

1 Title: Response of dark respiration to temperature in *Eriophorum vaginatum* from a 30 year old
2 transplant experiment in Alaska

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15 **Abstract**

16 Background: In the Arctic region, temperature increases are expected to be greater under
17 anticipated climate change than the global average. Understanding how dark respiration (R_d) of
18 common Arctic plant species acclimates to changes in the environment is therefore important for
19 predicting changes to the Arctic carbon balance.

20 Aims: To investigate the influence of genotype and growing environment on R_d , the temperature
21 response (Q_{10}) of R_d , and foliar N (N_{leaf}) of the Arctic sedge *Eriophorum vaginatum*.

22 Method: We measured R_d , its Q_{10} and N_{leaf} of *E. vaginatum* populations that were reciprocally
23 transplanted 30 years previously along a latitudinal transect of 370 km in northern Alaska.

24 Results: R_d and Q_{10} did not differ among populations (ecotypes) of *E. vaginatum*, but the local
25 environment had a significant effect on both variables. R_d as well as N_{leaf} was higher in northern,
26 colder sites, while Q_{10} was lower there.

27 Conclusions: R_d in the different populations of *E. vaginatum* is a very plastic trait and controlled
28 by growing environment, as is N_{leaf} . The lower Q_{10} values in the northern sites were most likely a
29 consequence of substrate inhibition of R_d at higher temperatures.

30 Keywords: Q_{10} , common garden experiment, leaf respiration, *Eriophorum vaginatum*, Arctic leaf
31 nitrogen, reciprocal transplant

32

33 **Introduction**

34 Autotrophic respiration is a key component of the carbon budget of an ecosystem, contributing
35 30-65% of the total CO₂ released into the atmosphere (e.g. Janssen et al 2001; Luo et al. 2007). It
36 is also widely acknowledged that understanding the long-term acclimation of autotrophic
37 respiration is important in light of the anticipated global increase in temperature (e.g. Atkin and
38 Tjoelker 2003; Luo et al. 2007; Atkin et al. 2008). Especially in the Arctic, temperature increases
39 are expected to be greater than the global average (Solomon et al. 2007). Observations have
40 already shown Arctic-wide warming trends since 1958 (0.11°C per decade (Kaufman et al.
41 2009), while Chapin et al. (2005) found that summer warming in arctic Alaska and western
42 Canada accelerated to about 0.3° to 0.4°C per decade between 1961–2004. Currently, the Arctic
43 acts as a modest carbon sink (McGuire et al 2009), but with changing temperatures it is
44 important to understand how climate change can affect different components of carbon fluxes,
45 such as autotrophic respiration.

46
47 Previous studies have shown that plant respiration acclimates to altered growth temperatures. For
48 example, when measured at the same temperature, plants that have acclimated to lower growing
49 temperatures had a higher foliar dark respiration (R_d) and a higher short-term temperature
50 responsiveness of R_d compared with plants that were acclimated to higher growing temperatures
51 (e.g. Strain and Chase 1966; Bolstad et al. 2003; Loveys et al. 2003; Bruhn et al. 2007; Campbell
52 et al. 2007; Tjoelker et al. 2008). The short-term temperature responsiveness of R_d can be
53 expressed by using Q_{10} , which represents the factor of change of R_d per 10 °C increase in
54 temperature, usually measured between 10°C and 20°C. Atkin and Tjoelker (2003) described
55 two different kinds of temperature acclimation of plant respiration: (1) altered temperature

56 sensitivity (i.e. a change in Q_{10}), and (2) a shift up or down in the overall temperature response
57 curve (with no change in Q_{10} , but with a change in the intercept of the response curve). The latter
58 form of acclimation is likely to be more common in newly developed tissue, while the former
59 occurs at a shorter time scale, in tissue that is already fully developed (e.g. Atkin et al. 2000; Ow
60 et al. 2008). Long-term cold acclimation is also often accompanied by an increase in leaf
61 nitrogen (N_{leaf}) (e.g. Tjoelker et al. 1999; Lee et al. 2005; Tjoelker 2008), which is associated
62 with increased investment in glycolytic and mitochondrial proteins. With more of these proteins,
63 higher R_d rates at the same temperature are possible and consequently cold acclimation of R_d in
64 the long-term (Atkin et al. 2005; Tjoelker et al. 2008).

65

66 One drawback of many studies of acclimation of respiration to temperature has been that the
67 acclimation period at a lower or higher temperature has often encompassed periods ranging from
68 one week or one growing season, which might not be a suitable time scale for studying effects of
69 climate change. In this study, we present results from a 30-year-old reciprocal transplant
70 experiment. In August 1980 and 1982, Shaver et al. (1986) established a latitudinal transect with
71 six common gardens along the Dalton Highway in Alaska, in which whole tussocks of the sedge
72 *Eriophorum vaginatum* L. were reciprocally transplanted over a distance of 370 km. Each of the
73 gardens was located more than 200 m from the road in order to avoid artefacts of the road traffic
74 (e.g., dust deposition). Each common garden included locally transplanted tussocks as well as
75 tussocks that originated from the other garden sites. *E. vaginatum* is one of the most common
76 and abundant species in northern Alaska (Britton 1966). It is a clonal species and individual
77 tillers typically live less than 8 years (Fetcher and Shaver 1983; Mark et al. 1985), meaning that
78 the entire biomass of the transplanted plants had been replaced at least 4 times before we

79 sampled them. The common gardens in the transect, which spans 3.30 degrees in latitude (~ 370
80 km), provided a unique opportunity to study the long-term acclimation of foliar respiration of
81 plants from one location. In addition, they allowed us to determine whether different populations
82 (ecotypes) of the same species had different physiological responses to changes in the growing
83 environment. For the populations in the transect, differences in morphology and growth between
84 ecotypes have been established previously (Shaver et al. 1986; Fetcher and Shaver 1990).
85 Bennington et al. (2012) showed that tussocks that were retransplanted into their sites of origin
86 had higher survival than tussocks from elsewhere on the transect, thus demonstrating home-site
87 advantage. Likewise, we were interested whether differences in R_d rates between ‘home and
88 away’ populations could be detected after 30 years of growth in the different sites. Additionally,
89 we wanted to investigate if observed differences in rates or the temperature response of R_d were
90 related to any changes in the values of N_{leaf} . The hypotheses tested in this study were: (1) There
91 is no difference within a site amongst the transplanted tussocks (local vs. non-local origin) in
92 their R_d rates, N_{leaf} , or Q_{10} values (i.e. there is no ecotypic variation). (2) Between sites
93 (gardens), the R_d values at a standardised temperature are higher at the northern sites that have
94 lower average temperatures. (3) The leaves from the colder, more northern sites have higher N_{leaf}
95 values. (4) The Q_{10} values remain identical between sites, though the intercept of the temperature
96 response curve differs).

97

98 **Material and methods**

99 Four of the six gardens described in Shaver et al. (1986) (No Name Creek, Coldfoot, Toolik
100 Lake, and Sagwon) were visited between 16 and 23 July 2011 (Table 1). Two of these gardens
101 are situated south of the Brooks Range (No Name Creek and Coldfoot), while the other two

102 (Toolik and Sagwon) are north of the Brooks Range. For 2011, the most northerly site (Sagwon)
103 and the most southerly site (No Name creek) differed over 5 °C in average annual temperature
104 (Table 1), and even more in the months leading up to the measurements (May-July 2011, Table
105 1). Additional details about the installation of the common gardens, environmental variation, and
106 variation in growth and flowering can be found in Shaver et al. (1986), Fetcher and Shaver
107 (1990), and Bennington et al. (2012). In this study, no individuals from the Coldfoot population
108 were measured and because not all the transplanted tussocks had survived, a balanced design of
109 measurements was not possible.

110 Temperature response curves for R_d were measured in situ between 9:00 am and 6:00 pm with
111 portable photosynthesis equipment fitted with an expanded temperature control kit (Li-Cor 6400
112 and Li-Cor 6400-88, Li-Cor, Inc, Lincoln, USA). For each replicate, a selection of *E. vaginatum*
113 leaves per tussock (3-9) was used. The mean \pm SD leaf temperatures (T_{leaf}) ranged between $10 \pm$
114 2.0 °C and 25 ± 1.9 °C for each curve and R_d measurements were taken at intervals of ~ 2.5 °C.
115 Each response curve took between 20 and 70 minutes, depending on how quickly the higher leaf
116 chamber temperatures were reached. After the respiration measurements, the leaf samples were
117 dried at 60 °C to a constant weight, ground and analysed for CHN with a Perkin-Elmer Series II
118 2400 CHNS/O Analyzer (LECO Corporation, U.S.A.). The response of R_d to T_{leaf} was fitted by
119 regression using a modified Arrhenius equation (e.g. Lloyd and Taylor 1994; Griffin et al. 2002):

$$120 \quad R_{dark} = a \cdot e^{bT_{leaf}}$$

121 where R_d is respiration rate, a and b are fitted parameters, respectively and T_{leaf} is leaf
122 temperature. The Q_{10} values of the temperature response curve were then derived from:

$$123 \quad Q_{10} = \frac{R_{dT+10}}{R_{dT}}$$

124 where R_{dT} and $R_{d(T+10)}$ are respiration rates at the temperature of T_{leaf} and $T_{\text{leaf}} + 10$. We chose
125 this relatively simple equation because the range of temperatures at which we could measure R_d
126 did not include the maximum temperature for leaf respiration, which is about 55 °C for *E.*
127 *vaginatum* (O. O'Sullivan, pers. comm.). This made fitting the temperature response to other
128 equations (for example, a polynomial equation) more difficult.

129 Statistical analyses were carried out in R with the *agricolae* package (R Development Core Team
130 2008). To analyse environmental (i.e. 'site' or 'garden') and genotype effects on R_d , Q_{10} , and
131 N_{leaf} , we used an additive main effects multiplicative interaction (AMMI) model. Before the
132 tests, the Q_{10} values were ln-transformed to obtain normally distributed data.

133

134 **Results**

135 The AMMI tests showed an effect of garden on R_d ($P < 0.04$), but no effect of population and no
136 interaction between genotype and garden ($P < 0.29$ and 0.62 , respectively). Hence, within the
137 gardens, the *E. vaginatum* leaves from different populations did not differ in their R_d . Between
138 gardens, leaves from Sagwon had the highest R_d at 10°C (Figure 1A). A similar result prevailed
139 for Q_{10} values, as the AMMI tests showed an effect of the environment (i.e. garden) on Q_{10} ($P <$
140 0.02), but no effect of population or interaction between population and garden ($P < 0.63$ and
141 0.89 , respectively). Overall, the northern sites Sagwon and Toolik Lake had significantly lower
142 values for Q_{10} than the two southern sites (Figure 1B). In contrast, both garden and garden *
143 population significantly influenced the values for N_{leaf} ($P < 0.001$ and $P < 0.04$, respectively),
144 with the northern gardens having larger values (Figure 1C), implying that N_{leaf} of the different
145 populations responded differently to the transplantation.

146

147 **Discussion**

148 The 30-year-old reciprocal transplant study showed that R_d and Q_{10} in *E. vaginatum* populations
149 were quite plastic. We found no significant effect of population within gardens on these traits,
150 therefore our first hypothesis (H1) was supported, which is also agrees with the general finding
151 of thermal acclimation of R_d in higher plants (e.g. Strain and Chase 1966; Bolstad et al. 2003;
152 Zaragossa-Castells et al. 2007; Tjoelker et al. 2008; Rodriguez-Calcerdera et al. 2010). However,
153 this result contrasts with the response of life history and morphological variables, such as tussock
154 survival rate and tiller size from the same experiment. For these traits, Bennington et al. (2012)
155 found home-site advantage (i.e. advantage for the population that originated in the common
156 garden) in tussock survival rates, as well as greater plasticity in tiller size in *E. vaginatum* that
157 originated from the southern sites. Therefore, the lack of difference between populations in
158 plasticity in R_d and Q_{10} (which are measured at the tissue level) cannot be extrapolated to the
159 functioning of *E. vaginatum* at the whole plant level, especially if some ecotypes produce fewer
160 tillers in their 'away' environment. In other words, although the physiological parameters on a
161 tissue scale do acclimate, there are some genetic based population differences (e.g. in survival
162 rate, tiller length) that can limit the ability of plants to respond to a change in environment.

163

164 No difference in Q_{10} was expected between research sites (gardens), as Atkin and Tjoelker
165 (2003) suggested that long-term thermal acclimation represents a shift up or down in the overall
166 temperature response curve (no change in Q_{10} , but with a change in the intercept of the response
167 curve). However, the lower Q_{10} values in the colder, northern Sagwon site do not support our
168 hypothesis (H4). Additionally, global differences in values of Q_{10} for R_d from Atkin and Tjoelker

169 (2003) show that colder, more northerly sites have higher, rather than lower Q_{10} values. In the
170 context of these global patterns, it would be expected that a site, such as Sagwon would have
171 higher, not lower, Q_{10} values when compared with the warmer, southern sites. It is possible that
172 the latitudinal range included in this study (3.3° latitude) is not large enough to reflect patterns
173 that are observed globally. In addition, the pattern of cold acclimation resulting in higher Q_{10}
174 values, as described by Atkin and Tjoelker (2003), requires that in colder environments plants
175 have a higher build-up of substrates (e.g. non-structural carbohydrates resulting from
176 photosynthesis) due to a changed balance between R_d and foliar C uptake. The higher amount of
177 substrate consequently allows for relatively higher R_d values with short-term warming, such as in
178 a temperature response curve (Atkin and Tjoelker 2003). In our study, data on the non-structural
179 carbohydrate content in the leaves is lacking. However, if this higher build-up of substrates did
180 not occur in the colder, northern sites this could explain why the pattern described by Atkin and
181 Tjoelker (2003) was not observed.

182 The increased values of N_{leaf} and R_d in the northern gardens (Figures 1A and 1C) supported our
183 Hypotheses 2 and 3, and suggest an increased investment in the respiratory apparatus. Higher
184 values for N_{leaf} at colder sites have been observed in boreal forest species (Tjoelker et al. 1999;
185 Tjoelker et al. 2008) while increased protein levels and investment in mitochondrial volume have
186 been found in cold-acclimated plants (Graham and Patterson 1983; Armstrong et al. 2006).
187 Therefore, although the values of Q_{10} in the colder, northern sites do not suggest acclimation of
188 R_d themselves, the higher values for N_{leaf} , together with those for R_d give indirect support for a
189 contrary conclusion. Higher values for R_d associated with lower values for Q_{10} at low
190 temperatures have been observed in other studies. Xiong et al. (2000) found a greater
191 temperature sensitivity of Antarctic species *Colobanthus quitensis* (Kunth) Bartl. and

192 *Deschampsia antarctica* E.Desv. when grown at higher (12 °C and 20 °C) rather than lower (7
193 °C) temperatures, but higher respiration in the cold-acclimated plants when measured at the same
194 temperature. Larigauderie and Körner (1995), however, showed that thermal acclimation of a
195 range of species can differ widely, both within genera, growth forms, and habitats. In sum, it
196 might be hard to observe the effects of thermal acclimation of R_d in cold-acclimated
197 environments through *in situ* measurements without factors, such as substrate limitation being
198 considered.

199 Overall, under the anticipated warming of the Arctic, the *E. vaginatum* populations in Alaska
200 will probably acclimate their R_d and the Q_{10} with higher temperatures. This implies that changes
201 in this species' abundance or biomass following Arctic warming are a more important factor to
202 consider when studying the effects of Arctic warming on the C balance of this ecosystem.

203

204 **Conclusions**

205 This study shows that R_d , Q_{10} and N_{leaf} are plastic traits in Alaskan populations of the species *E.*
206 *vaginatum*, since the growing environments, rather than the genotypes explained most of the
207 variation in these parameters. This thermal acclimation of R_d this species is probably facilitated
208 through changes in protein levels and mitochondrial volume as indicated by changes in N_{leaf} . It
209 has to be noted though that acclimation of R_d is a physiological response and that for the overall
210 effects of Arctic warming on *E. vaginatum* other plant traits are important as well.

211

212

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220

221 **References**

- 222 Atkin OK, Tjoelker MG. 2003. Thermal acclimation and the dynamic response of plant
223 respiration to temperature. *Trends in Plant Science* 8: 343–351.
- 224 Atkin, OK, Bruhn D, Hurry VM, and Tjoelker. MG. 2005. The hot and the cold: unravelling the
225 variable response of plant respiration to temperature. *Functional Plant Biology* 32:87-105.
- 226 Bennington CC, Fetcher, Vavrek MC, Shaver GR, Cummings K and McGraw JB. 2012. Home
227 site advantage in two long-lived arctic plant species: Results from two thirty-year reciprocal
228 transplant studies. *Journal of Ecology*.
- 229 Bolstad PV, Reich P and Lee T. 2003. Rapid temperature acclimation of leaf respiration rates in
230 *Quercus alba* and *Quercus rubra*. *Tree Physiology* 23: 969 –976.
- 231 Britton, ME. Vegetation of the arctic tundra. 1966. In Hanson, H. P. (ed.), *Arctic Biology*.
232 Corvallis: Oregon State University Press. pp. 67–130.

233 Chapin FS III, Shaver GR, Giblin AE, Nadelhoffer KJ and Laundre JA. 1995. Responses of
234 arctic tundra to experimental and observed changes in climate. *Ecology* 76: 694-711.

235

236 Chapin FS III, Sturm M, Serreze MC, McFadden JP, Key JR, Lloyd, AH, McGuire AD, Rupp
237 TS, Lynch AH, Schimel JP, Beringer J, Chapman WL, Epstein HE, Euskirchen ES, Hinzman
238 LD, Jia G, Ping CL, Tape KD, Thompson CDC, Walker DA and Welker JM. 2005. Role of
239 land-surface changes in Arctic summer warming. *Science* 310:657–60.

240

241 Fetcher N. and Shaver, GR. 1983. Life histories of tillers of *Eriophorum vaginatum* in relation to
242 tundra disturbance. *Journal of Ecology* 71: 131-147.

243 Fetcher N. and Shaver, GR. 1990. Environmental sensitivity of ecotypes as a potential influence
244 on primary productivity. *The American Naturalist* 136: 126-131.

245 Griffin KL, Turnbull M and Murthy R. 2002. Canopy position affects the temperature response
246 of leaf respiration in *Populus deltoides*. *New Phytologist* 154:609–619.

247 Janssens IA, Lankreijer H, Matteucci G, Kowalski AS, Buchmann N, Epron D, Pilegaard K,
248 Kutsch W, Longdoz B, Grünwald T, Montagnani L, Dore S, Rebmann C, Moors EJ, Grelle A,
249 Rannik Ü, Morgenstern K, Oltchev S, Clement R, Gudmundsson J, Minerbi S, Berbigier P,
250 Ibrom A, Moncrieff J, Aubinet M, Bernhofer C, Jensen NO, Vesala T, Granier A, Schulze E-D,
251 Lindroth A, Dolman AJ, Jarvis PG, Ceulemans R and Valentini R. 2001. Productivity
252 overshadows temperature in determining soil and ecosystem respiration across European forests.
253 *Global Change Biology* 7:269-278

254 Lee TD, Reich PB, Bolstad PV. 2005. Acclimation of leaf respiration to temperature is rapid and
255 related to specific leaf area, soluble sugars and leaf nitrogen across three temperate deciduous
256 tree species. *Functional Ecology* 19: 640-647.

257 Lloyd J, Taylor JA. 1994. On the temperature dependence of soil respiration. *Functional Ecology*
258 8: 315–323.

259 Mark AF, Fetcher N, Shaver GR and Chapin FS III. 1985. Estimated ages of mature tussocks of
260 *Eriophorum vaginatum* along a latitudinal gradient in Central Alaska, U.S.A. *Arctic and Alpine*
261 *Research* 17, 1-5.

262 McGuire DA, Anderson LG, Christensen TR, Dallimore S, Guo L, Hayes DJ, Heimann M,
263 Lorenson TD, Macdonald RW and Roulet N. 2009. Sensitivity of the carbon cycle in the Arctic
264 to climate change. *Ecological Monographs* 79(4) :23-555.

265 Ow LF, Griffin KL, Whitehead D, Walcroft AS and Turnbull MH. 2008. Thermal acclimation of
266 leaf respiration but not photosynthesis in *Populus deltoides x nigra*. *New Phytologist* 178: 123-
267 134.

268 Shaver GR, Fetcher N and Chapin FS III. 1986. Growth and flowering in *Eriophorum*
269 *vaginatum*: annual and latitudinal variation. *Ecology* 67: 1524-1535.

270 Solomon, S., D. Qin, M. Manning, R.B. Alley, T. Berntsen, N.L. Bindoff, Z. Chen, A.
271 Chidthaisong, J.M. Gregory, G.C. Hegerl, M. Heimann, B. Hewitson, B.J. Hoskins, F. Joos, J.
272 Jouzel, V. Kattsov, U. Lohmann, T. Matsuno, M. Molina, N. Nicholls, J. Overpeck, G. Raga, V.
273 Ramaswamy, J. Ren, M. Rusticucci, R. Somerville, T.F. Stocker, P. Whetton, R.A. Wood and D.
274 Wratt, 2007: Technical Summary. In: *Climate Change 2007: The Physical Science Basis*.

275 Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental
276 Panel on Climate Change [Solomon, S., D. Qin, M. Manning, Z. Chen, M. Marquis, K.B.
277 Averyt, M. Tignor and H.L. Miller (eds.)]. Cambridge University Press, Cambridge, United
278 Kingdom and New York, NY, USA

279 Tjoelker MG, Oleksyn J and Reich PB. 1999. Acclimation of respiration to temperature and CO₂
280 in seedlings of boreal tree species in relation to plant size and relative growth rate. *Global*
281 *Change Biology* 5: 679–691.

282 Tjoelker MG, Oleksyn J, Reich PB and Zytkowskiak R. 2008. Coupling of respiration, nitrogen,
283 and sugars underlies convergent temperature acclimation in *Pinus banksiana* across wide-
284 ranging sites and populations. *Global Change Biology* 14: 782–797.

285

286 Turnbull, M.H, Tissue DT, Griffin KL, Richardson SJ, Peltzer DA and Whitehead D. 2005.
287 Respiration characteristics in temperate rainforest tree species differ along a long-term soil-
288 development chronosequence. *Oecologia* 143: 271-279.

289 Xiong FS, Meuller EC and Day,TA. 2000. Photosynthetic and respiratory acclimation and
290 growth response of Antarctic vascular plants to contrasting temperature regimes. *American*
291 *Journal of Botany* 87: 700-710.

292 Zaragoza-Castells J, Sanchez-Gomez D, Valladares F, Hurry V and Atkin OK. 2007. Does
293 growth irradiance affect temperature dependence and thermal acclimation of leaf respiration?
294 Insights from a Mediterranean tree with long-lived leaves. *Plant, Cell and Environment* 30: 820–
295 833.

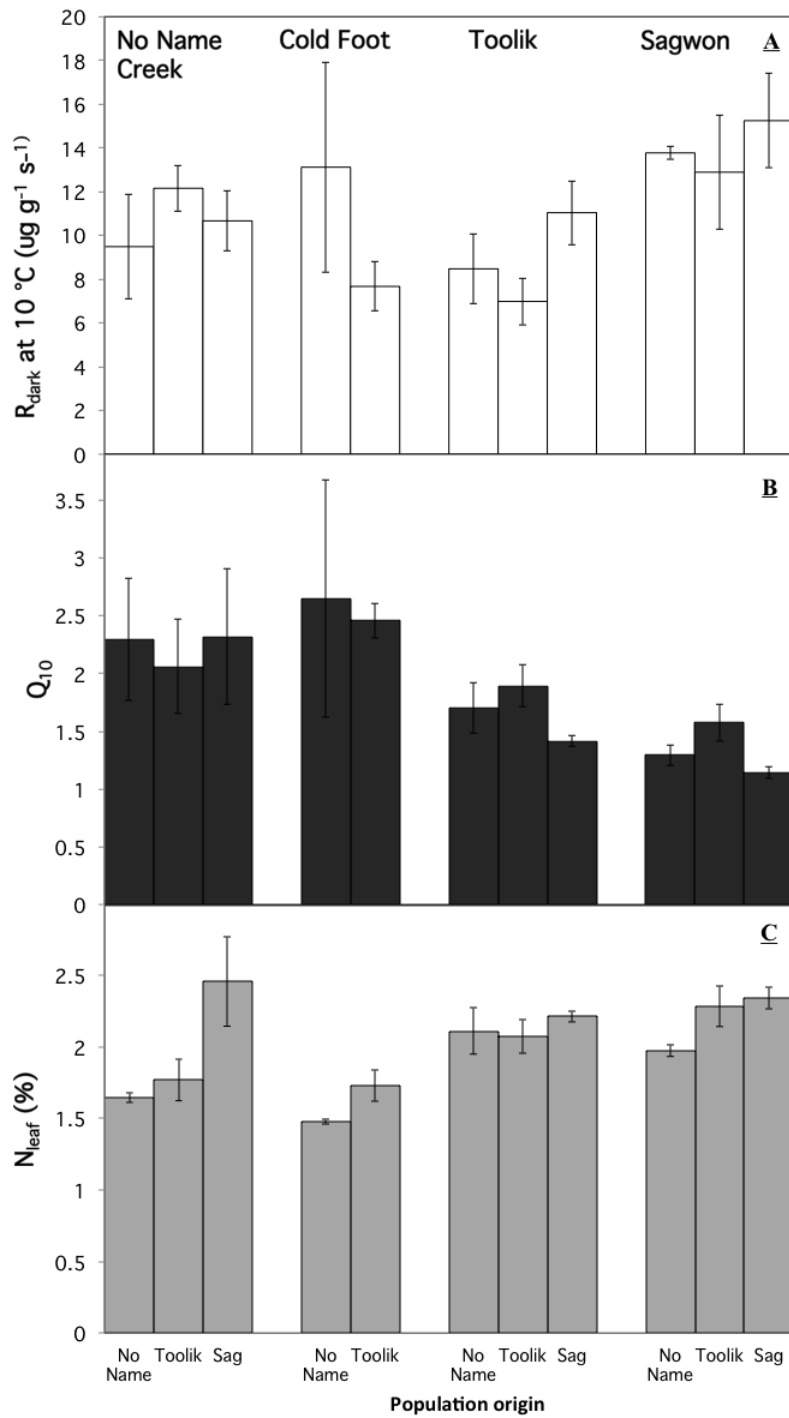
296 **Figure legends**

297

298 Figure 1. Average R_d at 10 °C (a), Q_{10} values of R_d (b) and average N_{leaf} (c) per population origin
299 (denoted below) and common garden (denoted above) and their standard errors.

300

301



302 **Figure 1.**

303

304