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Source: Arctic, Antarctic, and Alpine Research, 43(2) : 279-288

Published By: Institute of Arctic and Alpine Research (INSTAAR),
University of Colorado

URL: <https://doi.org/10.1657/1938-4246-43.2.279>

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Environmental Controls on Needle Gas Exchange and Growth of White Spruce (*Picea glauca*) on a Riverside Terrace near the Arctic Treeline

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Abstract

Recent studies have revealed positive and negative trends in the radial growth of treeline white spruce (*Picea glauca*) as temperatures have warmed in recent decades. Investigators have speculated that negative growth trends reflect the increasing importance of temperature-induced drought stress, yet direct observations of drought-induced stomatal closure have not been made in white spruce near the Arctic treeline. In this study, we measured needle gas exchange, a variety of needle traits, and branch growth in contrasting growing seasons on a riverside terrace near the Arctic treeline in Noatak National Preserve, northwest Alaska. Needle gas exchange was limited by cold soils (<7 °C), nighttime frosts, large vapor pressure deficits (VPD) and/or low soil water contents during the majority of our midday measurements. Near optimal conditions for needle gas exchange were consistently found in late August, when soils were relatively warm, air temperatures were moderate, and the VPD was relatively small. Defoliation during a two-year bud moth infestation (*Zeiraphera* spp.) substantially reduced branch growth, obscured potential relationships between needle gas exchange and growth, and revealed the importance of whole canopy gas exchange measurements. Results of our study show there is a very narrow window of environmental conditions for near optimal needle gas exchange in white spruce near the Arctic treeline. Although we identified many abiotic constraints on needle gas exchange, a single biological factor likely had the greatest effect on annual branch growth.

DOI: 10.1657/1938-4246-43.2.279

Introduction

Tree-ring studies of white spruce (*Picea glauca*) near the Arctic treeline in Alaska have revealed positive and negative growth trends during a period of rapid warming in the last half of the 20th century (e.g., Lloyd and Fastie, 2002; Wilmking et al., 2004). Investigators have speculated that negative growth trends reflect an increasing importance of temperature-induced drought stress and that increases in treeline stand density may be expected in mesic and wet areas, but not in dry areas, with future climate warming (e.g., Wilmking and Juday, 2005). There have been very few studies of tree physiology near the Arctic treeline (Vowinkel et al., 1975; Sveinbjörnsson, 1983; Goldstein et al., 1985; Sveinbjörnsson et al., 1992), yet process-level studies of tree physiology and growth may be required to develop a satisfactory understanding of the relationships between climate and tree performance. For instance, despite assertions that temperature-induced drought stress may be an increasingly important control on the performance of treeline trees, drought-induced stomatal closure has yet to be documented near the Arctic treeline in Alaska. The vast majority of research on drought stress has been carried out in warm and dry environments that exhibit large diurnal variation in air temperature. It is likely that stomatal limitations manifest differently in the Arctic, where plants may be less well adapted to drought, and where long days and smaller diurnal temperature variation may necessitate stomatal closure for

a greater proportion of the diurnal cycle during drought conditions.

In the present study, we set out to build on our limited understanding of the relationships between climate, needle physiology, and tree growth near the Arctic treeline. We measured needle gas exchange and branch growth of 18 white spruce trees during contrasting growing seasons along a riverside terrace near the Arctic treeline in Noatak National Preserve, northwest Alaska. We selected a riverside terrace for study, because it is the habitat in which white spruce reach their northernmost distribution. Riverside terraces generally have well-drained soils. Therefore, we anticipated that mid-summer drought stress may be an important control on tree performance. The study trees were evenly distributed along a gradient of parent material depth, with trees at the shallow and deep ends growing on approximately 15 and 50 cm, respectively, of sand and silt. We expected that trees growing on shallow parent material would be more likely to experience drought stress, because they may draw water from a smaller and drier volume of soil. Following the work of Goldstein et al. (1985) in the central Brooks Range, we anticipated that cold soils would limit needle gas exchange near the margins of the growing season. In general, we expected that needle gas exchange and branch growth would be greatest during growing seasons that are both warm and wet. An unexpected bud moth infestation (*Zeiraphera* spp.) during the second year of the project complicated relationships between climate and tree growth and provided

insights into the importance of biotic factors as controls on tree performance.

Methods

SITE AND TREATMENT DESCRIPTIONS

The study was carried out on a terrace along the Agashashok River in the Baird Mountains of the Brooks Range in Noatak National Preserve, Alaska (67°28'N, 162°12'W, 90 m a.s.l.). The study site is remote and accessed by bush plane in the summer months and snowmachine during the wintertime. The northernmost white spruce trees in the Agashashok watershed occur at 67°35'N, approximately 12 km north of the study site. The 0.75-km-long terrace is capped with a single layer of sand and silt that grades from approximately 15 cm depth at the upstream end, to 50 cm depth at the downstream end. Soil texture at the site is classified as a very fine sandy loam with 45–55% sand, 40–50% silt, and approximately 5% clay (Binkley et al., 1995). There is no evidence of permafrost. White spruce trees exist at similar density (~1200 stems/ha) along the full length of the parent material gradient. Binkley et al. (1995) collected increment cores from the largest trees on the terrace and found a maximum age of approximately 200 years, providing a minimum age for the terrace. Understory vegetation varies with parent material depth and is dominated by *Dryas integrifolia* at the shallow end. With increasing parent material depth, *Betula nana*, *Potentilla fruticosa*, *Shepherdia canadensis*, and shrubs of *Salix* spp. become increasingly prevalent.

STAND CLIMATE

The microclimate of the terrace was monitored using three meteorological stations, evenly distributed along the parent material gradient. Each station consisted of a CR1000 datalogger (Campbell Scientific, Logan, Utah) and sensors for air temperature, relative humidity (CS500, Campbell Scientific, Logan, Utah), and wind speed at 2 m (014A, Met One Instruments, Grants Pass, Oregon). All sensors for air temperature and relative humidity were housed within radiation shields. Sensors for soil temperature (CS107, Campbell Scientific, Logan, Utah) and soil water content (CS616, Campbell Scientific, Logan, Utah) were installed at 10 cm depth beneath each of the 18 study trees. The central station was also equipped with a solar radiation sensor (LI-200S, Licor Biosciences, Lincoln, Nebraska) and tipping bucket rain gauge (TE525, Texas Electronics, Dallas, Texas). Sensors were read at 30 second intervals and hourly averages were logged to memory. The atmospheric vapor pressure deficit (VPD) was calculated from air temperature and relative humidity data using the updated version of the equation presented in Buck (1981).

Measurements of soil water content were also made using a HydroSense probe (Campbell Scientific, Logan, Utah), which provided estimates of volumetric soil water content from 0 to 12 cm depth. In June, July, and August 2008, measurements made with the HydroSense were compared with direct measurements of volumetric soil water content made using soil cores (3.8 cm diameter) in an area adjacent to the study site. The relationship between the HydroSense measurements and the direct measurements was fit with a quadratic equation ($n = 35$, $r^2 = 0.86$, $P < 0.01$), and this calibration curve was applied to all measurements made using the permanently installed CS616 probes.

NEEDLE GAS EXCHANGE, NITROGEN CONCENTRATIONS, $\delta^{13}\text{C}$, AND XYLEM WATER POTENTIALS

Measurements of midday needle gas exchange were made at breast height on the west side of each of the 18 study trees using a LI-6400 portable photosynthesis system, equipped with an opaque 2×3 cm LED chamber and a CO_2 mixer (LI-COR Biosciences, Lincoln, Nebraska). Measurements were made on the youngest needle cohort at midday on 9 June, 19 July, and 31 August 2007, and 11 June, 21 July, and 24 August 2008. Bud break occurred in mid to late June during each year of the study. June measurements of needle gas exchange were, therefore, made on needles produced in the previous growing season, while measurements made in July and August were of needles produced during the current growing season. We are not aware of a study that has examined gas exchange as a function of needle age in white spruce. Hom and Oechel (1983) examined gas exchange and nutrition in different needle age classes of black spruce (*Picea mariana*) near Fairbanks, Alaska, and found no evidence of a difference in needle N concentrations or photosynthetic capacity in the four most recent age classes. Nevertheless, comparisons of gas exchange and needle $\delta^{13}\text{C}$ measurements made in June with those made in July and late August warrant some caution. In order to seal the chamber, approximately 10 needles were removed from each branch a minimum of 24 hours prior to the gas exchange measurements. Baddeley et al. (1994) found that removal of dead leaves from the arctic plant *Dryas octopetala* affected gas exchange of remaining live leaves for up to 30 minutes. We felt that a 24 hour wait period would be an appropriate and conservative approach, given that we were removing live needles.

Measurements were made of dark respiration and light-saturated net photosynthesis on each study tree. Because measurements were made on the branch tip, between one and three buds were present within the chamber. Gross photosynthesis was calculated as the difference between measurements made in the light and in the dark. Our calculations do not account for the possibility that respiration in the light may be lower than respiration in the dark (Krömer, 1995), meaning that we may have systematically overestimated gross photosynthesis. Given that all trees were measured at the same light levels, such an error would not affect relative comparisons across dates and parent material depths. During all measurements, needle temperature was held at 20 °C, the reference CO_2 concentration was set at 400 $\mu\text{mol/mol}$, and the flow rate was held constant at 400 $\mu\text{mol/sec}$, while the proportion of flow through the desiccant was adjusted to maintain a chamber RH of approximately 50%. Measurements of light-saturated needle gas exchange were made with the photosynthetic photon flux density (PPFD) set at 1500 $\mu\text{mol m}^{-2} \text{sec}^{-1}$. To ensure that 1500 $\mu\text{mol m}^{-2} \text{sec}^{-1}$ was an appropriate choice for measurements of light-saturated needle gas exchange, light response curves were measured periodically throughout the study. While photosynthetic rates were often more than 80% of maximum with light levels as low as 900 $\mu\text{mol m}^{-2} \text{sec}^{-1}$, slight increases were generally observed up to 1500 $\mu\text{mol m}^{-2} \text{sec}^{-1}$ (data not shown). On 22–23 July 2007 and 23–24 July 2008, diurnal measurements of dark respiration and light-saturated needle gas exchange were made on 6 trees growing on thin parent material (≤ 30 cm). Measurements were made at 2:00, 8:00, 14:00, and 20:00 Alaska Daylight Time. Chamber conditions during the diurnal measurements were the same as those used during the midday measurements on the 18 study trees.

Branch tips were harvested after completing the gas exchange measurements, such that different needles were measured on each

sampling date, but the same needles were monitored throughout the diurnal cycle. Needles were carefully removed from the branch within 6 hours and scanned fresh at 300 dpi. The scanned images were subsequently analyzed for needle projected area using unsupervised classifications in Erdas Imagine 9.1 (Leica Geosystems, Atlanta, Georgia). After scanning, the needle samples were returned to the laboratory, dried for 48 hours at 60 °C, ground to a fine powder using a ball mill, and analyzed for N concentration and $\delta^{13}\text{C}$ using a Costech 4010 Elemental Analyzer (Costech Analytical, Valencia, California) interfaced with a Thermo-Finnigan Delta Plus XP continuous-flow stable isotope ratio mass spectrometer (Thermo Electron Corp., Waltham, Massachusetts).

During the midday gas exchange measurements of July 2007 and June, July, and late August 2008, a second branch was selected from the same height and aspect of each experimental study tree for measurement of xylem water potential. Water potential measurements were made using a Scholander-type portable pressure chamber (PMS Instrument Co., Albany, Oregon). Care was taken to limit variation in the diameter of the cut stem and the amount of foliage within the chamber.

NEEDLE LENGTH, NEEDLE DENSITY, AND BRANCH GROWTH

Samples of the current year's needle cohort were collected in late August during each year of the study. In 2007 and 2008, these were the same needles on which gas exchange measurements were made. Needles were carefully removed from the branch and scanned fresh at 300 dpi. The scanned images were subsequently analyzed for needle length using WinSEEDLE (Regent Instruments Inc., Nepean, Ontario).

Retrospective measurements of 2005–2008 branch extension growth were made on the 18 study trees on 25 August 2008. The tree canopy was divided into four sections, corresponding with the cardinal directions, and one branch at breast height was harvested in each section. Care was taken to select a branch in which growth from the center bud had been dominant for a minimum of five years. Annual growth increments were identified using bud scars and measurements were made using digital calipers. For each growth increment, the number of branches originating at and between bud scars was recorded. The total number of branches originating between 2005 and 2008 was used to provide an index of branching frequency. Branches from the east and west sides of the trees were selected for retrospective analysis of needle density (# of needles/mm branch) during each year of the study. The wooden pegs at the base of each needle were counted within each growth increment, from 2005 to 2008, and expressed as needle number per unit branch length. This approach was used, rather than direct needle counts, because the pegs generally remain on the branch for several years after a needle has been lost.

BUD MOTH DAMAGE

A major outbreak of spruce bud moth (*Zeiraphera* spp.) became apparent following bud-break in June 2007 and persisted through the summer of 2008. On 25 August 2008, digital photographs were taken of one branch at breast height on each side (i.e., north, south, east, and west) of the study trees. The pictures showed between 5 and 20 active growing tips, which were visually classified as damaged and undamaged. Damaged growing tips were identified as those which showed withered needles or still retained the bud cap. The extent of damage was treated as the

percentage of tips which showed damage on each aspect of the tree.

STATISTICAL ANALYSES

Variations in microclimate, needle gas exchange, needle traits (length and density), and branch growth across years and months and with variation in parent material depth were examined using repeated measures analysis of variance (ANOVA) in the mixed model procedure of SAS 9.2 (SAS Institute, Cary, North Carolina). In all ANOVAs parent material depth was treated as a categorical variable (i.e., shallow: <25 cm; deep: >25 cm). The covariance structure which produced the lowest value of Akaike's Information Criterion was used in the repeated measures ANOVAs. Response variables that were not measured repeatedly over time on the same trees, such as branching and bud moth damage, were examined using ANOVAs in the general linear model procedure. Comparisons of interest beyond the main effects in all ANOVAs were made using Tukey's Honest Significant Difference. Data were \log_{10} -transformed when necessary to meet assumptions of normality and constant variance. The relationship between stomatal conductance and soil temperature was fit with a two-part linear function in Sigma Plot 11 (Systat Software Inc., San Jose, California). The two-part linear function includes an inflection point, which is a fitted value.

Results

STAND CLIMATE

The climate of the study site during the snow-free period differed strongly across the three years of observation (Fig. 1). During the snow-free period of 2006, hourly average air temperatures of 20 °C or greater were observed during only 49 hours and temperatures did not fall below 0 °C between 8 June and 20 August. Soil temperatures were similarly moderate during the snow-free period of 2006, varying between a minimum of 3.4 °C, recorded immediately after sensor installation on 13 June, and a maximum of 10.2 °C on 25 July. Precipitation during 2006 was fairly evenly distributed through time and much greater overall than observed during 2007 and 2008. Moderate temperatures and relatively high precipitation led to the highest and most consistent soil water contents observed during the three-year study. In 2006, volumetric soil water contents never fell below 33%.

The snow-free period of 2007 was markedly different than 2006. Hourly average air temperatures of 20 °C or greater were observed during 370 hours and temperatures did not fall below 0 °C between 30 May and 29 August. Soil temperatures were also very warm, reaching a maximum of 14.6 °C on 24 July. As observed in 2006, soil temperatures remained above 0 °C at 10 cm depth throughout the period from 1 June to 30 September. Precipitation during the snow-free period of 2007 was low, particularly during June and July. Low precipitation and very warm temperatures drove soil water contents to the lowest level (16%) observed during the three-year study. Low soil water contents were observed during warm periods that occurred in late July and early September, before and after a period of rain in early August.

The snow-free period of 2008 was the most variable in the three-year study. Air temperatures below 0 °C were again observed into the second week of June. In contrast with 2006 and 2007, there were four nights with sub-zero air temperatures during the mid-summer: three in late July and one in early August. Meanwhile, hourly average air temperatures of 20 °C or greater

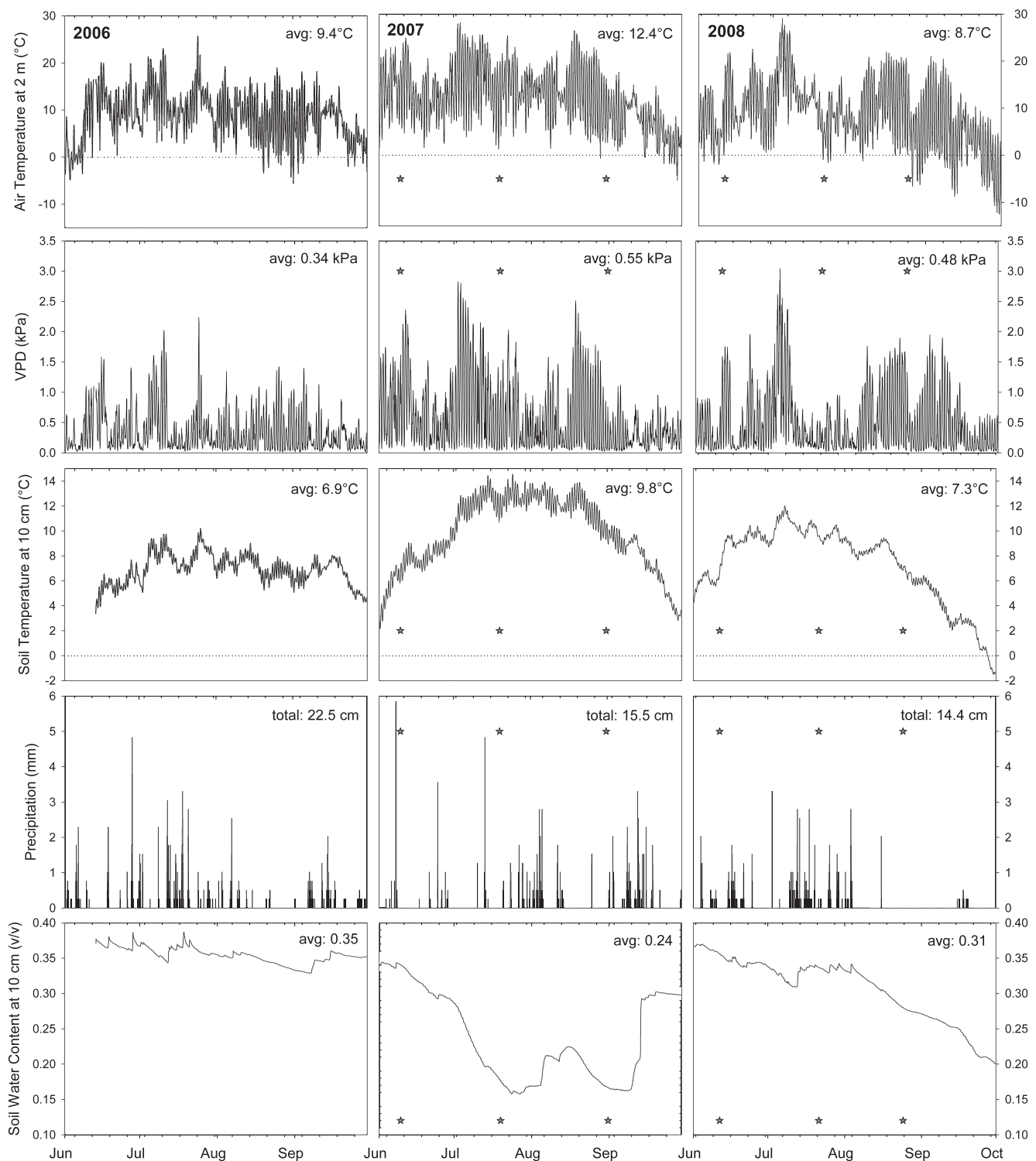


FIGURE 1. Hourly air temperature, atmospheric vapor pressure deficit, soil temperature, liquid precipitation, and soil water content between 1 June and 30 September in each year of the study. Soil temperature and soil water content were averaged across sensors installed beneath the drip line of each tree ($n = 18$). Stars indicate dates of needle gas exchange measurements.

were observed during 139 hours between 1 June and 30 September. During most of the 2008 snow-free period, soil temperatures were intermediate between those observed during 2006 and 2007, reaching a maximum of 12.0 °C on 7 July. There was very little precipitation during the latter half of the snow-free period in 2008, and soils dried to a water content of 0.20 v/v. Falling air temperatures and dry soils drove soil temperatures below 0 °C on 27 September. For comparison, average soil temperatures at 10 cm

depth did not fall below 0 °C until 30 October in 2006 and 20 October in 2007.

VARIATION IN TREE PHYSIOLOGY AND GROWTH ACROSS YEARS AND MONTHS

Measurements of light-saturated needle gas exchange were made on all of the study trees in June, July, and late August 2007

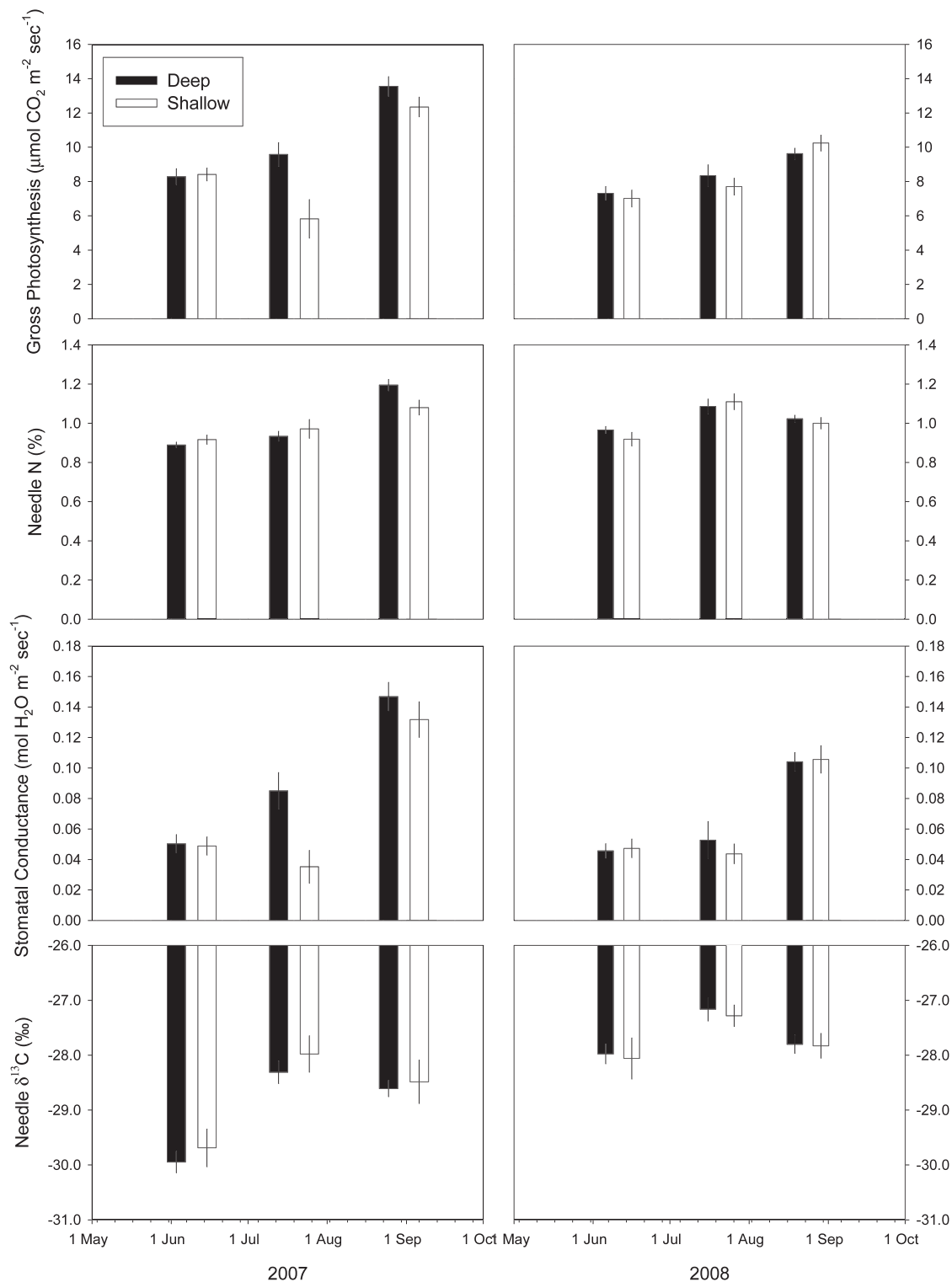


FIGURE 2. Variation in midday light-saturated needle gas exchange, needle N, and needle $\delta^{13}\text{C}$ measured in June, July, and late August 2007 and 2008 in trees growing in deep (>25 cm, $n = 10$) and shallow parent material (<25 cm, $n = 8$). Bars are 1.0 S.E.

and 2008. Gross photosynthesis and stomatal conductance were greater in 2007 than in 2008 and greater in late August than in June and July (Fig. 2). A plot of stomatal conductance as a function of soil temperature shows that cold soils in June were associated with low rates of needle gas exchange, while warmer soils in late August were associated with much higher stomatal conductance (Fig. 3). A two-part linear function was fit to the relationship between stomatal conductance and soil temperature

and an inflection point was identified at a soil temperature of 6.8 °C (S.E. = 0.8). Rates of gross photosynthesis and stomatal conductance were low in July 2007 and 2008, but environmental conditions differed strongly. When measurements were made in July 2007, air temperatures were warm (daily max: 20.0 °C), soil temperatures were very warm (daily max: 12.2 °C), and soil water contents were near the lowest levels observed during the three-year study (0.18 v/v). Diurnal measurements of needle gas exchange,

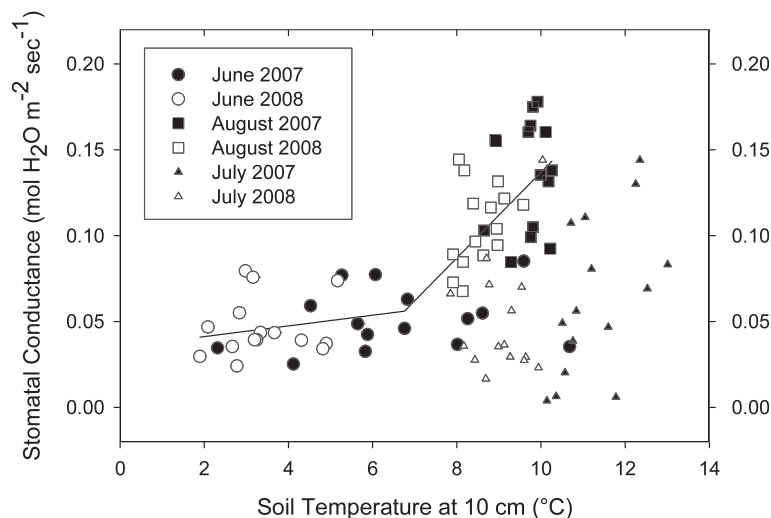


FIGURE 3. Relationship between soil temperature and midday light-saturated stomatal conductance across sampling dates ($n = 18/\text{date}$). A two-part linear model was fit to June and August data of 2007 and 2008. The model was not fit to July data. In July 2007, warm and dry conditions likely led to stomatal closure. In July 2008, a nighttime frost apparently reduced needle gas exchange during the subsequent midday measurements.

made three days later, showed that trees growing on shallow parent material were photosynthesizing at very low rates overall and likely had positive net assimilation rates only during the early morning hours (Fig. 4). When measurements were made in July 2008, air temperatures were cold (daily max: 7.1 °C), soil temperatures were modestly warm (9.6 °C), and soil water contents were relatively high (0.34 v/v). There was a light frost the evening prior to the midday gas exchange measurements, with a minimum temperature of -1.0 °C. Diurnal measurements of needle gas exchange were made two days later and there was a second frost during the diurnal measurements, in which temperatures fell to a minimum of -1.6 °C. The diurnal pattern of gross photosynthesis during mid-July 2008 followed a pattern almost exactly the opposite of that observed during mid-July 2007. In 2008, very low rates of gross photosynthesis were observed during the morning hours, while much higher rates were observed during the midday and evening hours. Measurements of xylem water

potentials made during the midday gas exchange measurements in July 2007 and 2008 were markedly different. Xylem water potentials averaged -1.6 MPa during the warm and dry conditions of 2007 and -0.8 MPa in the cold and comparatively wet conditions of 2008. Measurements of needle $\delta^{13}\text{C}$ correspond moderately well with measurements of needle gas exchange. Needle $\delta^{13}\text{C}$ showed strong enrichment ($+1.7\text{‰}$) between June and the warm and dry conditions in July 2007. Between July and late August 2007, needles became slightly more depleted in ^{13}C (-0.4‰). Needle $\delta^{13}\text{C}$ was relatively enriched throughout the snow-free period of 2008. The seasonal pattern in 2008 was similar to that observed in 2007, but the magnitude of variation was smaller.

Needle length, needle density (# of needles/mm branch) and branch extension growth varied across years. Needle length was shortest in 2006 (9.5 mm), intermediate in 2007 (10.5 mm), and longest in 2008 (11.9 mm). There was only weak evidence that

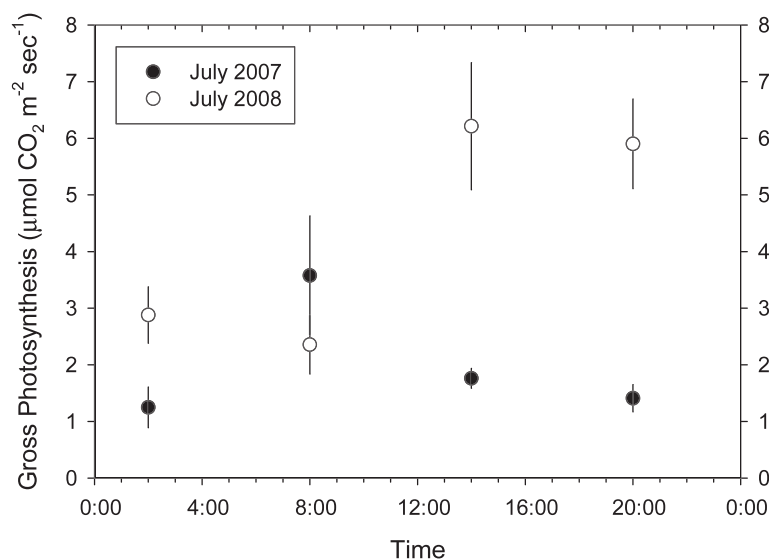


FIGURE 4. Diurnal patterns of light-saturated gross photosynthesis in trees growing on shallow parent material (≤ 30 cm) during mid-July 2007 and 2008 ($n = 6$). In July 2007, stomatal closure was observed, presumably in response to warm and dry conditions. In July 2008, needle gas exchange was apparently limited by nighttime frost.

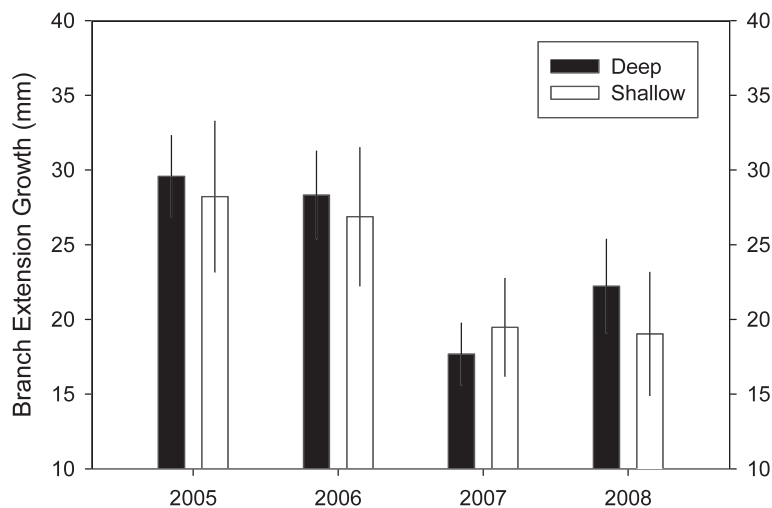


FIGURE 5. Branch extension growth in trees growing on deep (>25 cm, $n = 10$) and shallow parent material (<25 cm, $n = 8$). Bars are 1.0 S.E.

needle density varied across years. Needle density tended to be greatest in 2006 (2.8 needles/mm branch), lowest in 2007 (2.6 needles/mm branch) and intermediate in 2008 (2.7 needles/mm branch). Branch extension growth varied strongly across years (Fig. 5). Growth was relatively high and similar in 2005 and 2006 and substantially lower and similar in 2007 and 2008. An outbreak of spruce bud moth (*Zeiraphera* spp.) became apparent following bud-break in June 2007 and persisted at similar intensity through the summer of 2008. Overall, 40.4% of active growing tips were affected by bud moths when measurements were made in late August 2008.

EFFECTS OF PARENT MATERIAL DEPTH ON TREE PHYSIOLOGY AND GROWTH

Gross photosynthesis and stomatal conductance varied with parent material depth, but the effect of parent material depth depended upon the month of observation. In June 2007 and 2008 gross photosynthesis and stomatal conductance were greater on shallow than on deep parent material. During the warm and dry conditions of July 2007, gross photosynthesis and stomatal conductance were lower on shallow than on deep parent material (Fig. 6). Rates of gross photosynthesis were similar on shallow and deep parent material in late August 2007 and 2008. There was no evidence that needle N or needle $\delta^{13}\text{C}$ varied consistently with parent material depth, nor was there strong evidence that the effect of parent material depth on these variables depended upon the month of observation. Needle length did not vary with parent material depth, nor did needle density. Despite observed variation in needle gas exchange, there was no evidence that branch extension growth varied with parent material depth. There was, however, evidence that trees growing on shallow parent material produced fewer branches than trees on deep parent material. There was a non-significant trend toward lower bud moth infestation in trees growing on shallow parent material.

Discussion

CONSTRAINTS ON NEEDLE GAS EXCHANGE

We found reduced rates of needle gas exchange under both cold and warm conditions, indicating there is a very narrow range of environmental conditions that are optimal for needle gas

exchange of treeline white spruce. When measurements were made in June 2007 and 2008, white spruce needle gas exchange was constrained by cold soils (<7 °C), consistent with observations in the central Brooks Range (Goldstein et al., 1985). Cold soils are thought to reduce water flow into the roots by reducing membrane permeability and by increasing the viscosity of water (Kaufmann, 1975, 1977; Running and Reid, 1980). Warm and dry conditions in mid-July 2007 led to drought-induced stomatal closure, particularly on shallow parent material, where trees draw water from either a smaller soil volume or a soil volume that is more subject to evaporative water loss. Our observation that white spruce growing on shallow parent material were more likely to experience drought stress parallels recent findings in eastern Canada, where growth of black spruce trees on shallow organic layers was negatively affected by warm and dry conditions, while the reverse was true in trees growing on deep organic layers (Drobyshev et al., 2010). Several recent studies have suggested that negative growth trends of some treeline trees to period of rapid warming in the latter half of the 20th century may reflect the increasing importance of drought stress (e.g., Lloyd and Fastie, 2002; Wilmking et al., 2004). Our study provides the first direct observations of drought-induced stomatal closure near the Arctic treeline. Near optimal conditions for needle gas exchange were observed at midday in late August 2007 and, to a lesser extent, in late August 2008. Comparison of conditions in mid-July and late August 2007 is particularly instructive. On both sampling dates, soil water content was 0.17 v/v. Meanwhile, there was a VPD of 1.2 kPa in July and of 0.7 kPa in late August. Given that soil water contents did not vary between the two sampling dates, it is apparent that stomatal closure in mid-July was largely driven by the VPD. However, our observation that complete stomatal closure only occurred in trees growing on shallow parent material indicates that low soil water availability also contributes to drought stress.

IMPORTANCE OF HABITAT

White spruce trees occupy three major habitat types near the Arctic treeline: riverside terraces, hillslope forests, and treelines, where hillslope forests grade into a variety of different tundra types. Riverside terraces generally have well-drained soils, as do treelines that interface with dry tundra. Hillslope forests generally have relatively deep organic layers (≥ 20 cm) and moderately well-drained soils. Treelines that interface with moist and wet tundra

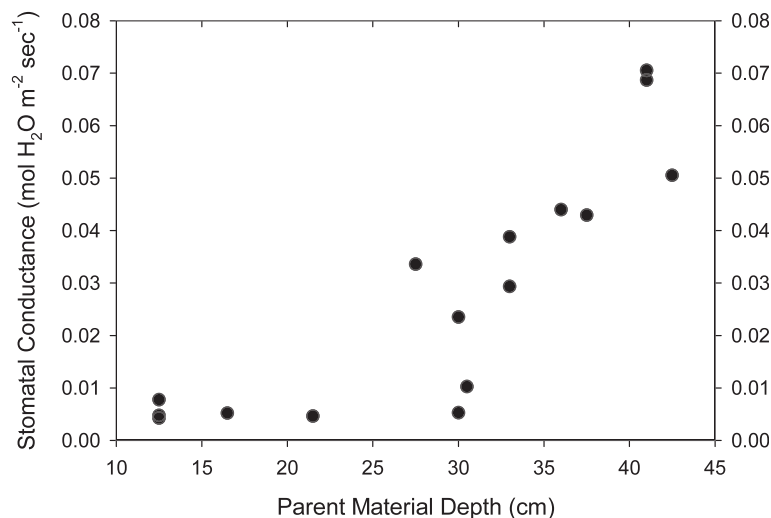


FIGURE 6. Midday light-saturated stomatal conductance as a function of parent material depth on 22 July 2007, during a period of warm and dry conditions.

types have soils that are underlain by permafrost and are, therefore, relatively poorly drained. We hypothesize that the relative importance of cold soils and the combination of dry soils and high evaporative demand for the water relations of white spruce near the Arctic treeline will depend upon habitat type. Our results and those of Goldstein et al. (1985) also suggest the combination of cold soils and high evaporative demand could lead to substantial reductions in white spruce needle gas exchange.

UTILITY OF $\delta^{13}\text{C}$ AS AN INDICATOR OF WARM TEMPERATURE-INDUCED DROUGHT STRESS

Needle $\delta^{13}\text{C}$ provides a time-integrated measure of intrinsic water-use-efficiency (iWUE), which is the ratio of photosynthesis to stomatal conductance (Farquhar et al., 1982). Plants generally increase iWUE in response to drought, and plant tissues constructed using C assimilated during the drought period are typically enriched in ^{13}C (Farquhar and Richards, 1984). Investigators working with white spruce in interior Alaska noted a trend toward reduced growth during recent warming (Barber et al., 2000), similar to the pattern observed in some treeline trees. Barber et al. (2000) found an inverse correlation between growth and $\delta^{13}\text{C}$ in tree ring cellulose and concluded, perhaps correctly, that reduced growth can be attributed to drought-induced stomatal closure. Our results show that soil temperature may be as important a control on iWUE as the VPD in white spruce near the Arctic treeline. The implication of this finding is that $\delta^{13}\text{C}$ in tree ring cellulose may not be a good indicator of warm temperature-induced drought stress in treeline trees. For example, needle $\delta^{13}\text{C}$ was more enriched near the end of the cold 2008 growing season, than near the end of the warm and dry 2007 growing season.

CONTROLS ON GROWTH

Needle length and branch extension growth both varied strongly across years. Needle length was shortest in 2006, intermediate in 2007, and longest in 2008. Branch growth, in contrast, was greatest in 2006 and similar in 2007 and 2008. The nearly inverse relationship between needle and branch growth is suggestive of a resource allocation tradeoff and highlights the potential importance of measuring growth in all major organs to

accurately characterize inter-annual variation in tree performance. This conclusion is consistent with observations made in the northern boreal forests of Siberia, where trees have apparently shifted allocation patterns in recent years, such that proportionately more biomass is being invested in wood and roots and less is being allocated to foliage (Lapenis et al., 2005).

It is tempting to attribute low branch growth in 2007 to drought stress. However, the 2007 drought affected trees on shallow parent material more than those on deep parent material, as indicated by lower rates of gross photosynthesis and stomatal conductance, yet there was no evidence that growth varied with parent material depth in 2007. Furthermore, there was no indication of drought stress during the snow-free period of 2008, yet branch growth remained low in 2008. We feel that low branch growth in 2007 and 2008 is most likely attributable to the bud moth infestation, which became apparent following bud break in 2007 and persisted through the summer of 2008. Our observation that branch growth was reduced during the two-year defoliation event provides some evidence that growth of white spruce on a riverside terrace near the Arctic treeline may become limited by carbohydrate availability (e.g., Susiluoto et al., 2010). It is also possible that bud moth herbivory could exacerbate nutrient limitations to growth. Results of a related experiment showed that trees at the study site are strongly limited by nutrient availability, as evidenced by a strong positive growth response to fertilization (P. Sullivan, unpublished data). If we accept that limitation of growth by carbon uptake can occur, then lower growth would be expected in a growing season with persistently cold soils or extensive drought. In this context, our results suggest that white spruce needle gas exchange and growth near the treeline will be greatest in warm summers with abundant precipitation.

The importance of occasional insect outbreaks to the structure and function of Arctic (Post and Pedersen, 2008) and boreal ecosystems (e.g., Berg et al., 2006; Payette, 2007) has gained prominence in recent years. In some cases, changes in the location, frequency, intensity, and/or duration of infestations have been linked to changes in climate (e.g., Berg et al., 2006; Hagen et al., 2007). The importance of moth herbivory is well known in mountain birch forests near the treeline in northern Scandinavia (Mjaaseth et al., 2005; Hagen et al., 2007), and spruce bark beetle infestation has been documented in white spruce forests near the Arctic treeline in northern Labrador (Payette, 2007), on the

TABLE 1

Results of ANOVAs designed to examine variation in tree physiology, growth and spruce bud moth damage across years, months, and with natural variation in parent material depth. Xylem water potential was measured in July 2007 and June, July, and August 2008. The effect of year reflects a comparison between July 2007 and July 2008. The other main effects and interactions pertain only to the 2008 xylem water potential data.

Variable	Year	Source of Variation		
		Month	Parent Material	Month \times Parent Material
Gross photosynthesis	$F = 5.2, P = 0.03$	$F = 35.8, P < 0.01$	$F = 3.9, P = 0.05$	$F = 6.1, P < 0.01$
Stomatal conductance	$F = 16.3, P < 0.01$	$F = 121.8, P < 0.01$	$F = 2.0, P = 0.16$	$F = 4.5, P = 0.01$
Xylem water potential	$F = 60.9, P < 0.01$	$F = 20.8, P < 0.01$	$F = 12.6, P < 0.01$	$F = 7.1, P < 0.01$
Needle N	$F = 1.8, P = 0.18$	$F = 35.9, P < 0.01$	$F = 0.3, P = 0.59$	$F = 3.3, P = 0.04$
Needle $\delta^{13}\text{C}$	$F = 182.8, P < 0.01$	$F = 73.9, P < 0.01$	$F = 0.1, P = 0.82$	$F = 0.0, P = 0.96$
Needle length	$F = 8.9, P < 0.01$	—	$F = 2.5, P = 0.14$	—
Needle density	$F = 1.3, P = 0.29$	—	$F = 0.0, P = 0.97$	—
Branch growth	$F = 37.8, P < 0.01$	—	$F = 0.6, P = 0.45$	—
Branch number	—	—	$F = 1.0, P = 0.33$	—
Bud moth damage	—	—	$F = 3.4, P = 0.07$	—

eastern coast of Hudson Bay (Caccianiga et al., 2008), on the Seward Peninsula (A. Lloyd, personal observation), and in dense stands within Noatak National Preserve (P. Sullivan, personal observation). We argue that insect outbreaks are an important and often overlooked control on treeline tree performance. It appears that insect herbivory increased sharply during the Paleocene–Eocene Thermal Maximum in northern Wyoming (Currano et al., 2008), and it is generally expected that insect outbreaks will become increasingly important drivers of ecosystem structure and function with future climate change in Arctic and boreal ecosystems (Post et al., 2009). We believe that further research into the history of insect outbreaks at the treeline and their importance as controls on tree performance and treeline position is warranted.

Acknowledgments

This project was supported by National Science Foundation grant 0528748 to Sullivan. We thank S. Cahoon, B. Yoder, K. Amerell, H. Walker, H. Ohms, and H. Eggleston for field assistance. CH2MHill Polar Field Services, Hagelands Aviation, Arctic Science Logistics, and the Western Arctic Office of the National Park Service provided valuable logistical support.

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MS accepted October 2010