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The ability of several high arctic plant species to utilize nitrate nitrogen under field conditions

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Abstract. The ability to utilize NO_3^- in seven high arctic plant species from Truelove Lowland, Devon Island, Canada was investigated, using an in vivo assay of maximum potential nitrate reductase (NR) activity and applications of ^{15}N. Plant species were selected on the basis of being characteristic of nutrient-poor and nutrient-rich habitats. In all species leaves were the dominant site of NR activity. Root NR activity was negligible in all species except *Saxifraga cernua*. NO_3^- availability per se did not appear to limit NR activity of the species typically found on nutrient-poor sites (*Dryas integrifolia*, *Saxifraga oppositifolia*, and *Salix arctica*), or in *Cerastium alpinum*, as leaf NR activities remained low, even after NO_3^- addition. $^{15}NO_3^-$ uptake was limited in *D. integrifolia* and *Salix arctica*. However, the lack of field induction of NR activity in *C. alpinum* and *Saxifraga oppositifolia* was not due to restricted nitrate uptake, as $^{15}NO_3^-$ labelled NO_3^- entered the roots and shoots of both species. Leaf NR activity rates were low in three of the species typical of nutrient-rich habitats (*O. digyna*, *P. radicatum* and *Saxifraga cernua*), sampled from a site containing low soil NO_3^-. Additions of NO_3^- significantly increased leaf NR activity in these latter species, suggesting that potential NR activity was limited by the availability of NO_3^-. ^{15}N labelled NO_3^- was taken up by *O. digyna*. *P. radicatum* and *Saxifraga cernua*. Although two species (*D. integrifolia* and *Salix arctica*) showed little utilization of NO_3^-, we concluded that five of the seven selected high arctic plant species (*C. alpinum*, *O. digyna*, *P. radicatum*, *Saxifraga cernua* and *Saxifraga oppositifolia*) do have the potential to utilize NO_3^- as a nitrogen source under field conditions, with the highest potential to utilize NO_3^- occurring in three of the species typically found on fertile habitats.

Key words: Arctic plants – Ammonium – Nitrate – Nitrate reductase – ^{15}N

The capacity for NO_3^- uptake and assimilation is thought to be a prerequisite for the utilization of nitrogen by plants in NO_3^- dominated ecosystems (Runge 1983). Before NO_3^- can be assimilated into organic nitrogen by plants, it must first be reduced to NO_2^- and then NH_4^+. The reduction of NO_3^- to NO_2^- is catalyzed by nitrate reductase (NR), an enzyme that is thought to be the rate limiting step in NO_3^- assimilation (Beevers and Hageman 1969; Campbell 1988). NR is a substrate-inducible enzyme (Beevers and Hageman 1969; Kaplan et al. 1974; Remmler and Campbell 1986), with the level of NR activity increasing within hours of NO_3^- application (Campbell 1988).

In contrast to the almost ubiquitous occurrence of NR in plants from NO_3^--rich environments, a number of plant species growing on NH_4^+-dominated soils appear unable to reduce significant amounts of NO_3^- due to inherently low levels of NR activity (Townsend and Blatt 1966; Routley 1972), even after NO_3^- application (Havill et al. 1974). This raises the possibility that high arctic plant species, which grow on soils dominated by NH_4^+ (Flint and Gersper 1974; Van Cleve and Alexander 1981), may also be unable to utilize NO_3^- nitrogen under field conditions due to low NR activity. However, no information is available concerning the activity and inducibility of NR in high arctic plants under field conditions.

The experiments described in this paper investigate the potential of several high arctic plant species, which typically grow on NH_4^+-dominated soils, to utilize NO_3^- nitrogen under field conditions, using an in vivo assay of the maximum potential NR activity and ^{15}N labelled NO_3^- applications. The relative amounts of NH_4^+ and NO_3^- taken up into roots and shoots were also determined using ^{15}N.

Materials and methods

Study site and plant material

The study was conducted at Truelove Lowland, Devon Island, Northwest Territories, Canada (75° 33′ N, 84° 40′ W) during July 1989 and July–August 1990. The habitats examined included a sparsely vegetated raised beach ridge that has low soil fertility (Walker and Peters 1977), and two fertile sites: a eutrophic region

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1–3 m below the camp outdoor toilet, and an area surrounding a lemming burrow on another raised beach ridge. Air temperatures on the beach ridges are usually below 7° C during the summer, with soil temperatures normally being much lower (Courtin and Labine 1977). The ecology of the lowland is comprehensively described in an International Biological Program study of the Truelove Lowland Tundra Biome (Bliss 1977).

Two groups of plant species were selected for study on the basis of being representative of habitats containing low or high levels of soil nutrients. *Dryas integrifolia* (M.), *Saxifraga oppositifolia* L., and *Salix arctica* Pall. were chosen as being characteristic of nutrient-poor, exposed, xeric environments (Porsild and Cody 1980). For species representative of fertile, mesic sites, we chose *Cerastium alpinum* L., Vahl, *Oxyria digyna* (L.) Hill, *Papaver radicatum* Rottb. and *Saxifraga cernua* L. (Porsild and Cody 1980). Despite differing in their characteristic habitats, all species could be sampled at the infertile Beach Ridge site. In addition, all the selected species could be sampled from the more fertile Camp Toilet site, with the exception of *P. radicatum*, which was sampled from the nutrient-rich Lemming Burrow site.

Soil sampling and analyses

As an index of NH_4^+ and NO_3^- available to the selected species, soil samples were collected and analyzed for exchangeable NH_4^+ and NO_3^-. Eight soil samples from 2–15 cm depth were collected from the crest of the Beach Ridge site at 1 m intervals. Soil was also collected around the upper 10 cm of roots in five species growing at the Beach Ridge site, from *Saxifraga cernua* growing at the Camp Toilet site, and from the roots of *P. radicatum* growing at the Lemming Hole site. The effect of NO_3^- application (see below) on pool sizes of NH_4^+ and NO_3^- in soils collected from close to the roots of three species growing at the Beach Ridge site (*D. integrifolia, Salix arctica,* and *Saxifraga oppositifolia*) was also assessed.

Samples were sieved through a 4 mm wire mesh, extracted for 1 h using a 1 M KCl solution, allowed to settle for 10 min, filtered through Whatman No. 42 paper, and the concentration of NH_4^+ and NO_3^- determined using an Orion model 95–10 NH_3 specific electrode (Orion Research Inc. Boston, USA; Myers and Paul 1968). Following the initial determination of NH_4^+ concentration in each sample, $TiCl_3$ reductant (Orion Research Inc.) was added, converting all NO_3^- to NO_2^- and subsequently to NH_3 (Orion Application Procedure Number 115). The concentration of NO_3^- was then calculated.

Plant sampling for NR activity measurements

When both root and leaf NR activity measurements were made in the NO_3^- application experiment, intact plants were excavated with the soil material retained. The plants were sealed in plastic bags, and transported to the field laboratory, where the soil was carefully removed by rinsing in distilled water. In earlier preliminary optimization studies, measurements of potential leaf NR activity were made using individual leaves sampled from non-excavated plants. In each case, leaves were detached from the plants using a new blade, and transported to the field laboratory for immediate assay.

Leaf and root in vivo NR activity measurements

NR activity was determined using an in vivo assay (Jaworski 1971 as modified by Havill et al. 1974), an assay that gave estimates of the maximum potential rate of NR activity, rather than the actual in situ rate of NO_3^- reduction. Fully expanded leaves and non-woody roots were sliced into 2 mm sections to facilitate greater penetration of incubation medium. Because of their small size, entire leaves were used from *Saxifraga oppositifolia.* Incubation of plant material in 5 mL of medium (100 mM phosphate buffer, pH 7.2) took place in the dark at 20° C, with 0.4 mL aliquots being removed after 24 and 54 min.

We determined the optimal concentrations of n-1-propanol and KNO_3 in the incubation medium (Havill et al. 1974) in leaves of each species, and roots of *P. radicatum* and *D. integrifolia.* As a result, the following concentrations of propanol and KNO_3 were used in subsequent assays of leaf NR activity: *P. radicatum*, 3% propanol, 10 mM KNO_3; *O. digyna*, 2% prop., 200 mM KNO_3; *C. alpinum*, 3% prop., 200 mM KNO_3; *Saxifraga cernua*, 3% prop., 50 mM KNO_3; *D. integrifolia*, 2% prop., 50 mM KNO_3; *Saxifraga oppositifolia*, 2% prop., 10 mM KNO_3; and *Salix arctica*, 2% prop., 20 mM KNO_3. 2% propanol and 50 mM KNO_3 were used in subsequent assays of root NR activity for all species.

Two minutes of vacuum infiltration were found to significantly increase NO_2^- production in the leaves of species that exhibited measurable NR activity and was, therefore, used in subsequent assays. NO_2^- concentration of each 24 and 54 minute aliquot was determined colorimetrically (Jaworski 1971). Production of NO_2^- was found to be linear between 24 and 54 min in all species. Checks for NO_2^- loss were periodically made by replacing the incubation medium's NO_3^- source (Havill et al. 1974) with 28 mM $NaNO_2$. NO_2^- loss, due to NO_2^- reductase activity, typically, represented less than 10% of the total NO_2^- liberated into the incubation media.

The plants chosen for the optimization and assay temperature experiments were sampled from the Camp Toilet site, or from around the Lemming Burrow site in the case of *P. radicatum.* Both sites had significant amounts of exchangeable NO_3^-. In this way, NO_3^- would have been naturally available to all species used in the optimization studies, increasing the potential for NR to be active.

NO_3^- applications

The effects of NO_3^- application on exchangeable soil NO_3^- and NH_4^+ concentrations, and on leaf and root NR activity, were assessed at the nutrient-poor Beach Ridge site. Individual plants at this site were sparsely distributed, often being separated from other plants by several metres. A 20×20 cm area surrounding each isolated plant was carefully watered with 40 mL of 0.24 M $NaNO_3$ solution (20 g[N] m^{-2}), and then immediately rinsed with 80 mL of distilled H_2O. To allow the solutions to penetrate the soil below each plant, and to allow sufficient time for NO_3^- uptake and induction of NR, plants were sampled 10 days after initial fertilization. In each case, four treated and four non-treated plants of each species were measured. Subsequent analyses of extractable soil nitrogen demonstrated that the resultant pool sizes of NO_3^- at the level of the roots were within the range experienced at the nutrient-rich sites (e.g. Camp Toilet, see results section).

Labelled ^{15}N uptake study

To assess the ability of the arctic species to take up NO_3^- and NH_4^+, $NaNO_3$ and NH_4Cl solutions were labelled with 5% atom excess ^{15}N (Cambridge Isotope Laboratories, USA) and spread at the rate of 20 g (N) m^{-2} around individual plants growing at the Beach Ridge site. To reduce surficial contamination of the fertilized plants, we rinsed each plant with 80 mL of distilled water immediately after the nutrient addition. At harvest, the excised roots and shoots were rinsed in distilled water. As it rained on several days before and during the ^{15}N treatment experiment, ^{15}N uptake would not have been affected by a lack of soil moisture. Small plant size necessitated pooling of the replicate samples for subsequent analysis. Non-treated plants were used as controls. Following excavation and rinsing, the plants were oven dried at 60° C for 2 days.

Chemical analyses of ^{15}N-labelled tissue

Upon return to the University of Toronto, the samples were redried (70° C for 1 d) and ground. Total nitrogen of Kjeldahl destruction

samples was determined colorimetrically using indophenol blue (Novozamsky et al. 1974). NO_3^- was determined colorimetrically by nitrification of salicylic acid from water extracts (Cataldo et al. 1975). The atom proportion of ^{15}N-nitrogen in each pooled sample was determined by optical emission spectroscopy, using a modified Dumas method (Preston et al. 1981). The amount of NO_3^- and NH_4^+ fertilizer taken up by the roots and shoots during the 10 day treatment period was then calculated using the enriched atom proportion of ^{15}N and the total nitrogen concentration. In each case, the background ^{15}N was subtracted from the enriched treatment values.

As the total yield of each treatment was low, even after pooling, we were only able to conduct a single extraction of total N and NO_3^- from each pooled sample. Three replicate measurements were then made of each total N and NO_3^- extraction. Duplicate measurements of the atom proportion of ^{15}N-nitrogen in each pooled sample were made. There was no difference between the species background percentage of ^{15}N (0.36%) in the roots or shoots of the seven species.

Statistical analyses

Data were analyzed with the SYSTAT statistical package using the one and two way analyses of variance and Tukey's multiple comparison options (Wilkinson 1990). Statistical significance was determined at $p<0.05$.

Results and discussion

Soil nitrogen concentrations

The concentration of extractable nitrogen, and in particular NO_3^-, was very low in the untreated soils collected from the Beach Ridge site and in soils collected from around the roots of plants growing on the beach ridge, except around *O. digyna*, where the concentration of NH_4^+ was significantly greater than in any other species ($p<0.001$; Table 1). Additions of $NaNO_3$ to the beach ridge soils resulted in a significant increase in exchangeable NO_3^- levels around the roots of *Salix arctica*, *Saxifraga oppositifolia* and *D. integrifolia* ($p<0.001$; Table 1).

In contrast, soils from around the roots of *Saxifraga cernua* at the Camp Toilet and *P. radicatum* at the Lemming Burrow site had high concentrations of extractable NH_4^+ and NO_3^- (Table 1). This suggests that NR activity could not have been limited by soil NO_3^- availability per se at the Camp Toilet and Lemming Burrow site.

Leaf and root NR activities

The level of maximum potential in vivo NR activity in leaves and roots was low in untreated plants of all species at the Beach Ridge site, with the potential for NR activity (per unit of fresh weight) being greater in the leaves than roots in five of the seven plant species (Fig. 1). The lowest

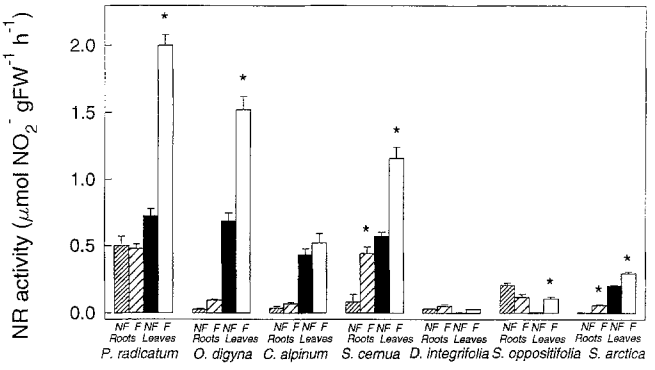

Fig. 1. The effect of NO_3^- applications on potential in vivo *NR* activity in leaves and roots of seven high arctic plant species growing at the nutrient-poor Beach Ridge site. Values are means ($n=4$, $\pm$SE). Abbreviations: *NF*, Non fertilized plants: *F*, $NaNO_3$ fertilized plants. Significant effects of NO_3^- treatment on root and leaf *NR* activity are designated by the * symbol ($p<0.05$)

Table 1. Variation in KCl-extracted available soil NH_4^+ and NO_3^- concentrations. Samples were collected from either soil alone or from around roots of 10 day $NaNO_3$ treated or untreated plants. Values represent the mean of 8 and 4 ($\pm$ SE) determinations for soil alone and plant-soil samples respectively

Soil/species	Site/date	Treatment	Available N Concentration (ppm)	
			NH_4^+	NO_3^-
Soil alone	BR/26 June	None	0.5 ± 0.2	0.1 ± 0.1
	BR/2 July	None	1.7 ± 0.4	0.8 ± 0.3
	BR/7 July	None	0.4 ± 0.1	0.1 ± 0.1
	BR/15 July	None	1.5 ± 0.9	0.4 ± 0.2
Salix arctica	BR/7 July	None	0.5 ± 0.2	1.0 ± 0.2
	BR/7 July	NO_3^- application	0.9 ± 0.3	23.8 ± 5.8
Saxifraga oppositifolia	BR/7 July	None	0.4 ± 0.1	0.5 ± 0.2
	BR/7 July	NO_3^- application	0.5 ± 0.1	13.5 ± 3.5
Dryas integrifolia	BR/8 July	None	2.1 ± 0.5	0.4 ± 0.2
	BR/8 July	NO_3^- application	2.1 ± 0.1	67.3 ± 14.0
Saxifraga cernua	BR/12 July	None	2.9 ± 0.5	0.3 ± 0.2
	CT/12 July	None	144.5 ± 30.0	20.7 ± 3.6
Oxyria digyna	BR/12 July	None	11.5 ± 0.8	0.3 ± 0.2
Papaver radicatum	LB/12 July	None	195.6 ± 50.2	10.7 ± 3.2

BR, Beach Ridge site; *CT*, Camp Toilet site; *LB*, Lemming Burrow site

levels of NR activity occurred in the three species most characteristic of the beach ridge habitat (*D. integrifolia*, *Salix arctica* and *Saxifraga oppositifolia*). Soil NO_3^- availability did not appear to be responsible for the low NR activity in *D. integrifolia* or *C. alpinum*, as additions of $NaNO_3$ failed to induce leaf or root NR activity in these species (Fig. 1). Similarly, the rates of NR in *Salix arctica* and *Saxifraga oppositifolia* remained low after NO_3^- supplementation, despite the significant induction of NR activity by NO_3^- in leaves and roots of *Salix arctica*, ($p<0.05$ and 0.01 respectively) and leaves of *Saxifraga oppositifolia* ($p<0.05$). The suggestion that NO_3^- was not responsible for the low NR activity in the above species is also supported by the observation that rates of leaf NR activity in *D. integrifolia*. *Salix arctica*, *Saxifraga oppositifolia* and *C. alpinum* were no greater in plants sampled at the fertile Camp Toilet site (Fig. 2) than at the infertile Beach Ridge site (Fig. 1).

NO_3^- supplementations at the Beach Ridge site induced NR activity in leaves of three of the species characteristic of more fertile sites (*P. radicatum*, *O. digyna* and *Saxifraga cernua*; $p<0.001$ in all three species), and in roots of *Saxifraga cernua* ($p<0.05$; Fig. 1). *P. radicatum* and *O. digyna* leaf NR activity rates were also significantly greater in plants sampled from the fertile Lemming Burrow and Camp Toilet sites, respectively (Fig. 2), than in the untreated plants at the Beach Ridge site ($p<0.001$ in both species; Fig 1). These results suggest that *P. radicatum*, *O. digyna* and *Saxifraga cernua* were capable of assimilating NO_3^-, and that soil NO_3^- availability was limiting NR activity in these species at the Beach Ridge site.

Despite the induction of leaf and root NR activity in *Saxifraga cernua* following NO_3^- supplementations at the Beach Ridge site (Fig. 1), no differences in leaf NR activity were found between untreated plants at the Beach Ridge site (Fig. 1) and plants sampled from the NO_3^--rich Camp Toilet site (Fig. 2). High concentrations of NH_4^+ at the Camp Toilet site (145 ppm, Table 1) relative to that of the Beach Ridge site (3 ppm) may provide an explanation for this discrepancy, as NH_4^+ can inhibit the uptake and assimilation of NO_3^- (Frith 1972; Srivastava 1980).

Despite the lack of induction of leaf NR activity in *C. alpinum* moderate levels of leaf NR activity were found in the leaves collected from the untreated plants at the Beach Ridge (Fig. 1) and Camp Toilet sites (Fig. 2). *C. alpinum* therefore appears to have the potential to utilize NO_3^- nitrogen under field conditions. The lack of further induction of NR activity indicates that soil NO_3^--deficiencies per se were not limiting induction of additional enzyme activity in *C. alpinum*.

Effect of assay temperature on NR activity

Increases in assay temperature significantly increased enzyme rates ($p<0.001$) in leaves of the four species characteristic of the more fertile habitats (*P. radicatum*, *O. digyna*, *Saxifraga cernua* and *C. alpinum*; Fig. 3). The standard assay temperature (20° C) therefore provided an overestimate of the potential amount of NO_3^- that could be reduced under the colder field conditions. A similar conclusion on the effect of assay temperature on NR activity has been reported previously (Jónsdóttir and Callaghan 1990). Assay temperature had no significant effect on leaf NR activity in *Saxifraga oppositifolia*, *D. integrifolia* or in *Salix arctica*.

Chemical composition of NO_3^- and NH_4^+ treated beach ridge plants

Could limited NO_3^- uptake explain the limited induction of NR activity in *D. integrifolia*, *Salix arctica*, *Saxifraga oppositifolia* and *C. alpinum* following NO_3^- supplementation (Fig. 1)? Additions of $^{15}NO_3^-$ had almost no effect on root or shoot total N of *D. integrifolia* and *Salix arctica* at the Beach Ridge site (Table 2). Furthermore, exposure to high levels of soil NO_3^- at the Camp Toilet site did not result in shoot NO_3^- concentrations of *Salix arctica* being any greater than that of the untreated beach ridge plants (Table 3). These results suggest, therefore, that NO_3^- uptake was limited in *D. integrifolia* and *Salix arctica*.

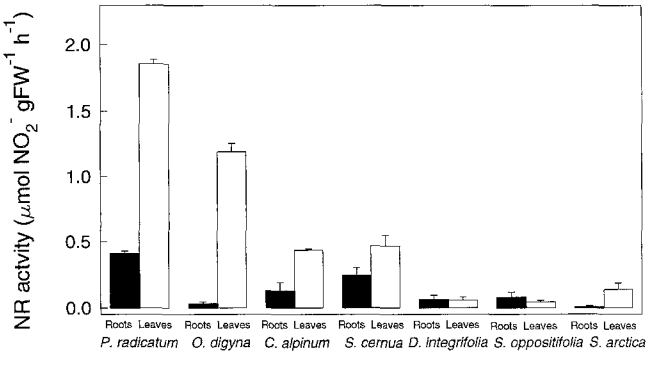

Fig. 2. Rates of potential in vivo NR activity in leaves and roots of plants growing at the nutrient-rich Camp Toilet and Lemming Burrow sites. All species were sampled from near the Camp Toilet, except for *P. radicatum*, which was sampled from the Lemming Burrow site. Values are means ($n=4$, ±SE)

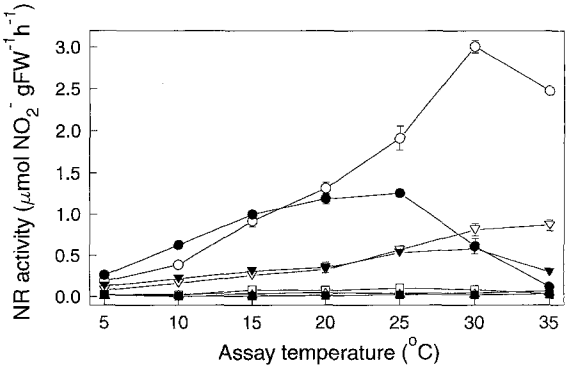

Fig. 3. Effect of assay temperature on in vivo leaf NR activity of seven high arctic plant species, collected from the Camp Toilet or Lemming Burrow sites. Values are means ($n=4$, ±SE) of *P. radicatum* (○), *O. digyna* (●), *C. alpinum* (▽), *Saxifraga cernua* (▼), *D. integrifolia* (△), *Saxifraga oppositifolia* (■) and *Salix arctica* (□)

Table 2. The effect of N applications on the net increase in total N (mmol N g^{-1} [DW]) of pooled samples of plants growing on the beach ridge. The concentrations of total N in untreated plants are given for reference. The absolute amount of $^{15}NO_3^-$ and $^{15}NH_4^+$ labelled nitrogen taken up over the 10 day period (Net enrichment values; mmol N g^{-1} [DW]) and the percentage of the total N that the labelled nitrogen accounted for in the samples after 10 days are given. The total N concentrations of shoots from selected species from the Beach Ridge (BR), Camp Toilet (CT) and Lemming Burrow sites (LB) sites are also given for reference. n/a denotes that measurements of net % ^{15}N increase were not made for *O. digyna*, due to insufficient ^{15}N solutions

Species		Treatment				
		None	$^{15}NO_3^-$ application		$^{15}NH_4^+$ application	
			Net increase in total N	(% total N)	Net increase in total N	(% total N)
Shoots						
P. radicatum	BR	0.40	0.09	(14.5%)	0.05	(9.5%)
	LB	1.12				
O. digyna	BR	0.51	n/a	n/a	n/a	n/a
	CT	1.75				
C. alpinum		0.52	0.14	(23.2%)	0.12	(19.2%)
S. cernua		0.37	0.28	(43.9%)	0.17	(35.9%)
D. integrifolia		0.40	0.02	(4.8%)	0.05	(10.4%)
S. oppositifolia		0.34	0.18	(34.1%)	0.12	(24.2%)
S. arctica	BR	0.81	0.02	(2.2%)	0.03	(3.4%)
	CT	0.89				
Roots						
P. radicatum.		0.56	0.08	(14.8%)	0.07	(12.5%)
O. digyna		0.66	n/a	n/a	n/a	n/a
C. alpinum		0.50	0.11	(16.9%)	0.14	(20.6%)
S. cernua		0.39	0.06	(20.9%)	0.11	(31.3%)
D. integrifolia		0.30	0.02	(6.1%)	0.06	(10.4%)
S. oppositifolia		0.38	0.05	(13.7%)	0.04	(12.9%)
S. arctica		0.40	0.01	(2.4%)	0.03	(7.2%)

Table 3. The concentrations of tissue NO_3^- (mmol N g^{-1}[DW] and as a percentage of total N) in pooled samples of untreated and 10 day NO_3^--treated plants growing on the beach ridge. The concentrations tissue NO_3^- in shoots from selected species from the Beach Ridge (BR), Camp Toilet (CT) and Lemming Burrow sites (LB) sites are given

Species		Treatment			
		None		$^{15}NO_3^-$ application	
		mmol N g^{-1}[DW]	(% total N)	Net increase	(% total N)
Shoots					
P. radicatum	BR	0.10	(25.0%)	0.09	(14.5%)
	LB	0.13	(11.6%)		
O. digyna	BR	0.12	(23.5%)	0.12	(22.5%)
	CT	0.10	(5.7%)		
C. alpinum		0.11	(21.1%)	0.16	(26.5%)
S. cernua		0.10	(27.8%)	0.14	(21.9%)
D. integrifolia		0.10	(25.0%)	0.13	(31.1%)
S. oppositifolia		0.08	(23.5%)	0.08	(15.2%)
S. arctica	BR	0.12	(14.8%)	0.09	(9.9%)
	CT				
Roots					
P. radicatum		0.05	(8.9%)	0.04	(7.4%)
O. digyna		0.09	(13.6%)		
C. alpinum		0.06	(12.0%)	0.08	(12.3%)
S. cernua		0.05	(12.8%)	0.24	(83.6%)
D. integrifolia		0.06	(20.0%)	0.05	(15.3%)
S. oppositifolia		0.03	(7.9%)	0.03	(8.2%)
S. arctica		0.07	(17.5%)	0.08	(19.2%)

However, the limited induction of NR activity in *Saxifraga oppositifolia* does not appear to have been due to limitations in NO_3^- uptake, as $^{15}NO_3^-$ applications led to substantial net increases in total N of *Saxifraga oppositifolia* shoots (Table 2). Furthermore, the net increase in total N of *Saxifraga oppositifolia* following NO_3^- treatment was unlikely to have been due to the accumulation of NO_3^-, as there was little difference in the tissue NO_3^- concentrations of the untreated controls and plants treated with NO_3^- (Table 3).

Discussion

Our results demonstrate that the plant species characteristic of the infertile Beach Ridge soils (*D. integrifolia* and *Salix arctica*) have only limited ability to utilize increases in NO_3^- availability under field conditions. This was shown by their very low rates of in vivo NR activity both before and after NO_3^- supplementation (Fig. 1) and limited uptake of $^{15}NO_3^-$ (Table 2). However, NH_4^+ uptake and assimilation may also be limited in these two species,

as little difference was observed in the uptake of $^{15}NO_3^-$ and $^{15}NH_4^+$ in *D. integrifolia* or *Salix arctica* (Table 2). Similar amounts of $^{15}NO_3^-$ and $^{15}NH_4^+$ uptake also occurred in the five other selected plant species (Table 2).

What was the cause of the apparent limited ability of *D. integrifolia* and *Salix arctica* to utilize both forms of inorganic nitrogen? Slow growth imposed by environmental or genetic constraints may provide an explanation, as rates of NO_3^- uptake and NR activity are often lower in slow growing plant species (Clement et al. 1978a, b; Gharbi and Hipkin 1984; Runge 1983). Alternatively, *D. integrifolia* and *Salix arctica* may have been relying on internal nutrient reserves to support new growth, as reported for other arctic plant species (Chapin et al. 1986; Marion and Kummerow 1990).

The ability of *Saxifraga oppositifolia* to take up NO_3^- (Table 2) contrasts with its apparent inability to reduce NO_3^- (Fig. 1). This discrepancy may have been due to an underestimate of NR activity, as penetration of incubation medium into the unsliced *Saxifraga oppositifolia* could have been limited. Alternatively, the $^{15}NO_3^-$ taken up may have been converted to an alternative nitrogen form (eg. NH_4^+ or organic nitrogen) before uptake, possibly by mycorrhizae. Some mycorrhizae are able to assimilate NO_3^- (Ho and Trappe 1980; Lundeberg 1970; Sarjala 1990). Furthermore, extensive ectomycorrhizal hyphal growth on the surface of and within the roots of *Saxifraga oppositifolia* has been reported at Truelove Lowland (Bledsoe et al. 1990) and elsewhere in the Canadian High Arctic (Kohn and Stasovski 1990). However, regardless of the involvement of mycorrhizae, and/or whether NR activity was underestimated, our results demonstrate that *Saxifraga oppositifolia* was able to utilize NO_3^- supplementations, as $^{15}NO_3^-$ (or a reduced product of $^{15}NO_3^-$) was taken up without being stored (Tables 2 and 3).

In contrast to *D. integrifolia* and *Salix arctica*, the species commonly found on fertile habitats (*C. alpinum*, *O. digyna*, *P. radicatum* and *Saxifraga cernua*) were capable of taking up (Table 2) and assimilating NO_3^- (Figs.1 and 2). This potential to utilize NO_3^- was perhaps not surprising, given the relatively high concentrations of NO_3^- in their characteristic habitats (e.g. animal burrows, Table 1). Other arctic plant species have also been shown to possess the capacity to take up and assimilate NO_3^- nitrogen, despite growing on soils dominated by NH_4^+ (Koch et al. 1991).

While the maximum rates of NR in *C. alpinum*, *O. digyna*, *P. radicatum* and *Saxifraga cernua* were far greater than that observed in *D. integrifolia*, *Salix arctica* and *Saxifraga oppositifolia*, they were considerably less than the maximum potential rates exhibited by some temperate crop species, which can exhibit rates in excess of 15 μmol NO_2^- $gFW^{-1}h^{-1}$ (Janiesch 1973 as cited by Smirnoff and Stewart 1985; Havill et al. 1974; Runge 1983). While the difference in values may be due in part to the growth conditions and methodology used, our results indicate that maximum potential NR activity is lower in high arctic plant species under arctic field conditions, relative to temperate crop species grown under more favorable conditions. In fact, the maximum potential NR rates of the selected high arctic plant species remain lower than that of a temperate crop species (*Hordeum vulgare* cv Steptoe) when all plant species are grown under identical controlled environment conditions (20° C; Atkin unpublished data). Similar differences between the potential rate of NR activity in arctic and temperate plant species under controlled environment conditions have been recently reported (Chapin et al. 1993).

The maximum potential rates of NR activity in *C. alpinum*, *O. digyna*, *P. radicatum* and *Saxifraga cernua* may have, however, been insufficient to allow growth to occur on substrates containing NO_3^- as the sole nitrogen source. To assess this question, we calculated the reduced nitrogen demands imposed by a constant relative growth rate (RGR) and plant nitrogen concentration (PNC) in *O. digyna*. Semikhatova et al. (1992) reported that the RGR of *O. digyna* under field conditions was approximately 100 mg g(dry weight)$^{-1}$ d^{-1}, a value presumably determined from plants grown on fertile sites. If one assumes a PNC of 1.1 mmol N g(dry weight)$^{-1}$ (the mean PNC value for *O. digyna* in Table 2), and a fresh to dry weight ratio of 12 (Atkin unpublished data), then the amount of NO_3^- that would needed to be taken up and reduced by *O. digyna* would be 0.4 μmol NO_3^- g(fresh weight)$^{-1}$ h^{-1}. This calculated value is considerably less than the maximum potential rate exhibited by *O. digyna* under field conditions (1.5 μmol NO_3^- g(fresh weight)$^{-1}$ h^{-1}, Fig. 1), suggesting that the rate of maximum potential NR activity would have been sufficient to allow *O. digyna* to rely on NO_3^- as its sole nitrogen source.

The above calculation was based on the assumption that maximum potential rates of in vivo NR activity were an accurate estimate of actual NO_3^- reduction rates. This is unlikely to have been the case, given the relatively high assay temperature used, and the provision of exogenous NO_3^- in the assay media, both of which would have resulted in an overestimate of the rate of NO_3^- reduction occurring in situ. The rate of NR activity in situ may not therefore, have been sufficient to completely satisfy the reduced nitrogen requirements of the selected plant species. Nevertheless, our results do suggest that a substantial proportion of the nitrogen requirements of the species characteristic of fertile habitats (*C. alpinum*, *O. digyna*, *P. radicatum* and *Saxifraga cernua*) could potentially be met by NO_3^-, when available.

Despite growing on soils containing very small pool sizes of NO_3^-, all species in our study accumulated large amounts of NO_3^- as a proportion of total N (Table 3). This indicates that the selected high arctic plant species may acquire a substantial proportion of their nitrogen as NO_3^-, even when the apparent availability of NO_3^- is low. The low rates of NR activity in *D. integrifolia* and *Salix arctica* (Fig. 1) would limit the ability of these two species to take advantage of any available NO_3^-.

In conclusion, our results demonstrate that five of the seven selected high arctic plant species do have the potential to utilize NO_3^- as a nitrogen source under field conditions. The highest potential to utilize NO_3^- was observed in the species characteristic of fertile habitats, while the lowest potential was observed in the species characteristic of the infertile environments. Further studies are needed to assess the actual NO_3^- assimilation rates in the selected plant species under field conditions, and the importance of inherent and/or environmental characteristics in

determining the potential of the selected high arctic to induce NR activity.

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