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Out of Sight, Out of Mind: Thermal Acclimation of Root Respiration in Arctic *Ranunculus*

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Abstract

Respiration rates, thermal sensitivity, and thermal acclimation potential of root respiration were investigated in *Ranunculus* from the Arctic. Comparisons of three species (*R. glacialis*, *R. nivalis* and *R. acris* subsp. *pumilus*) used plants grown on a mountain or in a glasshouse for 6 wk at contrasting soil temperatures (5.4 and 14.5°C, respectively). Northern and southern ecotypes of two species of *Ranunculus* (*R. pygmaeus*, and *R. acris* subsp. *acris*), together ranging from Svalbard (79 °N) to Scotland (56°N), were similarly compared after 2 wk in a growth cabinet at 5 and 15°C. Respiration rates varied at standard measurement temperatures; *R. nivalis* and *R. pygmaeus* grown on the mountain or at 5°C had the highest respiration, followed by other alpine snowbed species (*R. glacialis* and *R. acris* subsp. *pumilus*) and *R. acris* subsp. *acris* from the arctic lowland; *R. acris* subsp. *acris* from Scotland had lowest rates. Respiration was temperature sensitive for all populations, increasing progressively between 5 and 20°C ($Q_{10}^{(5-15)}$: 1.2–2.4).

Extent and type of acclimation of root respiration varied with no clear latitudinal pattern emerging. Acclimation to a 10°C increase in growth temperature was achieved through: change in temperature sensitivity (shown by changes in $Q_{10}^{(5-15)}$ values) (*R. acris* subsp. *pumilus*); or reduction in absolute rates (*R. pygmaeus* from Svalbard, *R. acris* subsp. *pumilus* and *R. nivalis*). Complete acclimation occurred in *R. acris* subsp. *pumilus* and *R. pygmaeus*, whereas *R. acris* subsp. *acris* from Scotland and *R. glacialis* did not acclimate. Plants that adjust root respiration (e.g., *R. pygmaeus* from Svalbard and *R. acris* subsp. *pumilus*) to maintain a positive carbon balance, may tolerate predicted temperature increases in arctic regions. Plants with high rates of root respiration and/or high sensitivity to temperature as well as poor acclimation potential, (e.g., *R. glacialis*) may only persist in cold microhabitats.

Introduction

Root respiration is an important but often overlooked component of plant performance. The balance between rates of photoassimilate production by green tissue and their use in respiration determines a plant's capacity to survive and grow. Root and rhizome respiration accounts for 10 to 66% of the carbon fixed daily by a plant (Lambers, 1989; van der Werf et al., 1994), and up to 60% of total soil respiration (Bowden et al., 1993). Northern or alpine plant species or ecotypes often have higher root respiration rates than their southern or lowland counterparts (Higgins and Spomer, 1976; Crawford and Palin, 1981; Sowell and Spomer, 1986; Graves and Taylor, 1988), particularly at cooler growth temperatures. Respiration is generally more temperature sensitive than photosynthesis, meaning that increased temperatures brought about by global climate change (IPCC 2001), may result in the respiration of a significantly higher proportion of the carbon fixed by photosynthesis (Woodwell, 1990; Loveys et al., 2002). In arctic plants, root respiration is of major importance because of the large proportion of biomass allocated belowground (Wielgolaski, 1972; Shaver and Chapin, 1991), high respiration rates and high temperature sensitivity. The risk of a negative carbon balance with increased growth temperature in these plants may be reduced if they are able to thermally acclimate, by reducing either their absolute rates of root respiration or the thermal sensitivity of respiration.

Despite the importance of root respiration, few studies document its response to increased growth temperatures; particularly so for arctic plants. Some species adjust to increased growth temperatures by reducing root respiration rates by up to 40% (Higgins and Spomer,

1976; Abebe, 1990; Tjoelker et al., 1999; Atkin et al., 2000a; Atkin and Tjoelker, 2003). This is achieved through changing the proportions of control exerted by adenylates, substrates, and enzyme capacity on respiratory flux (Covey-Crump et al., 2002). The extent to which plants reduce their absolute respiration rates and thermal sensitivity of respiration varies greatly between species, with no clear pattern yet emerging (Atkin and Tjoelker, 2003).

This study investigated respiration rates, thermal sensitivity, and the potential for thermal acclimation of root respiration to experimental warming for plants from a range of sites—from High Arctic to temperate latitudes and upland to lowland altitudes. Three arctic *Ranunculus* species (*R. glacialis*, *R. nivalis* and *R. acris* subsp. *pumilus*) grown on a mountain or in a glasshouse for 6 wk at contrasting soil temperatures (5.4 and 14.5°C, respectively) were compared. Northern and southern ecotypes of two species of *Ranunculus* (*R. pygmaeus* (from Svalbard and Sweden) and *R. acris* subsp. *acris* (from Sweden and Scotland)) were similarly compared after 2 wk in a growth cabinet at 5 and 15°C. Acclimation is defined as the adjustment of root respiration rate to compensate for a change in growth temperature. Plants may acclimate their respiration rates partially or fully, with full acclimation providing homeostasis (Atkin et al., 2000b), i.e. identical respiration rates in plants grown and measured at contrasting temperatures. Acclimation ability is indicated by the long-term ratio (LTR) $_{10}^{(5-15)}$ (Larigauderie and Körner, 1995), i.e. the ratio of respiration rate of the plants grown and measured at 15 and at 5°C, with a value of 1.0 showing complete acclimation. Acclimation can occur by reductions in thermal sensitivity of root respiration at increased growth temperature, as measured by $Q_{10}^{(5-15)}$ values ("Type I" acclimation, Atkin and Tjoelker, 2003);

TABLE 1

Details of study sites. Dates and sources of the data are as follows: Svalbard: 1969–1992, Norwegian Meteorological Office, 1985; Sweden: 1961–1990 ANS records; Scotland: 1931–1960 British Meteorological Office. Mean soil temperature and daily amplitude of soil (6 cm depth) and air (5 cm) are shown for a warm 5-d period during July (GRANT Squirrel data logger). *Ranunculus* species used in ^{a)}field experiment, ^{b)}growth cabinet experiment.

Site	Latitude	Longitude	Altitude, m a.s.l.	Mean annual temp, °C	Mean June-Aug. temp, °C	July maximum °C	Amplitude air °C	Amplitude soil °C	Mean soil °C	Species used
Drumochter Hills, Scotland	56°51'N	4°15'W	500	6.2	11.7	30.0	—	—	—	<i>R. acris</i> subsp. <i>acris</i> ^b
Abisko, Sweden	68°21'N	18°49'E	380	−0.8	9.7	21.3	—	—	—	<i>R. acris</i> subsp. <i>acris</i> ^b
Slättajäkka Mountain, Sweden	68°21'N	18°49'E	830	—	—	—	—	—	—	<i>R. acris</i> subsp. <i>pumilus</i> ^a
			1190	—	—	—	13	2	6	<i>R. glacialis</i> ^a
			1190	—	—	—	13	2	6	<i>R. nivalis</i> ^a
			1190	—	—	—	13	2	6	<i>R. pygmaeus</i> ^b
Ny-Ålesund, Svalbard	79°56'N	11°50'E	25	−6.0	3.6	15.6	10	5	11	<i>R. pygmaeus</i> ^b

and reductions in absolute rate of respiration (“Type II” acclimation, Atkin and Tjoelker, 2003). Q_{10} was calculated at 5 and 15°C since this investigation concerns respiration at soil temperatures experienced by plants in the Arctic. Thus, the complementary field and laboratory experiments in the present study evaluate the acclimation potential in arctic, temperate, alpine, and lowland species of the same genus.

Methods

SPECIES AND SITES

The genus *Ranunculus* includes species with contrasting latitudinal ranges within Europe, from High Arctic to temperate ecosystems. Study species were herbaceous perennials with small rhizomes and nonmycorrhizal roots (Harley and Harley, 1987; Cooper, 1996). They were *R. acris* subsp. *acris* L., *R. acris* subsp. *pumilus* (Wahlenb.) Å. and D. Löve, *R. glacialis* L., *R. nivalis* L., and *R. pygmaeus* Wahlenb.; nomenclature follows Tutin et al. (1993). *Ranunculus acris* occurs in wet meadows and habitats (Harper, 1957); *R. nivalis* is found in wet meadows, along the edges of mountain streams, on tundra, and in snowbeds (Polunin, 1959); *R. pygmaeus* grows in snowbeds to at least 2000 m a.s.l. (Hultén, 1968) and in moist places on tundra (Polunin, 1959). *Ranunculus glacialis* is characteristic of wet snowbeds with stony ground and sparse vegetation (Gjærevoll, 1956; Gjærevoll and Bringer, 1965) and is the species found at the highest altitudes in the European Alps (up to 4275 m a.s.l., Crawford, 1989).

Plant material was collected from sites at three latitudes comprising a gradient from upland temperate, through lowland and upland subarctic, through to High Arctic (Table 1). In Svalbard the *R. pygmaeus* site lay 1.5 km northwest of Ny-Ålesund, in a late melting snowbed on a well drained southwest-facing moraine at 25 m a.s.l. In northern Sweden, *R. pygmaeus*, *R. nivalis*, and *R. glacialis* were

collected on Slättajäkka mountain (1190 m a.s.l.) from late-melting snowbeds that were constantly damp and cold, while *R. acris* subsp. *pumilus* was collected on the same mountain (at 830 m a.s.l.) in an area snow covered in June but with drier soils by the end of summer. *Ranunculus acris* subsp. *acris* was collected just outside the Abisko Research Station (380 m a.s.l.), Sweden, and a Scottish population of *R. acris* subsp. *acris* was collected from a wet meadow community on a west-facing slope above Drumochter Pass (500 m a.s.l.).

FIELD EXPERIMENT

Individually potted plants from Slättajäkka (*R. nivalis*, *R. glacialis* and *R. acris* subsp. *pumilus*) were grown on the mountain at 1000 m a.s.l., or under natural lighting in a glasshouse at Abisko Research Station. Mean soil and air temperatures were $5.4 \pm 1.9^\circ\text{C}$ and $6.3 \pm 3.2^\circ\text{C}$ (mountain) and $14.5 \pm 2.9^\circ\text{C}$ and $14.7 \pm 3.3^\circ\text{C}$ (glasshouse). Pots in the glasshouse were watered regularly and 100 ml of nutrient solution containing 19.5 mg N, 3 mg P, and 14.1 mg K applied weekly. Root respiration rates for six randomly selected plants of each species were determined after 6 wk at 5 and 15°C, using an infrared gas analyzer (IRGA, model LCA3, ADC, Herts., UK) and a leaf chamber with water jacket. The same roots were used at both temperatures and stored in air-saturated water between measurements. The aboveground tissues experienced a photosynthetic photon flux density (PPFD) of $500 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ throughout. Root mass was oven dried at 60°C and weighed for calculation of respiration rate.

GROWTH CABINET EXPERIMENT

Ranunculus pygmaeus from Svalbard and Slättajäkka, and *R. acris* subsp. *acris* from Abisko and Scotland, were grown in a glasshouse at

TABLE 2

$Q_{10(5-15)}$ s for root respiration. ‘ $Q_{10(5-15)}$ cool’: plants grown on Slättajäkka mountain, Sweden, and in a growth cabinet at 5 °C. ‘ $Q_{10(5-15)}$ warm’: plants grown in a glasshouse in Abisko, Sweden) and in a growth cabinet at 15 °C. Significant difference indicated by * ($P < 0.05$). Where no significant difference exists, the average $Q_{10(5-15)}$ value is shown.

Experiment	Origin	Species	$Q_{10(5-15)}$ cool	$Q_{10(5-15)}$ warm	t	df	P	sig	average $Q_{10(5-15)}$
Field	Slättajäkka	<i>R. nivalis</i>	1.7 ± 0.1	2.1 ± 0.2	2.079	8.6	0.069	ns	1.9
	Slättajäkka	<i>R. glacialis</i>	2.1 ± 0.2	2.3 ± 0.2	0.730	9.9	0.483	ns	2.2
	Slättajäkka	<i>R. acris</i> subsp. <i>pumilus</i>	1.2 ± 0.1	2.2 ± 0.4	2.459	6.4	0.047	*	—
Growth Cabinet	Slättajäkka	<i>R. pygmaeus</i>	1.9 ± 0.4	1.5 ± 0.2	−1.071	7.0	0.319	ns	1.7
	Svalbard	<i>R. pygmaeus</i>	2.0 ± 0.3	1.5 ± 0.3	−1.076	9.8	0.308	ns	1.8
	Abisko	<i>R. acris</i> subsp. <i>acris</i>	1.7 ± 0.1	2.0 ± 0.1	1.371	9.6	0.202	ns	1.9
	Scotland	<i>R. acris</i> subsp. <i>acris</i>	2.4 ± 0.2	2.1 ± 0.1	−1.726	8.6	0.120	ns	2.3

TABLE 3

Tests for homeostasis and mean long term respiration ratios ($LTR_{10(5-15)}$) ($\pm SE$, $n = 6$) for root respiration of plants grown on Slättjåkka, (Sweden) and measured at 5°C compared with those grown in the glasshouse at Abisko (Sweden) and measured at 15°C. Likewise plants grown and measured at 5°C in a growth cabinet are compared with plants grown and measured at 15°C. T-test (t) results are indicated as follows: *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$, ns = not significant (= complete acclimation). An LTR Value of 1.0 indicates complete acclimation; as the value increases, the acclimation ability decreases.

Experiment	Origin	Species	t	df	P	sig	$LTR_{10(5-15)}$
Field	Slättjåkka	<i>R. nivalis</i>	-4.89	9.6	<0.001	***	1.6 \pm 0.2
	Slättjåkka	<i>R. glacialis</i>	-5.23	6.3	0.002	**	2.0 \pm 0.3
	Slättjåkka	<i>R. acris</i> subsp. <i>pumilus</i>	-0.88	9.9	0.402	ns	1.1 \pm 0.1
Growth Cabinet	Slättjåkka	<i>R. pygmaeus</i>	-2.00	9.3	0.075	ns	1.5 \pm 0.2
	Svalbard	<i>R. pygmaeus</i>	0.16	6.5	0.0876	ns	1.2 \pm 0.2
	Abisko	<i>R. acris</i> subsp. <i>acris</i>	-3.79	8.2	0.005	*	1.4 \pm 0.2
	Scotland	<i>R. acris</i> subsp. <i>acris</i>	-3.52	9.8	0.006	**	2.0 \pm 0.3

Bradford University, UK. Nonflowering plants of equivalent sizes were cleaned of soil and grown in full strength Rorison's solution (Gigon and Rorison, 1972) in a Birchover growth cabinet with continuous light (PPFD of 400 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), mimicking the arctic growing season. Relative humidity (RH) was 50 to 70%. Plants were kept at a constant 5 or 15°C for 2 wk, and then the roots of six intact plants from each population were measured at 5, 10, 15, and 20°C using an IRGA. The same plants were measured at all temperatures and aboveground tissues received PPFD of 400 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ throughout. Respiration rate was measured on four successive days using temperature order 15, 5, 20, 10°C and plants were returned to their growth conditions between measurements. Roots were dried at 60°C and weighed.

STATISTICAL ANALYSES

Data were analyzed using the "R" statistical package (<http://www.r-project.org/>). Respiration rates in the field experiment were analyzed by a two-way ANOVA with interactions on all data (variables: species, treatment, measurement temperature) and for each species separately (variables: treatment, measurement temperature). Growth cabinet experiment data was analyzed by repeated-measures ANOVA with interactions on all data (variables: species, ecotype, treatment, measurement temperature) and individually for each ecotype (variables: treatment, measurement temperature). The Welch two-sample *t*-test was used for treatment effects on $Q_{10(5-15)}$, and to test for homeostasis of root respiration.

Results

ABSOLUTE RATES OF ROOT RESPIRATION

Root respiration rates are summarized in Figures 1 and 2. Absolute respiration rates varied between species (species effect; field experiment: $F_{(2,60)} = 57.78$, $P < 0.001$; growth cabinet experiment: $F_{(1,40)} = 24.56$, $P < 0.001$), and between northern and southern ecotypes of *R. pygmaeus* but not *R. acris* subsp. *acris* (growth cabinet: species*ecotype interaction, $F_{(1,40)} = 15.19$, $P < 0.001$). *Ranunculus nivalis* and *R. pygmaeus* grown on the mountain or at 5°C had the highest respiration, followed by other snowbed species (*R. glacialis* and *R. acris* subsp. *pumilus*) and *R. acris* subsp. *acris* from Abisko; *R. acris* subsp. *acris* from Scotland had lowest rates. Respiration rates of plants grown at 5°C were higher for the High Arctic population of *R. pygmaeus* than the alpine subarctic population (ecotype effect at 5°C growth, growth cabinet: $F_{(1,10)} = 13.95$, $P = 0.004$).

TEMPERATURE SENSITIVITY OF RESPIRATION

Root respiration rates increased with measurement temperature (field: $F_{(1,60)} = 184.23$, $P < 0.001$; growth cabinet: $F_{(3,120)} = 132.42$,

$P < 0.001$). For example, rates for *R. pygmaeus* from Svalbard grown at 5°C increased from 14.8 to 32.9 $\text{nmol CO}_2 \text{g}^{-1} \text{s}^{-1}$ between 5 and 20°C. The mean $Q_{10(5-15)}$ values for the mountain and 5°C grown plants (Table 2) were 1.2 to 2.4; those of glasshouse and 15°C grown plants ranged from 1.5 to 2.2.

ACCLIMATION

The extent and type of acclimation to a 10°C increase in growth temperature varied, with no clear latitudinal pattern emerging. Type I acclimation (change in temperature sensitivity shown by changes in $Q_{10(5-15)}$ values): only *R. acris* subsp. *pumilus* differed significantly in $Q_{10(5-15)}$ between mountain (1.2) and glasshouse (2.2) grown plants ($t = 2.46$, $df = 6.39$, $P = 0.047$). Type II acclimation (reduction in absolute rates): root respiration of glasshouse and 15°C grown plants were lower than for those of corresponding cooler growth conditions (treatment effects, field: $F_{(1,60)} = 16.47$, $P < 0.001$; growth cabinet: $F_{(1,40)} = 22.41$, $P < 0.001$). For example, at 15°C, Svalbard *R. pygmaeus* grown at 15°C respired 14.3 $\text{nmol CO}_2 \text{g}^{-1} \text{s}^{-1}$, compared to 25.5 $\text{nmol CO}_2 \text{g}^{-1} \text{s}^{-1}$ for plants grown at 5°C. Significantly lower respiration rates at the warmer growth treatment occurred for Svalbard *R. pygmaeus* ($F_{(1,10)} = 15.47$, $P = 0.003$) in the growth cabinet and *R. acris* subsp. *pumilus* and *R. nivalis* ($F_{(1,20)} = 16.52$, $P < 0.001$ and $F_{(1,20)} = 4.80$, $P = 0.040$, respectively) in the field experiment.

Homeostasis was measured in *R. acris* subsp. *pumilus* and both ecotypes of *R. pygmaeus* (Table 3). $LTR_{10(5-15)}$ indicate that complete acclimation occurred in *R. acris* subsp. *pumilus* and in Svalbard *R. pygmaeus*; partial acclimation in *R. acris* subsp. *acris* from Abisko and in *R. pygmaeus* from Slättjåkka, whereas *R. acris* subsp. *acris* from Scotland and *R. glacialis* did not acclimate.

Discussion

Respiration rates of plants grown experimentally on the mountain and in the growth cabinet at 5°C were similar to those of undisturbed arctic *Ranunculus* in the field (Cooper, 1996). High rates of root respiration, especially in cold soils emerging from snow at the beginning of the growth season, enable rapid growth of leaves for effective use of diurnal sunlight for photosynthesis. No clear latitudinal pattern emerged in response of root respiration to growth temperature. The ecotype acclimating most to a 10°C increase in growth temperature was *R. pygmaeus* from Svalbard; its site was poorly vegetated and supported thin dark soil that dried out following snowmelt, warmed quickly and subsequently followed air temperature. In contrast, the Slättjåkka snowbed had higher vegetation cover, was continually fed by melting snow and thus the soil remained damp and cold all summer. An insulating vegetation layer buffers arctic soil temperature against

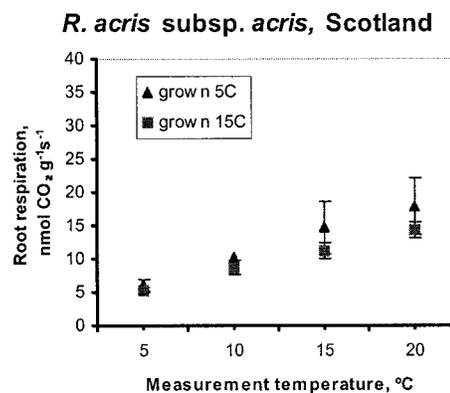
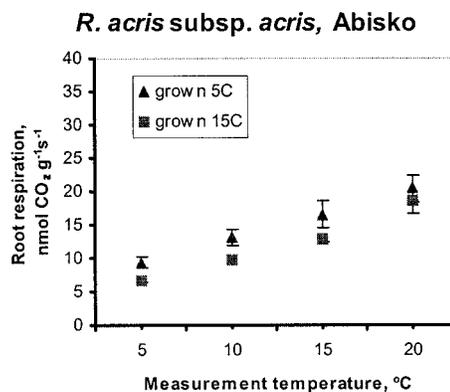
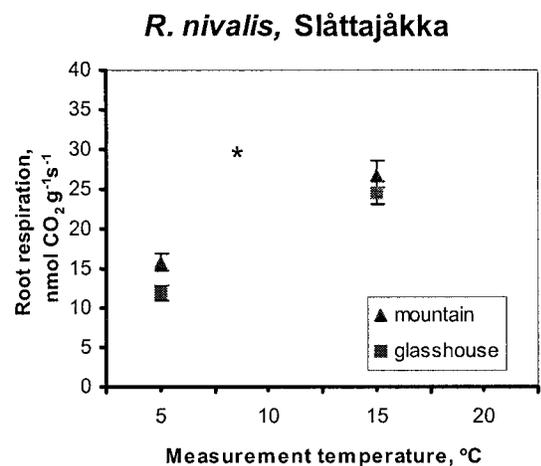
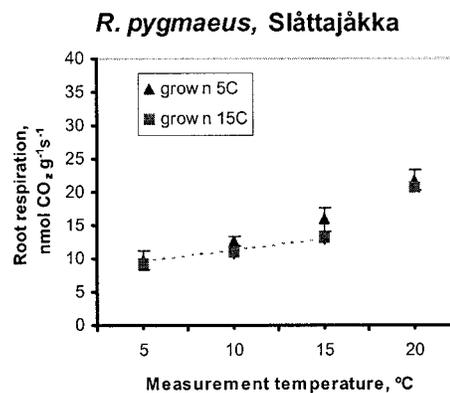
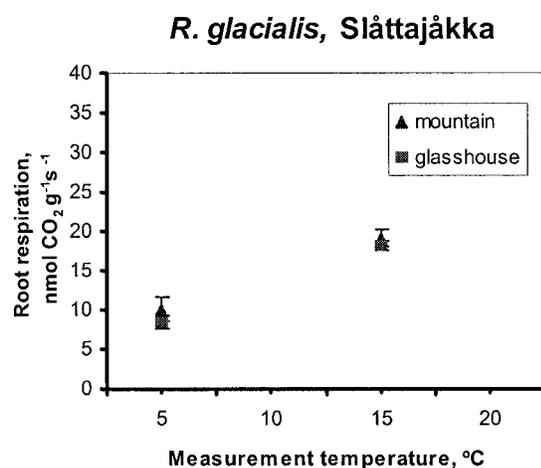
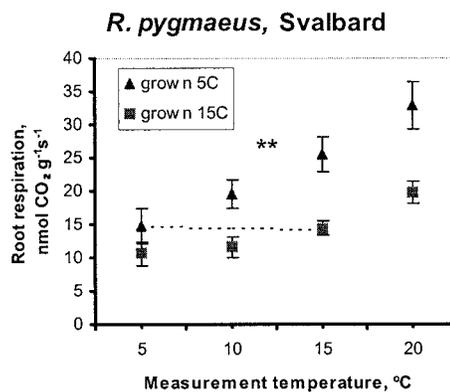
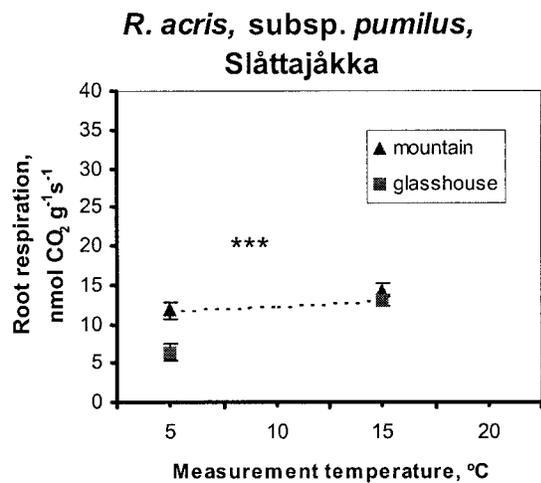


FIGURE 1. Belowground respiration rates (mean \pm SE, $n = 6$) ($\text{nmol CO}_2 \text{ g dry wt}^{-1} \text{ s}^{-1}$) at 5 and 15°C for arctic-alpine *Ranunculus* species grown on Slåttajäkka and in a glasshouse at Abisko, Sweden. The dotted line shown for *R. acris* subsp. *pumilus* represents homeostasis. Significant differences in rates between mountain and glasshouse grown plants are indicated by * $P < 0.05$, ** $P < 0.01$.

FIGURE 2. Belowground respiration rates (mean \pm SE, $n = 6$) ($\text{nmol CO}_2 \text{ g dry wt}^{-1} \text{ s}^{-1}$) of *R. pygmaeus* from Svalbard and Slättajåkka (Sweden), and *R. acris* from Abisko (Sweden) and Scotland grown in a growth cabinet at 5 or 15°C, and measured at 5 to 20°C. Dotted lines shown for both *R. pygmaeus* populations represent homeostasis. Significant differences in rates between the plants grown at 5 and 15 °C are indicated by ** $P < 0.01$.

the warming effect of the sun and reduces melting of permafrost (Coulson et al., 1993; van der Wal and Brooker, 2004). Dry soils also warm faster than wet soils (Coulson et al., 1993). The Svalbard site therefore, may have been warmer during part of the growing season with larger diurnal temperature amplitude than the snowbed site on top of Slättajåkka. Differential moisture content and thermal stability of the sites of origin may explain the differences in acclimation potential between *R. pygmaeus* from Svalbard and Slättajåkka. Likewise, *R. acris* subsp. *pumilus*, originating from a site susceptible to summer drying and warming, thermally acclimated to warmer growth temperatures, in contrast with *R. glacialis*, originating from a damper and colder site.

It appears that there are two strategies for arctic and arctic-alpine plants: (i) plants with limited or no potential for acclimation of root respiration are restricted to damp, cold, relatively thermally stable soil environments; (ii) plants able to thermally acclimate by reducing the rates or temperature sensitivity of root respiration can survive in widely fluctuating or warmer soils. Plants that can thermally acclimate (e.g., *R. pygmaeus* from Svalbard and *R. acris* subsp. *pumilus* from Slättajåkka) may survive increases in summer temperature, whereas those unable to do so (e.g., *R. glacialis*) may only survive if their belowground habitats remain cold. High rates and temperature sensitivities of root respiration, coupled with limited ability to thermally acclimate their root respiration rates may explain the decline or disappearance of typical snowbed species from central Norway and Finnish Lapland (Virtanen et al., 2003). They may also account for the recent rise in the lower altitudinal limit for *R. glacialis* and other snowbed species in the European Alps and the Jotenheimen mountains, Norway (Grabherr et al., 1994, 1995; Klanderud and Birks, 2003).

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References Cited

Abebe, T., 1990: The effect of high root temperature and mild water stress on the partitioning of carbon in barley. M. phil. thesis. University of Wales, Bangor. 94 pp.

Atkin, O. K., Edwards, E. D., and Loveys, B. R., 2000a: Response of root respiration to changes in temperature and its relevance to global warming. *New Phytologist*, 147: 141–154.

Atkin, O. K., Holly, C., and Ball, M. C., 2000b: Acclimation of snow gum (*Eucalyptus pauciflora*) leaf respiration to seasonal and diurnal variations in temperature: the importance of changes in the capacity and temperature sensitivity of respiration. *Plant, Cell and Environment*, 23: 15–26.

Atkin, O. K., and Tjoelker, M. G., 2003: Thermal acclimation and the dynamic response of plant respiration to temperature. *Trends in Plant Science*, 8(7): 343–351.

Bowden, R. D., Nadelhoffer, K. J., Boone, R. D., Melillo, J. M., and Garrison, J. B., 1993: Contributions of aboveground litter, belowground litter and root respiration to total soil respiration in a temperate mixed hardwood forest. *Canadian Journal of Forest Research*, 23: 1402–1407.

Cooper, E. J., 1996: An ecophysiological investigation of some species of Arctic and temperate *Ranunculus* L. with respect to climatic warming: Responses of above- and below-ground growth and carbon dioxide exchange to season and temperature. PhD thesis, University of Bradford. 283 pp.

Coulson, S. J., Hodkinson I. D., Strathdee A. T., Bale J. S., Block W., Worland M. R., and Webb N. R., 1993: Simulated climate change: the interaction between vegetation type and microhabitat temperatures at Ny-Ålesund, Svalbard. *Polar Biology*, 13: 67–70.

Covey-Crump, E. M., Attwood, R. G., and Atkin, O. K., 2002: Regulation of root respiration in two species of *Plantago* that differ in relative growth rate: the effect of short- and long- term changes in temperature. *Plant, Cell and Environment*, 25: 1501–1513.

Crawford, R. M. M., 1989: *Studies in Plant Survival: Ecological Case Histories of Plant Adaptation to Adversity*. Oxford: Blackwell Scientific Publications. 296 pp.

Crawford, R. M. M. and Palin, M. A., 1981: Root respiration and temperature limits to the North-South distribution of four perennial maritime plants. *Flora*, 171: 338–54.

Gigon, A. and Rorison, I. H., 1972. Response of some ecologically distinct plant species to nitrate-nitrogen and to ammonium-nitrogen. *Journal of Ecology*, 60: 93–102.

Gjærevoll, O. 1956: The plant communities of the Scandinavian alpine snow-beds. *Kunlige Norske Videnskaps Selskab Skrifter*, 1: 1–405.

Gjærevoll, O. and Bringer, K.-G., 1965: Plant cover of the alpine regions. *Acta Phytogeographica Suecica*, 50: 257–268.

Grabherr, G., Gottfried, M., Gruber, A., and Pauli, H., 1995: Pattern and current changes in alpine plant diversity. In Chapin, F. S., III and Körner C. (eds.), *Arctic and Alpine Biodiversity: Patterns Causes and Ecosystem Consequences*. Ecological Studies 113. Berlin-Heidelberg: Springer-Verlag, 167–181.

Grabherr, G., Gottfried, M., and Pauli, H., 1994: Climate effects on mountain plants. *Nature*, 369: 448.

Graves, J. D. and Taylor, K., 1988: A comparative study of *Geum rivale* L. and *G. urbanum* L. to determine those factors controlling their altitudinal distribution. II. Photosynthesis and respiration. *New Phytologist*, 108: 297–304.

Harley, J. L. and Harley, E. L., 1987: A check list of mycorrhiza in the British Flora. *New Phytologist*, 105: 1–102.

Harper, J. L., 1957: Biological flora of the British Isles No. 33. *Ranunculus acris*, L., *Ranunculus repens*, L. and *Ranunculus bulbosus*, L. *Journal of Ecology*, 45: 289–342.

Higgins, P. D. and Spomer, G. G., 1976: Soil temperature effects on root respiration and the ecology of alpine and subalpine plants. *Botanical Gazette*, 137: 110–120.

Hultén, E., 1968. *Flora of Alaska and Neighboring Territories. A Manual of the Vascular Plants*. Stanford, Calif.: Stanford University Press. 1008 pp.

IPCC (Intergovernmental Panel on Climate Change), 2001: *Climate Change 2001: The Scientific Basis. Contribution of Working Group I to the Third Assessment Report of the Intergovernmental Panel on Climate Change*. Houghton, J. T. et al. (eds.) Cambridge: Cambridge University Press. 881 pp. (Also available at www.ipcc.ch)

Klanderud, K. and Birks, H. J. B., 2003: Recent increases in species richness and shifts in altitudinal distributions of Norwegian mountain plants. *The Holocene*, 13: 1–6.

Lambers, H., Freijns, N., Poorter, H., Hirose, T., and van der Werf, A., 1989: Analysis of growth based on net assimilation rate and nitrogen productivity. In Lambers, H., Cambridge, M. L., Konings, H., and Pons, T. L. (eds.), *Causes and Consequences of Growth and Productivity of Higher Plants*. The Hague: SPB Academic Publishing, 1–17.

Larigauderie, A. and Körner, C., 1995: Acclimation of leaf dark respiration to temperature in alpine and lowland plant species. *Annales de Botany*, 76: 245–252.

- Loveys, B. R., Scheurwater, I., Pons, T. L., Fitter, A. H., and Atkin, O. K., 2002: Growth temperature influences the underlying components of relative growth rate: an investigation using inherently fast- and slow-growing plant species. *Plant, Cell and Environment*, 25: 975–987.
- Polunin, N., 1959. *Circumpolar Arctic Flora*. Oxford: The Clarendon Press. 514 pp.
- Shaver, G. R. and Chapin, F. S., III, 1991: Production: biomass relationships and element cycling in contrasting Arctic vegetation types. *Ecological Monographs*, 61: 1–31.
- Sowell, J. B. and Spomer, G. G., 1986: Ecotypic variation in root respiration rate among elevational populations of *Abies lasiocarpa* and *Picea engelmannii*. *Oecologia*, 68: 375–379.
- Tjoelker, M. G., Oleksyn, J., and Reich, P. B., 1999: Acclimation of respiration to temperature and CO₂ in seedlings of boreal tree species in relation to plant size and relative growth rate. *Global Change Biology*, 49: 679–691.
- Tutin, T. G., Burges, N. A., Chater, A. U., Edmundson, J. R., Heywood, V. H., Moore, D. M., Valentine, D. H., Walters, S. M., and Webb, D. A. (eds.), 1993: *Flora Europaea*. Vol.1. Cambridge University Press, Cambridge. 581 pp.
- van der Wal, R. and Brooker, R.W., 2004: Mosses mediate grazer impacts on grass abundance in arctic ecosystems. *Functional Ecology*, 18: 77–86.
- van der Werf, A., Poorter, H. and Lambers, H., 1994: Respiration as dependent on a species inherent growth rate and on the nitrogen supply to the plant. In Roy, J. and Garnier, E. (eds.). *A Whole-plant Perspective of Carbon-nitrogen Interactions*: The Hague: SPB Academic Publishing, 61–77.
- Virtanen, R., Eskelinen, A., and Gaare, E., 2003: Long term changes in Alpine plant communities in Norway and Finland. In Nagy, L., Grabherr, G., Körner, Ch, Thompson, D. B. A. (eds.), *Alpine Biodiversity in Europe*. Ecological Studies, Vol. 167. Berlin-Heidelberg: Springer-Verlag, 411–422.
- Wielgolaski, F. E., 1972: Vegetation types and plant biomass in tundra. *Arctic and Alpine Research*, 4: 291–305.
- Woodwell, G., 1990: The effects of global warming. In Leggart, J. (ed.), *Global Warming: the Greenpeace Report*. Oxford: Oxford University Press, 116–132.

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