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Nitrate reductase activity in vegetation below an arctic bird cliff, Svalbard, Norway

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Abstract. Vegetated sites below bird-nesting cliffs are uniquely nutrient-rich habitats in the otherwise nutrient-poor arctic environment. Plants from six distinct vegetation zones below such a cliff at 79° N, Svalbard, Norway, were collected for analysis under greenhouse conditions. Leaf nitrate reductase activity (NRA) was analysed in 42 species representing 25 % of the Svalbard vascular flora. The species mean NRA values ranged from 0.37 to 8.34 µmols of nitrite ions formed per gram of plant fresh weight per hour. Species in the vegetated zone growing closest to recent guano deposits had the highest NRA values, (mean = 4.47) whereas plants growing farther below the cliff had significantly lower values (mean = 0.55).

A similar pattern was detected in a duplicate set of plants induced with 15 mM KNO_3; vegetation zone means for NRA ranged from 5.08 to 0.98 µmols of nitrite ions formed per gram of plant fresh weight per hour. Maximally induced species NRA values were highest in the first zones below the cliff and decreased downslope. This gradient paralleled the steep soil nitrate gradient, which decreased from 13.84 mg/l at the cliff-base to 1.03 mg/l downslope. Correspondingly, soil ammonium ions in the vegetation zones ranged between 1.96 mg/l at the cliff-base to 0.03 mg/l downslope. Correlations between NRA and soil nitrate provide a systematic basis for assigning scalar 'nitrogen figures' as indicators of habitat preference, here for the first time applied to arctic species.

Keywords: Ammonia; Guano; Nitrogen indication; Soil nitrate.

Nomenclature: Rønning (1979).

Introduction

Nitrogen, the element taken up in greatest amounts by plants from soil, is of major significance in plant ecology because of its involvement in plant growth and metabolism. Nitrogen constitutes as much as 6 % of the total dry weight in some plants (Lee & Stewart 1978) and is essential for all activities of living cells, including the synthesis of organic compounds such as amino-acids, proteins, and nucleic acids. Although in a few cases NH_4^+ provides the exclusive form of available soil N , in some soils NO_3^- is the predominant form available for uptake. The capacity for NO_3^- reduction in plants is therefore a prerequisite for, and an indication of, the optimal utilization of the natural N supply. Of the enzymes participating in reduction, nitrate reductase (NR) determines the rate of the reaction as a whole (Beevers & Hageman 1969). Occurrence and activity of NR are therefore of considerable ecological interest.

Low nitrogen levels limit plant growth over much of the biosphere and especially at high latitudes (Shaver & Chapin 1980; Maessen et al. 1983). Moreover, in the Arctic, nitrogen availability is limited by abiotic factors, e.g., low temperatures, little precipitation, slow chemical weathering of bedrock, poor soil aeration, low evapotranspiration, and impeded drainage of soils underlain by permafrost. Biotic processes such as slow natural decomposition rates, aggravated by the dominance of wet, snowy, and ice-covered surfaces, severely hinder nutrient cycling during the short 6 to 8 week growing season in the Arctic.

Exceptional nitrogen-rich 'oases' occasionally exist in the generally nitrogen-poor landscape of the Arctic. Large colonies of migratory birds transport nitrogen from sea to land during cliff-nesting activities in the spring and summer. The ornithogenic soils associated with these nesting sites receive seasonal flushes of nutrients during snowmelt-runoff. Later in the season rainfall redistributes these deposits of rich organic material to maintain a typical steep nitrogen gradient characterized by high levels at the cliff-base and lower concentrations downslope. Distinct identifiable zones of lush vegetation are present along this rich nitrogen gradient, and are best developed on the south-facing slopes where net solar radiation is highest.

A bird cliff habitat at 79° N on Svalbard provides a unique 'natural experiment' where the competitive advantage of effective nitrate assimilation can be investigated in plants growing along a natural nitrate gradient. The aim of this study was to investigate the relationship between the distribution of plant species in bird cliff vegetation and the amount of soil nitrate available in the region of sea-bird guano deposition. The species' capacity to synthesize NR may be a key factor for plant

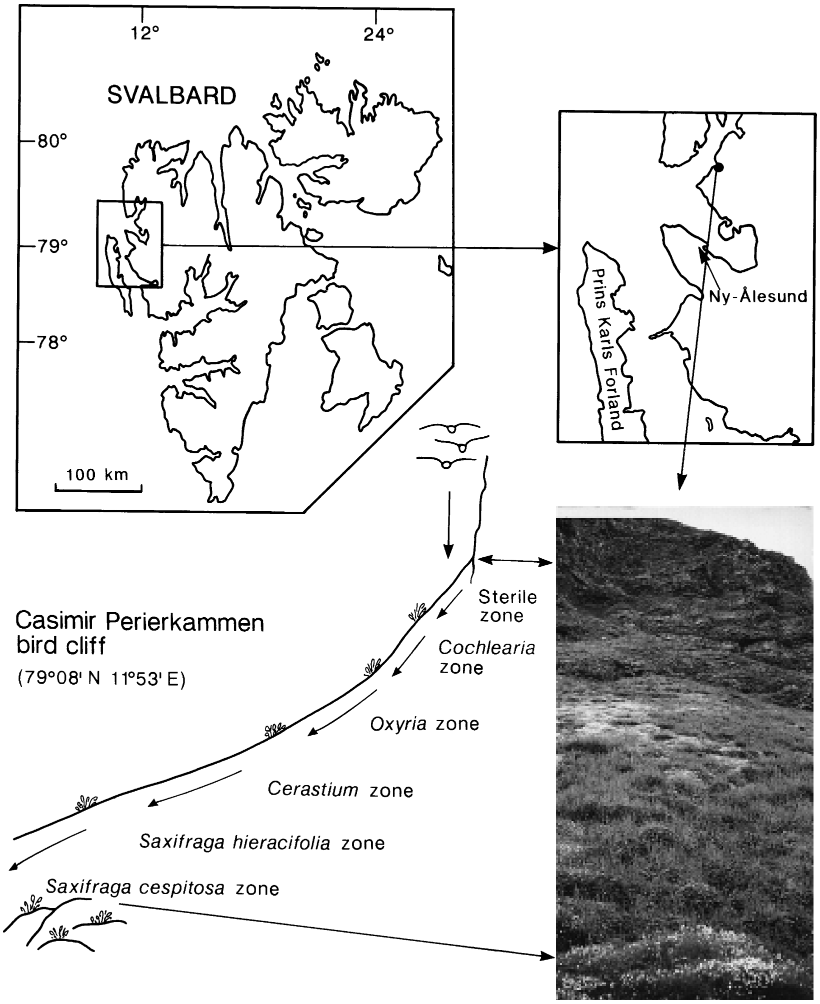

Fig. 1. Location map and vegetation below the Casimir Perierkammen bird cliff on NW Svalbard.

survival and distribution along the vegetation zonation. To test this hypothesis, constitutive NRA analyses were conducted on plants collected in their natural soils and transported to a controlled greenhouse environment. At the same time, induction capacity of the nitrate assimilating enzyme was investigated in a nitrate application-fertilization experiment conducted on a subset of the collected plants. Field investigations of NR activity have been conducted on temperate and boreal species from various environments (Gigon & Rorison 1972; Havill et al. 1974; Lee & Stewart 1978; Gebauer et al. 1988; Högbom & Ohlson 1991). This study is the first field investigation of NR activity in arctic plants.

Site description

The investigation focused on the vegetation zones under the Casimir Perierkammen bird cliff, (79° 08' N 11° 53' E) in the Krosfjorden region on northwest Svalbard (Fig. 1). Summers are cool with a June to August mean temperature of 4 °C and midday temperatures reaching 15 °C. Annual precipitation of 385 mm has been recorded in Ny-Ålesund, 15 km distant (Aune 1982). Ca. 3000 pairs of Kittiwakes (*Rissa tridactyla*) and 3000 Brunnich's guillemots (*Uria lomvia*) nest on a vertical south-facing cliff and deposit about 150 kg of guano per day on the vegetated slopes below the cliffs. Zones of low-growing herbaceous plants cover a vertical drop of more than 100 m below the cliffs. Mats of accumulated organic material are greater than 1 m thick in the lower zones. Bedrock consists of gneisses and magmatites, with some calcareous rocks in the lower slopes. There are 24 h of sun from April 17 to August 25 with the bird cliff receiving ca. 11 h of potential direct sun during this period.

Immediately below the bird cliff is a 30-m wide 'sterile' zone (45° slope). Guano and other organic matter (e.g. nesting material) accumulate in this area; seedling establishment is restricted, mainly due to the lack of soil, repeated local mechanical disturbance caused by litter and rock fall, and a high osmotic gradient in the guano. Below this zone a series of vegetated zones fan out to more than 200 m at the base (Fig. 1).

Cochlearia groenlandica dominates the first vegetated zone of ca. 500 m^2 . Fine moist litter material on the 45° slope is stabilized by a network of shallow *C. groenlandica* roots (Fig. 1). A 2-m strip of vegetatively reproducing *Puccinellia angustata* is located at the top of the zone and a few individuals of *Draba arctica* and *D. norvegica* are located close to the cliff side-walls. See Table 1 for species composition of each zone.

Oxyria digyna dominates the next zone, characterized by a moderate slope (20 - 30°) and undulating topography due to the accumulated rockfall. The substrate is moist and emits a pungent urea odour. *Oxyria* plants are robust with thick tuberous roots and completely cover the 700 m^2 of this zone.

Cerastium arcticum dominates an area of 1000 m^2. The zone has a slight slope (10 - 15°) and interdigitates with the lower boundary of the *Oxyria* zone. Species diversity increases in the *Cerastium* zone and is at a maximum in two *Saxifraga* zones with *S. hieracifolia* and *S. cespitosa* farther downslope. The combined *Saxifraga* zones are 200 m wide and support a continuous mat of the moss, *Aulacomnium palustre*, which is present to a depth of over 1 m and extends into the permafrost. The tundra area has rolling topography and abutts this lower edge of the bird cliff site.

Table 1. Species composition by vegetation zone (mid-zone altitude in m a.s.l.) in order of abundance. Constitutive and induced NRA, nitrate reductase activity (μmol $NO_2^-/g_{fw}/h$) for 42 vascular species below the Casimir Perierkammen bird cliff. Effect is given as the difference between NRA values. Number of samples (*n*), mean (*x*) and standard error (SE) are given for green leaf tissue for constitutive field and fertilized (15 mM KNO_3) groups. For N-figure, see Discussion.

	NRA							
Vegetation zone /species	Constitutive			Fertilized			Eff.	N-fig.
	n	*x*	SE	*n*	*x*	SE	*x*	
Cochlearia zone (95 m)								
Cochlearia groenlandica	18	3.55	0.50	18	4.35	0.37	0.80	8.1
Puccinellia angustata	6	3.11	0.89	5	5.28	1.00	2.17	6.7
Draba arctica	4	7.73	1.27	1	9.11	-	1.38	9.1
D. norvegica	3	8.34	1.08	1	13.00	-	4.66	13.0
Oxyria zone (80 m)								
Oxyria digyna	21	3.32	0.55	17	6.06	0.86	2.74	14.0
Poa pratensis	8	2.02	0.28	6	5.48	0.90	3.46	9.5
Draba alpina	9	6.54	1.21	5	7.84	2.03	1.30	12.6
D. daurica	16	4.66	0.33	11	7.89	0.87	3.23	12.8
D. oblongata	3	6.71	1.58	2	6.61	-	–0.10	9.1
***Cerastium* zone** (45 m)								
Cerastium arcticum	12	1.91	0.37	12	4.26	0.30	2.35	6.9
Taraxacum brachyceras	1	1.56	-	4	2.68	0.17	1.12	3.2
Chrysosplenium tetrandrum	17	1.04	0.16	15	1.56	0.16	0.52	2.7
Poa arctica	11	3.05	0.32	6	4.79	0.52	1.74	6.0
P. alpina	4	4.26	0.26	4	5.66	1.59	1.40	8.5
Trisetum spicatum	3	1.38	0.88	5	4.28	1.16	2.90	8.5
Polygonum viviparum	6	0.72	0.19	7	3.03	0.87	2.31	7.4
Cardamine nymanii	5	1.68	0.37	6	4.48	0.47	2.80	6.5
Ranunculus sulphureus	8	1.00	0.09	2	3.59	-	2.59	4.7
Potentilla hyparctica	5	0.68	0.10	6	3.41	0.49	2.73	4.4
Melandrium apetalum	4	2.27	0.41	3	1.71	0.21	–0.56	2.1
***Saxifraga hieracifolia* zone** (25 m)								
Saxifraga hieracifolia	10	1.11	0.11	9	1.36	0.13	0.25	2.0
S. cernua	6	0.86	0.06	3	0.94	0.38	0.08	1.6
Ranunculus pygmaeus	3	1.33	0.09	1	1.37	-	0.04	1.4
Saxifraga rivularis	5	1.18	0.29	4	2.35	0.34	1.17	3.0
Luzula arcuata ssp. *confusa*	2	0.44	-	2	1.72	-	1.28	2.1
Colepodium vahlianum	2	1.91	-	2	3.30	-	1.39	3.3
***Saxifraga cespitosa* zone** (6 m)								
Saxifraga cespitosa	4	0.51	0.11	3	1.23	0.37	0.72	1.8
Silene acaulis	3	0.63	0.09	2	1.02	-	0.39	1.2
Salix polaris	5	0.46	0.11	3	0.75	0.20	0.29	1.1
Saxifraga nivalis	5	0.81	0.06	2	1.07	-	0.26	1.4
Sagina intermedia	2	0.37	-	2	0.63	-	0.26	0.6
Erigeron humilis	4	0.43	0.08	4	1.08	0.30	0.65	1.9
Tundra zone (4 m)								
Dryas octopetala	4	0.38	0.13	6	1.10	0.08	0.72	1.3
Saxifraga oppositifolia	4	0.57	0.03	4	0.67	0.12	0.10	1.0
Salix reticulata	4	0.52	0.12	2	0.37	-	–0.15	0.4
Cassiope tetragona	6	0.61	0.11	5	0.46	0.05	–0.15	0.6
Carex misandra	3	0.82	0.35	7	2.83	0.24	2.01	3.5
C. rupestris	3	0.97	0.29	2	3.51	-	2.54	3.5
C. nardina	2	1.59	-	2	3.36	-	1.77	3.4
Pedicularis dasyantha	2	0.60	-	7	0.38	0.05	–0.22	0.6
Saxifraga aizoides	3	0.57	0.04	5	1.33	0.08	0.76	1.6
Pedicularis hirsuta	2	1.34	-	3	1.79	0.34	0.45	2.4

Methods

Soil nutrients

Samples ($n = 7$) were collected from the top 10 cm of soil in each of the vegetation zones. Nitrate, ammonium, phosphate (mg/l), and pH were determined on fresh soil samples immediately after collection (from Odasz 1988), and on dry samples from tundra sites (Odasz 1989). Nitrate and ammonium were extracted in calcium chloride and phosphate was extracted in ammonium lactate.

NRA analyses

Plants of 42 species were collected from the bird cliff vegetation following a random sampling design within each zone. Replicates of all species were collected in their original soil during the peak growing season (22-26 July). The number of replicates varied because some species were small and more abundant allowing for easy collection, resulting in many replicates while plants showing signs of stress after field collection were excluded from analyses. Each individual plant was placed in a 120-mm diameter, 120-mm tall plastic pot and transported by boat for 2 h (15 km) to a greenhouse located in Ny-Ålesund (Fig. 1). Plants of each species were randomly separated into two groups both of which were analysed for NRA. One group represents constitutive enzyme activity values and these plants were kept in natural soil conditions. The second group was fertilized regularly with 15 mM KNO_3 to test if species had induction capacity of nitrate reductase activity above the field, or constitutive, levels. Plants were maintained at 9 - 12 °C to simulate field conditions.

NRA was determined during 1-21 August, a period with minimal spectral variation (Hisdal 1987). Analyses were standardized using fresh leaf material, in mid-day sunlight at constant temperature, to minimize potential variation in enzyme activity associated with different plant organs (Lee & Stewart 1978; Gebauer et al. 1988), circadian rhythms and leaf-age (Hipkin et al. 1984; Lillo 1984), or the influence of light and temperature (Nicholas et al. 1976; Margolis et al. 1988). NRA was estimated by measuring the amount of nitrite reduced from nitrate following the methods of Guerrero (1985). The bioassay was conducted on leaves because root reduction is a minimal portion of total plant NRA when large amounts of nitrate are available (Gebauer et al. 1988; Muller & Garnier 1990). Within each species, care was taken to use 0.5 - 1.0 g young leaf material. Because of between-species differences in leaf size, the sampled mass corresponds to different numbers of leaves. These were cut into ca. 1 mm × 2 mm pieces which were placed in test tubes with phosphate buffer containing propanol–1 and 100 mM KNO_3 and incubated in the dark for 1 h at 28 °C in a water bath. Activity was stopped by immersion in boiling water for 25 min. The product, NO_2^-, was dyed with N(1-naphtyl) ethylene diamine dichloride, sulphamide, and 3 M HCl, and measured at 540 nm with a spectrophotometer (Schimadzu, model UV-240). NRA was calculated and reported as µmol of nitrite ions formed per gram of fresh weight of the plant per hour (µmol $NO_2^-/g_{fw}/h$). The standard assay was conducted on all species.

Analysis of variance was used for statistical comparisons among vegetation zones and treatments. Correlation analyses were conducted on constitutive and induced NRA, and on NRA and soil nitrate values (Statview plus, Machintosh). The difference between the NRA values measured in the fertilization treatments and those in natural soil conditions indicates increase in enzyme activity due to induction.

In this study I used the maximally induced nitrate reductase activities of species to establish nitrogen indicator figures for arctic plants, thus extending the system of Ellenberg (1991) for central-European plants for different levels of nitrogen, using a scalar system from 1, environments poor in N, through 9, rich in N.

Results

Soil nutrients

Soil nutrient values decrease downslope with the sole exception of a relatively high phosphate level in the *Oxyria* zone (Table 2). The nitrate gradient, decreases downslope from 13.84 mg/l to 1.03 mg/l. Correspondingly, the soil ammonium ranged from 1.96 mg/l at the top to 0.03 mg/l downslope. The ratio $NO_3^- : NH_4^+$ decreased downslope; the high value for *Saxifraga cespitosa* zone is accounted for by extremely low soil NH_4^+ (Table 2). The soil pH, on the other hand, increases downslope. Sea-bird guano contains a wide range of phosphate minerals (Tatur & Barczuk 1985) and the concentrations found in this site are unlikely to be limiting to plant growth (Table 2).

NRA in natural soil conditions

NRA was detectable in all 42 species tested in natural soil. Mean NRA ranged from 0.37 µmol $NO_2^-/g_{fw}/h$ in the *Saxifraga* zone to 8.34 µmol $NO_2^-/g_{fw}/h$ in the *Cochlearia* zone (Table 1). Thus a decrease in values of over an order of magnitude was detected for species along a gradient downslope from the guano deposition site. Only nine species (mean NRA= 4.3 µmol $NO_2^-/g_{fw}/h$) grow in the two richest vegetation zones, while a total of 23 species (mean NRA= 1.12 µmol $NO_2^-/g_{fw}/h$) thrive in the lower zones where nutrients are less concentrated. In Table 2 the significant differences between mean NRA values for each zone are indicated by different letters, i.e. 'a' is significantly different from the

Table 2. Mean NRA values for constitutive field NRA and 15mM KNO_3 treatment for all individuals (*n*) of the species sampled in each vegetation zone below the Casimir Perierkammen bird cliff. Means (*x*) and one standard error (SE) for soil nutrients in mg/l, and mean, minimum and maximum pH, (data from Odasz 1988) and the $NO_3^- : NH_4^+$ ratios are from fresh soil samples from each vegetation zone. Tundra data are from dry soil samples, mg/100g (Odasz 1989). Letters indicate significant differences ($P < 0.001$) for parameters between vegetation zones (see text for details).

	NRA				Soil nutrients,mg/l										
	Constitutive		15 mM			NO_3^-		NH_4^+		PO_4^-		pH			
Vegetation zone	*n*	*x*	*n*	*x*	*n*	*x*	SE	*x*	SE	*x*	SE	*x*	min.	max.	ratio
Cochlearia zone	31	4.47^{a}	25	5.08^{a}	7	13.84^{a}	4.59	1.96^{a}	0.77	15.94^{a}	5.39	5.2^{a}	4.2	6.4	7.06
Oxyria zone	57	4.13^{a}	41	6.71^{b}	7	5.94^{b}	2.73	1.60^{a}	0.34	20.91^{a}	7.85	5.8^{b}	4.9	6.2	3.71
Cerastium zone	76	1.71^{b}	70	3.41^{c}	7	3.32^{b}	2.22	1.41^{a}	0.44	13.73^{a}	3.56	6.2^{c}	6.1	6.4	2.35
Saxifraga hieracifolia zone	28	1.10^{bc}	21	1.71^{d}	7	1.07^{c}	0.35	0.81^{ab}	0.10	4.74^{ab}	0.72	6.9^{d}	6.5	7.2	1.32
Saxifraga cespitosa zone	23	0.55^{c}	16	0.98^{d}	6	1.03c	0.50	0.03^{b}	0.01	1.23^{b}	0.19	8.9^{e}	8.8	9.0	34.3
Tundra	33	0.72c	43	1.41^{d}	7	0.0074^{d}	0.0004	nd		0.013c	0.0016	6.8^{d}	6.3	7.2	nd

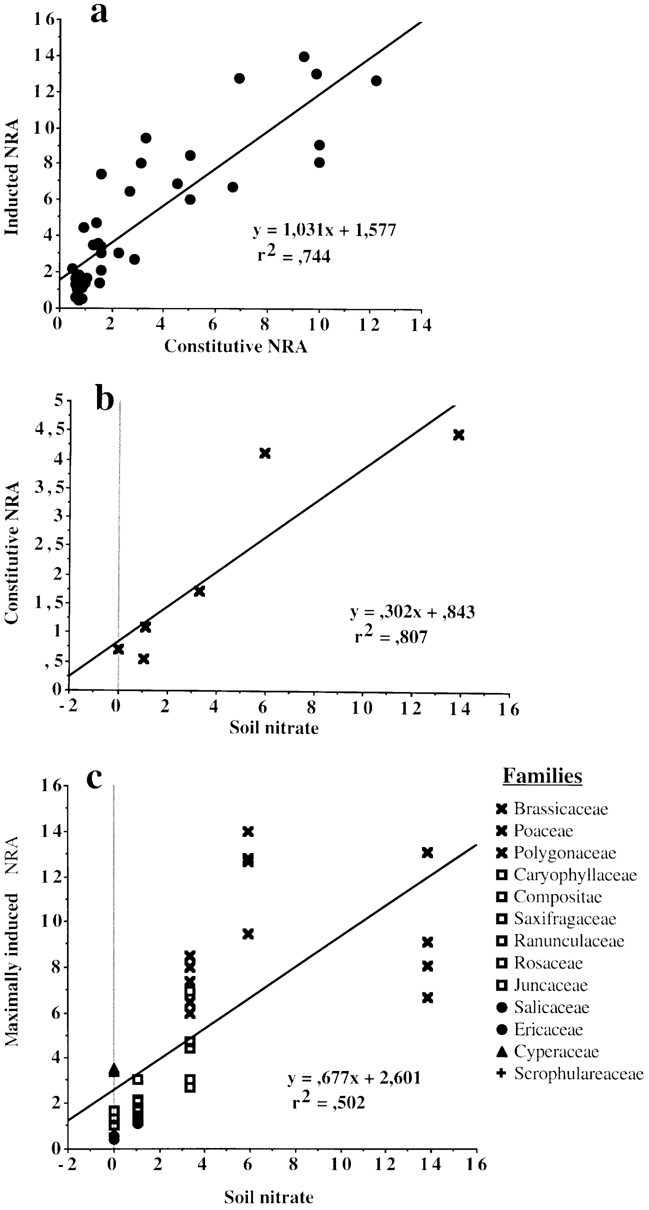

Fig. 2. Regressions relating **a.** Constitutive and induced NRA (μmol $NO_2^-g/_{fw}/h$) by species; **b.** mean constitutive NRA and soil nitrate (mg/ l) by zone; **c.** maximally induced NRA for all species and zone soil nitrate, with point symbols representing significant differences between family groups as differentiated by the ANOVA.

zones indicated by 'b', but is not different from zones indicated by 'a', etc.

Induction of NRA in natural soil conditions

The NRA of most plants induced with 15 mM KNO_3 increased above the constitutive values and ranged from 0.63 to 13.00 μmol $NO_2^-/g_{fw}/h$ (Table 1). Species in the two *Saxifraga* zones and in the Tundra zone had lowest NRA.

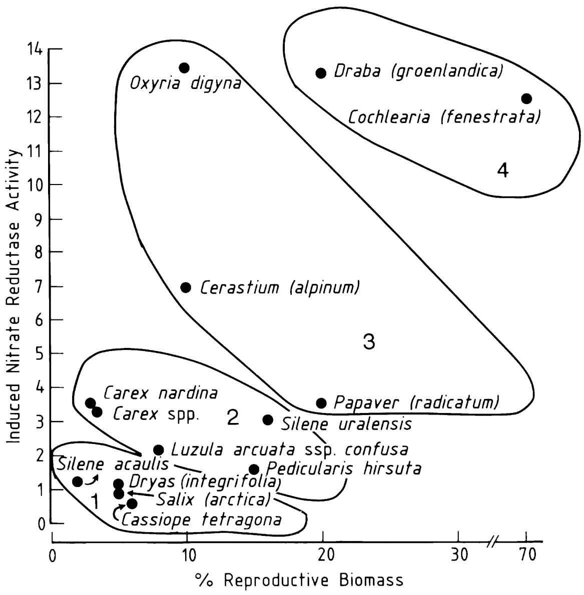

Fig. 3. Induced NRA values for selected species related to % biomass allocated to reproductive tissues. Biomass data are from Canada (Maessen et al. 1983). Species names in parentheses are relatives of species in this study. Species are grouped according to % reproductive tissues and NRA. 1 = lowest values to 4 = highest values.

Draba norvegica, in the *Cochlearia* zone, showed the greatest induced increase in NRA amounting to 4.66 μmol μmol $NO_2^-/g_{fw}/h$ above the constitutive NRA value (Table 1). In the *Oxyria* zone, *Poa pratensis* ssp. *alpigea* increased 3.46 μmol $NO_2^-/g_{fw}/h$ and *Draba daurica* increased 3.23 μmol $NO_2^-/g_{fw}/h$ above the constitutive values. Six species of the *Cerastium* zone showed NRA increases of over 2 μmol $NO_2^-/g_{fw}/h$ whereas in the *Saxifraga hieracifolia* zone three species were 1 μmol over the constitutive value (Table 1).

The mean induced NRA for the vegetation zones ranged from 0.98 μmol $NO_2^-/g_{fw}/h$ in the *Saxifraga cespitosa* zone to 5.08 μmol $NO_2^-/g_{fw}/h$ in the *Cochlearia* zone. Induced NRA values for the dominant species in each zone decreased significantly downslope: *Cochlearia groenlandica*: 4.35; *Oxyria digyna*: 6.06; *Cerastium arcticum*: 4.26; *Saxifraga hieracifolia*: 1.36; *Saxifraga cespitosa:* 1.23; and *Dryas octopetala* representative of the tundra sites: 1.10 (Table 2).

Accordingly, constitutive and induced NRA for all samples and for all species decreased significantly downslope (Table 1). Species with high constitutive enzyme activity also had additional capacity for considerable induction of the enzyme (Fig. 2a). All correlations between NRA and soil NO_3^-, for both mean NRA values for the entire data set and maximum NRA values for each species were significant ($p < 0.0001$) (Fig. 2b). The correlations of zone mean for all mean NRA values and maximum NRA values of the dominant species of each zone were not significant; correlation coefficients were similar here, but there were fewer degrees of freedom.

Plants from specific taxonomic groups showed similarities in habitat preference along the guano gradient. Species from the *Brassicaceae*, *Poaceae* and *Polygonaceae* families were growing high on the slope, nearest the cliff, on soils with the most concentrated nitrate levels, and had capacity for the greatest NRA (Fig. 2c).

The capacity for enzyme activity is also related to the growth strategy of plants and the amount of biomass allocated to reproductive tissues (Fig. 3). The distribution of the species in the vegetation and their capacity for maximally induced NRA was the basis for assigning N-figures (referring to Ellenberg et al. 1991) to species of this study, values ranged from 0.4 for *Salix reticulata* to a maximum of 14.0 for *Oxyria digyna*. Values are highest in the top zones and decrease downslope.

Discussion

Nitrate reductase activity

Species dominating the vegetation zones with concentrated soil nitrate showed greater capacity to synthesize NR than species growing in areas of lower nitrate (Tables 1 and 2). Such evidence supports the suggestion that the differential capacity for NRA in vascular species results in the development and maintenance of distinct vegetation zones in the bird cliff meadow.

Ecological strategies

Effective assimilation of nitrate may provide a competitive edge in interspecific establishment and growth of arctic plants in ornithogenic soils. *C. groenlandica* and *O. digyna* appear to out-compete most other species in their respective zones. Genetic differentiation may have resulted in specially adapted populations of these species. By means of effective nitrate assimilation (mean induced NRA = 4.35, and 6.06 μmol $NO_2^-/g_{fw}/h$, respectively) and probable tolerance to concentrated ammonia and other nutrients in the sites, these robust species thrive in a dense, high biomass vegetation (plant cover - 100%) and grow rapidly to heights of over 45 cm in the bird cliff vegetation. The large individuals of these two species may be a result of great growth response due to abundant useable nutrients in the mesic bird cliff meadow.

Draba species, however, have high NRA, but they may be genetically constrained to a small size and must compete for sunlight through the dense stands of the dominating *C. groenlandica* and *O. digyna* plants. Field-based habitat studies such as these are prerequisites for understanding ecological behavior which is not necessarily identical with physiological demands measured in isolation under laboratory conditions.

The r- vs. K- selection (Stearns 1976) may be useful in describing growth strategies which relate to species differences in NRA. *C. groenlandica* is short-lived, has a fast growth rate, high productivity, and high reproductive achievement (Fig. 3, group 4), high capacity for photosynthesis and nutrient absorption, and the ability to exploit nutrient-rich environments. The rapid assimilation of absorbed nitrate into tissues and the capacity to store large concentrations of nitrate in stems and leaves allows concordant high NRA in nitrophilous ruderal species (Lee & Stewart 1978).

On the other hand, smaller, slow-growing species such as *Cassiope tetragona* and *Silene acaulis* are more typical of K-strategists. These tend to live longer and allocate less biomass to reproduction (Fig. 3, group 1). A combination of low capacity for NRA and the small size of these K-strategists makes sunlight competition with the fast growing species difficult. The K-strategists in group 1 (Fig. 3) are known to be long-lived, *Dryas*: 108 yr, *Silene*: 100 yr, *Salix*: 59 yr (Callaghan & Emanuelsson 1985), and these show low NRA values both before and after fertilization. In group 2, the longevity of *Luzula* exceeds 10 yr, whereas in group 3, *Cerastium* may reach 10 yr, *Oxyria*, 50 yr, and in group 4, *Cochlearia* lives to a maximum of 5 yr. Group 2 species all have relatively high NRA. Thus, life expectancy is inversely related to NRA and reproductive biomass.

In the upper vegetation zones, however, the position of the two species, *Cochlearia* and *Oxyria*, contradicts the otherwise direct correlation between plant NRA and soil nitrate. The mean induced NRA for *Oxyria*, 6.06 μmol $NO_2^-/g_{fw}/h$, is greater than the mean of 4.35 μmol $NO_2^-/g_{fw}/h$ for *Cochlearia*, which is growing on more concentrated soil nitrate (Table 1). Species establishment is influenced by substrate composition, and *Cochlearia* roots form a shallow network which stabilizes the dry unconsolidated nesting litter fall. In contrast, the thick long-lived tuberous *Oxyria* roots act to stabilize the undulating topography of the rockfall prevalent in the next zone. *Oxyria* produces greater root biomass in arctic than alpine stands (Mooney & Billings 1961), and, once established, *Oxyria* prevents most other species from germinating in its understory where limited light also restricts potential NRA.

Furthermore, the relationship between root morphology and the ability to establish and stabilize in the contrasting substrate types may also be regulated by root size and ion flux at root surfaces. Small roots, like those of *Cochlearia*, have higher demand per unit root surface area (Clarkson et al. 1986), which may explain the dominance of this species at high soil nitrate levels. Water availability and limitation of micronutrients at different pH levels are potential limitations depending on root and substrate conditions.

The 'natural experiment' of this bird cliff provides an example of how extremes in abiotic conditions limit species diversity. In nutrient-rich habitats, inorganic N nutrition usually prevails, NO_3^- is the dominant form and NRA is of ultimate importance (Lee & Stewart 1978). However, in poor sites species have other strategies for improving nutrient status such as nitrogen-fixing mutualists, ericoid, or ectomycorrhizal symbioses which utilize complex organic sources of N. Conversely some species have preference for ammonium. Often species commonly mycorrhizal in nutrient-poor sites do not develop the association when growing in rich habitats. Cyanobacteria, for example, were found associated with moss in the bird cliff vegetation but the high nutrient levels inhibited nitrogen-fixation (B. Solheim pers. comm.). Väre et al. (in press) found that although *Polygonum viviparum*, *Silene acaulis* and *Saxifraga oppositifolia* are ectomycorrhizal in other areas, they did not have this association in Svalbard habitats. Some species can increase the amount of nitrate uptake per unit root as nitrate becomes limiting. Another adaptive strategy is to reduce growth rather than produce nutrient-deficient tissue.

Among families, assimilation of $N0_3^-$ is most pronounced in the *Brassicaceae*, dominating the top vegetation zone and represented by *Draba* species in the next zone (Fig. 2c). High levels of NRA may be the most important explanation for the successful ruderal habit of this phylogenetic group. *Poaceae* (*Puccinellia angustata*, *Poa pratensis*), and *Polygonaceae* (*Oxyria digyna*) dominate the richer soils, whereas *Salicaceae*, *Ericaceae* and *Scrophulariaceae* have a significantly lower capacity to induce NRA and dominate lower zones (Fig. 2c). The two *Scrophulariaceae* species in this study, *Pedicularis dasyantha* and *P. hirsuta*, are hemiparasitic plants with low NRA. Hemiparasitic plants have access to nitrate in host plant xylem sap and are not solely dependent on nitrate assimilation from the soil (Lee et al. 1986).

Naturally fertilized habitats

Constitutive NRA values in the bird cliff, ranging from 0.37 to 8.34 $NO_2^-/g_{fw}/h$ for the 42 species, are within reported mean values for other fertilized sites such as areas where cattle congregate, which reach values as high as 13.33 $\mu mol\ NO_2^-/g_{fw}/h$ (Gebauer et al. 1988). Gradients in NRA have been recognized along successional series, ruderal to climax species (Lee et al. 1986) and from old field ruderals to forest climax species (Franz & Haines 1977). The importance of nitrogen as an ecological factor is emphasized by comparing nitrate reductase activity values for diverse habitats, fellfield = 0.23, bog = 0.02, woodland = 1.32, and ruderal = 4.58 (mean constitutive NRA in $NO_2^-/g_{fw}/h$) (Lee et al. 1986).

Other habitats influenced by ornithogenic soils have been investigated in penguin rookeries in Antarctica (Speir & Cowling 1984; Tartur & Barczuk 1985), in an Estuary in Canada (Bedard et al. 1980), and on the coast of South Africa (Bosman et al. 1986). Surface soil horizons from sites receiving continuous additions of fresh penguin guano had high soil enzyme activity. On the coast of South Africa guano deposition by colonial sea birds was found to enhance intertidal algal growth.

N-figures

NRA and soil nitrate status of the 42 species analysed in the present study provide a basis for assigning scalar N-figures to arctic plants for the first time. In a similar way, Gebauer et al. (1988) related nitrate and nitrate reduction levels of some central-European plants to the N-figures of Ellenberg (1979; Ellenberg et al. 1991). In the arctic bird cliff vegetation, values of maximally induced NRA reach 14.0 in the top two zones and decrease to 0.4 in lower zones; they provide appropriate scalar N-figures for the 42 species. Ellenberg and Gebauer et al. did not use figures above 9, and in order to relate to their system the N-figures would have to be converted. It is not yet clear how this should be done. A check on the Ellenberg-values for some species included both in his list (as alpine and montane species) and in mine gave confusing results; *Oxyria digyna*, the relatively most nitrophilous species on the arctic cliff, has an Ellenberg value of only 3. The N-figures as based on the maximally induced NRA figures are included in Table 1.

N-figures can be used to predict changes in species composition and distribution following changes in nitrogen supply. Nitrogenous fertilizers are known to produce marked changes in vegetation species composition (e.g. Thurston 1969), thus leading us to predict changes in bird cliff vegetation if nitrogen supply (e.g. decline or increase in seabird populations). In addition, plants with high N figures may be quick to respond to managed fertilization and be useful in revegetating disturbed areas in the Arctic.

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