

## Variation in white spruce needle respiration across the species range

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## 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 enigmas. Working 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*<sub>25</sub>) 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

## 43 Introduction

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

59 Physiological processes such as photosynthesis, respiration and growth all respond strongly to  
60 local environmental conditions. Together these processes constrain plant carbon balance and thus  
61 contribute to a species distribution range (part of the physiological filter of Lambers & Oliveira,  
62 2019). Here we concentrate on leaf respiration. This flux is less well studied than photosynthesis,  
63 provides a crucial link between photosynthesis (carbon gain) and growth (carbon sequestration)  
64 and has been hypothesized to control the range distribution of individual species (Criddle et al.,  
65 2003). Furthermore, respiration is highly temperature sensitive, making it an important  
66 determinant of ecosystem productivity (Valentini et al., 2000). *GlobResp*, a global database of  
67 plant respiratory characteristics, identifies latitudinal gradients in leaf respiration measured at a  
68 common temperature that increase with absolute latitude. These findings suggest that species  
69 with a large range should exhibit variable rates of respiration across their distribution, although  
70 this hypothesis has not been explicitly tested (Atkin et al., 2015). Furthermore, Patterson et al.  
71 (2018) quantified respiratory rates and responses to temperature in 16 tree species growing in a  
72 common location, grouping them by their relative location within their individual species  
73 distributions. The results show that northern ranged species growing near their southern range  
74 limit had 71% higher respiration rates (measured at 20°C) than southern ranged species growing  
75 near the northern edge of their range limits. Quantifying respiratory characteristics of individuals  
76 growing near the margins of their species range distributions can thus elucidate physiological  
77 controls of the current distribution.

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

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 Heskell 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.

## 127 **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<sub>2</sub> 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 Heskell 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<sup>-1</sup> and the CO<sub>2</sub>

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<sup>-1</sup>.

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<sup>2</sup> g<sup>-1</sup>) 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<sup>-1</sup>) 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 Heskell et al.  
191 (2016) by fitting a second-order polynomial model to the log transformed respiration rates  
192 between 10 and 45 °C.

$$\ln R = a + bT + cT^2 \quad (\text{Equ. 1})$$

193  
194  
195  
196 Where *a* represents the basal respiration rate (y-intercept), while *b* and *c* describe the slope and  
197 curvature of the response (Heskell et al. 2016). The respiration rate at a common temperature of  
198 25°C (*R*<sub>25</sub>) was also calculated and the temperature where the maximum respiration rate was  
199 reached (*T*<sub>max</sub>) 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 *justification 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 Heskell *et al.*, (2016)  
205 using R 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*<sub>25</sub>. All traits were transformed as necessary to fulfill  
210 assumptions of normality. To test our third hypothesis, we compared our model estimates with  
211 those of Heskell *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 *T*<sub>max</sub> 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 ( $23.1 \pm 1.99$  vs.  $16.6 \pm 0.68$  cm), but similar in height ( $9.9 \pm 0.73$  vs.  $9.36 \pm 0.41$  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 Heskell  
235 et 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  $-1.82 \pm 0.12$ ,  $0.090 \pm 0.003$  and  $-0.00030 \pm 0.0001$  ( $a$ ,  $b$  and  $c$   
237 respectively, mean  $\pm$  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, Heskell 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  $0.75 \pm 0.08$   $\mu\text{mol CO}_2 \text{ m}^{-2}$  leaf  
251 area  $\text{s}^{-1}$ , which is 68% lower than the average rate at the northern location ( $2.35 \pm 0.88$   $\mu\text{mol CO}_2$   
252  $\text{m}^{-2}$  leaf area  $\text{s}^{-1}$ ). 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  $\pm 0.09$   $\mu\text{mol m}^{-2} \text{ s}^{-1}$  vs.  $0.61 \pm 0.10$   $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) 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  $58.5 \pm 0.5$  °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 ( $57.6 \pm 0.36$  °C). However, the maximum rate of respiration ( $R_{\max}$ ) of the upper canopy southern  
261 location leaves at  $T_{\max}$  ( $7.43 \pm 0.78$   $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ) was 40% higher than the  $R_{\max}$  of the lower  
262 canopy leaves ( $5.29 \pm 0.66$   $\mu\text{mol m}^{-2} \text{ s}^{-1}$ ), and the southern location average  $R_{\max}$  was 59% lower  
263 than the northern location average, a difference of more than  $9.3$   $\mu\text{mol CO}_2 \text{ m}^{-2}$  leaf area  $\text{s}^{-1}$   
264 (Figure 4c). None of the major respiratory parameters ( $R_{25}$ ,  $a$  or  $R_{\max}$ ) was significantly related to  
265 leaf N ( $\text{mg N m}^{-2}$ ) ( $p > 0.05$ , data not shown), although the trend was always for increasing rates

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 al.*,  
283 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 al.*,  
311 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 adaptive  
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 Heskell 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.

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443

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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<sup>-1</sup> 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.

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

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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

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

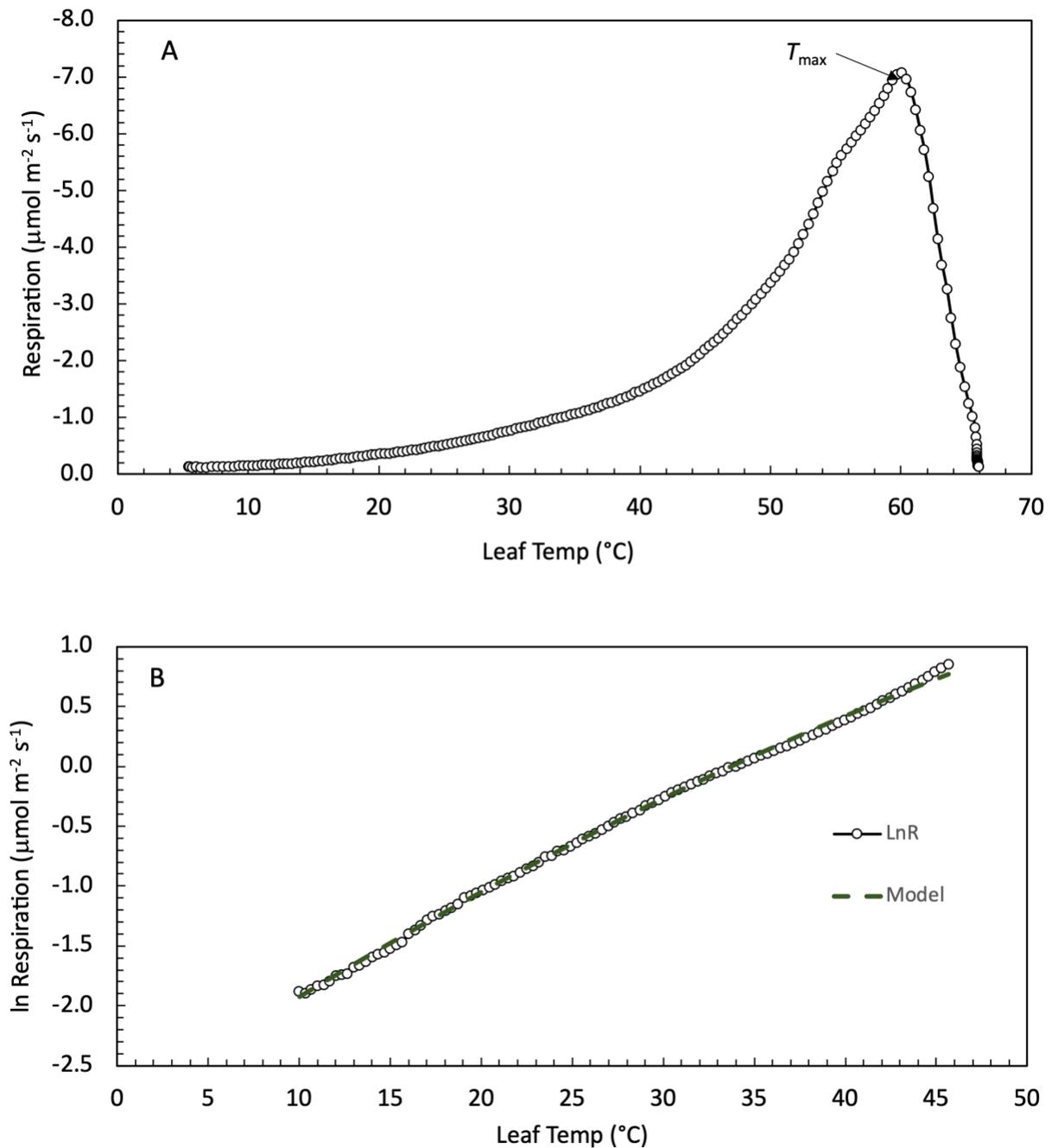
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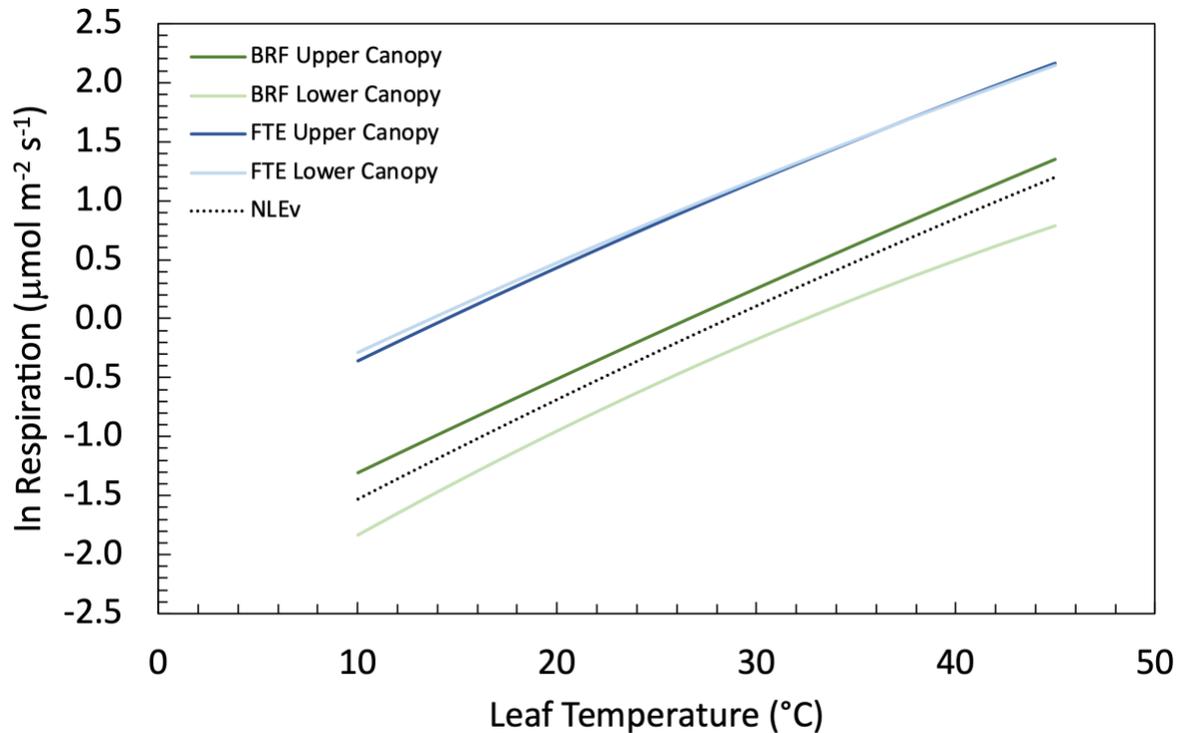
739 **Figure 1.** Species range distribution for *Picea glauca*. The southern range limit site, Black Rock  
740 Forest, Cornwall NY, is marked with the red star. The arctic treeline site in northern Alaska is  
741 marked with a yellow star. Map from U.S. Geological Survey, Department of the Interior/USGS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

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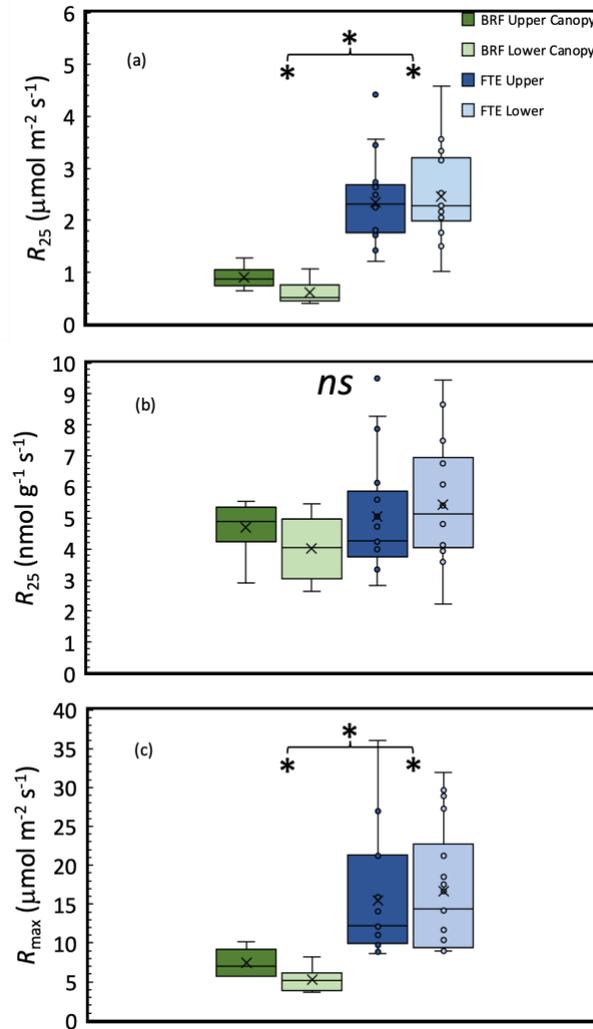
745 **Figure 2.** Leaf respiration as a function of temperature in *Picea glauca* measured at the southern  
746 end of the species distribution in Black Rock Forest, Cornwall, NY USA. Panel A (top) is an  
747 example high-resolution temperature response curve measured from 5 to 65°C. Air temperature  
748 was heated at a rate of  $1^{\circ}\text{C min}^{-1}$  while the rate of  $\text{CO}_2$  release and other gas-exchange parameters  
749 were recorded every 20 seconds. Panel B (bottom) is the log of measured respiration rate and  
750 model fit ( $\ln R = a + bT + cT^2$  – see text for full description) between 10 and 45  $^{\circ}\text{C}$  for the same  
751 sample.



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753 **Figure 3.** Average model results (log of leaf respiration) for the bottom of canopy (light green  
754 and blue lines) and top of the canopy (dark green and blue lines), of *Picea glauca* trees growing  
755 at either the south-eastern edge of the species range (green lines) in Black Rock Forest, NY  
756 USA, or the northern edge of the species range limit (blue lines) in the Forest Tundra Ecotone  
757 (FTE) in northcentral AK, USA. Line presents the mean response (n=6 (BRF) or 18(FTE) and  
758 shaded area = 95% confidence interval for each canopy position. Also shown is the average  
759 response for Needle-Leaved Evergreen species (NLEv) from the global survey of Heskell et al  
760 (2016) (black dotted line). Model parameters are presented in table 2.

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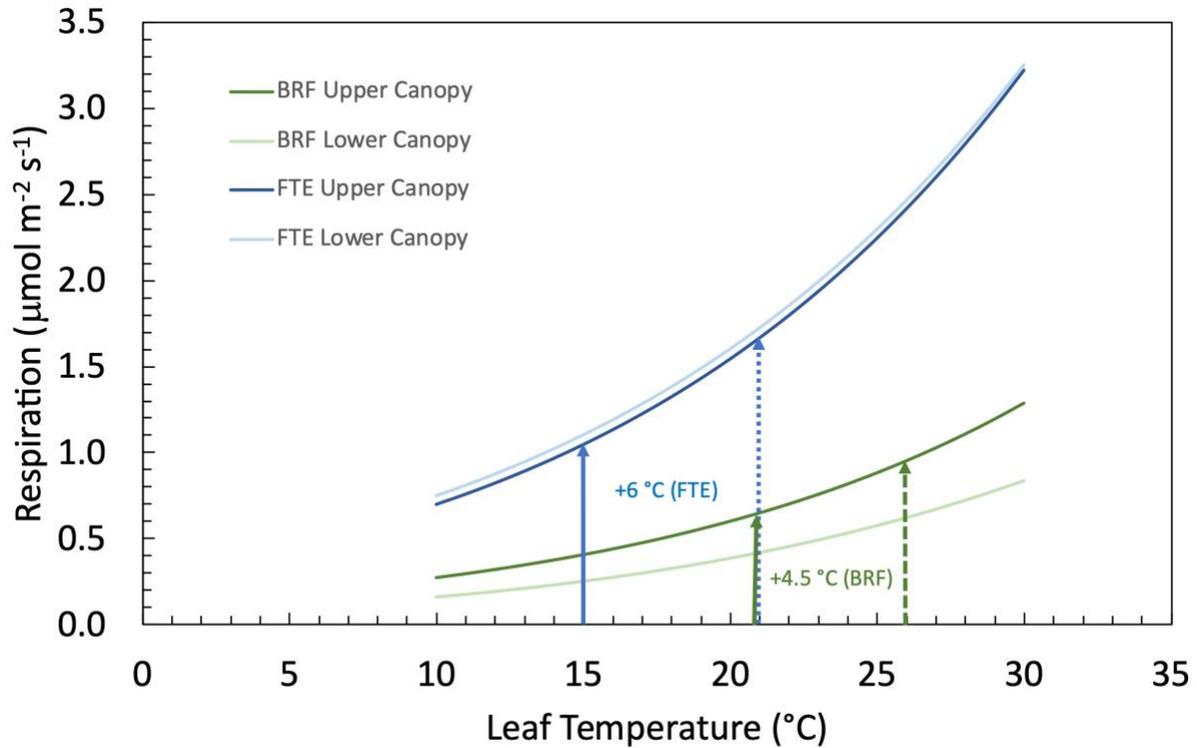


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763 **Figure 4.** Respiration of White Spruce (*Picea glauca*) foliage measured from the upper (dark  
764 green) or lower (light green) canopy in the southern location (Black Rock Forest, NY USA), and  
765 the upper (dark blue) or lower (light blue) canopy from the northern location (Forest Tundra  
766 Ecotone, AK USA). Respiration was measured at a leaf temperature of 25°C either on a  
767 projected leaf area basis (panel a, top), leaf mass basis (panel b, center) as well as the maximum  
768 rate of respiration from a temperature response curve, expressed on a leaf area basis (panel c,  
769 bottom). The middle line of the box represents the median, the x represents the mean. The box is  
770 drawn between the first and third quartiles and the whiskers extend to the minimum and  
771 maximum values. \* = statistical significance ( $p < 0.05$ , panels a and c). ns = not significant (panel  
772 b). n = 6 (BRF) – 18 (FTE)

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