Trends in tree biomass along topgraphically- and climatically-induced permafrost gradients in the Mackenzie Valley, NWT

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ABSTRACT
With permafrost distribution controlled largely by topography and climate, this study examines the influence of climate and permafrost conditions on standing tree biomass along a climatic gradient extending from the Mid-Boreal Ecoclimatic Region in the southern Northwest Territories to the High Subarctic environments near the arctic tree line at Inuvik. At each of 25 sites, plots were established in areas of permafrost-affected peatlands (peat plateaux), areas of permafrost thaw (collapse scars), and adjacent forest environments occurring on mineral soils (upland forests). Significant (α=0.05) changes in tree biomass were observed along both the climatic and topographic gradients examined with results demonstrating the complexities of permafrost environments.

RÉSUMÉ
La répartition du pergélisol dépend principalement de la topographie et du climat. Dans le cadre de la présente étude, on a examiné l'effet du climat et de l'état du pergélisol sur la biomasse d'arbres sur pied qui se situe le long d'un gradient climatique s'étendant de la région écoclimatique des terres boréales moyennes, dans les Territoires du Nord-Ouest, jusqu'à la région du haut-subarctique, près de la limite septentrionale des arbres d'Inuvik. À chacun des 25 sites de l'étude, on a établi des placettes dans des tourbières pergélisolées (plateaux de tourbières), des zones de dégel du pergélisol (tourbières oligotrophes effondrées) et des zones forestières adjacentes situées sur des sols minéraux (forêts des hautes terres). Des changements significatifs (α = 0,05) ont été observés dans la biomasse d'arbres le long des gradients climatiques et topographiques qui ont été examinés. Les résultats de l'étude illustrent la complexité des milieux pergélisolés.

1 INTRODUCTION

Permafrost (earth materials having a temperature below 0˚C for at least two consecutive years, Harris et al. 1988) is an important component of northern landscapes, underlying 25% of the northern hemisphere (Anisimov and Nelson 1996). In Canada, the Continuous and Discontinuous Permafrost Zones cover approximately half of the country's land area (Heginbottom et al. 1995). A thermal phenomenon, the permafrost distribution is broadly determined by mean annual air temperatures. On a local or regional level, however, the interaction of topography, hydrology, and soil materials exert a greater influence on permafrost distribution. Peat soils, in particular, have a strong association with permafrost.

Peatlands are also characteristic of northern landscapes, formed as slow decomposition of plant materials in waterlogged soils results in an accumulation of this organic matter (peat) on the ground surface. Through autogenic successional processes, a series of plant communities continue to thicken the peat deposit until the peatland surface is raised above the water table far enough that peatland plants are no longer in contact with the regional ground water (Vitt 1994). The resulting peatland is termed a bog, and if this bog occurs north of the 0˚C isotherm, dry surface peat layers may provide enough insulation that soils frozen over winter will be protected from the summer heat and remain frozen year-round. With the establishment of permafrost, the bog surface is now further raised above the surrounding landscape due to volumetric expansion, and peat mosses characteristic of bogs are replaced by the more drought tolerant lichens. These peatlands, with established permafrost cores, are now termed peat plateaux (Robinson and Moore 2000). A dynamic environment, if the insulating surface layers of the peat plateau are disturbed by such things as fire, compaction, or peat fissures (Thie 1974, Zoltai 1993) this may allow for thawing of the permafrost during the summer and collapse scars will be formed within the peat plateau. With the loss of underlying ice volume, the ground surface of collapse scars subsides and forms a wet depression, often prevented from drainage by the surrounding peat plateau. This wet, collapse scar environment is ideal for peat accumulation and, if the climate is amenable, continued vertical peat accumulation will again result in dry, insulating surface layers and reestablishment of permafrost (Zoltai 1993).

With complex interactions between northern peatland soils, vegetation, and permafrost, a thorough understanding of forest and peatland ecology is required in order to predict climate change responses in these sensitive northern landscapes. In northwestern Canada, the Mackenzie Valley presents a unique opportunity to study tree biomass in a region rich in peat deposits, spanning a climatic gradient of 6ºC mean annual temperature and 121 mm mean annual precipitation (Environment Canada 2002), in what is predicted to be one of the most sensitive areas to climate warming in Canada (Kettles and Tarnocai 1999).

2 STUDY REGION

Extending from the Alberta border to the northern extent of the Taiga Plains Ecozone (level II ecoregion; Ecosystem Classification Group 2007) north of Inuvik, the forested ecoregions of the Mackenzie Valley encompass a latitudinal gradient of almost nine degrees. This climatic gradient is reflected in the permafrost zonation, with the Sporadic Discontinuous, Extensive Discontinuous, and Continuous Permafrost Zones replacing each other from south to north, underlying 10-50%, 50-90%, and 90-100% of the terrain, respectively (Figure 1). Ecological classifications of the region also reflect this north to south variability, while incorporating influences of the large-scale topography. A prime example is the Ecoclimatic Regions of Canada (Ecoregions Working Group 1989) which delineate the Mid Boreal, High Boreal, Low Subarctic and High Subarctic ecoclimatic regions within the Mackenzie Valley (Figure 1). .

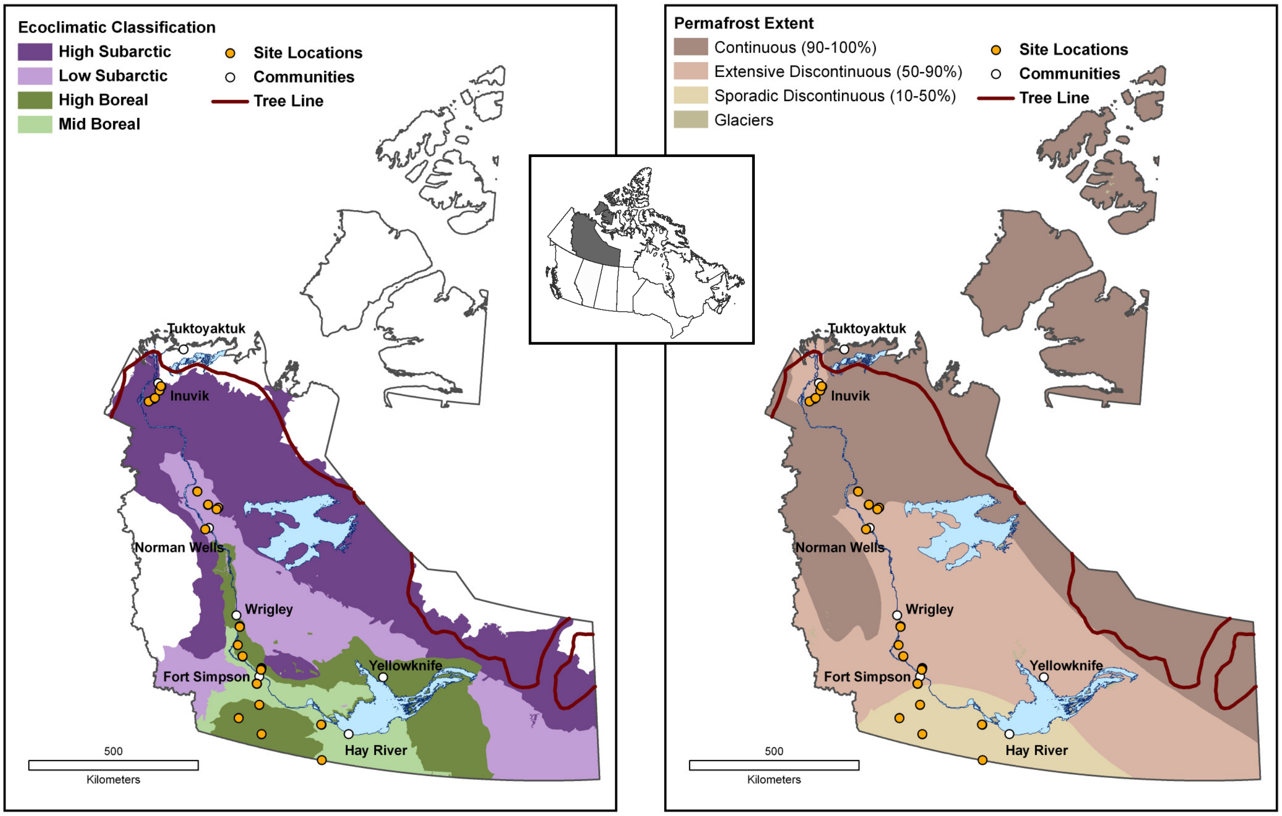

Figure 1. The 25 site locations in the Mackenzie Valley region of Canada's Northwest Territories are depicted with respect to the Ecoclimatic Classification (left) and Permafrost Zone (right), where the Ecoclimatic Classification is derived from the Ecoregions Working Group (1989) and the original permafrost map data was provided by The Atlas of Canada http://atlas.gc.ca/ © 2007, and was produced under licence from Her Majesty the Queen in Right of Canada, with permission of Natural Resources Canada.

3 METHODS

3.1 Field Methods

Sixty nine plots were established throughout the Mackenzie Valley during the summers of 2007 and 2008 (Figure 1). At each of the 25 sites, plots were located in areas of permafrost-affected peatlands (peat plateaux), areas of permafrost thaw (collapse scars), and adjacent forest environments occurring on mineral soils (upland forests). (Figure 2). Because of climatic limitations in the High Subarctic, Continuous Permafrost Zone, near Inuvik, no collapse scar plots were included in the six most northern sites.

Each plot was laid out as a 20 x 20 m square, with standard mensuration data recorded within fixed plot areas. Mensuration included tree species, height, and diameter (DBH, diameter at breast height – 1.3 m) for each tree in a randomly selected 10 x 10 m plot quadrant. Trees shorter than 1.3 m were tallied by size class within the same quadrant, while data for trees larger than 5 cm DBH were recorded for all trees within the entire 20 x 20 m plot.

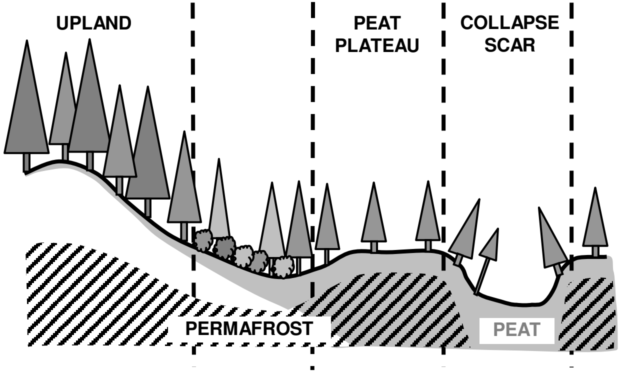

Figure 2. The topographic gradient examined at each site includes plots in upland, peat plateau, and collapse scar environments. Soils and active layer depths vary along this gradient as is evident with a transition from mineral (white) soils, in the upland, to organic (grey) soils in the peat plateau and collapse scar. Shallowest active layer depths are found in the peat plateaux, while permafrost is absent from collapse scars.

Active layer depth for each plot was determined through the use of a peat probe or in the plot soil pit. The peat probe (an extendable metal rod) was inserted at 13 locations per plot to determine the depth to permafrost (active layer depth) or mineral soil (peat depth). Because active layer depth could only be recorded when it was shallower than the peat layer, active layer depths were only obtained for upland plots where permafrost was reached within the 60 cm depth of a standard soil pit. Depth of the water table was also recorded, when present, in soil pits.

3.2 Analysis Methods

Tree level biomass was calculated using a mixed model (Lambert et al. 2005) for trees taller than 2 m. The Lambert functions are accurate for larger trees, but all approach zero biomass at a height of 1.3 m. Although this small error would be negligible in many mature, southern stands, with the large number of small trees in these northern study sites, we felt it prudent to make an adjustment for small trees (Eq. 1). For trees less than 2 m tall, an average biomass (in tonnes) for 2 m tall trees was calculated at each site (C) and the adjusted biomass (B), also in tonnes, was calculated for each tree as a linear function of the cube of the tree height (h) in metres.

$$B = C * \frac{h^3}{2^3} \qquad [1]$$

The biomass of all trees measured in each fixed area plot was summed and divided by the plot area, to yield a biomass per unit land area (t ha^{-1}).

Tree biomass was then normalized with a natural logarithm transform [ln(biomass + 1)] in order to meet assumptions of normality and equal variances inherent in Analysis of Variance (ANOVA) and regression procedures (Zar 1999). Subsequently, a univariate analysis of variance was conducted, through the SPSS GLM procedure (SPSS Inc. 2003). The ANOVA included normalized biomass as the dependant variable, and a single fixed factor which combined the topographic plot types (collapse scars, peat plateaux and upland forests) and the ecoclimatic regions (high subarctic, low subarctic, high boreal, and mid boreal). Post hoc comparisons were then performed using Dunnett's T3 (Dunnett 1980), to indicate significant ($\alpha = 0.05$) differences between group means.

Linear regressions were developed to examine the relationship between normalized biomass and climatic parameters. With sparse climatic stations in the NWT, Mean Annual Temperature (MAT) and Mean Annual Precipitation (MAP) were derived from 1961-1990 monthly climate station normals interpolated for 10 km grid cells (McKenney et al. 2006) using the ANUSPLIN software (Hutchinson 2004).

In order to determine if the relationships differed significantly between topographic types, regression equations were compared through the use of dummy variable coding in a multiple regression model (Kleinbaum and Kupper 1978). Linear regression procedures were conducted in SPSS (SPSS Inc. 2003) with subsequent F-tests calculated by hand in Microsoft Excel (Microsoft 2003).

4 RESULTS

Results of the ANOVA indicate significant ($\alpha = 0.05$) changes in tree biomass along both the ecoclimatic and topographic gradients examined. Post hoc tests illustrate three groupings evident in Figure 3. The greatest tree biomass was found in the Mid and High Boreal uplands, while High and Low Subarctic uplands had comparable biomass to the Boreal peat plateaux. In turn, Subarctic peat plateaux have very low biomass, comparable to that found in collapse scars from all regions. Tree biomass varied from a mean of 76.2 ± 0.2 (SE) t ha^{-1} in the Mid-Boreal uplands to an absence of trees in the Low Subarctic collapse scars.

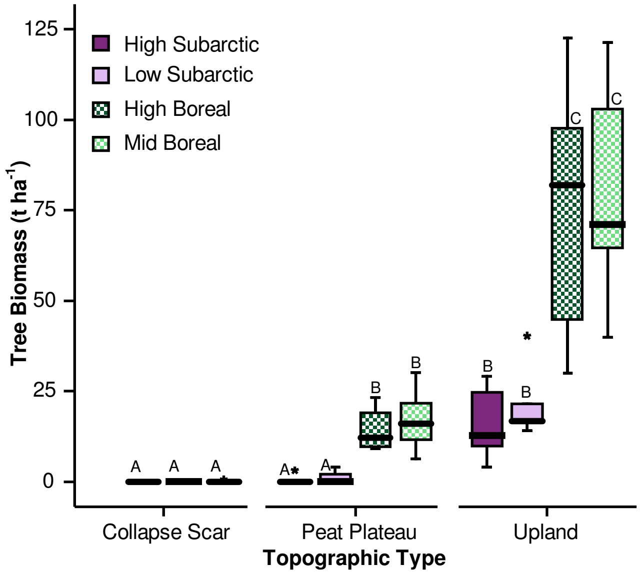

Figure 3. Tree biomass grouped according to topographic plot types, and ecoclimatic region. Letters above box plots denote significant groupings as determined by Dunnett's T3 post hoc tests.

A more direct climatic influence was detected with linear dependence of normalized tree biomass on both MAT, and MAP, with significantly (α = 0.05) different relationships between topographic landforms in both cases (Figures 4 & 5). Mean annual temperature and precipitation were found to be highly correlated (r = 0.84, p = 0.000) in the study region, however, and temperature demonstrated the stronger relationship with biomass.

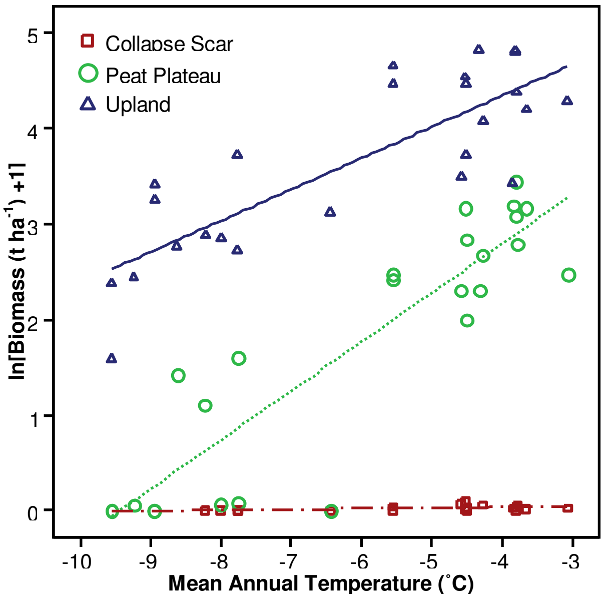

Figure 4. Linear relationships between ln-transformed biomass (t ha^{-1}) and mean annual temperature (˚C) for different topographic landscape features.

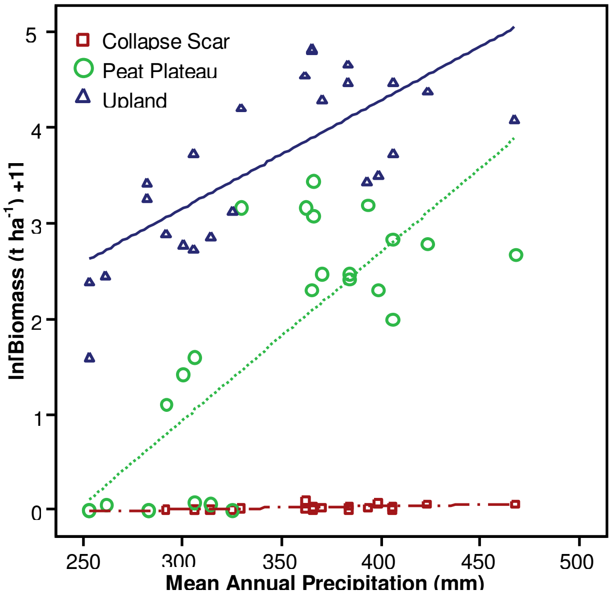

Figure 5. Linear relationships between ln-transformed biomass (t ha^{-1}) and annual precipitation (mm) for different topographic landscape features.

Active layer depth was recorded in all peat plateau plots, and in approximately one quarter of the upland plots (Figures 6 & 7). Active layer depths ranged from 26 cm in a High Subarctic upland, to 73 cm in a High Boreal peat plateau. Tree biomass in these permafrost – restricted plots ranged from a minimum of zero in a number of Low and High Subarctic peat plateaux to a maximum of 30 t ha^{-1} in a Mid Boreal peat plateau.

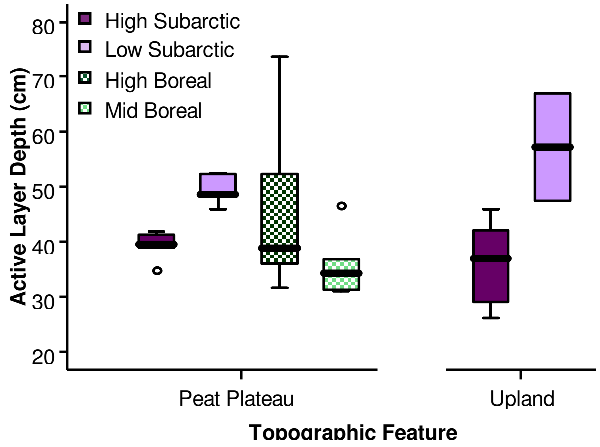

Figure 6. Box plots showing the variation in active layer depth (cm) across ecoclimatic regions for peat plateaux and for the upland plots where the active layer was accessible for probe measurement.

While permafrost was absent from collapse scars, by definition, shallow water table depths were measured in all plots, ranging from 3 cm above to 29 cm below the ground surface.

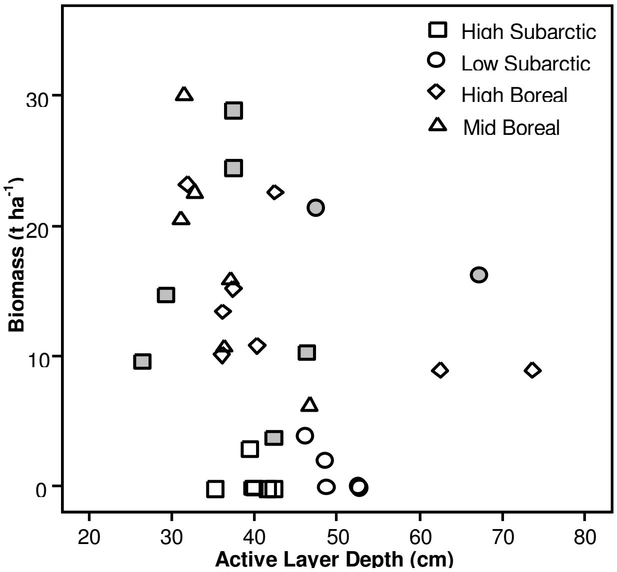

Figure 7. Scatterplot of tree biomass and active layer depth. Peat plateau plots are represented by open symbols, while filled symbols depict upland plots. Symbols shape identifies the ecoclimatic region.

5 DISCUSSION

Results of this study demonstrate that tree biomass is influenced both by climatic and local site factors. The local site conditions examined reflect differences in permafrost conditions, water table depths, and in soil materials. Highest tree biomass was found in mineral soil uplands, with intermediate tree biomass in the peat plateaux, and very low tree biomass in the, essentially treeless, collapse scars. This general trend of decreasing biomass from upland to peat plateau, to collapse scar, is consistent within an ecoclimatic region but, on a broader scale, is complicated by the impact of climatic conditions. While tree biomass is greatest in the Mid and High Boreal upland plots, shallow active layers limit tree biomass in the, more northerly, Low and High Subarctic uplands. Similar active layer depths, of the Boreal peat plateaux and Subarctic uplands, result in similar tree biomass values, indicating active layer depth to be a limiting factor, constraining tree biomass. Because active layer depth is determined not only by the regional climatic conditions, but also by the insulative value of the soil and overlying vegetation, tree biomass is effectively determined by the interaction of climatic conditions, and local site factors as expressed through the active layer depth.

Tree biomass in collapse scars throughout the Mackenzie Valley is, by definition, not limited by the presence of permafrost. These areas are, instead, limited by the high water tables resulting from the surface subsidence associated with localized permafrost thaw. This subsidence and drastic increase in the water table, relative to the ground surface has been seen to drown tree roots (Vitt et al. 1994, Camill and Clark 1998, Zoltai 1993) and resulting collapse features are essentially treeless, with a few small seedlings resulting in negligible biomass.

With shorter growing seasons, and shallow active layers, northerly, Low and High Subarctic, peat plateaux have very few trees and, consequently, the very low tree biomass is not significantly different from that found in collapse scars throughout the Mackenzie Valley. While shallow active layer depths in these Subarctic peat plateaux certainly restrict tree rooting zones, data do not demonstrate active layers of Subarctic peat plateaux to be any shallower than those of the Boreal peat plateaux, despite the significantly lower Subarctic tree biomass. This discrepancy may be partially attributed to the timing of active layer measurements which occurred slightly earlier in the season for Boreal sites (a mean measurement date of July 21, as compared to August 7). Measurement timing cannot completely explain the consistently lower biomass, however, as dates of measurement overlapped considerably, while biomass values did not.

Cool air and soil temperatures are known to limit tree growth and are commonly cited as factors controlling the treeline position on a landscape level (Gehrig-Fasel et al. 2008, Grace et al. 2002, Danby and Hik 2007), although the specific mechanisms limiting growth, reproduction, and survival of trees at the tree line are poorly understood (Grace et al. 2002). Annual variations in growing season length have also been documented as a primary factor impacting tree growth in Boreal and Subalpine sites (Suni et al. 2003, Wieser 2000). Assuming similar active layer depths and growing season soil temperatures between the Boreal and Subarctic peat plateaux, cooler summer air temperatures, coupled with shorter growing seasons in the Subarctic regions, likely restrict the tree biomass growth and account for observed regional differences.

Direct analysis of climatic parameters demonstrates that while tree growth in collapse scars is clearly limited by high water tables and is invariable with respect to MAT or MAP, in both upland and peat plateau sites tree biomass increases in response to MAT and MAP. Although strong correlation of MAT and MAP in the Mackenzie Valley makes it impossible to disentangle temperature and precipitation growth responses, the stronger relationship of biomass with MAT, coupled with the lower slope, moisture-receiving positions of most sites, makes it much more likely that temperature rather than moisture is limiting tree biomass in the Mackenzie Valley.

On a local scale, limiting site factors such as shallow water tables or active layer depths appear to account for the different tree biomass values seen between collapse scar, peat plateau and upland sites. On a landscape scale, climatic parameters, such as air temperature or growing season length, have a greater influence on tree biomass.

5.1 Climate Change Implications

Most general circulation models predict climate warming in the high latitudes of western North America (McCarthy et al. 2001), continuing the general trend observed since 1966 (Serreze et al. 2000). The Mackenzie Valley lies within one of the most strongly impacted areas of the globe and, as results demonstrate, is comprised of ecosystems strongly influenced by thermal factors, with tree biomass responding to air temperature and permafrost conditions.

Superficially, the observed relationship between biomass and MAT indicates that warming climate conditions would result in increased tree biomass for both peat plateaux and upland forests throughout the Valley. While this is probable, at least in the short term, for upland forests, in peat plateaux the interaction of permafrost with warming climate is anticipated to be more complex (Camill and Clark 1998). In sites where warming air temperatures do not cause permafrost collapse in peat plateaux, tree biomass can be expected to increase. If, however, warming climates cause degradation of the peat plateau permafrost, tree biomass will decline.

Although permafrost aggradation and collapse has been shown to be a cyclic phenomenon (Zoltai 1993) recent climate warming has resulted in net degradation of permafrost, documented in the Sporadic Discontinuous and Isolated Patches Permafrost Zones of southern NWT, and in continental western Canada (Beilman and Robinson 2003, Beilman et al. 2001, Halsey et al. 1995). Degradation of peat plateaux to collapse scars will result in a dramatic decline in tree biomass, at the local level, and may result in a net decline in tree biomass across a landscape, depending on the extent of permafrost collapse. Even if these recently degraded peat plateaux were to accumulate peat to the point where site conditions were, again, suitable for permafrost aggradation this process would be expected to take a minimum of 600 years (Zoltai 1993).

The process of aggradation is only possible where climate conditions are conducive to permafrost formation, and warming climates since the Little Ice Age (circa 1500 to 1700 A.D., Luckman 1986) have resulted in relict permafrost features occurring south of the 0˚C isotherm (Thie 1974, Camill and Clark 1998, Halsey et al. 1995). In such a situation, climate is no longer capable of supporting permafrost, even under insulating peat layers, and degraded peatlands will not be capable of future permafrost aggradation unless climatic conditions cool. With continued climate warming, the 0˚C isotherm will shift North, resulting in more relict permafrost on the landscape. As permafrost slowly degrades into equilibrium with the climate, connectivity of collapsing features will drain the landscape (Beilman and Robinson 2003). Increased connectivity will alter local peatland hydrology, replacing peat plateaux and collapse scars with the bogs and fens, while also changing the landscape-level hydrology, with consequent impacts on tree growth throughout the landscape.

Because northern peatland environments exhibit complex interactions of vegetation, climate and hydrology, both local, autogenic, processes must be considered in tandem with landscape-level processes in order to understand the impacts of climate change. Because both the vegetation and soil conditions impart a degree of inertia into the system, time lags must also be considered as the ecosystems adapt to new conditions (Camill and Clark 1998).

6 CONCLUSION

The Mackenzie Valley region of Canada provides a unique opportunity to investigate the impact of a range of climatic conditions on tree biomass in a permafrost-affected region rich in peat deposits. The Mackenzie Valley spans a MAT gradient of 10ºC and a MAP range of 227 mm, in what is predicted to be one of the most sensitive areas to climate warming in Canada (Kettles and Tarnocai 1999). Although northern peatland environments exhibit complex interactions of vegetation, climate and hydrology, a number of results help to elucidate climatic controls on standing tree biomass in the Mackenzie Valley.

Results of this study clearly demonstrate that tree biomass is influenced both by climatic and local site factors. On a local scale, limiting site factors such as shallow water tables or active layer depths appear to account for the different tree biomass values seen between collapse scar, peat plateau and upland sites. On a landscape scale, climatic parameters such as air temperature, or growing season length, are more important in determining tree biomass. An example of these interacting factors is the revelation that shallower active layers in peat plateaux result in tree biomass values comparable to more northerly upland forests. Specifically, tree biomass in Boreal peat plateaux is comparable to Subarctic uplands, while Subarctic peat plateaux are effectively treeless (the definition of Arctic uplands). Biomass in the, temperature limited, peat plateau and upland sites is seen to increase significantly with MAT, while the tree biomass of collapse scars (limited by high water tables) has a very low response to MAT.

Although the observed relationship between biomass and MAT imply that warming climate conditions would result in increased tree biomass for the peat plateaux and upland forests, complex interactions of vegetation, climate and hydrology prevent such a simplification. When considering landscapes with the presence of both peatlands and permafrost, local, autogenic, processes must be considered in tandem with landscape-level processes in order to understand the impacts of climate change. Additionally, because both the vegetation and soil conditions affect the local microclimate, time lags must also be considered as the ecosystems adapt to new conditions.

While research is still needed to understand northern boreal and subarctic ecosystems' response to climate change, the sites described here have been established as part of a permanent monitoring network enabling continued monitoring of complex ecosystem responses to a warming climate.

ACKNOWLEDGEMENTS

This project was made possible with the generous support of the Government of Canada Program for International Polar Year, the Government of Canada MVP Program and Natural Resources Canada, Canadian Forest Service. Many thanks are also due to Steve Gooderham, Mike Gravel, Tom Lakusta and Paul Rivard, from the Forest Management Division, Government of the Northwest Territories, as well as Michael Brady and Diana Boylen from the Northern Forestry Centre, Canadian Forest Service. Without the valuable contributions of field and laboratory staff, this project would not have been possible and we would like to acknowledge the hard work of: Patrick Hurdle, Sydney Kjellander, Meghan Klaudt, Isaac Lennie, Claire Marchildon, Catherine McNalty, Natalka Melyncyky, Valerie Mucciarelli, Stephanie Nelson, Molly Patterson, Cody Renz, Michelle Riopel, Natalia Startsev, Nancey Stevens-Whiteman, and Peter Sugawara.

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