Variation in white spruce needle respiration across the species range — Source link ↗

Kevin L. Griffin, Kevin L. Griffin, Zoe M. Griffin, Stephanie C. Schmiege ...+5 more authors

Institutions: Columbia University, Lamont–Doherty Earth Observatory, New York Botanical Garden, University of Idaho

Related papers:

- Characteristics of stem respiration in black spruce (Picea mariana) stand, interior Alaska

- Foliar respiration and its temperature sensitivity in trees and lianas: in situ measurements in the upper canopy of a tropical forest.

- Evidence of soil nutrient availability as the proximate constraint on growth of treeline trees in northwest Alaska

- Responses of white spruce (Picea glauca) to experimental warming at a subarctic alpine treeline

- Effects of canopy position on climate-growth relationships of Qinghai spruce in the central Qilian mountains, northwestern China

Share this paper: 𝐟 🐦 in ✉

Variation in white spruce needle respiration across the species range

1   **Kevin L. Griffin[1,2,3]*, ORCID 0000-0003-4124-3757, Zoe M. Griffin[4], 0000-0003-4821-9557, Stephanie C.**
2   **Schmiege[2,5], ORCID 0000-0001-9054-5538, Sarah G. Bruner[2], 0000-0001-7103-9664, Natalie T. Boelman[3],**
3   **ORCID 0000-0003-3716-2372, Lee A. Vierling[6], ORCID 0000-0001-5344-1983, Jan U. H. Eitel[6,7], ORCID 0000-0003-**
4   **1903-3833**

5

6   [1]Department of Earth and Environmental Sciences, Columbia University, Palisades, NY 10964,
7   USA.

8   [2]Department of Ecology, Evolution and Environmental Biology, Columbia University, New
9   York, NY 10027, USA

10   [3]Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY 10964, USA

11   [4]Department of Geography & Environmental Sustainability, SUNY Oneonta, Oneonta, NY
12   13820, USA

13   [5] New York Botanical Garden, Bronx, NY 10458, USA

14   [6]Department of Natural Resources and Society, College of Natural Resources, University of
15   Idaho, Moscow, ID 83843, USA

16   [7]McCall Outdoor Science School, College of Natural Resources, University of Idaho, McCall, ID
17   83638, USA

18   *** Correspondence:**
19   Kevin L. Griffin
20   griff@LDEO.columbia.edu
21   Orcid ID 0000-0003-4124-3757

22   **Abstract**

23   White spruce (*Picea glauca*) spans a massive range from arctic treeline to temperate forests. Yet
24   the variability in respiratory physiology and the implications for tree carbon balance at the
25   extremes of this distribution remain enigmasWorking at Arctic and Temperate sites more than
26   5000 km apart, we measured the short-term temperature response of dark respiration (R/T) at
27   upper and lower canopy positions. R/T curves were fit to a polynomial model and model
28   parameters (*a*, *b*, and *c*) were compared between locations, canopy positions, or with published
29   data. Respiration measured at 25°C (R_{25}) was 68% lower at the southern location than the
30   northern location, resulting in a significantly lower *a* parameter of the R/T response in temperate
31   trees Only at the southern location did upper canopy leaves have a steeper temperature response
32   than lower canopy leaves, likely reflecting steeper canopy gradients in light. No differences were
33   manifest in the maximum temperature of respiration. At the northern range limit, respiration
34   appears extreme. This high carbon cost likely contributes to the current location of northern
35   treeline. We find that respiration will increase with end-of-the-century warming and will likely
36   continue to constrain the future range limits of this important boreal species.

37   **Keywords: *Picea glauca*, Canopy gradients, Carbon balance, Dark Respiration, Arctic**
38   **Treeline**

39   **Summary Statement:** White spruce (*Picea glauca*) needle respiration at the northern limit of
40   the species range is three times higher than at the southern range limit. This extreme carbon cost
41   likely challenges tree survival and contributes to the location of the northern treeline.
42

Introduction

The distribution range of a species delineates the geographical location where historical, physiological and biotic filters combine to result in its successful growth and reproduction (Lambers & Oliveira, 2019). The niche-breadth hypothesis explains species distributions based on envelopes of environmental conditions tolerated (Lowry & Lester, 2006), yet to this day there is still no universally accepted "cause" delineating a species' range despite a long history of debate (see Casazza et al., 2005; Kruckeberg & Rabinowitz, 1985; Kunin & Gaston, 1993; Lavergne et al., 2004; Stebbins, 1942; Watson, 1833). Clearly many other evolutionary and ecological factors influence species range distributions, including genetic diversity, phenotypic plasticity, mating systems and metapopulation dynamics (*reviewed in* Brown et al., 1996; Gaston, 1996; Lowry & Lester, 2006). Still the role of the growth environment is undeniable and links a species' distribution to its physiological performance. Using a physiological approach to understand the complex relationships between climate and the distribution of species can be preferable to simple climate envelope models because the former is capable of predicting species distributions under a variety of possible environmental conditions (Hijmans & Graham, 2006; Malanson et al., 1992; Prentice et al., 1992).

Physiological processes such as photosynthesis, respiration and growth all respond strongly to local environmental conditions. Together these processes constrain plant carbon balance and thus contribute to a species distribution range (part of the physiological filter of Lambers & Oliveira, 2019). Here we concentrate on leaf respiration. This flux is less well studied than photosynthesis, provides a crucial link between photosynthesis (carbon gain) and growth (carbon sequestration) and has been hypothesized to control the range distribution of individual species (Criddle et al., 2003). Furthermore, respiration is highly temperature sensitive, making it an important determinant of ecosystem productivity (Valentini et al., 2000). *GlobResp*, a global database of plant respiratory characteristics, identifies latitudinal gradients in leaf respiration measured at a common temperature that increase with absolute latitude. These findings suggest that species with a large range should exhibit variable rates of respiration across their distribution, although this hypothesis has not been explicitly tested (Atkin et al., 2015). Furthermore, Patterson et al. (2018) quantified respiratory rates and responses to temperature in 16 tree species growing in a common location, grouping them by their relative location within their individual species distributions. The results show that northern ranged species growing near their southern range limit had 71% higher respiration rates (measured at 20°C) than southern ranged species growing near the northern edge of their range limits. Quantifying respiratory characteristics of individuals growing near the margins of their species range distributions can thus elucidate physiological controls of the current distribution.

Recently we reported that white spruce (*Picea glauca* (Moench) Voss) growing at the arctic treeline (which marks the transition between the boreal forest and treeless tundra occurring in the Forest Tundra Ecotone (FTE)) exhibit exceptionally high respiratory costs (Griffin et al., 2021). This species has a transcontinental range in North America and while it is one of the most common tree species defining the FTE (Sutton, 1969), it also has a remarkably large species distribution stretching from the west coast of Alaska to the east coast of Canada and New England (US Geological Survey, 1999) (Figure 1). One of the hardiest coniferous species, white spruce has a suite of structural and functional traits that are adapted to cold temperatures and short growing seasons. However, ambient environmental conditions at the southern edge of its

3

87   range distribution can be markedly different from those at treeline. Perhaps surprising given its
88   large geographical range, several studies show that white spruce has limited physiological
89   plasticity (Benomar et al., 2018; Man & Lieffers, 1997; McNown & Sullivan, 2013;
90   Prud'Homme et al., 2018; Stinziano & Way, 2017; Weger & Guy, 1991). However, McNown &
91   Sullivan (2013) working across a gradient that included terrace, forest and treeline sites,
92   demonstrated that the physiological capacity of white spruce can vary due to other site factors
93   such as soil properties and nutrition, even when climatic variables like temperature are constant.
94   To our knowledge no studies have compared the respiratory characteristics of this species at the
95   opposite ends of its distribution where climate and light conditions differ dramatically.

96   The goal of this research was to gain a better understanding of how respiration varies across the
97   white spruce species range, and to explore the potential impact of respiration on leaf carbon
98   balance, tree growth and survival. This is done by taking advantage of our recent detailed
99   assessment of white spruce respiratory physiology at the Alaskan FTE, and then using identical
100 techniques, we compare this to the physiological function of spruce growing more than 5000 km
101 away at the opposite end of the species distribution. We test four research hypotheses. First, that
102 leaf respiration measured at 25°C (R_{25}) in will decrease with latitude (Atkin et al., 2015). We
103 extend this to examine the overall temperature response of respiration. Second, while our
104 previous study did not find canopy position differences in respiration at the FTE (Griffin et al.,
105 2021), we hypothesize that at our southern site upper canopy leaves will have higher respiration
106 rates and be less responsive to temperature than lower canopy leaves. Light acclimation has been
107 shown to affect respiration rates in white spruce dramatically (Awada & Redmann, 2000) and
108 there are intra-canopy gradients in light absorption in the dense canopy at Black Rock Forest
109 (Schmiege et al., *pers com*). Furthermore, the top of the canopy is often the most physiologically
110 active portion of a tree crown and has been shown to affect both average respiration rates and the
111 response of respiration to temperature of leaves at various canopy depths (Griffin et al., 2001,
112 2002). Third we hypothesize that southern but not northern spruce respiration will be similar to
113 the average for the Needle leaved Evergreen (NLEv) plant functional type to which they belong.
114 To quantify white spruce respiratory temperature response and make these comparisons, we use
115 the global polynomial model of Heskel et al. (2016). Fourth, we hypothesize that trees from the
116 southern edge of the species range will have a higher temperature tolerance than trees from the
117 northern edge of the distribution. To test this, we quantify T_{max}, the leaf temperature at which the
118 maximum rate of respiration is reached, from the respiratory temperature response to curves.
119 Finally, we examine the general relationships between respiratory traits and leaf traits. The two
120 specific locations of this study are Black Rock Forest, located in the Hudson highlands of NY,
121 and the FTE in north central AK, USA (Figure 1. Referred to as the "southern location" and
122 "northern location" respectively). Our southern site is the same location as the species range
123 study described earlier (Patterson et al., 2018) and represents an extreme southerly location for
124 white spruce. By quantifying these variables at the extremes of the species distribution, we
125 characterize the mechanistic contribution of respiration to the current and potential future
126 distribution of white spruce.

Materials and Methods

128 *Site Descriptions and Leaf Material*: This research was conducted at two sites representing the
129 opposite ends of the species range, Black Rock Forest (BRF), New York, USA (41°24' 03.91" N
130 latitude, 74°01'28.49" W longitude – southern location) and the Forest Tundra Ecotone (FTE),

131   AK USA (67°59' 40.92" N latitude, 149°45'15.84" W longitude – northern location). The sites
132   are more fully described elsewhere (Eitel et al., 2019, Patterson et al 2018). Briefly, the average
133   annual precipitation at the southern location is 1285 mm and mean annual temperature is 10.9°C
134   (Arguez et al., 2010). The northern location is spruce dominated evergreen forest (Eitel et al.,
135   2019), while the southern location is a northern temperate deciduous forest that is oak dominated
136   (Patterson et al., 2018; Schuster et al., 2008). The southern location is to the south of the natural
137   species range distribution presented by Little (1999). White spruce was probably introduced into
138   BRF as nursery stock for forestry trials in the early 1930's but has since expanded naturally. The
139   trees used for this study were naturally seeded on the forest edge along Continental Road, a dirt
140   trail established during the Revolutionary War to facilitate troop travel between West Point and
141   the encampment of the Continental army in New Windsor. While the trail represents a break in
142   the forest canopy it gets limited use and has only a minor impact on the canopy-dominant study
143   trees located at least 15 m from the road.
144
145   Leaves used for the respiration measurements from the southern site were from south facing
146   branches collected in late June and early July of 2018 from six study trees and came from the
147   upper (1 m below the apical meristem) and lower (1.37 m from the ground) canopy positions. As
148   in our FTE study (Griffin et al., 2021), the terminal portions of several branches were cut with
149   sharp pruners and the removed portion of the stem was immediately wrapped with wet paper
150   towels, sealed in a plastic bag with ample air and placed in cooler where they could be kept dark
151   and transported to the lab. The top of the canopy was accessed with an articulating boom lift.
152   Once returned to the lab, the stem pieces were recut underwater and then placed in a beaker
153   containing enough water to submerge the cut end until analyzed, typically within 8 (but no more
154   than 24) hours. Leaves from the northern site are a subset of data used by Griffin et al., (2021)
155   and thus are described fully there. The motivation of that study was to assess the effect of tree
156   size (saplings vs. trees) and test current hypotheses about the location of treeline. No saplings
157   were sampled at the southern location and the effect of tree size/development is not specifically
158   of interest here. Thus, the Griffin et al. (2021) dataset was trimmed to exclude all saplings (stems
159   < 10cm DBH), leaving 18 individual trees ($\geq$ 10 cm DBH) and re-analyzed for the present study.
160   No part of the analysis presented here was included in the earlier publication.
161
162   *Respiration Temperature Response Curves*: The techniques employed here were identical to
163   those used in our treeline study in order to facilitate this direct comparison. Thus, methods are
164   described more fully in Griffin et al., (2021). Briefly, CO_2 exchange rates were measured on
165   needles that were carefully removed from the stems, weighed to determine the initial fresh mass
166   (g) and placed in a fine nylon mesh bag. The mesh bag containing the leaves was placed inside a
167   custom-made cuvette (Patterson et al. 2018, Li et al. 2019, Schmiege et al. 2021) with computer
168   controlled thermoelectrical cooling (CP-121 Thermoelectric Peltier Cooling Unit, TE
169   Technology, Traverse City, MI USA). The custom cuvette was interfaced with a portable
170   photosynthesis system (Li-6400XT, LiCor Lincoln, Nebraska USA) which recorded all gas
171   exchange and environmental parameters every 20 seconds.
172
173   After equilibrating the system to 5°C, the mesh bag holding the leaves was sealed inside. Once
174   stability was reached the instrument was zeroed and the response curve was measured as
175   described in Heskel et al. (2016), O'Sullivan et al. (2013), and Schmiege et al. (2021). During
176   measurements the flow rate through the cuvette was set to 500 ml min^{-1} and the CO_2

177   concentration to 400 ppm. The air was dried using a Li-6400XT desiccant column and then

178   transpiration was allowed to humidify the cuvette. During the measurement the cuvette

179   temperature was ramped up from 5 to 65°C at a constant rate of 1°C min^{-1}.

180

181   *Leaf Traits:* Measured leaves were subsequently photographed with a known scale and *ImageJ*

182   was used to determine their projected area (Schneider et al., 2012). The leaves were dried at

183   65°C for a minimum of 48 hours and again weighed to determine leaf dry mass (g). Specific leaf

184   area (SLA cm^2 g^{-1}) was calculated and used to determine mass-based respiratory fluxes from the

185   area-based fluxes. Leaf water content (%) and leaf dry matter content (LDMC g g^{-1}) were

186   calculated from the fresh and dry masses. Leaf nitrogen was estimated using the %N measured

187   from these same trees, sampled at the same canopy locations in 2017 (Schmiege et al. *pers*

188   *comm*).

189

190   *Data Analyses:* The respiration temperature response curves were analyzed as in Heskel et al.

191   (2016) by fitting a second-order polynomial model to the log transformed respiration rates

192   between 10 and 45 °C.

193

194    $$LnR = a + bT + cT^2 \qquad \text{(Equ. 1)}$$

195

196   Where *a* represents the basal respiration rate (y-intercept), while *b* and *c* describe the slope and

197   curvature of the response (Heskel et al. 2016). The respiration rate at a common temperature of

198   25°C (R_{25}) was also calculated and the temperature where the maximum respiration rate was

199   reached (T_{max}) was recorded. The modeled temperature response was also used to quantify the

200   possible effect of warming on respiration rates (in the absence of thermal acclimation – *see*

201   *justificaiton below*), based on the current growing season average temperatures for the two sites

202   and projections for end of the century warming (US Federal Government, 2021).

203

204   Respiration vs. temperature curves were fit to the polynomial model of Heskel *et al.,* (2016)

205   using ʀ v. 3.6.3 (R Core Team, 2020). Due to the unequal sample size (n BRF = 6; n FTE = 18),

206   a one-way ANOVA was used to test our first hypothesis regarding respiration across the species

207   range. To test our second hypotheses regarding the main effects of canopy position on respiration

208   *within* each of the two sites, paired t-test were used to compare each of the model parameters *a*, *b*

209   and *c* (see Equ. 1), and model predictions of R_{25}. All traits were transformed as necessary to fulfil

210   assumptions of normality. To test our third hypothesis, we compared our model estimates with

211   those of Heskel *et al.*, (2016) by means of an independent sample t-test based on the mean,

212   confidence intervals and sample size for the NLEv PFT (as reported in their Table 1). Our fourth

213   hypothesis regarding the $\underline{T}_{max}$ of respiration was tested similarly to hypotheses 1 & 2 described

214   above. Finally, regression equations were used to assess the general relationships between leaf

215   traits and leaf respiration, and in particular ability of leaf N (per unit leaf area) to predict the rate

216   of respiration (Atkin et al., 2015). All data analysis other than the initial R/T curve fitting was

217   done in Excel (version 16.51 for Mac, Microsoft, Redmond, Washington, U.S.A.) with both the

218   Solver and *RealStatistics* (Release 7.6, Zaiontz 2021) add-ins.

219

220   **Results**

221   *Tree and leaf traits:* The average tree in this study was 18.3±1.02 cm in DBH (1.37 m from the

222   ground) and 9.5 ±0.46 m tall (Table 1). Trees from the southern location tend to be larger in

223   diameter (23.1±1.99 vs. 16.6±0.68 cm), but similar in height (9.9 ±0.73 vs. 9.36±0.41 m)
224   compared to the northern location trees.

225   The leaf dry matter content, leaf nitrogen content and leaf water content (LWC) did not differ by
226   canopy position at either location, but LDMC was 32% lower, LWC was 37% higher, and leaf N
227   was 25% higher at the southern location compared to the northern location (Table 1). The
228   specific leaf area (SLA) of the upper canopy leaves was 23% lower than that of the lower canopy
229   leaves at the southern location, which on average had 37% higher LWC than the northern
230   location (Table 1).

231   *Respiration temperature response curves*: In all trees, respiration increased exponentially
232   between 5 and 45 °C, then slowed briefly before increasing rapidly to a maximum rate (R_{max})
233   defining the T_{max} (Figure 2a). Measured respiration rates between 10 and 45°C were used to
234   model the ecologically relevant response (Figure 2b). The global polynomial model of Heskel et
235   al (2016) fit all log normal respiration temperature curves with an $r^2 \geq 0.99$ (Figure 3). Overall,
236   the three model coefficients averaged -1.82±0.12, 0.090±0.003 and -0.00030±0.0001 (*a*, *b* and *c*
237   respectively, mean ± SEM, Table 2). At the southern location, leaves from the top of the canopy
238   had a 24% lower intercept (coefficient *a*), than leaves from the bottom of the canopy (p=0.04,
239   Table 2). Canopy position did not affect the model coefficients at the northern location. The
240   temperature response of white spruce growing at the southern location is quite similar to the
241   average model coefficients for the plant functional type to which this species belongs, needle-
242   leaved evergreen (NLEv, Heskel et al. 2016), and only the curvature (*c*) of the southern location
243   upper canopy leaves was statistically different from the average NLEv response (Figure 3).
244   However, the southern location measurements from both canopy positions were significantly
245   different when compared to their counterparts from northern location (Figure 3). The differences
246   include lower intercepts for both the BRF canopy positions, as well slight differences in both the
247   slope and curvature of the upper canopy leaves. The response of respiration to temperature at the
248   northern site was significantly different from the NLEv PFT response (higher *a*).

249   *Respiration at a common temperature & R_{max}*: Across all samples at the southern location, the
250   average rate of respiration at a common temperature of 25°C was 0.75 ± 0.08 μmol CO_2 m^{-2} leaf
251   area s^{-1}, which is 68% lower than the average rate at the northern location (2.35±0.88 μmol CO_2
252   m^{-2} leaf area s^{-1}). The rate differed significantly by canopy position at the southern but not the
253   northern location. R_{25} was 48% higher in upper canopy leaves than in lower canopy leaves (0.90
254   ± 0.09 μmol m^{-2} s^{-1} vs. 0.61 ± 0.10 μmol m^{-2} s^{-1}) from the southern location (Figure 4a). Due to
255   significantly lower SLA of the southern location upper canopy leaves compared to the lower
256   canopy leaves, there were no significant differences in the mass based R_{25} (Figure 4b). Leaves
257   from the southern location, at both canopy positions continued to respire until leaf temperature
258   reached 58.5 ± 0.5 °C (T_{max}) before respiration quickly decreased as the leaves died. This is a
259   slightly higher, but statistically similar temperature to the T_{max} of northern location trees
260   (57.6±0.36 °C). However, the maximum rate of respiration (R_{max}) of the upper canopy southern
261   location leaves at T_{max} (7.43 ± 0.78 μmol m^{-2} s^{-1}) was 40% higher than the R_{max} of the lower
262   canopy leaves (5.29 ± 0.66 μmol m^{-2} s^{-1}), and the southern location average R_{max} was 59% lower
263   than the northern location average, a difference of more than 9.3 μmol CO_2 m^{-2} leaf area s^{-1}
264   (Figure 4c). None of the major respiratory parameters (R_{25}, *a* or R_{max}) was significantly related to
265   leaf N (mg N m^{-2}) (p>0.05, data not shown), although the trend was always for increasing rates

7

266 of respiration with increasing leaf N. Estimated in situ rates of respiration at the average growing
267 season temperature (June/July/August) were significantly higher at the northern location than
268 they were at the southern location (indicated as solid vertical lines on Figure 5), as are the
269 estimated rates for the projected end of century temperatures (indicated by dotted vertical lines
270 on Figure 5).

271 **Discussion**
272 We found dramatic differences in white spruce leaf respiration across the species range, from
273 New York State at the south-eastern edge of the distribution to the Forest Tundra Ecotone, more
274 than 5000 km away in Arctic north-central AK. The differences are extreme, and represent a
275 significant physiological response to changes in ambient environmental conditions. Across the
276 vast range of this species, many environmental gradients/differences exist, including day length
277 and associated effects on light energy, air and soil temperatures and moisture, and pollutant
278 exposure and edaphic factors, all of which are moderated differently by the distinctive forest
279 canopy structures of the sites. Of the above environmental factors, the response of white spruce
280 foliage to air temperature is of particular interest for three reasons: 1) temperature is known to
281 have strong effects on the rate of respiration (Heskel *et al.*, 2016); 2) temperature is increasing
282 rapidly and unevenly across the species range (warming is more rapid at high latitudes (Cohen et
283 al., 2014; Huang et al., 2017); and 3) ecosystem models calculate the temperature response of
284 respiration to scale over both time and space (Atkin et al., 2014; Heskel, Atkin, et al., 2016;
285 Heskel et al., 2016; Huntingford et al., 2017a). Across the species range of white spruce, average
286 growing season (June, July August) temperatures differ by nearly 6 °C, from approximately 21
287 °C at the southern location (US Federal Government, 2021) to slightly less than 15°C at the
288 northern location (Harris *et al.*, 2020; Zepner *et al.*, 2021). This 29% decrease in average
289 temperature is associated with a tripling of the respiration rate in white spruce measured at a
290 common temperature of 25°C, and a doubling of the rate at the *in situ* average growing season
291 temperature. The much higher rates of respiration at the northern range limit of this species do
292 not support our first research hypothesis but may help explain not only why white spruce is not
293 found further to the north, but also why the boreal forest biome transitions to tundra at these high
294 northern latitudes (Griffin et al., 2021). Plants acclimated to cold temperatures often have higher
295 rates of respiration measured at a common temperature and a steeper respiratory temperature
296 response (Atkin & Tjoelker, 2003; Körner, 1989; Reich & Oleksyn, 2004) as a means to
297 maintain metabolic function in cold environments. The high respiratory rates coupled with slow
298 growth rates (Jensen et al., pers com) at the northern range limit suggest that northern trees
299 experience large carbon losses that are likely related to high maintenance and other metabolic
300 costs. These costs are not incurred in white spruce at the southern edge of its distribution.
301
302 The response of respiration to temperature in trees at either end of the species range provides
303 additional insights into the regulation of respiration and the root cause of the observed
304 differences. First, we find differences in the measured rates of respiration at both cold and warm
305 temperatures. This is consistent with Type II acclimation (Atkin & Tjoelker, 2003) and suggests
306 that there are differences in respiratory capacity, efficiency or perhaps mitochondrial numbers
307 and structure (Atkin & Tjoelker, 2003; Klikoff, 1966; Kornfeld et al., 2013; Miroslavov &
308 Kravkina, 1991; Patterson et al., 2018). Second, the measured T_{max} of white spruce needle
309 respiration does not differ significantly across the entire range. This indicates that overall thermal
310 tolerance is not plastic but a fixed species trait in white spruce (Heskel et al., 2014; O'Sullivan et
311 al., 2013, 2017). Third, we find differences in the temperature response of respiration across the

312   species range, with northern white spruce also exhibiting a significantly different response to that
313   of the needle leaved evergreen plant functional type. This suggests that the northern range limit
314   is an extremely challenging environment for this species, and that the high respiration rates may
315   be affecting leaf carbon balance and ultimately tree survival (Heskel et al., 2016; Huntingford et
316   al., 2017b; Patterson et al., 2018). And fourth, despite the indication of a Type II acclimation
317   response (Atkin & Tjoelker, 2003) the adjustments in respiratory physiology do not result in
318   homeostasis with regards to maintaining observed rates of respiration at the local temperatures
319   during the growing season. Rates of respiration at the northern edge of the species range are
320   extremely high and respond strongly to temperature, most likely stemming from biochemical and
321   physiological responses to the extreme environmental conditions of the Arctic.
322
323   We gained further insights into the response of white spruce to local environmental conditions
324   across its range by examining leaf traits and the relationships between leaf traits and respiratory
325   physiology. Needles from the northern edge of the species distribution tend to be thicker, or
326   perhaps denser, than needles from the southern location, likely reflecting large differences in
327   ambient temperatures (Atkin et al., 2006; Rosbakh et al., 2015). Increasing leaf structure is
328   potentially adaptive in the harsh environmental conditions at the arctic treeline where, in addition
329   to cold temperatures, leaves must survive high winds and abrasion, prolonged winters and the
330   possibility of large snow or ice loads while remaining metabolically active for many years.
331   While we found that variation in leaf structural characteristics were consistent with expected
332   relationships with cold temperatures, the biochemical characteristics were not. Leaf nitrogen
333   usually correlates negatively to temperature (Yin, 1993), and positively to leaf respiration (Atkin
334   et al., 2015) and latitude (Körner, 1989) yet these trends did not hold across the species range of
335   white spruce. The small difference in leaf nitrogen at the northern compared to the southern
336   range limit likely reflects the effects of the environment (*e.g.* temperature, hydrology, permafrost
337   dynamics and bedrock geology, (Nadelhoffer et al., 1991; Schimel et al., 2004) and
338   biogeochemistry (limited nitrogen fixation, slow decomposition rates, rapid uptake rates and
339   microbial competition (Schimel & Chapin, 1996; Schimel & Bennett, 2004; Yano et al., 2010))
340   on nitrogen availability and certainly suggests the presence of nitrogen limitation at the northern
341   location. Despite lack of a statistical difference in leaf N content, we found that the rate of white
342   spruce needle respiration and its response to temperature remained extremely high at the
343   northern location compared to the southern location, limiting the effectiveness of leaf N as a
344   proxy of respiration (Atkin et al. 2015). The patterns in leaf traits suggest the general adaptative
345   strategy in white spruce necessary to survive harsh northern conditions, and implicates the local
346   environmental conditions as directly and indirectly driving the respiratory physiology across the
347   species range.
348
349   We found support for our second hypothesis, that needles from the top of the tree would have
350   higher rates of respiration than needles from the bottom of the tree at the southern range limit
351   where canopy complexity creates resource gradients. The nature of the tree crown and the forest
352   canopy differs significantly at our two sites. The southern location trees are strongly conical and
353   compete for above ground resources in a mostly closed canopy surrounded by deciduous
354   hardwood species. The FTE trees, however, are more cylindrical and arranged in mostly open
355   canopies composed of individual trees or small groups of trees with only limited competition for
356   space and aboveground resources such as light. As a result, strong intra canopy light gradients
357   exist at the southern location but are much less pronounced at the northern location. Light, VPD,

358   wind and air temperature microclimates could all be affected by these differences in canopy
359   structure (Walcroft et al., 2005; Whitehead et al., 2001; Whitehead, Walcroft, et al., 2004), but
360   light is the most plausible driver of the observed respiratory response (*similar to* Bond et al.,
361   1999). The upper canopy leaves at the southern location receive full light and as a result have
362   higher photosynthetic rates than the lower canopy leaves which experience self-shading and
363   generally lower ambient light conditions (Schmiege et al., *pers com).* Higher photosynthetic rates
364   and more rapid growth in the upper canopy require higher respiration to support the ensuing
365   growth and maintenance costs of these needles (Bond et al., 1999; Griffin et al., 2001, 2002;
366   Tissue et al., 2002; Whitehead et al., 2004). By contrast, the combination of the open canopy,
367   low sun angles and narrow unbranching crown morphology of white spruce at the northern
368   location has the effect of homogenizing the light environment, and thus equalizing both
369   photosynthetic capacities, and the rates of respiration throughout the canopy. Clearly spruce trees
370   at either end of the species distribution must dynamically respond and adapt to different
371   environmental conditions over multiple spatial and temporal scales. However, our findings show
372   that it is the interplay between the environment and tree form and function that contributes to,
373   and ultimately determines, the geographic location of the species range. At the southern edge of
374   its range, white spruce exhibits unique respiratory responses in the upper vs lower canopy
375   needles to persist. At the northern limits, the unequal distribution of metabolic activity amongst
376   the different canopy positions is not observed and presumably not needed.
377
378   Climate change has, and will continue, to increase air temperature across the white spruce range
379   (Tamarin-Brodsky et al., 2020). This may increase rates of respiration and exacerbate increases
380   in respiratory carbon loss from the southern to the northern range limits of this species. The
381   short-term temperature response curves presented here can be cautiously used to infer how
382   respiration might change with continued warming. We note that thermal acclimation of
383   respiration could directly alter the predicted response (Atkin et al., 2008; Slot & Kitajima, 2015;
384   Vanderwel et al., 2015), most likely lessening the effect of climate warming. However, the noted
385   lack of thermal acclimation of respiration in this species implies that the short-term respiration
386   temperature response may be used to predict the long-term effect of climate warming in white
387   spruce (Benomar et al., 2016). Using the current growing season temperature and the predicted
388   rate of temperature increase by the end of the century (U.S. Climate Resilience Toolkit Climate
389   Explorer), we calculate that white spruce respiration may increase by 67% at the northern range
390   limit regardless of canopy location and by 53% at the southern range limit, where the upper
391   canopy needles are likely to increase more than the lower canopy (46 vs. 60% respectively).
392   These are massive estimated changes in the leaf carbon flux to the atmosphere that, if unmatched
393   by similar increases in photosynthesis or mediated by thermal acclimation, would have dramatic
394   effects on leaf carbon balance (Ow et al., 2008; Ow et al., 2008). Combining the R_{25} rates with
395   these projected rates of increase suggests that any increase in respiration is likely to be more
396   detrimental to the carbon balance of white spruce at the northern range limit than at the southern
397   range limit. The ecological effects of these physiological changes on the competitiveness of this
398   species and the future species range are unknown but clearly the metabolic adjustments needed
399   to respond to the changing environmental conditions are likely to play a role. We suggest these
400   effects are at least as severe, if not significantly more so, at the northern end of the range limit
401   than they are at the southern edge. This calls into question the suggestions (ACIA 2005; Zhang et
402   al. 2013; Pearson et al. 2013), that species migrations will tend to shift species ranges north and
403   more specifically to move the arctic treeline north in response to climate change.

404
405
406 **Conclusions**
407 The natural distribution of white spruce extends not just across strong environmental gradients,
408 but also to the very limit of tree growth form. North of its current range limit, not only is white
409 spruce not found, but neither are trees of any species. The results presented here may help
410 explain these linked observations. We clearly show that respiration rates of white spruce at the
411 northern range limit are not only higher than those from trees growing at the southern range
412 limit, but that these rates are extreme. Furthermore, we show that canopy position has a strong
413 influence on the distribution of respiratory activity at the southern range limit but not at the
414 northern range limit, a pattern that likely reflects differences in metabolic activity driven by light.
415 Despite the large differences in respiration, leaf traits in this species often remain constant across
416 the species range. Additionally, when leaf traits do change, they do not explain patterns in
417 respiratory activity. As a result, common techniques used to estimate respiration, such as
418 predictions based on leaf nitrogen, were ineffective. The model of Heskel et al., (2016) was
419 successfully fit to our data and demonstrates that the temperature response of respiration at the
420 southern end of the species distribution is statistically indistinguishable from the NLEv tree plant
421 functional type used in their global survey. In contrast, the northern range limit trees have much
422 higher rates of respiration and differ significantly from the NLEv PFT. Our work supports the
423 conclusion of Griffin et al. (2021), that white spruce needles at the northern range edge respire at
424 what are likely the species extreme limits, and that this carbon cost likely contributes to the
425 location of northern treeline. Using the short-term temperature response curves to constrain the
426 potential response of respiration to predicted end-of-the-century warming, we show that
427 respiration will have a significant impact on leaf carbon balance that is likely to contribute to
428 future range limits of this species. We question the assertion that species like white spruce will
429 simply shift their range distributions northward in response to warming and suggest that, without
430 a detailed understanding of the myriad ways photosynthesis, respiration and growth will respond
431 to changing climatic conditions, range shifts will be difficult to predict.

432 **Conflict of Interest**

433 *The authors declare that the research was conducted in the absence of any commercial or*
434 *financial relationships that could be construed as a potential conflict of interest.*

435 **Author Contributions**

436 K.L.G., S.C.S., N.B., L.A.V. and J.U.H.E. designed the research. They were assisted in data
437 collection by Z.M.G. & S.B.. S.C.S, Z.M.G. & K.L.G. analyzed the data. K.L.G wrote the first
438 draft of the manuscript. All authors contributed to the revisions, editing and submission of the
439 final manuscript.

440 **Acknowledgements**

443

Literature Cited

ACIA. (2005). Arctic climate impact assessment scientific report. Fairbanks (USA): University of Alaska, Cambridge University Press. 1020 pp.

Arguez, A., Durre, I., Applequist, S., Squires, M., Vose, R., Yin, X., & Bilotta, R. (2010). *NOAA's U.S. Climate Normals (1981-2010)*.

Atkin, O. K., Atkinson, L. J., Fisher, R. a., Campbell, C. D., Zaragoza-Castells, J., Pitchford, J. W., Woodward, F. I., & Hurry, V. (2008). Using temperature-dependent changes in leaf scaling relationships to quantitatively account for thermal acclimation of respiration in a coupled global climate-vegetation model. *Global Change Biology*, *14*(11), 2709–2726. https://doi.org/10.1111/j.1365-2486.2008.01664.x

Atkin, O. K., Bloomfield, K. J., Reich, P. B., Tjoelker, M. G., Asner, G. P., Bonal, D., Bönisch, G., Bradford, M. G., Cernusak, L. A., Cosio, E. G., Creek, D., Crous, K. Y., Domingues, T. F., Dukes, J. S., Egerton, J. J. G., Evans, J. R., Farquhar, G. D., Fyllas, N. M., Gauthier, P. P. G., … Zaragoza-Castells, J. (2015). Global variability in leaf respiration in relation to climate, plant functional types and leaf traits. *New Phytologist*, *206*(2), 614–636. https://doi.org/10.1111/nph.13253

Atkin, O. K., Loveys, B. R., Atkinson, L. J., & Pons, T. L. (2006). Phenotypic plasticity and growth temperature: understanding interspecific variability. *Journal of Experimental Botany*, *57*(2), 267–281. https://doi.org/10.1093/jxb/erj029

Atkin, O. K., Meir, P., & Turnbull, M. H. (2014). Improving representation of leaf respiration in large-scale predictive climate-vegetation models. *New Phytologist*, *202*(3), 743–748. https://doi.org/10.1111/nph.12686

Atkin, O. K., & Tjoelker, M. G. (2003). Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science*, *8*(7), 343–351. https://doi.org/10.1016/S1360-1385(03)00136-5

Awada, T., & Redmann, R. E. (2000). Acclimation to light in planted and naturally regenerated populations of white spruce seedlings. *Canadian Journal of Botany-Revue Canadienne De Botanique*, *78*(12), 1495–1504. https://doi.org/10.1139/b00-121

Benomar, L., Lamhamedi, M. S., Pepin, S., Rainville, A., Lambert, M. C., Margolis, H. A., Bousquet, J., & Beaulieu, J. (2018). Thermal acclimation of photosynthesis and respiration of southern and northern white spruce seed sources tested along a regional climatic gradient indicates limited potential to cope with temperature warming. *Annals of Botany*, *121*(3), 443–457. https://doi.org/10.1093/aob/mcx174

Benomar, L., Lamhamedi, M. S., Rainville, A., Beaulieu, J., Bousquet, J., & Margolis, H. A. (2016). Genetic adaptation vs. ecophysiological plasticity of photosynthetic-related traits in young *Picea glauca* trees along a regional climatic gradient. *Frontiers in Plant Science*, *7*(FEB2016), 1–15. https://doi.org/10.3389/fpls.2016.00048

12

482   Bond, B. J., Farnsworth, B. T., Coulombe, R. A., & Winner, W. E. (1999). Foliage physiology
483   and biochemistry in response to light gradients in conifers with varying shade tolerance.
484   *Oecologia*, *120*(2), 183–192.

485   Brown, J. H., Stevens, G. C., & Kaufman, D. M. (1996). The geographic range: Size, shape,
486   boundaries, and internal structure. *Annual Review of Ecology and Systematics*, *27*, 597–623.
487   https://doi.org/10.1146/annurev.ecolsys.27.1.597

488   Casazza, G., Barberis, G., & Minuto, L. (2005). Ecological characteristics and rarity of endemic
489   plants of the Italian Maritime Alps. *Biological Conservation*, *123*(3), 361–371.
490   https://doi.org/10.1016/j.biocon.2004.12.005

491   Cohen, J., Screen, J. A., Furtado, J. C., Barlow, M., Whittleston, D., Coumou, D., Francis, J.,
492   Dethloff, K., Entekhabi, D., Overland, J., & Jones, J. (2014). Recent Arctic amplification
493   and extreme mid-latitude weather. *Nature Geoscience*, *7*(9), 627–637.
494   https://doi.org/10.1038/ngeo2234

495   Criddle, R. S., Church, J. N., Smith, B. N., & Hansen, L. D. (2003). Fundamental causes of the
496   global patterns of species range and richness. *Russian Journal of Plant Physiology*, *50*(2),
497   192–199. https://doi.org/10.1023/a:1022969029867

498   Eitel, J. U. H. J. U. H., Maguire, A. J. A. J., Boelman, N., Vierling, L. A. L. A., Griffin, K. L. K.
499   L., Jensen, J., Magney, T. S. T. S., Mahoney, P. J. P. J., Meddens, A. J. H. A. J. H., Silva,
500   C., & Sonnentag, O. (2019). Proximal remote sensing of tree physiology at northern
501   treeline: Do late-season changes in the photochemical reflectance index (PRI) respond to
502   climate or photoperiod? *Remote Sensing of Environment*, *221*(October 2018), 340–350.
503   https://doi.org/10.1016/j.rse.2018.11.022

504   Gaston, K. J. (1996). Species-range-size distributions: Patterns, mechanisms and implications.
505   *Trends in Ecology & Evolution*, *11*(5), 197–201. https://doi.org/10.1016/0169-
506   5347(96)10027-6

507   Griffin, K. L., Tissue, D. T., Turnbull, M. H., Schuster, W., & Whitehead, D. (2001). Leaf dark
508   respiration as a function of canopy position in Nothofagus fusca trees grown at ambient and
509   elevated CO_2 partial pressures for 5 years. *Functional Ecology*, *15*(4), 497–505.
510   https://doi.org/10.1046/j.0269-8463.2001.00539.x

511   Griffin, K. L., Turnbull, M., & Murthy, R. (2002). Canopy position affects the temperature
512   response of leaf respiration in *Populus deltoides*. *New Phytologist*, *154*(3), 609–619.
513   https://doi.org/10.1046/j.1469-8137.2002.00410.x

514   Griffin, K.L., Schmiege, S.C., Bruner, S.G., Boelman, N.T., Vierling, L.A., Eitel J.U.H. (2021)
515   High Leaf Respiration Rates May Limit the Success of White Spruce Saplings growing in
516   The *Kampfzone* at The Arctic Treeline. *Frontiers in Plant Science – Plant Physiology*, in
517   review - bioRxiv 2021.08.10.455813; doi: https://doi.org/10.1101/2021.08.10.455813

518   Harris, I., Jones, P., Osborn, T. (2020) CRU TS4.04: Climatic Research Unit (CRU) Time-Series
519   (TS) Version 4.04 of High-resolution Gridded Data of Month-by-Month Variation in

520   Climate (Jan. 1901-Dec. 2019).In Unit UoEACR. East Anglia: Centre for Environmental
521   Data Analysis.

522 Heskel, M. A., Atkin, O. K., O'Sullivan, O. S., Reich, P., Tjoelker, M. G., Weerasinghe, L. K.,
523   Penillard, A., Egerton, J. J. G., Creek, D., Bloomfield, K. J., Xiang, J., Sinca, F., Stangl, Z.
524   R., Martinez-De La Torre, A., Griffin, K. L., Huntingford, C., Hurry, V., Meir, P., &
525   Turnbull, M. H. (2016). Empirical versus process-based approaches to modeling
526   temperature responses of leaf respiration. *Proceedings of the National Academy of Sciences*
527   *of the United States of America*, *113*(41), E5996–E5997.
528   https://doi.org/10.1073/pnas.1612904113

529 Heskel, M. A., Greaves, H. E., Turnbull, M. H., O'Sullivan, O. S., Shaver, G. R., Griffin, K. L.,
530   & Atkin, O. K. (2014). Thermal acclimation of shoot respiration in an Arctic woody plant
531   species subjected to 22 years of warming and altered nutrient supply. *Global Change*
532   *Biology*, *20*(8), 2618–2630. https://doi.org/10.1111/gcb.12544

533 Heskel, M. A., O'Sullivan, O. S., Reich, P. B., Tjoelker, M. G., Weerasinghe, L. K., Penillard,
534   A., Egerton, J. J. G., Creek, D., Bloomfield, K. J., Xiang, J., Sinca, F., Stangl, Z. R.,
535   Martinez-De La Torre, A., Griffin, K. L., Huntingford, C., Hurry, V., Meir, P., Turnbull, M.
536   H., & Atkin, O. K. (2016). Convergence in the temperature response of leaf respiration
537   across biomes and plant functional types. *Proceedings of the National Academy of Sciences*
538   *of the United States of America*, *113*(14), 3832–3837.
539   https://doi.org/10.1073/pnas.1520282113

540 Hijmans, R. J., & Graham, C. H. (2006). The ability of climate envelope models to predict the
541   effect of climate change on species distributions. *Global Change Biology*, *12*(12), 2272–
542   2281. https://doi.org/10.1111/j.1365-2486.2006.01256.x

543 Huang, J. B., Zhang, X. D., Zhang, Q. Y., Lin, Y. L., Hao, M. J., Luo, Y., Zhao, Z. C., Yao, Y.,
544   Chen, X., Wang, L., Nie, S. P., Yin, Y. Z., Xu, Y., & Zhang, J. S. (2017). Recently
545   amplified arctic warming has contributed to a continual global warming trend. *Nature*
546   *Climate Change*, *7*(12), 875–879. https://doi.org/10.1038/s41558-017-0009-5

547 Huntingford, C., Atkin, O. K., Martinez-De La Torre, A., Mercado, L. M., Heskel, M. A.,
548   Harper, A. B., Bloomfield, K. J., O'Sullivan, O. S., Reich, P. B., Wythers, K. R., Butler, E.
549   E., Chen, M., Griffin, K. L., Meir, P., Tjoelker, M. G., Turnbull, M. H., Sitch, S., Wiltshire,
550   A., & Malhi, Y. (2017). Implications of improved representations of plant respiration in a
551   changing climate. *Nature Communications*, *8*(1). https://doi.org/10.1038/s41467-017-
552   01774-z

553 Klikoff, L. G. (1966). Temperature dependence of the oxidative rates of mitochondria in
554   *Danthonia intermedia*, *Penstemon davidsonii* and *Sitanion hystrix*. *Nature*, *212*(5061), 529–
555   530.

556 Körner, C. (1989). The nutritional status of plants from high altitudes. *Oecologia*, *81*(3), 379–
557   391.

14

558 Kornfeld, A., Heskel, M., Atkin, O. K., Gough, L., Griffin, K. L., Horton, T. W., & Turnbull, M.
559   H. (2013). Respiratory flexibility and efficiency are affected by simulated global change in
560   Arctic plants. *New Phytologist*, *197*(4), 1161–1172. https://doi.org/10.1111/nph.12083

561 Kruckeberg, A. R., & Rabinowitz, D. (1985). BIOLOGICAL ASPECTS OF ENDEMISM IN
562   HIGHER-PLANTS. *Annual Review of Ecology and Systematics*, *16*, 447–479.
563   https://doi.org/10.1146/annurev.es.16.110185.002311

564 Kunin, W. E., & Gaston, K. J. (1993). The biology of rarity - patterns, causes and consequences.
565   *Trends in Ecology & Evolution*, *8*(8), 298–301. https://doi.org/10.1016/0169-
566   5347(93)90259-r

567 Lambers, H., & Oliveira, R. S. (2019). Plant physiological ecology. In *Plant Physiological*
568   *Ecology*. Springer US. https://doi.org/10.1007/978-3-030-29639-1

569 Lavergne, S., Thompson, J. D., Garnier, E., & Debussche, M. (2004). The biology and ecology
570   of narrow endemic and widespread plants: a comparative study of trait variation in 20
571   congeneric pairs. *Oikos*, *107*(3), 505–518. https://doi.org/10.1111/j.0030-
572   1299.2004.13423.x

573 Lowry, E., & Lester, S. E. (2006). The biogeography of plant reproduction: Potential
574   determinants of species' range sizes. *Journal of Biogeography*, *33*(11), 1975–1982.
575   https://doi.org/10.1111/j.1365-2699.2006.01562.x

576 Malanson, G. P., Westman, W. E., & Yan, Y. L. (1992). Realized versus fundamental niche
577   functions in a model of chaparral response to climatic-change. *Ecological Modelling*, *64*(4),
578   261–277. https://doi.org/10.1016/0304-3800(92)90026-b

579 Man, R. Z., & Lieffers, V. J. (1997). Seasonal photosynthetic responses to light and temperature
580   in white spruce (*Picea glauca*) seedlings planted under an aspen (*Populus tremuloides*)
581   canopy and in the open. *Tree Physiology*, *17*(7), 437–444.

582 Marion, G. M., Hastings, S. J., Oberbauer, S. F., & Oechel, W. C. (1989). Soil-plant element
583   relationships in a tundra ecosystem. *Ecography*, *12*(3), 296–303.
584   https://doi.org/10.1111/j.1600-0587.1989.tb00849.x

585 McNown, R. W., & Sullivan, P. F. (2013). Low photosynthesis of treeline white spruce is
586   associated with limited soil nitrogen availability in the Western Brooks Range, Alaska.
587   *Functional Ecology*, *27*(3), 672–683. https://doi.org/10.1111/1365-2435.12082

588 Miller, A. E., Schimel, J. P., Sickman, J. O., Skeen, K., Meixner, T., & Melack, J. M. (2009).
589   Seasonal variation in nitrogen uptake and turnover in two high-elevation soils:
590   mineralization responses are site-dependent. *Biogeochemistry*, *93*(3), 253–270.
591   https://doi.org/10.1007/s10533-009-9301-4

592 Miroslavov, E. A., & Kravkina, I. M. (1991). Comparative analysis of chloroplasts and
593   mitochondria in leaf chlorenchyma from mountain plants grown at different altitudes.
594   *Annals of Botany*, *68*(3), 195–200.

595 Nadelhoffer, K. J., Giblin, A. E., Shaver, G. R., & Laundre, J. A. (1991). Effects of temperature
596   and substrate quality on element mineralization in six arctic soils. *Ecology*, *72*(1), 242–253.

597 O'Sullivan, O. S., Heskel, M. A., Reich, P. B., Tjoelker, M. G., Weerasinghe, L. K., Penillard,
598   A., Zhu, L., Egerton, J. J. G., Bloomfield, K. J., Creek, D., Bahar, N. H. A., Griffin, K. L.,
599   Hurry, V., Meir, P., Turnbull, M. H., & Atkin, O. K. (2017). Thermal limits of leaf
600   metabolism across biomes. *Global Change Biology*, *23*(1), 209–223.
601   https://doi.org/10.1111/gcb.13477

602 O'Sullivan, O. S., Weerasinghe, K., Evans, J. R., Egerton, J. J. G., Tjoelker, M. G., & Atkin, O.
603   K. (2013). High-resolution temperature responses of leaf respiration in snow gum
604   (*Eucalyptus pauciflora*) reveal high-temperature limits to respiratory function. *Plant Cell*
605   *and Environment*, *36*(7), 1268–1284. https://doi.org/10.1111/pce.12057

606 Ow, L. F., Griffin, K. L., Whitehead, D., Walcroft, A. S., & Turnbull, M. H. (2008a). Thermal
607   acclimation of leaf respiration but not photosynthesis in *Populus deltoides* x nigra. *New*
608   *Phytologist*, *178*(1), 123–134. https://doi.org/10.1111/j.1469-8137.2007.02357.x

609 Ow, L. F., Whitehead, D., Walcroft, A. S., & Turnbull, M. H. (2008b). Thermal acclimation of
610   respiration but not photosynthesis in *Pinus radiata*. *Functional Plant Biology*, *35*(6), 448–
611   461. https://doi.org/10.1071/FP08104

612 Patterson, A. E., Arkebauer, R., Quallo, C., Heskel, M. A., Li, X. M., Boelman, N., & Griffin, K.
613   L. (2018). Temperature response of respiration and respiratory quotients of 16 co-occurring
614   temperate tree species. *Tree Physiology*, *38*(9), 1319–1332.

615 Pearson, R.G,, Phillips, S.J., Loranty, M.M,. Beck, P.S.A., Damoulas, T., Knight, S.J., Goetz,
616   S.J. (2013). Shifts in Arctic vegetation and associated feedbacks under climate change.
617   *Nature Climate Change*, 3, 673–677.

618 Prentice, I. C., Cramer, W., Harrison, S. P., Leemans, R., Monserud, R. A., & Solomon, A. M.
619   (1992). A global biome model based on plant physiology and dominance, soil properties
620   and climate. *Journal of Biogeography*, *19*(2), 117–134. https://doi.org/10.2307/2845499

621 Prud'Homme, G. O., Lamhamedi, M. S., Benomar, L., Rainville, A., DeBlois, J., Bousquet, J.,
622   Beaulieu, J., Prud'Homme, G. O., Lamhamedi, M. S., Benomar, L., Rainville, A., DeBlois,
623   J., Bousquet, J., & Beaulieu, J. (2018). Ecophysiology and growth of white spruce seedlings
624   from various seed sources along a climatic gradient support the need for assisted migration.
625   *Frontiers in Plant Science*, *8*(January), 1–17. https://doi.org/10.3389/fpls.2017.02214

626 Reich, P. B., & Oleksyn, J. (2004). Global patterns of plant leaf N and P in relation to
627   temperature and latitude. *Proceedings of the National Academy of Sciences of the United*
628   *States of America*, *101*(30), 11001–11006. https://doi.org/10.1073/pnas.0403588101

629 Rosbakh, S., Römermann, C., & Poschlod, P. (2015). Specific leaf area correlates with
630   temperature: new evidence of trait variation at the population, species and community
631   levels. *Alpine Botany*, *125*(2), 79–86. https://doi.org/10.1007/s00035-015-0150-6

632   Schimel, J. P., & Bennett, J. (2004). Nitrogen mineralization: Challenges of a changing
633   paradigm. *Ecology*, *85*(3), 591–602.

634   Schimel, J. P., Bilbrough, C., & Welker, J. A. (2004). Increased snow depth affects microbial
635   activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biology &*
636   *Biochemistry*, *36*(2), 217–227. https://doi.org/10.1016/j.soilbio.2003.09.008

637   Schimel, J. P., Chapin, F. S., & Stuart Chapin, F. (1996). Tundra plant uptake of amino acid and
638   NH_4^+ nitrogen in situ: Plants compete well for amino acid N. *Ecology*, *77*(7), 2142–2147.
639   https://doi.org/10.2307/2265708

640   Schmiege, S. C., Buckley, B. M., Stevenson, D. W., Heskel, M. A., Cuong, T. Q., Nam, L., &
641   Griffin, K. L. (2021). Respiratory temperature responses of tropical conifers differ with leaf
642   morphology. *Functional Ecology*. https://doi.org/10.1111/1365-2435.13814

643   Schneider, C. A., Rasband, W. S., & Eliceiri, K. W. (2012). NIH Image to ImageJ: 25 years of
644   image analysis. *Nature Methods*, *9*(7), 671–675. https://doi.org/10.1038/nmeth.2089

645   Schuster, W. S. F., Griffin, K. L., Roth, H., Turnbull, M. H., Whitehead, D., & Tissue, D. T.
646   (2008). Changes in composition, structure and aboveground biomass over seventy-six years
647   (1930-2006) in the Black Rock Forest, Hudson Highlands, southeastern New York State.
648   *Tree Physiology*, *28*(4). https://doi.org/10.1093/treephys/28.4.537

649   Slot, M., & Kitajima, K. (2015). General patterns of acclimation of leaf respiration to elevated
650   temperatures across biomes and plant types. *Oecologia*, *177*(3), 885–900.
651   https://doi.org/10.1007/s00442-014-3159-4

652   Stebbins, G. L. (1942). The genetic approach to problems of rare and endemic species. *Madrono*,
653   *6*(8), 241–258.

654   Stinziano, J. R., & Way, D. A. (2017). Autumn photosynthetic decline and growth cessation in
655   seedlings of white spruce are decoupled under warming and photoperiod manipulations.
656   *Plant Cell and Environment*, *40*(8), 1296–1316. https://doi.org/10.1111/pce.12917

657   Sutton, R. F. (1969). *The Silvics of White Spruce (Picea glauca (Moench) Voss)* (Vol. 1250).
658   Forest Research Division, Forestry Branch, Canada.

659   Tamarin-Brodsky, T., Hodges, K., Hoskins, B. J., & Shepherd, T. G. (2020). Changes in
660   Northern Hemisphere temperature variability shaped by regional warming patterns. *Nature*
661   *Geoscience*, *13*(6), 414–421.

662   Tissue, D. T., Lewis, J. D., Wullschleger, S. D., Amthor, J. S., Griffin, K. L., & Anderson, O. R.
663   (2002). Leaf respiration at different canopy positions in sweetgum (*Liquidambar*
664   *styraciflua*) grown in ambient and elevated concentrations of carbon dioxide in the field.
665   *Tree Physiology*, *22*(15–16), 1157–1166. https://doi.org/10.1093/treephys/22.15-16.1157

666   US Federal Government. (2021). U.S. Climate Resilience Toolkit Climate Explorer. [Online]
667   https://crt-climate-explorer.nemac.org/ Accessed August 2021.

668   US Geological Survey. (1999). *Digital representation of "Atlas of United States Trees" by*
669   *Elbert L. Little Jr.* US Geological Survey Professional Paper 1650.

670   Valentini, R., Matteucci, G., Dolman, A. J., Schulze, E. D., Rebmann, C., Moors, E. J., Granier,
671   A., Gross, P., Jensen, N. O., Pilegaard, K., Lindroth, A., Grelle, A., Bernhofer, C.,
672   Grunwald, T., Aubinet, M., Ceulemans, R., Kowalski, A. S., Vesala, T., Rannik, U., …
673   Jarvis, P. G. (2000). Respiration as the main determinant of carbon balance in European
674   forests. *Nature*, *404*(6780), 861–865. https://doi.org/10.1038/35009084

675   Vanderwel, M. C., Slot, M., Lichstein, J. W., Reich, P. B., Kattge, J., Atkin, O. K., Bloomfield,
676   K. J., Tjoelker, M. G., & Kitajima, K. (2015). Global convergence in leaf respiration from
677   estimates of thermal acclimation across time and space. *New Phytologist*, *207*(4), 1026–
678   1037. https://doi.org/10.1111/nph.13417

679   Walcroft, A. S., Brown, K. J., Schuster, W. S. F., Tissue, D. T., Turnbull, M. H., Griffin, K. L.,
680   & Whitehead, D. (2005). Radiative transfer and carbon assimilation in relation to canopy
681   architecture, foliage area distribution and clumping in a mature temperate rainforest canopy
682   in New Zealand. *Agricultural and Forest Meteorology*, *135*(1–4), 326–339.
683   https://doi.org/10.1016/j.agrformet.2005.12.010

684   Watson, H. C. (1833). Observations on the affinities between plants and subjacent rocks.
685   *Magazine of Natural History*, *6*, 424–427.

686   Weger, H. G., & Guy, R. D. (1991). Cytochrome and alternative pathway respiration in white
687   spruce (Picea glauca) roots - effects of growth and measurement temperature. *Physiologia*
688   *Plantarum*, *83*(4), 675–681.

689   Whitehead, D., Griffin, K. L., Turnbull, M. H., Tissue, D. T., Engel, V. C., Brown, K. J.,
690   Schuster, W. S. F., & Walcroft, A. S. (2004). Response of total night-time respiration to
691   differences in total daily photosynthesis for leaves in a *Quercus rubra* L. canopy:
692   Implications for modelling canopy CO_2 exchange. *Global Change Biology*, *10*(6), 925–938.
693   https://doi.org/10.1111/j.1529-8817.2003.00739.x

694   Whitehead, D., Leathwick, J. R., & Walcroft, A. S. (2001). Modeling annual carbon uptake for
695   the indigenous forests of New Zealand. *Forest Science*, *47*(1), 9–20.
696   https://doi.org/10.1093/forestscience/47.1.9

697   Whitehead, D., Walcroft, A. S., Griffin, K. L., Tissue, D. T., Turnbull, M. H., Engel, V., Brown,
698   K. J., & Schuster, W. S. F. (2004). Scaling carbon uptake from leaves to canopies: Insights
699   from two forests with contrasting properties. In *Forests at the land-atmosphere interface*
700   (pp. 231–254).

701   Yano, Y., Shaver, G. R., Giblin, A. E., Rastetter, E. B., & Nadelhoffer, K. J. (2010). Nitrogen
702   dynamics in a small arctic watershed: Retention and downhill movement of [15]N. *Ecological*
703   *Monographs*, *80*(2), 331–351. https://doi.org/10.1890/08-0773.1

704   Yin, X. (1993). Variation in foliar nitrogen concentration by forest type and climatic gradients in
705   North America. *Canadian Journal of Forest Research*, *23*(8), 1587–1602.

706   Zepner, L., Karrasch, P., Wiemann, F., Bernard, L. (2021) ClimateCharts.net - an interactive
707   climate analysis web platform. *International Journal of Digital Earth* **14**(3): 338-356.

708   Zhang, W., Miller, P.A., Smith, B., Wania, R., Koenigk, T., Döscher, R. (2013). Tundra
709   shrubification and tree-line advance amplify arctic climate warming: results from an
710   individual-based dynamic vegetation model. *Environ Res Lett*. 8, 034023.
711
712

713   **Tables**
714
715   **Table 1.** Top of canopy leaf and bottom of canopy leaf characteristics of *Picea glauca* trees
716   growing at either the south-eastern edge of the species range limit in Black Rock Forest, NY
717   USA, or at the northern edge at the Forest Tundra Ecotone (FTE) in northcentral Alaska, USA.
718   DBH = diameter at breast height (1.37m), SLA = specific leaf area, LDMC = leaf dry matter
719   content (g dry mass g-1 fresh mash, LWC = leaf water content and N = leaf nitrogen %. * Leaf
720   nitrogen data collected from the same trees in 2017, (Schmiege et al. *pers com*). Lowercase
721   letters following the canopy position means (within a site) and uppercase letters following the
722   location means (across the canopy positions) denote statistically significant differences (p<0.05).
723   n = 6-47, all values mean±1 standard error.
724

	DBH cm	Height m	SLA $cm^2\ g^{-1}$	LDMC	LWC %	N^* %
BRF	23.1 ± 1.99 **B**	9.9 ± 0.73 **A**	61.34±4.53 **B**	368.93±6.79 **A**	63.1±0.78 **B**	1.10 ± 0.04 **B**
Upper Canopy	-	-	53.19±4.43 **a**	375.99±5.27 **a**	62.4±0.53 **a**	1.11 ± 0.03 **b**
Lower Canopy	-	-	69.50±6.62 **b**	361.87±12.45 **a**	63.8±1.25 **a**	1.10 ± 0.08 b
FTE	16.6±0.68 **A**	9.36±0.41 **A**	44.90±1.46 **A**	540.03±3.15 **B**	46.0±0.32 **A**	0.88 ± 0.10 **A**
Upper Canopy	-	-	44.15±3.51 **a**	542.19±4.55 **a**	45.8±0.46 **a**	0.79 ± 0.11 **a**
Lower Canopy	-	-	45.64±1.46 **a**	537.99±4.44 **a**	46.2±0.44 **a**	0.96 ± 0.06 **a**
All Trees	*18.31±1.02*	*9.47±0.46*	*53.12±1.88*	*496.34±11.37*	*50.4±1.14*	*0.99 ± 0.05*

725
726
727
728
729   **Table 2.** Model parameters fit to the measured high-resolution leaf respiration temperature
730   response curves collected from either the top of canopy leaves or bottom of canopy leaves of
731   *Picea glauca* trees growing at either the southern edge of the species range limit in Black Rock
732   Forest, NY USA, or the northern edge of the species range limit in the Forest Tundra Ecotone
733   (FTE) in northcentral AK, USA. Lowercase letters following the canopy position means and
734   uppercase letters following the location means denote statistically significant differences
735   (p<0.05). n = 6-47, all values mean±1 standard error.
736

|	a	b	c
BRF	-2.48±0.56 **B**	0.094±0.009 **A**	-0.00034±0.0001 **A**
Upper Canopy	-2.166±0.105 **a**	0.084±0.006 **a**	-0.00014±0.0001 **a**
Lower Canopy	-2.829±0.371 **b**	0.104±0.017 **a**	-0.00053±0.0003 **a**
FTE	-1.15±0.09 **A**	0.086±0.003 **A**	-0.00027±0.0001 **A**
Upper Canopy	-1.20±0.29 **a**	0.087±0.004 **a**	-0.00028±0.0001 **a**
Lower Canopy	-1.10±0.27 **a**	0.084±0.005 **a**	-0.00026±0.0003 **a**
All Trees	*1.82±0.12*	*0.090±0.003*	*-0.00030±0.0001*

737

738

Figure 1. Species range distribution for *Picea glauca.* The southern range limit site, Black Rock Forest, Cornwall NY, is marked with the red star. The arctic treeline site in northern Alaska is marked with a yellow star. Map from U.S. Geological Survey, Department of the Interior/USGS based on original data from Little (1999).

743
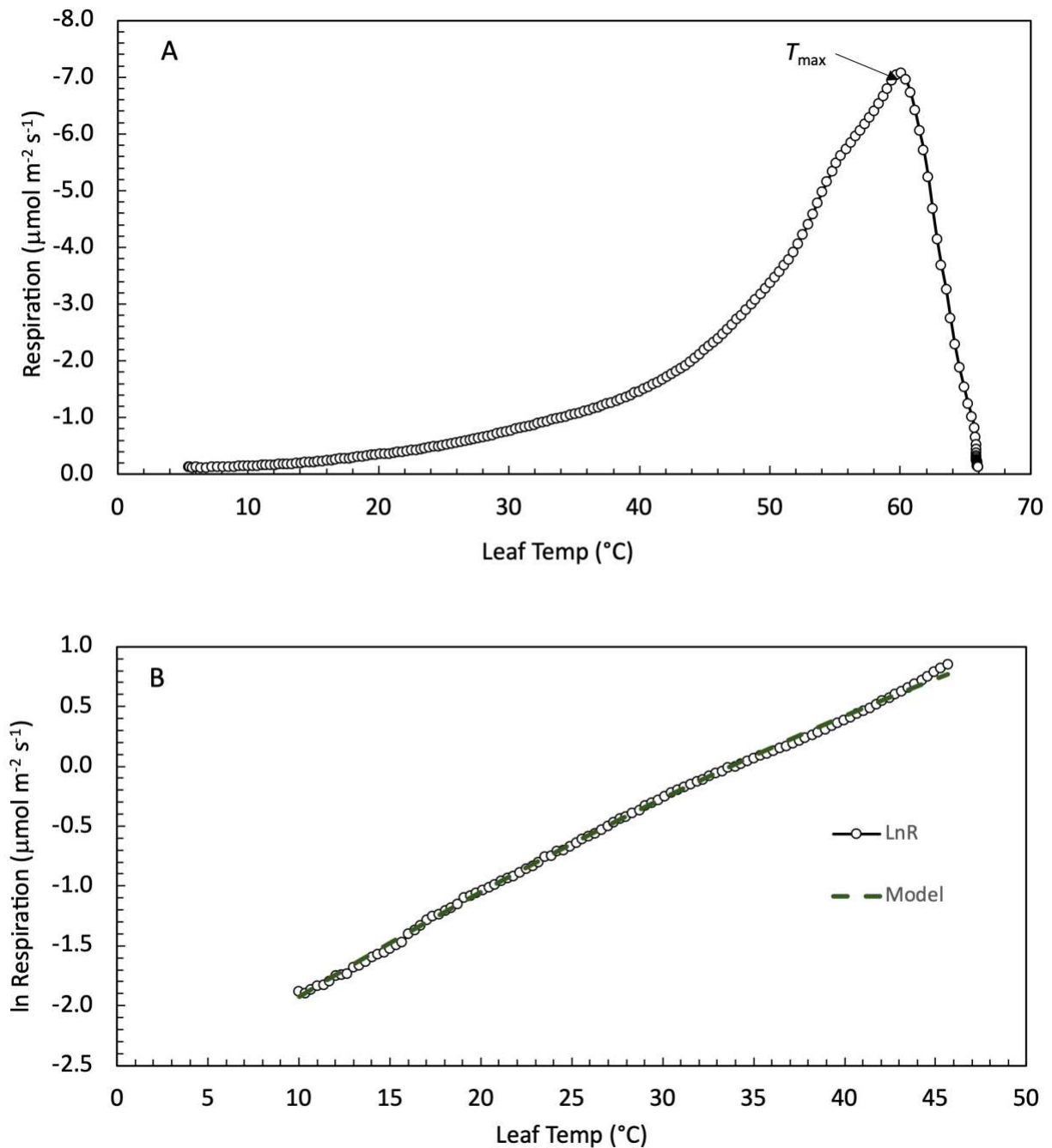
Figure 2. Leaf respiration as a function of temperature in *Picea glauca* measured at the southern end of the species distribution in Black Rock Forest, Cornwall, NY USA. Panel A (top) is an example high-resolution temperature response curve measured from 5 to 65°C. Air temperature was heated at a rate of 1°C min^{-1} while the rate of CO_2 release and other gas-exchange parameters were recorded every 20 seconds. Panel B (bottom) is the log of measured respiration rate and model fit ($lnR = a + bT + cT^2$ – see text for full description) between 10 and 45 °C for the same sample.
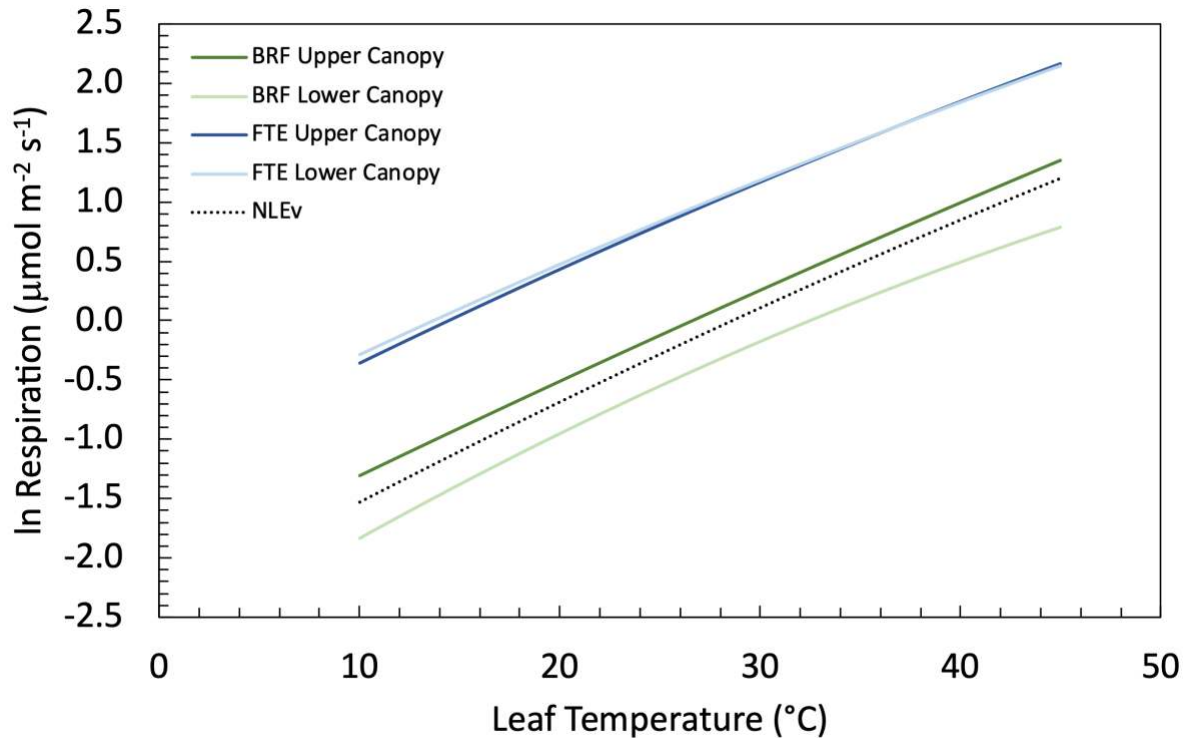
Figure 3. Average model results (log of leaf respiration) for the bottom of canopy (light green and blue lines) and top of the canopy (dark green and blue lines), of *Picea glauca* trees growing at either the south-eastern edge of the species range (green lines) in Black Rock Forest, NY USA, or the northern edge of the species range limit (blue lines) in the Forest Tundra Ecotone (FTE) in northcentral AK, USA. Line presents the mean response (n=6 (BRF) or 18(FTE) and shaded area = 95% confidence interval for each canopy position. Also shown is the average response for Needle-Leaved Evergreen species (NLEv) from the global survey of Heskel et al (2016) (black dotted line). Model parameters are presented in table 2.
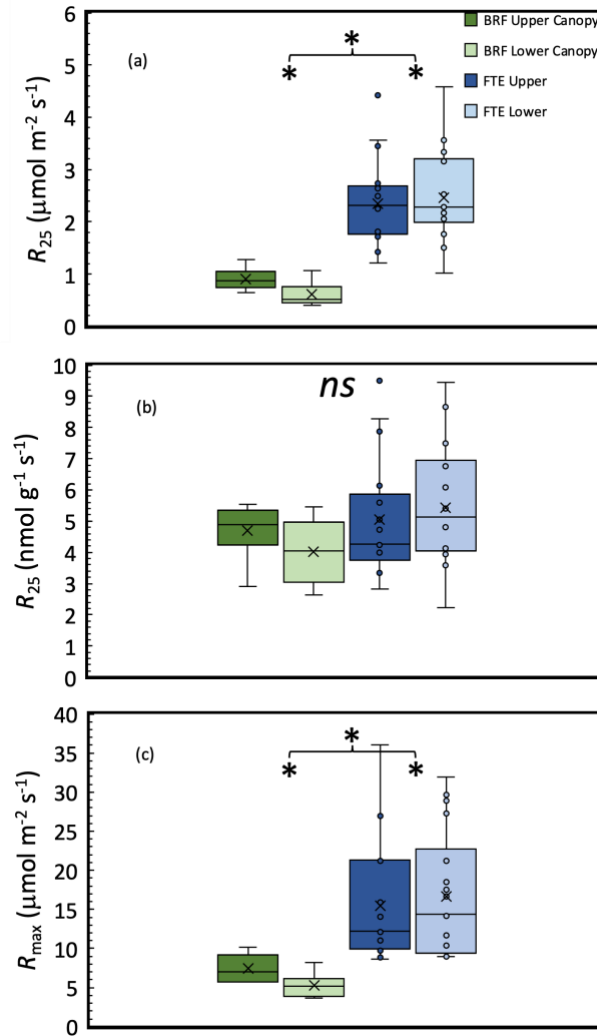
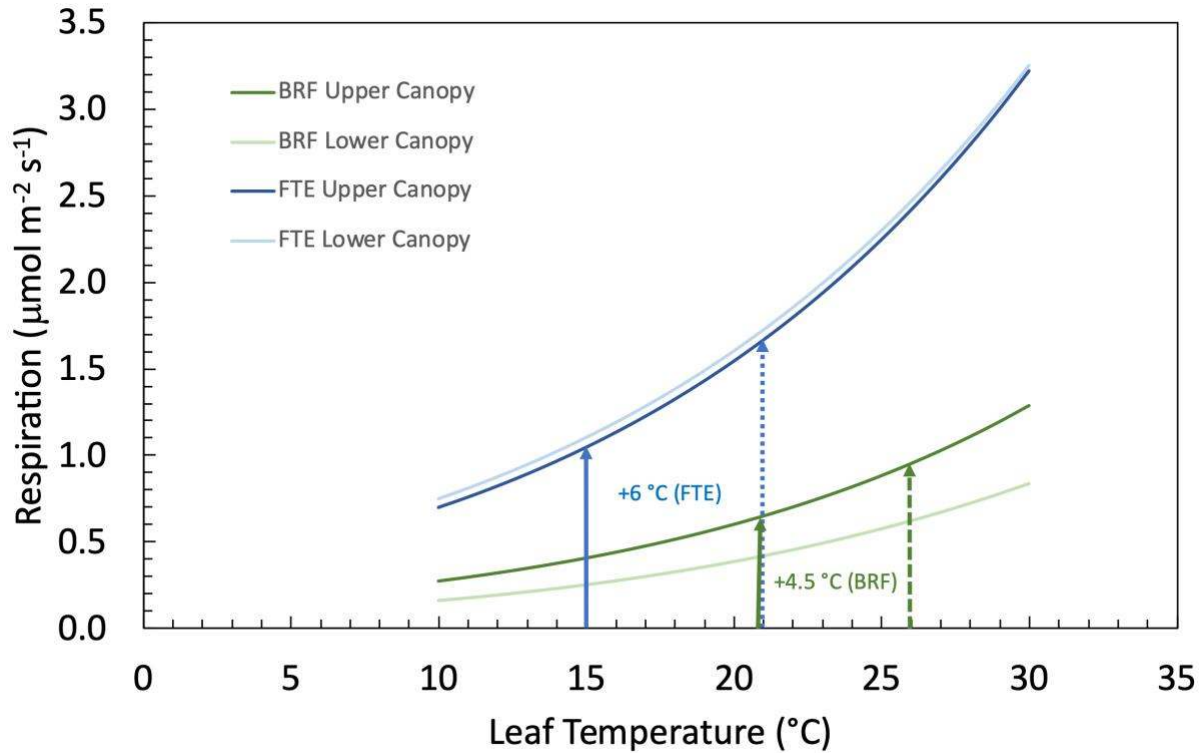**Figure 4**. Respiration of White Spruce (*Picea glauca*) foliage measured from the upper (dark green) or lower (light green) canopy in the southern location (Black Rock Forest, NY USA), and the upper (dark blue) or lower (light blue) canopy from the northern location (Forest Tundra Ecotone, AK USA). Respiration was measured at a leaf temperature of 25°C either on a projected leaf area basis (panel a, top), leaf mass basis (panel b, center) as well as the maximum rate of respiration from a temperature response curve, expressed on a leaf area basis (panel c, bottom). The middle line of the box represents the median, the x represents the mean. The box is drawn between the first and third quartiles and the whiskers extend to the minimum and maximum values. * = statistical significance ($p < 0.05$, panels a and c). *ns* = not significant (panel b). n = 6 (BRF) – 18 (FTE)

24

Figure 5. Modeled rates of White Spruce (_Picea glauca_) foliage respiration vs. leaf temperature from two canopy positions at either the northern or southern range limits of the species. Lines display the average modeled response from the upper (dark green) or lower (light green) canopy from the southern location (Black Rock Forest, NY USA, n= 6), and the upper (dark blue) or lower (light blue) canopy from the northern location (Forest Tundra Ecotone, AK USA, n = 18). Vertical arrows represent the average June, July, August temperatures from each of the field sites (solid blue = FTE, solid green = BRF) and the projected end of century increases (dashed blue = FTE projection, dashed green = BRF projections, see text for more information).