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PHYSIOLOGICAL ECOLOGY - ORIGINAL PAPER

Variation in carbohydrate source–sink relations of forest and treeline white spruce in southern, interior and northern Alaska

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Abstract Two opposing hypotheses have been presented to explain reduced tree growth at the treeline, compared with growth in lower elevation or lower latitude forests: the carbon source and sink limitation hypotheses. The former states that treeline trees have an unfavorable carbon balance and cannot support growth of the magnitude observed at lower elevations or latitudes, while the latter argues that treeline trees have an adequate carbon supply, but that cold temperatures directly limit growth. In this study, we examined the relative importance of source and sink limitation in forest and treeline white spruce (*Picea glauca*) in three mountain ranges from southern to northern Alaska. We related seasonal changes in needle nonstructural carbohydrate (NSC) content with branch extension growth, an approach we argue is more powerful than using needle NSC concentration. Branch extension growth in the southernmost Chugach Mountains was much greater than in the White Mountains and the Brooks Range. Trees in the Chugach Mountains showed a greater seasonal decline in needle NSC content than trees in the other mountain ranges, and the seasonal change in NSC was correlated with site-level branch growth across mountain ranges. There was no evidence of a consistent difference in branch growth between the forest and treeline sites, which differ in elevation by approximately 100 m. Our results point to a continuum between source and sink limitation of growth, with high-elevation trees in northern and interior Alaska showing greater evidence of sink limitation, and those in southern Alaska showing greater potential for source limitation.

Keywords Growth · Nonstructural carbohydrates · *Picea glauca* · Temperature · Treeline

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Introduction

Treeline positions have important implications for surface energy budgets (Rouse 1984; Bonan et al. 1992; Thompson et al. 2004; Beringer et al. 2005) and carbon cycling (LaFleur et al. 2001; Steltzer 2004; Wilmking et al. 2006) in high-latitude landscapes. Air temperatures are increasing at unprecedented rates in arctic and boreal regions (e.g., Chapman and Walsh 1993; Serreze et al. 2000) and tree growth at latitudinal and elevational treelines is changing (Paulsen et al. 2000; Lloyd and Fastie 2002; Wilmking et al. 2004; Wilmking and Juday 2005). In several instances, recent increases in the growth of treeline trees have been linked to treeline advance (Suarez et al. 1999; Lloyd and Fastie 2003). An improved understanding of the environmental constraints on treeline tree growth may, therefore, provide insights into the trajectory of treeline positions in a changing climate.

Of the many hypotheses purporting to explain the control of treeline tree growth, two competing hypotheses have dominated the recent literature: the carbon source and sink limitation hypotheses. Tree growth is considered source limited when carbon assimilation through photosynthesis is insufficient to meet growth requirements (Schulze et al. 1967; Sveinbjörnsson 2000; Sveinbjörnsson et al. 2002). Source limitation is most likely to arise through low nutrient availability, drought stress or the loss or damage of tissues responsible for carbon or nutrient acquisition. Nutrient availability is generally lower at the treeline than in the forest (Sveinbjörnsson et al. 1995; Loomis et al. 2006), although investigators have drawn contrasting conclusions about nutrient limitations at the treeline. Sveinbjörnsson et al. (1992) showed that mountain birch growth responses to fertilization with nitrogen (N) increased with elevation, and Schulze et al. (1994) found a positive relationship between growth and needle N content and concluded that N was limiting to the growth of treeline spruce. Conversely, Sveinbjörnsson (2000) fertilized treeline and forest white spruce in the Chugach Mountains, found similar positive responses at both elevations, and concluded that differential N limitation could not explain lower growth at the Chugach treeline. Several recent studies have identified inverse relationships between temperature and growth of treeline white spruce, particularly in dry areas, leading investigators to suggest that drought stress may limit photosynthesis at some sites (Lloyd and Fastie 2002; Wilmking et al. 2004). Evergreen treeline trees may experience extensive winter needle death, as a result of dehydration following incomplete cuticle development and/or abrasion by wind-blown snow and ice (Baig et al. 1974; Hadley and Smith 1983; 1986; 1989), and winter loss of photosynthetic tissue may restrict growth during the subsequent growing season. Climate warming may influence source limitations on treeline tree growth through increases in nutrient availability (Sveinbjörnsson et al. 1992), increases in growing season length (Sveinbjörnsson 2000), alleviation of cold temperature limits on leaf gas exchange (Goldstein et al. 1985), increases in the frequency or duration of drought stress (Lloyd and Fastie 2002; Wilmking et al. 2004), or direct effects of elevated temperature on leaf gas exchange (Vowinkel et al. 1975; Black and Bliss 1980).

Trees are considered carbon sink limited when there is an abundant supply of the resources necessary to support growth, but growth itself is directly limited by environmental conditions (Dahl and Mork 1959; Skre 1972; Dahl 1986; Bonan and Shugart 1989; Körner 1998). Sink limitation of treeline tree growth is most likely to occur as a result of low temperature, and recent work suggests that treeline positions across the globe are well correlated with growing season soil temperature (Körner 1998; Jobbagy and Jackson 2000; Körner and Paulsen 2004). The observation that nonstructural carbohydrate (NSC) concentrations tend to increase in tissues with proximity to the treeline has been used as evidence that growth is limited by carbon sink strength (Hoch et al. 2002; Hoch and Körner 2003, 2005; Shi et al. 2006, 2008). Recent work in the laboratory also points to the potential for sink limitation at the treeline. Seedlings of treeline trees grown in cold temperatures (6°C) showed substantially lower growth and higher tissue NSC concentrations than seedlings grown in comparatively warm temperatures (12°C) (Hoch and Körner 2009).

In this study, we examined the relative importance of source and sink limitation in forest and treeline white spruce (*Picea glauca*) in three mountain ranges along a gradient from southern to northern Alaska. Treeline and forest site contrasts were chosen, as these have generally demonstrated a significant difference in tree growth and reproduction and have therefore been frequently used to test the source–sink limitation hypotheses, allowing a direct comparison of our results to a rich literature. We elected to work along a south-to-north transect, which spanned the entire boreal forest in Alaska, to capture a wide range of environmental conditions and associated carbohydrate relations. To avoid pseudo-replications and allow a greater generalization of our results, we chose to work on paired treeline and forest sites in three separate watersheds within each mountain range.

Dilution of foliar nutrient concentrations has been consistently shown in CO_2-enrichment experiments, not because of reduced nutrient uptake, but because of increased carbohydrate contents (e.g., Norby et al. 1986; Kuehny et al. 1991). Similarly, we expected that changes in the abundance of other leaf constituents could lead to variation in NSC concentration in the absence of changes in NSC content. Therefore, we considered the NSC content or pool size in each needle cohort, examined seasonal changes in NSC concentration and content, and compared our NSC measurements with branch extension growth. Instead of considering a tree either source- or sink-limited, we interpreted our results in the context of a continuum. We considered trees with relatively low growth and little or no seasonal change in needle NSC content to be more sink limited. In contrast, we argue that trees which show substantial seasonal reductions in needle NSC content have a greater potential for source limitation of growth. Previous work in the Chugach Mountains showed that treeline trees experience extensive needle loss, presumably from wind-blown snow (Sveinbjörnsson 2000). We also anticipated that trees in the Chugach Mountains experience a more favorable thermal regime than trees in interior and northern Alaska. We expected that treeline trees in the Chugach

would reduce NSC contents to a greater extent than trees in interior and northern Alaska, reflecting relatively greater source limitation of growth, as a result of greater needle loss and a potentially more favorable growth environment. We anticipated that the pattern would be reversed in interior and northern Alaska (i.e., relatively greater sink limitation of growth at the treeline than in the forest), where we expected lesser mechanical damage from wind-blown snow.

Methods

Site descriptions

This study was carried out within three mountain ranges along a 785-km transect in Alaska (Table 1). The southernmost sites were established in the western Chugach Mountains east of Anchorage, AK, USA. The interior sites were situated in the White Mountains, northeast of Fairbanks, AK, USA. The northernmost, arctic sites were established in the Brooks Range, both north and south of Coldfoot, AK, USA. Mean annual precipitation does not differ strongly across the sites and is approximately 400–600 mm $year^{-1}$. Within each range, paired treeline and forest sites were selected in each of three watersheds. In this study we use the term "treeline" for the zone of generally smaller and/or fewer upright trees beyond the contiguous forest (Callaghan et al. 2002; Sveinbjörnsson et al. 2002). Nomenclature in this article follows Hultén (1968) for vascular plants and Vitt et al. (1988) for bryophytes and lichens.

Chugach Mountains

Three watersheds 10–25 km east of Anchorage were selected for study: Site Summit, Art's Ridge, and Near Point. The Art's Ridge site has been the subject of previous treeline research (Abadie 1991; Sveinbjörnsson et al. 1995; Sveinbjörnsson 2000). The forest limit occurs at approximately 600 m elevation and the treeline ecotone extends approximately 1,500 m from mature forest to isolated krummholz. The sites are dominated by *Picea glauca,* with isolated patches of *Tsuga mertensiana* and *Picea mariana*. Site Summit is somewhat unusual in the sense that the stand density of live trees is greater at the treeline than in the forest. This difference is attributable to the large number of forest trees that have recently died from bark beetle infestation. The western Chugach Mountains have a maritime climate with moderate winter and summer temperatures (Table 2). Summers are typically dry during May and June, followed by a wet season that extends through October.

White Mountains

Three watersheds were selected for study in the White Mountains, between 75 and 100 km northeast of Fairbanks: 12-Mile Summit, Eagle Summit and Nome Creek. In all three watersheds, *P. glauca* is the only tree species at the treeline, which begins at an elevation of 770–950 m. The treeline ecotone is more abrupt than in the western Chugach, transitioning from closed forest to krummholz within 800 m.

Brooks Range

The three watersheds selected for study in the Brooks Range lie along the Dalton Highway, both north and south of Coldfoot, AK: Gobbler's Knob, Snowden and Dietrich River. *P. glauca* is the only tree species found at treeline at the average elevation of 750 m a.s.l., where there is a sharp transition from mature forest to tundra over approximately 800 m. The northernmost Dietrich River site lies within 2 km of the latitudinal treeline for *P. glauca*. Stand density is generally high in the Brooks Range forest sites, and particularly at the Snowden site. The short growing season, combined with low temperatures, low evaporation rates and permafrost, create wet soil conditions at the Brooks Range sites.

Microclimate

One watershed within each mountain range was selected for comprehensive microclimate monitoring: Site Summit, 12-Mile Summit and Dietrich River. At these sites, 3 m high meteorological towers were established at both forest and treeline sites, with sensors for air temperature and relative humidity, wind speed, solar radiation, precipitation, soil water content and soil temperature. Air temperature and relative humidity sensors were housed within radiation shields, while soil sensors were installed at a depth of 5 cm. Sensors were read every 30 s, and 15 min averages were logged to a CR10x datalogger (Campbell Scientific Inc., Logan, UT, USA). Long-term records (1952–2001) for the first-order climate stations in Anchorage, Fairbanks and Bettles, AK, USA were obtained from the Alaska Climate Research Center at the Geophysical Institute, University of Alaska Fairbanks.

Needle NSC

At each of the 18 study sites, needles were harvested during four time periods: fall of 2000, spring of 2001, summer of 2001 and fall of 2001. We selected five trees at each forest and treeline site and harvested one leeward branch at breast height from each tree. Where wind direction was not

Table 1 Characteristics of the study sites within each mountain range. Vegetation community classification is based on Viereck et al. (1992)

Site	Location	Slope (°)	Aspect	Elevation (m)	Stand density (stems ha^{-1})	Tree height (m)	Tree basal diameter (cm)	Community description
Chugach Range								
Site Summit								
Treeline	61°15′N	10	NW	600	466.6 ± 68.9	1.4 ± 0.0	10.8 ± 0.4	*Vaccinium* tundra
Forest	149°34′W	20	N	510	263.4 ± 18.6	3.8 ± 0.1	18.9 ± 0.4	Open white spruce forest
Art's Ridge								
Treeline	61°10′N	15	W	621	26.9 ± 2.1	3.0 ± 0.1	20.0 ± 0.6	*Vaccinium* tundra
Forest	149°39′W	15	SW	492	290.7 ± 78.8	5.8 ± 0.2	25.6 ± 1.0	Open white spruce forest
Near Point								
Treeline	61°9′N	15	W	590	24.3 ± 3.1	2.9 ± 0.1	18.9 ± 0.9	*Vaccinium* tundra
Forest	149°40′W	2	W	388	70.6 ± 11.0	5.6 ± 0.3	17.5 ± 1.2	Open white spruce forest
White mountains								
Eagle Summit								
Treeline	65°30′N	12	S	997	336.0 ± 31.0	2.1 ± 0.0	8.1 ± 0.2	Low open shrub birch
Forest	145°21′W	15	S	936	863.3 ± 56.7	6.5 ± 0.1	18.2 ± 0.3	Open white spruce forest
Twelve-Mile Summit								
Treeline	65°23′N	10	NW	1,010	38.2 ± 4.4	1.5 ± 0.0	8.0 ± 0.2	Sedge-willow tundra
Forest	145°56′W	5	NW	960	379.2 ± 16.0	4.8 ± 0.1	18.3 ± 0.4	Open white spruce forest
Nome Creek								
Treeline	65°21′N	2	NW	770	69.1 ± 3.9	2.2 ± 0.1	10.0 ± 0.3	*Vaccinium* tundra
Forest	146°42′W	5	NW	715	254.1 ± 19.2	7.8 ± 0.1	25.0 ± 0.4	Open white spruce forest
Brooks range								
Dietrich								
Treeline	68°01′N	25	SE	820	337.0 ± 71.9	3.3 ± 0.1	9.6 ± 0.3	Low open shrub birch
Forest	149°41′W	15	SE	670	457.3 ± 28.6	5.5 ± 0.1	14.1 ± 0.3	Open white spruce forest
Snowden								
Treeline	67°49′N	25	W	790	302.2 ± 56.8	2.5 ± 0.0	5.4 ± 0.2	Low open shrub birch
Forest	149°48′W	15	W	610	2,380.9 ± 274.6	4.2 ± 0.1	10.3 ± 0.2	Closed white spruce forest
Gobbler's Knob								
Treeline	66°44′N	2	S	620	15.7 ± 1.8	2.1 ± 0.1	6.6 ± 0.1	*Vaccinium* tundra
Forest	150°40′W	5	S	520	550.3 ± 49.0	6.9 ± 0.1	12.7 ± 0.2	Open white spruce forest

All treeline sites have less than 10% tree cover and are therefore classified based on shrub vegetation

obvious, we harvested down slope branches. To prevent a pruning effect on carbohydrate levels in the selected trees, we selected two sets of five trees within each site so that each tree was harvested only twice. On each sampling date, the entire branch was cut near the bole of the tree and needle cohorts or age classes were identified and separated using bud scars along the main axis of the branch. Annual growth increments (1991–2001) were measured using calipers, and needle samples were frozen in liquid nitrogen within 6 h of sampling. Needle samples were dried to constant mass at 60°C, weighed, and ground to a fine powder using a ball mill grinder.

After an exploratory analysis of the NCS concentration in all needle age classes, the current year's needles (age 0) and 1 and 2, 5, 9 and 14 year old needles were selected for NSC analysis. NSC, including sucrose, glucose, fructose and starch, were analyzed following the protocol outlined in Wong (1990). Samples (8–10 mg) were extracted for 30 min in 2 ml of distilled water. Starch was broken down into glucose using dialyzed Validase, followed by submersion in a 60°C water bath overnight. After centrifugation at 5,000 rpm, a 500 µl sample of the extract was treated with 10 µl of isomerase and 100 µl of invertase to convert fructose and sucrose into glucose. After enzymatic conversion to gluconate-6-phosphate, total glucose was determined photometrically in a spectrophotometer at 340 nm. Pure starch, pure glucose and plant material of known composition were used to ensure reproducibility.

Table 2 Comparison of annual and summer (June, July and August) air and soil temperatures at treeline and subalpine forest sites along a latitudinal gradient in Alaska

Mountain Elevation	Annual air (°C, 2 m)	Annual soil (°C, 5 cm)	Summer air (°C, 2 m)	Summer soil (°C, 5 cm)	Frost-free days
Chugach					
Forest	2.2	3.3	12.8	7.5	191
Treeline	1.8	3.0	12.1	7.1	176
White					
Forest	−3.2	1.4	11.2	6.9	179
Treeline	−3.5	0.4	10.1	6.1	172
Brooks					
Forest	−8.3	−0.2	11.2	6.0	136
Treeline	−4.9	−1.5	10.8	6.3	136

Frost-free days were calculated as the number of days with soil temperatures continuously greater than 0°C

Needle NSC values are expressed as both concentration (% dry mass) and content (mg).

The seasonal change in needle NSC was calculated using several different approaches. The change was calculated between June and July, which is thought to correspond to the period of branch extension growth, and between June and August, which should also include radial and root growth. Seasonal changes in NSC were calculated using both concentration and content. A related study showed that the three most recent needle cohorts contribute to branch extension growth, while older needles do not ("ESM" S1). Therefore, the seasonal change in NSC was calculated using concentration and content averaged over the three most recent needle cohorts. Such a calculation necessitates a mismatch, however, as a new cohort of needles emerged between our June and July sampling dates. Therefore, we also calculated the seasonal change in NSC using just the two needle cohorts common to both sampling dates. Because needles were harvested from different trees on consecutive sampling dates, the seasonal change in NSC was calculated using site-level means.

The seasonal change in NSC was related to our measurements of branch growth to examine the relationship between sink activity (growth) and the pool of carbohydrates available to support the sink activity. This analysis assumes that carbohydrate pool size is governed strictly by the balance between supply (photosynthesis) and demand (growth), and not by other factors. There is, however, some evidence to suggest that plants may accumulate carbohydrates as a stress-tolerance strategy (e.g., Chapin et al. 1990, Smith et al. 2003). In other words, some tree populations may control carbohydrate pool sizes above a threshold level. We recognize that such a strategy could complicate the use of NSC to make inferences about the limitations on growth, and we suggest that future research should examine the potential for genetic differences in the control of carbohydrate pool sizes.

Statistical analyses

Data were tested for normality using Shapiro–Wilk's test and for heteroscedasticity using Levene's test. When necessary, data were log-transformed to meet assumptions of the analyses. Needle NSC content per cohort was calculated as NSC concentration multiplied by needle mass. Needle NSC concentration and content were analyzed using ANOVA, with sampling date, mountain range and elevation (treeline vs. forest) as main effects in the general linear model procedure of SAS 9.1 (SAS Institute, Cary, NC, USA). The study sites were treated as replicates in all analyses. NSC analyses were restricted to data collected in the spring, summer and fall of 2001, as NSC content data were not available for the White Mountain sites in the fall of 2000. Needle NSC concentration data were not available for four of the 18 study sites in August of 2001, and needle mass data were not available for one additional site. Therefore, NSC content data were not available for five of the study sites in August of 2001. We recognize that samples collected over time at the same site may not be statistically independent. Because needle samples were collected from different trees on consecutive sampling dates, we were forced to assume independence, and the data were analyzed using fixed-effects ANOVA. Retrospective measurements of branch extension growth were analyzed using repeated-measures ANOVA in the mixed model procedure of SAS 9.1. Comparisons of interest in all ANOVAs were made using Tukey's honest significant difference. The relationships between branch extension growth and the seasonal change in NSC content were examined using Pearson's correlation in the correlation procedure of SAS 9.1. The seasonal change in NSC content was also examined as a percent of the NSC content in June, at the beginning of the growth period [i.e., (July–June/June) × 100]. The relationship between branch extension growth and the seasonal change in NSC content, expressed as a percent of June NSC content, was nonlinear and fitted

with a negative exponential curve using the nonlinear modeling procedure of SAS 9.1.

Results

Needle NSC

Averaging across the three most recent needle cohorts, needle NSC concentration varied with sampling date ($F_{2,44} = 13.8$, $P < 0.01$), but not with mountain range ($F_{2.44} = 0.6$, $P = 0.56$), nor with elevation ($F_{1,44} = 0.2$, $P = 0.64$) (Fig. 1). The highest needle NSC concentration was observed in June, when it was significantly greater than in July ($P = 0.03$) and August ($P < 0.01$). NSC content per needle cohort (NSC concentration × needle mass) varied with sampling date ($F_{2,43} = 12.4$, $P < 0.01$) and mountain range ($F_{2,43} = 6.2$, $P < 0.01$). However, there was no difference in needle NSC content between forest and treeline trees when averaged across mountain ranges ($F_{1,43} = 0.3$, $P = 0.56$). NSC content tended to be greater in June than in July ($P = 0.22$), and was significantly greater in June than in August ($P < 0.01$). The greatest NSC content per needle cohort was observed in the Chugach, where NSC content was higher than in either the White Mountains ($P = 0.02$) or the Brooks Range ($P < 0.01$), in contrast with observations of needle NSC concentration. The same analyses were also conducted using the two needle cohorts common to all sampling dates, and very similar results were obtained.

Seasonal change in needle NSC

The seasonal change in needle NSC was calculated using concentration and content, while averaging across the three most recent needle cohorts. Between June and July (i.e., July–June), the change in NSC concentration varied with mountain range ($F_{2,14} = 4.5$, $P = 0.04$), but not between forest and treeline ($F_{1,14} = 1.1$, $P = 0.31$). In both analyses, the change in NSC concentration between June and July was greatest in the Brooks Range. Between June and July, the change in NSC content varied with mountain range ($F_{2,14} = 4.8$, $P = 0.03$), but not between forest and treeline ($F_{1,14} = 0.3$, $P = 0.57$). NSC content declined to a greater extent in the Chugach than in the White Mountains ($P = 0.03$), and there was a trend toward a greater decline in the Chugach Mountains than in the Brooks Range ($P = 0.08$). Qualitatively similar results were obtained when the analyses were restricted to the two needle cohorts present on all sample dates, and when the analyses were conducted using the change in NSC content between the June and August sampling dates.

Branch extension growth

Repeated-measures ANOVA of retrospective annual branch extension growth (1991–2001) revealed significant effects of mountain range ($F_{2,169} = 19.2$, $P < 0.01$) and year ($F_{10,169} = 2.7$, $P < 0.01$) (Fig. 2). There was no evidence of an overall difference in growth between the treeline and forest ($F_{1,14} = 0.0$, $P = 0.92$). The effect of

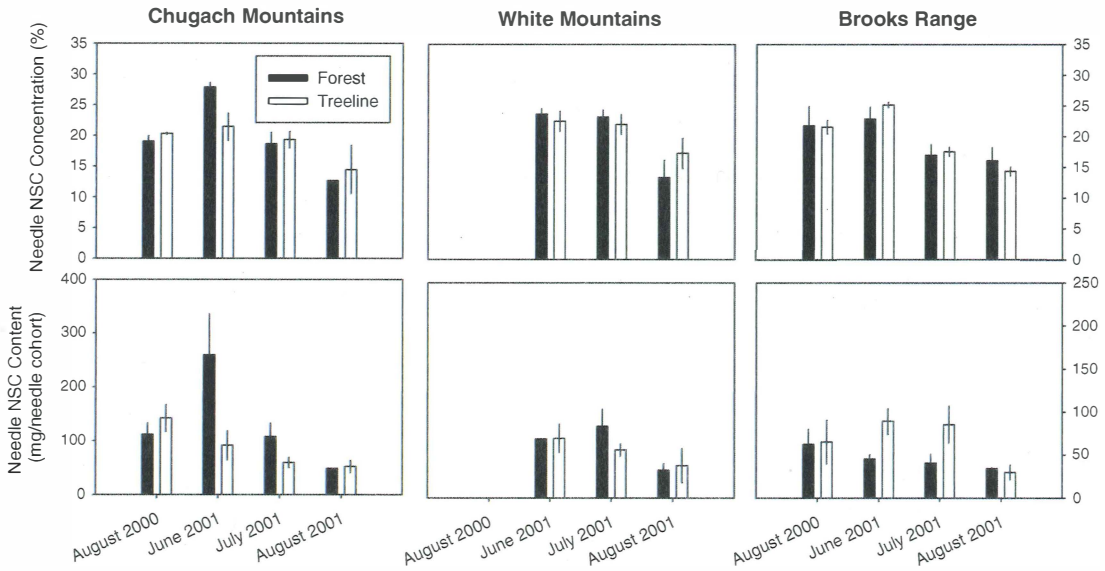

Fig. 1 Seasonal variation in needle NSC concentrations (*upper row*) and NSC content per needle cohort (*lower row*), averaged across ages 0–2, at treeline and forest sites along a latitudinal gradient in Alaska ($n = 3$). *Bars* are ±1.0 SE

mountain range was driven by significantly greater branch growth in the Chugach Mountains relative to the White Mountains ($t = 5.1$, $P < 0.01$) and the Brooks Range ($t = 5.6$, $P < 0.01$). Branch extension growth during 2001 (when needle NSC was measured) showed patterns similar to the long-term record (Fig. 3). There was a significant effect of mountain range ($F_{2,14} = 15.9$, $P < 0.01$) and no evidence of difference in growth between treeline and forest ($F_{1,14} = 0.3$, $P = 0.57$). In 2001, growth was greater in the Chugach Mountains than in the White Mountains ($P < 0.01$) and Brooks Range ($P < 0.01$).

Relationships between needle NSC and branch growth

Across sites, branch extension growth was not significantly correlated with the seasonal change in needle NSC concentration in the three most recent needle cohorts when the change was examined between the June to July ($n = 18$, $r = -0.26$, $P = 0.31$) or the June to August time periods ($n = 18$, $r = -0.31$, $P = 0.21$). Similar results were obtained when the analyses were restricted to the two needle cohorts present on both sampling dates. In contrast, there was a negative linear correlation between site-level branch extension growth and the seasonal change in NSC calculated as the difference between NSC content in June and July ($n = 18$, $r = -0.65$, $P < 0.01$) (Fig. 4) and between June and August ($n = 18$, $r = -0.61$, $P < 0.01$). Again, similar results were obtained when the analyses were restricted to the two needle cohorts present on both sampling dates. The seasonal change in NSC content of the three most recent needle cohorts was also examined as a percent of NSC content in June. When the change in NSC content between June and July was expressed as a percent of June NSC content, a negative exponential relationship emerged ($n = 18$, $r^2 = 0.38$, $P = 0.03$).

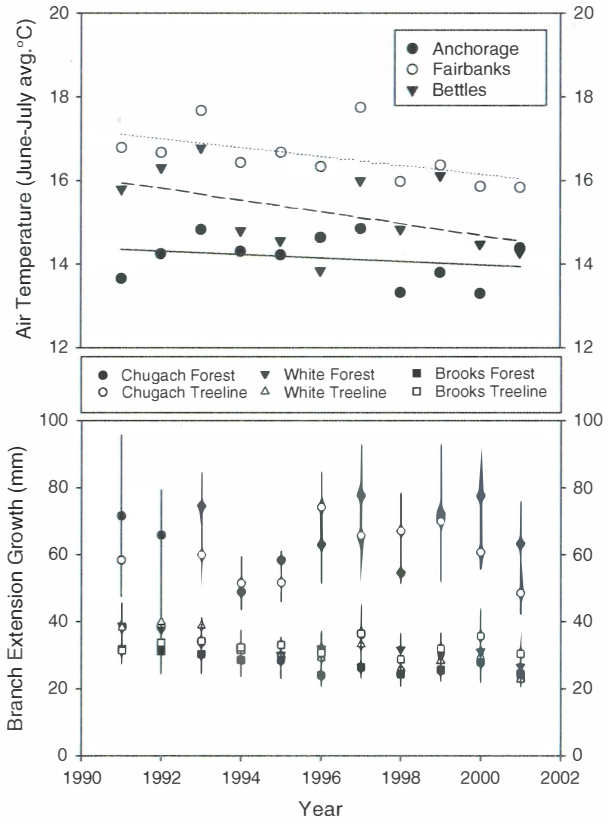

Fig. 2 Air temperature trends (June–July) at first-order climate stations in Anchorage, Fairbanks and Bettles, AK, USA, along with corresponding measurements of retrospective branch extension growth averaged across three forest and three treeline sites in three mountain ranges along a gradient from south- to north-central Alaska ($n = 3$). *Bars* are ±1.0 SE

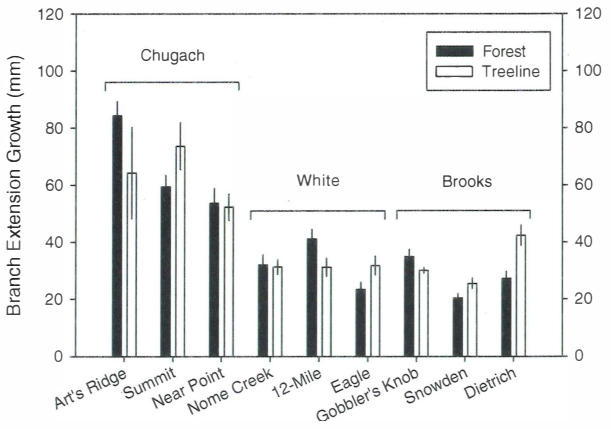

Fig. 3 Average annual branch extension growth (1991–2001) at paired treeline and forest sites in three mountain ranges along a latitudinal gradient in Alaska ($n = 5$). *Bars* are ±1.0 SE

Discussion

Seasonal changes in needle NSC concentration and content

Needle NSC concentration varied seasonally, with the highest levels observed in June and lower levels observed in July and August of 2001, much like previous observations in the Chugach Mountains (Abadie 1991). The higher June NSC concentration likely reflects differences in the phenology of photosynthesis and growth. Relatively high rates of net photosynthesis in white spruce (>30% of annual maximum) have been observed in April, when soils are still covered by ~40 cm of snow in south-central Alaska (Abadie 1991), while growth does not begin until late May (Abadie 1991; Sveinbjörnsson 2000). Prior to our June sampling event, needle NSC concentration probably increased in the absence of strong sinks. NSC

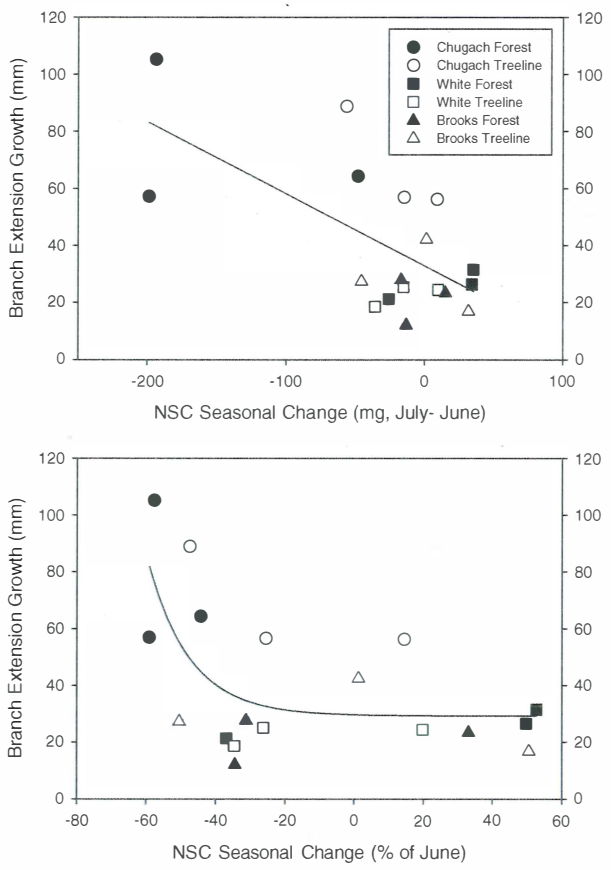

Fig. 4 Relationships between branch extension growth and the seasonal change in NSC content, averaged across the three most recent needle cohorts, between June and July of 2001. The seasonal change in NSC content is expressed as both a difference (July–June, mg) and as a percent of June NSC [(July–June/June) × 100, %]. Measurements were made at paired treeline and forest sites distributed across three mountain ranges along a gradient from southern to northern Alaska ($n = 18$)

concentration and content generally declined from June to mid-July, although the trend depended strongly upon mountain range. The early summer decline in needle NSC concentration and content probably reflects the demands of branch and leader extension growth. Branch and leader extension growth likely ceased just before our July collections, but NSC concentration and content declined further during the second half of the growing season. The decline in NSC concentration and content during the second half of the growing season is likely due to the demands of radial growth and fine root production, with the former continuing until August and the latter into September (Chapin and Tryon 1983; Tryon and Chapin 1983; Ruess et al.1998).

Seasonal trends in needle NSC concentration agreed well with trends in NSC content in the Chugach and White Mountains. In the Brooks Range, however, NSC concentration declined substantially from June to July of 2001, while NSC content remained unchanged. These divergent trends were observed whether the calculations were made using the three most recent needle cohorts or the two cohorts common to both sampling dates. Such a trend probably reflects the accumulation of other leaf constituents between June and July, such as nutrients, tannins, lignin and lipids. Regardless of the cause, our observations in the Brooks Range highlight the potential error in using needle NSC concentration to make inferences about the limits on growth. Changes in the abundance of other needle constituents could change NSC concentration, while NSC content remains unchanged. Conversely, changes in NSC content could be masked by parallel changes in other leaf constituents, leaving NSC concentration unchanged.

Elevational patterns

Growing season soil temperatures at our forest and treeline sites are within the narrow range (5.9–7.5°C) that has been correlated with global treeline positions (Körner 1998; Körner and Paulsen 2004). Summer soil temperatures were slightly cooler at treeline compared with forests in our watersheds of the Chugach and White Mountains, but slightly warmer than in the neighboring forests in our Brooks Range watersheds. Retrospective measurements of branch extension growth (1991–2001) and those restricted to 2001 showed no overall effect of elevation. Similarly, there was no evidence of an elevation effect in measurements of NSC concentration, content or the seasonal change in NSC. Examination of the elevation effect on growth within the mountain ranges showed contrasting trends in the Chugach Mountains and the Brooks Range, and no evidence of an elevation effect in the White Mountains. In the Chugach, there was a trend toward greater growth in the forest than at the treeline, while growth was greater at the treeline than in the forest in the Brooks Range.

The trend toward greater growth in the forest than at the treeline in the Chugach was driven by large differences in 1992 and 1993. Measurements of white spruce branch and leader growth in the summers of 1988 and 1989 also showed much higher growth in the forest and the valley than at the treeline on Art's Ridge in the Chugach Mountains (Abadie 1991; Sveinbjörnsson 2000).

In the Brooks Range, branch extension growth was greater at the treeline than in the forest. This observation is consistent with our measurements of soil temperature, which show that forest soils were slightly colder than the treeline soils. Colder soils in the forest than at the treeline likely reflect the shading effect associated with greater stand density and canopy leaf area. Greater stand density in the forest may also mean greater competition for resources such as light and nutrients. Our forest sites in the Brooks

Range, and particularly Snowden, had much higher stand density than our forest sites in the other mountain ranges.

Our study is not the first to show no overall difference in growth between treeline and forest trees. Paulsen et al. (2000) examined radial growths of trees along elevation transects in the European Alps and showed that trees near the treeline have not differed in growth from trees in lower elevation forests since 1940. Between 1800 and 1940, however, there was generally a linear decline in growth with increasing elevation, leading the authors to conclude that the current treeline position was determined by past climates. In our study and that of Paulsen et al. (2000), it is possible that current treeline positions are controlled by factors that govern recruitment of new trees beyond the forest limit, rather than factors affecting the growth of mature treeline trees (Smith et al. 2003).

Patterns across mountain ranges

Branch extension growth in the Chugach Mountains was much greater than observed in the two more northern ranges. Our 11-year record of branch extension growth showed negative growth trends in the White Mountains and Brooks Range and no overall trend in the Chugach Mountains. The negative growth trends in the White Mountains and Brooks Range closely mirror declining trends in June–July average air temperatures measured over this period in Fairbanks and Bettles, AK, USA. A causal relationship between cooling temperatures and declining growth of trees in the White Mountains and Brooks Range would be consistent with our observation that trees in these mountain ranges did not draw down needle NSC content during growth.

Needle NSC concentration also varied across mountain ranges. Trees in the White Mountains generally showed the highest needle NSC concentration, while those in the Chugach Mountains and the Brooks Range had lower needle NSC concentrations that were statistically indistinguishable from one another. Differences in needle mass per cohort across mountain ranges were sufficient to reverse this trend when needle NSC content was examined. Trees in the Chugach Mountains maintained lower needle NSC concentrations and tended to lose needles at a greater rate than in the other mountain ranges (Smith 2005), but still maintained greater needle mass and greater NSC content per needle cohort (ages 0–2) than trees in the two more northern ranges, where NSC contents were similar.

Relating branch extension growth to needle NSC

Previous treeline studies that examined tissue NSC concentration found no difference or an increase in tissue NSC from the closed forest to the treeline, and concluded that photoassimilate availability is probably not an important constraint on tree growth (Hoch et al. 2002; Hoch and Körner 2003, 2005; Shi et al. 2006). We found an increase in needle NSC concentration from the Chugach Mountains to the White Mountains, commensurate with a substantial decline in branch extension growth. A similar decline in growth, however, was observed between the Chugach Mountains and the Brooks Range, but there was no evidence of a change in needle NSC concentration. This latter observation suggests that needle NSC concentration is not a sensitive indicator of changes in branch extension growth.

We found a stronger correlation with growth when seasonal changes in needle NSC content were examined. The seasonal change in needle NSC content of the three most recent cohorts was calculated by subtracting NSC content measured in July and August of 2001 from contents measured before the period of branch extension growth, in early June of 2001. In both instances, we found a negative correlation between the seasonal change in NSC content and branch extension growth, with the best correlation obtained using the difference between July and June NSC data. It is not surprising that the change in NSC content between June and July was better correlated with growth, given that white spruce branch extension growth begins in late May or early June and concludes in early to mid July. White spruce trees in the Chugach Mountains drew down needle NSC content to a greater extent and showed far greater growth than trees in the White Mountains and the Brooks Range, where needle NSC content was only slightly reduced from June to July and from June to August. The relatively high needle NSC concentration and limited seasonal change in needle NSC content of trees of the White Mountains and Brooks Range suggest that growth was not limited by photoassimilate availability, but instead by the ability of the trees to invest those raw materials in branch extension growth. Our observation of limited growth and a failure to reduce needle NSC content in trees of the more northern mountain ranges is consistent with observed differences in soil temperature across the latitudinal gradient and with trends in branch growth during a period of cooling temperatures. The spread of our data in plots of growth versus the seasonal change in NSC content indicates that source–sink relations of white spruce vary in space along a continuum between source and sink limitation of growth. Variation along the same continuum likely occurs over time in individual trees. Our observation that white spruce source–sink relations vary along a continuum between source and sink limitation contrasts with the framework of many previous studies, which have generally considered treeline trees to be either source- or sink-limited. Our argument that treeline trees may vary between source and sink limitation in space and time is

consistent with the observations of Bansal and Germino (2008), who found that conifer seedlings grown at different altitudes showed a strong inverse correlation between starch concentration and respiration, consistent with sink limitation, while they also found an equally strong positive correlation between seedling growth and assimilation, consistent with source limitation.

We have argued that trees in the Chugach Mountains show a greater potential for source limitation because they drew down needle NSC pools by as much as 80% during the period of branch extension growth. We do not think the Chugach trees were completely source limited during the 2001 growing season, because there was no evidence of saturation or a decline in branch growth at high levels of seasonal decline in NSC content. If NSC content is reduced by much more than 80% during the growth period, we expect that the curve would begin to saturate and then steeply decline. At the outset, we expected that treeline trees in the Chugach would show the greatest evidence of source limitation of growth, as a result of greater needle loss and a potentially more favorable growth environment. Our findings suggest that Chugach trees were indeed relatively more source limited than trees in the other mountain ranges, but there was no clear difference in carbohydrate relations between forest and treeline trees in the Chugach, suggesting that greater needle loss at the treeline did not predispose the trees to greater source limitation. In the White Mountains and the Brooks Range, we anticipated less favorable thermal conditions, reduced growth, and a greater tendency toward sink limitation of growth at the treeline than in the forest. We found no evidence of consistent differences between forest and treeline in any of these variables.

Our observations across a 785-km gradient from southern to northern Alaska have revealed three important complexities in the source–sink relations and growth patterns of high-elevation white spruce. First, comparison of source–sink inferences made using NSC concentration and content showed that relating seasonal changes in NSC content to measurements of growth provides a powerful framework to compare source–sink relations across elevations and mountain ranges. Use of NSC concentration, in contrast, was likely confounded by changes in other leaf constituents over space and time. Second, we found no evidence of a consistent difference in growth and source–sink relations between trees at our treeline and forest sites, which differed in elevation by an average of 113 m. This may indicate a present decoupling of mature tree performance and population processes, and highlights the danger of using growth trends in mature trees to infer potential changes in treeline positions. Third, our results indicate that source–sink relations of high elevation white spruce vary along a continuum between source and sink limitation over space, and likely over time. One important implication of this finding is that one cannot conclude that a tree is sink limited by simply showing it is not source limited.

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