whether landscape position (edge versus interior) affected growth trends of trees over time (i.e., increasing/decreasing BAI). The proportion of trees exhibiting increasing/decreasing BAI responses in the edge versus interior locations was compared using a chi-square test in the package gmodels [Warnes *et al.*, 2015b]. To determine whether growth was higher in trees on the interior of plateaus compared to trees on degrading plateau edges, a Welch two-sample *t* test was used to compare the 2010 BAI of edge and interior trees. We used only the 2010 BAI for this analysis to match the time period in which edge versus interior classifications were made. Determining BAI over a longer period would mask the possible effect of edge conditions on BAI, simply because trees are not likely experiencing edge conditions over long time frames.

We determined the relationship between stand thaw rate and the proportion of increasing BAI/decreasing BAI trees by using a multinomial logistic regression in the package “mlogit” [Croissant, 2013]. We also investigated the relationship between thaw rate and the 2010 BAI of all trees within each stand by using a weighted linear regression.

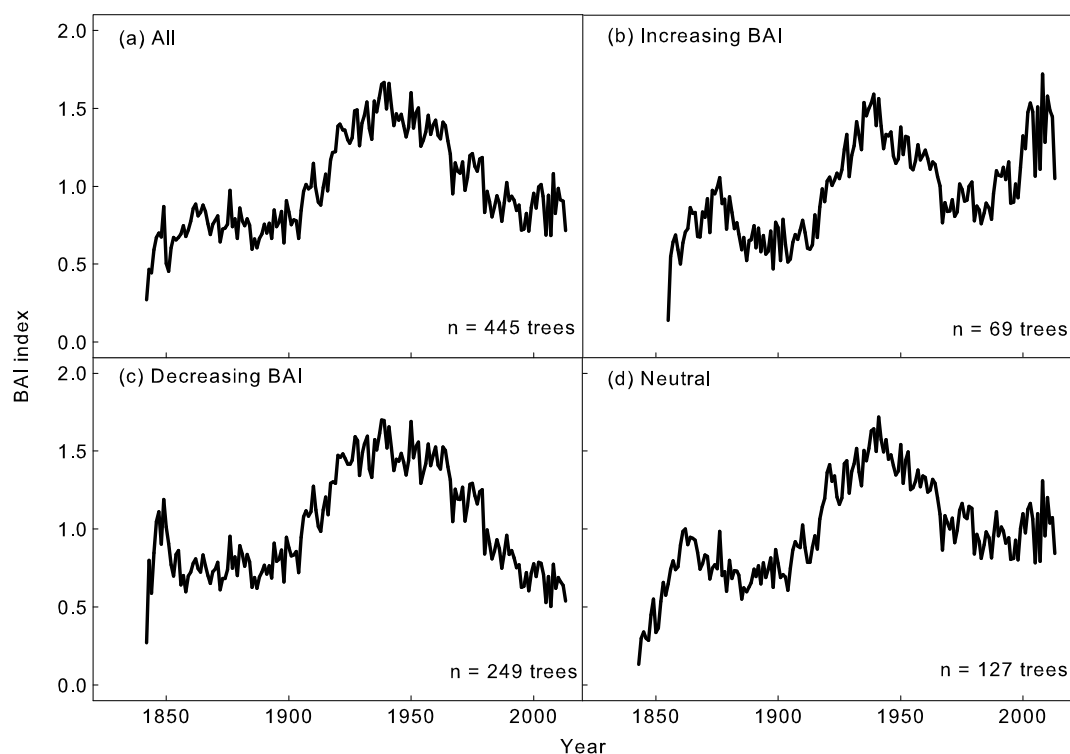


Figure 4. Average annual basal area index (BAI; calculated using the C-method) of black spruce at Scotty Creek NT. (a) The master chronology. (b–d) The chronologies for the individuals demonstrating increasing BAI/decreasing BAI/neutral trends. A table comparing the slopes of these four chronologies pre-1970 and post-1970 is shown in Table S2.

3. Results

3.1. Growth Patterns and Climate-Growth Relationships

The average annual BAI growth curve for black spruce showed a fairly consistent BAI from 1850 to 1900 before increasing until approximately 1950 (due to a period of rapid recruitment; Figure S6), at which point BAI declined steadily (Figure 4a). We also found that there was considerable divergence in this trend among individuals from 1950 to present—69 trees demonstrated increasing BAI trends and 249 trees exhibited decreasing BAI, while 127 trees did not show any directional growth trend (Figure 4).

The proportion of trees responding positively to annual average temperature decreased significantly between the early and late periods (Figure 5 and Table 1). While this shift occurred, there was a large increase in the proportion of trees demonstrating a negative growth response to temperature (Figure 5 and Table 1). There was also a significant difference in the proportions of trees exhibiting positive and negative growth responses to total annual precipitation, total annual snowfall, and annual CMI, with a reduction in the proportion of individuals demonstrating significant responses to these climate variables in the late time period (i.e., weakening relationships between growth and these three climate variables; Figure 5 and Table 1). In all cases reductions were attributable to decreases in positive responders, which was particularly marked in the relationship between growth and snowfall (Figure 5). However, in these precipitation and CMI comparisons there was no directional change in the relative proportions of positive and negative responders between the early and late periods (Figure 5).

We found a significant difference in the proportion of trees from the increasing and decreasing BAI groups responding to temperature; while there was little difference in the proportion of positive and negative temperature-growth relationships among the increasing BAI trees, the trees classified as decreasing BAI had a much greater proportion of negative temperature-growth responses (Fisher's exact test, $p = 0.0050$; Figure 6). There were no significant differences found in the proportion of positive/negative climate-growth responses to the other three climate variables among the increasing BAI and decreasing BAI chronologies (prec—Fisher's exact test, $p = 0.54$; snow—Fisher's exact test, $p = 0.16$; CMI—Fisher's exact test, $p = 0.97$).

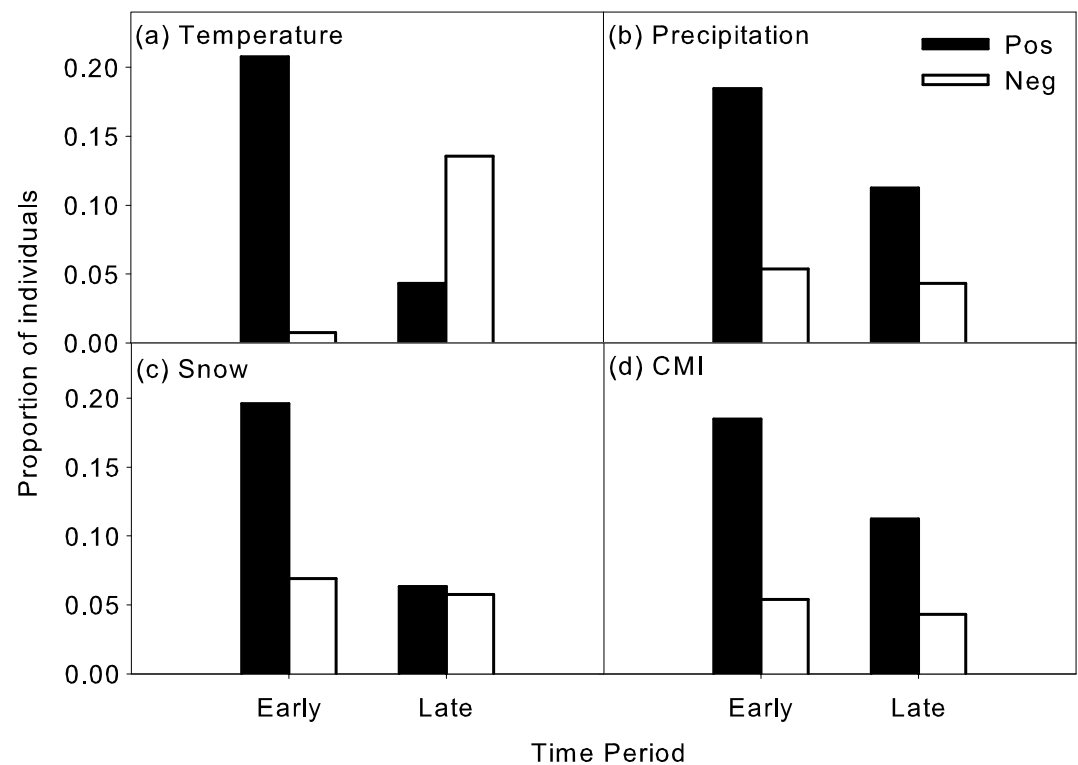


Figure 5. Proportion of trees responding to (a) average annual temperature, (b) total annual precipitation, (c) annual snowfall, and (d) annual climate-moisture index (CMI) in an early (1930–1970) and late (1971–2011) time period. Pos (Positive) and Neg (Negative) indicate the series' correlation to the given climate variables. There were significant changes in the number of responders to each variable over the two time periods. Only positive and negative responders are shown, but the proportions sum to unity with the remainder being neutral responders. All pairwise comparisons of both early/late and positive/negative results were significant ($p < 0.05$), with the exception of precipitation positive versus negative populations ($p = 0.67$).

3.2. Influence of Permafrost Change on Growth Dynamics

Of the trees that we sampled, 72% fell within the 10 m edge zone where permafrost plateaus transition into wetland features. The proportion of trees exhibiting an increasing BAI/decreasing BAI trend demonstrated significant differences between trees within edge zones versus on the interior parts of plateaus ($\chi^2 = 8.74$, d.f. = 2, $p = 0.013$; Figure 7). There was no significant difference in 2010 BAI between edge and interior trees ($t_{260} = 0.647$, $p = 0.52$). Thaw rate did not influence the proportion of trees within the stand exhibiting increasing BAI or decreasing BAI trends (log-likelihood: -430.1 , likelihood ratio test: $\chi^2 = 4.83$, $p = 0.089$). There was also no significant relationship found between thaw rate and the 2010 BAI of trees within each stand ($F_{1,5} = 2.372$, $p = 0.184$, adjusted $R^2 = 0.186$; Figure 8).

4. Discussion

In this study, we investigated the growth patterns of black spruce and the potential climatic drivers behind these patterns, as well as how landscape position (edge versus interior) and rate of lateral permafrost thaw influence growth patterns. We found that individual growth patterns have largely exhibited

Table 1. Results of Chi-Square Tests Comparing the Proportion of Trees Responding Positively and Negatively to Each of the Four Annual Climate Variables in an Early (1930–1970) and Late (1971–2011) Time Period

Climate Variable	χ^2	d.f.	p -value
Temperature	65.7	2	$p < 0.0001$
Precipitation	7.02	2	$p = 0.029$
Snow	25.2	2	$p < 0.0001$
CMI	19.2	2	$p < 0.0001$

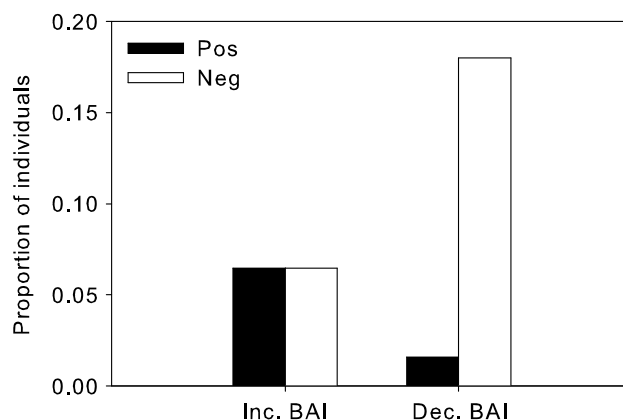


Figure 6. Proportions of individual trees demonstrating a positive (pos) and negative (neg) growth response to annual average temperature within the increasing BAI (Inc.BAI) and decreasing BAI (Dec.BAI) chronologies (Fisher's exact test, $p = 0.0050$).

declining trends since the mid-1900s. These patterns coincide with a shift in the temperature-growth relationships of trees, which change from a predominantly positive response during the 1930–1970 time period to a predominantly negative response during the 1971–2011 time period. Neither precipitation nor climate moisture index (CMI) played a direct role in these changing responses, which undermines the idea that evapotranspirative drought stress is driving growth declines at this site.

We found that landscape position influenced the growth trends of individual trees, with there being more increasing BAI and less decreasing BAI trends observed in trees on the interior of plateaus in comparison to those on the edge of plateau-wetland interfaces. Interestingly, we found no apparent effect of the rate of lateral permafrost thaw on the magnitude of black spruce growth despite rapid changes in permafrost conditions at this site. We suggest that warming-induced permafrost thaw leading to active layer thickening (vertical thaw) may be driving changes in soil moisture conditions that are directly impacting growth and productivity in boreal forests.

4.1. Growth Patterns and Climate-Growth Relationships

Our results show that black spruce has been experiencing growth declines since the mid-1900s, with over 50% of the 445 trees sampled exhibiting decreasing BAI trends (Figure 4). The growth decline observed at this site is temporally consistent with the literature on boreal forest growth dynamics. Many studies of these high-latitude forests have shown a decline in annual tree growth occurring since the middle- to late-1900s, particularly in spruce-dominated forests [e.g., Lloyd and Fastie, 2002; D'Arrigo et al., 2004; Lloyd and Bunn, 2007; Girardin et al., 2014]. Furthermore, this is consistent with normalized difference vegetation index trends that have reported declining productivity across the boreal forest in Northwestern North America [e.g., Angert et al., 2005; Bunn and Goetz, 2006; Beck et al., 2011]. Though a decline in annual BAI could be driven by tree senescence, productivity of black spruce forests on organic soils typically begins to decline at approximately 200 years [Viereck and Johnston, 1990]. Because the longevity of this species is considerably higher than the

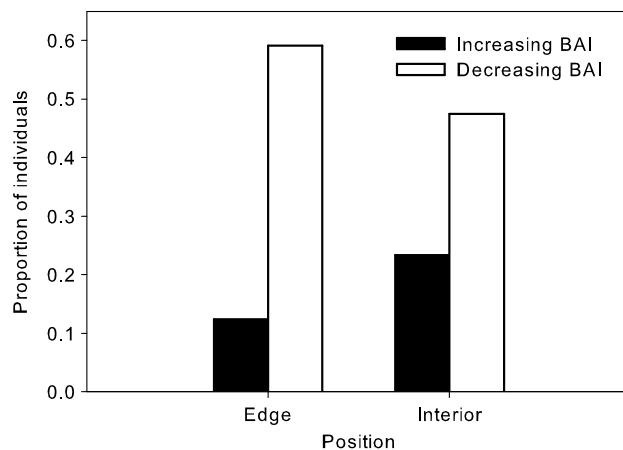


Figure 7. Proportions of trees exhibiting increasing BAI/decreasing BAI trends on the edge of plateaus (within 10 m of permafrost plateau-wetland interface) versus interior of plateaus ($\chi^2 = 8.74$, d.f. = 2, $p = 0.013$).

average age of the trees in this study (mean age = $96.1 \text{ years} \pm 30.3 \text{ SD}$), the decline in average annual growth is not likely to be attributable to tree senescence, and therefore, it is more likely to be driven by other processes such as the changing climate regime. However, growth declines at such a large scale could also be driven by widespread disease or pest outbreaks, neither of which have been documented for black spruce in this region.

It is widely accepted that in the boreal region, “forest browning” (decreasing productivity) is a result of rising temperatures driving increases in evapotranspirative water loss and drought stress [e.g., Lloyd and Fastie, 2002;

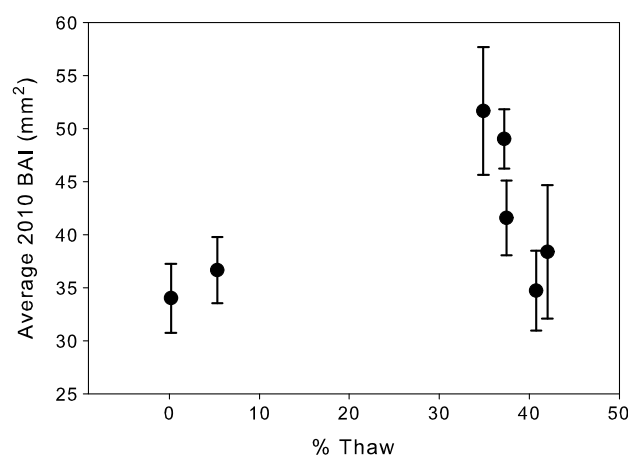


Figure 8. Relationship between the thaw rate of stands (calculated as % lateral permafrost thaw between 1977 and 2010) and averaged 2010 total basal area increment (BAI) for individuals at each site ($F_{1,5} = 2.372$, $p = 0.184$, adjusted $R^2 = 0.186$). Error bars represent the standard error of average 2010 BAI of all trees at each site.

Driscoll et al., 2005; Wilmking et al., 2005]. Similar to the widespread negative temperature-growth responses across the transition from the interior of a permafrost plateau to the wetland interface that we observed in this study, Walker and Johnstone [2014] found climate-growth relationships in black spruce were largely negative despite sampling across a regional moisture gradient in Alaska and the Yukon Territory. Carbon isotope analysis revealed widespread drought stress signals that are thought to be in part due to soil-based processes that influenced water availability to trees [Walker et al., 2015]. Similarly, we show that increases in precipitation, snowfall, and CMI over the late (1971–2011) time period have not promoted an increase

in positive climate-growth responses despite our hypothesis that these could counteract effects of increased evapotranspirative water losses associated with warming temperatures.

Of the climatic variables examined, annual average temperature over the late 1900s is the strongest predictor of the decline in productivity. While early growth responses to annual average temperature were predominantly positive (i.e., warmer years promoted growth), there was a shift in the late period toward a much higher frequency of negative responses (Figure 5). Such shifts from positive to negative responses have been documented in several studies of annual growth dynamics in boreal forests [e.g., Lloyd and Fastie, 2002; Porter and Pisaric, 2011]. These have largely been attributed to evapotranspirative drought stress driven by warming temperatures that are not tracked by precipitation (atmospheric-driven evapotranspirative drought stress). Here we propose that these late time period temperature-growth response trends are a result of warming-induced permafrost thaw and associated soil moisture stressors amplifying drought stress driven by a soil moisture deficit. At Scotty Creek and many boreal peatlands [e.g., Thie, 1974; Christensen et al., 2004; Lara et al., 2016], warming drives the thaw and loss of permafrost with dramatic implications for surficial hydrology. The widespread decreasing BAI trends and negative temperature-growth correlations without corresponding responses to precipitation or CMI support the hypothesis that changes to surface hydrology driven by active layer thickening (vertical permafrost thaw) may be playing a major role in influencing access by trees to soil water.

4.2. Influence of Permafrost Change on Growth Dynamics

The rapidly changing landscape within boreal peatlands on discontinuous permafrost drives heterogeneity in microsite conditions. Trees directly at permafrost plateau-wetland interfaces demonstrate reduced radial growth and sap flow compared to those on the interior of plateaus (>10 m from a wetland boundary [Baltzer et al., 2014; Patankar et al., 2015]). Because the gradient in abiotic conditions (e.g., active layer thickness and soil moisture) penetrates as much as ~10 m from the plateau edge [Baltzer et al., 2014], we expected to see growth trends reflect the edge conditions. We indeed found that there was a greater proportion of trees exhibiting increasing BAI trends within the interior grouping than the edge and, additionally, more decreasing BAI in the edge than interior (Figure 7). However, the proportion of trees with decreasing BAI trends was still overwhelmingly larger than increasing BAI in both edge and interior groups (Figure 7) and there was no difference in the magnitude of growth in 2010 between edge and interior trees ($t_{260} = 0.647$, $p = 0.52$). This suggests that the part of the transition between permafrost plateaus and wetlands that drives documented physiological declines and associated reductions in tree growth is isolated to the immediate plateau-wetland interface. In other words, the penetration of the biotic edge effects of permafrost thaw may be much more limited than those of abiotic changes. We investigated whether there was a discernable

continual pattern between growth and distance from edge; however, we found no clear trend (Figure S7). This is consistent with our proposed hypothesis that negative effects are constrained to the immediate edge.

The rate of land cover change (as quantified through lateral thaw rates) does not appear to be a driver of the growth dynamics (Figure 8), despite the tight associations between permafrost presence and forest cover in this ecosystem [Quinton *et al.*, 2011]. This result was unexpected as the stands sampled range from very stable with little change in areal permafrost extent since the 1970s to extensively degraded with little remaining permafrost. However, we only sampled seven stands and none of these fell within the mid-range of thaw rates, which may have restricted our ability to detect trends in the growth dynamics of these trees with respect to rate of thaw. Alternatively, our results may reflect the complex dynamics of permafrost thaw wherein both vertical and lateral thaw processes impact surface hydrology and tree growth processes [Quinton and Baltzer, 2013; Patankar *et al.*, 2015; Warren, 2015].

Given the high moisture availability in boreal peatlands on discontinuous permafrost [Zoltai, 1972] and the moisture gradient moving from edge to interior of a permafrost plateau [Baltzer *et al.*, 2014], it seemed improbable that these widespread negative growth responses at Scotty Creek could be driven by drought stress. There is already evidence for reduced root function [Baltzer *et al.*, 2013] and consequently sap flow of trees experiencing waterlogged conditions at the edges of degrading permafrost plateaus [Patankar *et al.*, 2015], which makes this site an unlikely candidate for experiencing drought. Though lateral permafrost thaw is most apparent in the discontinuous permafrost zone, it is coupled with vertical thaw [Quinton and Baltzer, 2013], which could be a major factor in the declining growth of black spruce at this site.

Patankar *et al.* [2015] and Warren [2015] linked a seasonal decline in black spruce sap flow at Scotty Creek with active layer thickening and surface soil drying. A conceptual diagram outlining the impacts of thaw processes on soil moisture with respect to the rooting zone and its implications for sap flow in black spruce is shown in Patankar *et al.* [2015]. This clearly parallels the widespread negative temperature-growth relationships across regional moisture gradients as found by Walker and Johnstone [2014]; despite large variability in moisture conditions, the shallow rooting structure of black spruce (~20 cm [Gale and Grigal, 1987]) renders the species unable to access the water table as the active layer thickens.

In peat-dominated soils, water-holding capacity of the upper layer of soil is low and the water table perches upon the impenetrable frost table. As the active layer thickens and the depth to frost table increases, the depth to the water table also increases [Quinton and Baltzer, 2013]. The current active layer thickness at Scotty Creek ranges from 35 to >150 cm at our forest stands (Figure S8); meaning for black spruce, the deepening of the water table due to vertical thaw could lead to soil moisture deficits despite increases in precipitation and CMI. In other words, more precipitation is entering the system but because of warming-induced active layer thickening, less is available to the trees for growth. Indeed, Warren [2015] found that at this site, black spruce sap flow correlates most closely with soil moisture in the top 10 cm. Increasing snowfall may likewise amplify the effects of drought stress. As we observed in our climate-growth analysis, there were high proportions of positive growth responses to snowfall pre-1970, with many fewer positive responders in the post-1970 time period (Figure 5), despite increasing snowfall (Figure 3) [Connon *et al.*, 2014]. Snow serves an important role in the insulation of soils from cold temperatures over the winter months. With the increased snowfall at this site, the warmer soils would thaw earlier in the spring. We propose that this increasing snowfall in combination with the warming-induced permafrost thaw in the late 1900s is exacerbating active layer thaw and decreasing access to soil moisture for the black spruce forests at this site.

5. Conclusions

From this study, we have been able to conclude that climatically driven drought stress is not the mechanism behind the widespread growth declines in this boreal peatland system, as there have not been major shifts toward positive growth responses to either precipitation or CMI. However, there is evidence suggesting that the thickening of the active layer as warming continues in this region coupled with the low water holding capacity of peat is resulting in water limitations within the rooting zone of black spruce [Quinton and Baltzer, 2013; Patankar *et al.*, 2015; Warren, 2015]. Such soil moisture deficits would be expected to contribute to the prevalence of negative growth—temperature relationships apparent in recent years in this thawing permafrost peatland as warming-induced active layer thickening may be affecting access to the water table for shallow-rooting black spruce. This mechanism is also influenced by the insulation of soils by the deeper

snowpacks experienced in recent years; deeper snowpack can promote earlier soil thaw, active layer thickening, and further limit water availability within the rooting zone. This hypothesis is supported by our findings of reduced positive growth responses to snowfall in recent decades. Further investigation of rooting distribution and plasticity in light of the effects of thawing permafrost on the soil moisture profile will be required to understand and predict responses of black spruce to warming. However, this study has provided notable additions to the ever-growing body of knowledge on the response of the boreal forest to climate change. As this study was one of the first to specifically test permafrost conditions as a mechanism driving individual growth patterns within a site, we have provided important insights into the underlying causes of growth patterns of black spruce in a landscape that has experienced and is expected to continue to undergo dramatic change.

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