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Growth of the cushion-forming lichen, *Cladonia portentosa*, at nitrogen-polluted and unpolluted heathland sites

M. Hyvärinen *, P.D. Crittenden

Department of Life Science, University of Nottingham, University Park, Nottingham, NG7 2RD, UK

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Abstract

Biomass increments in the cushion-forming heathland lichen *Cladonia portentosa* were measured at five heathland sites differing in precipitation acidity, wet nitrogen deposition and annual rainfall. Preweighed thalli were placed in the field to grow; one half of the material was native to the sites and the second half was transplanted from a background site in northernmost Scotland. After 1 year lichens were harvested, weighed and the total N concentration in transplanted lichens was measured in the apical 5 mm of thalli (apices) and in a stratum between 40 and 50 mm from the top (base). Site means for 1 year's biomass yield varied between 20 and 60% and relative growth rates (RGRs) (mg mg^{-1} year^{-1}) ranged between 0.13 and 0.43. No significant regional differences in the growth of native lichens were encountered which may have implications for pollution monitoring. Transplanted thalli grew significantly slower than native material suggesting a poor adaptivity to alien environments. Nitrogen concentration in both apices and bases of transplanted lichens increased significantly during the year at those sites subject to high N deposition but, owing to retarded growth at these locations, estimated total N uptake by the lichen (N concentration in the thallus base × mass increment) was broadly similar at all sites. Thus, at the site with the highest wet N deposition load, N input greatly exceeded uptake whereas at the background site the two quantities were similar. In contrast, estimated N uptake in lichens native to each site was similar to the site-specific quantity of wet deposited N.

Keywords: *Cladonia portentosa*; Lichen; Growth rate; Nitrogen; Heathland

1. Introduction

The effect of acid rain and increased rates of N deposition on different components of temperate heathland and moorland ecosystems has been the subject of several recent studies. Much of this research has focused on the impact on shrubs and grasses, and the integrity of their mycorrhizal symbioses (Caporn et al., 1994; Heijne et al., 1994, 1996; Yesmin et al., 1996) whereas cryptogams, especially lichens, have received less attention. In previous reports, we demonstrated that changes in chemical characteristics of the common heathland lichen, *Cladonia portentosa*, pro-

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* Corresponding author. Present address: Department of Biology, University of Oulu, P.O. Box 333, FIN-90571, Oulu, Finland. Tel.: +358 8 5331510; fax: +358 8 5531061; e-mail: marko.hyvarinen@oulu.fi

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vided relatively precise biomarkers both for rainfall acidity and total N deposition (Hyvärinen and Crittenden, 1996; Hyvärinen, 1997). First, the cation concentration ratios of total K^+:total Mg^{2+} and total intracellular Mg^{2+}:total extracellular Mg^{2+} in the thallus apices were positively correlated with precipitation acidity ($[H^+]_{ppt}$). Second, the total N concentration in the thallus ($[N]_{lichen}$), particularly in the deeper basal parts of lichen cushions ($[N]_{base}$), was positively correlated with total N deposition. The results of field experiments by Kytöviita (1993), in which the mat-forming lichens *Cladonia stellaris* and *Stereocaulon paschale* were subjected to simulated acid rain treatments, suggest that these relationships are causal. Thus, we hypothesised that elevated tissue N concentration in lichen subjected to high N deposition load is a result of increased N uptake. However, increase in lichen N concentration might also result from reduced growth dilution of the element if growth were retarded. Accordingly, it was of interest to explore whether these chemical shifts are associated with changes in growth rate. We now report a comparative study of the growth of *C. portentosa* at five British heathland sites subject to different levels of acid and N deposition. Dry mass increment was measured in lichen native to the sites and also in thalli transplanted to the sites from a background location. The rate of change in [N] in the transplanted lichen was also examined.

2. Materials and methods

2.1. Growth measurements

Biomass increment in *Cladonia portentosa* (Dufour) Coem. was measured between October 1994 and October 1995 at five heathland sites (15, 17, 24, 28 and 32 in Fig. 1 and Table 1; numbering following Hyvärinen and Crittenden (1996)). At each site *C. portentosa* was collected at 12 spots ≥ 10 m apart in order to reduce the likelihood of collecting genetically identical lichen material. These samples, each comprising aggregates (approx. 20 mm diameter) of about 4–6 interconnected podetia, were returned to the laboratory in the wet state, cut to a standard length of 50 mm and cleaned of extraneous debris using forceps. The thalli were allowed to air dry and equilibrate for 24 h on a laboratory bench in a well-ventilated room (approx. 20°C and approx. 40% RH), then weighed and tagged for identification purposes with small acetate labels attached by polyester thread. The oven dry mass (12 h at 80°C) of each podetium (M_0) was estimated from air dry mass:oven dry mass ratios determined for 50 dummy lichen samples (10 from each heathland site) that were treated in an identical manner to the test material. The tagged podetia were then returned to the field sites to grow. Each podetium was inserted into a cylindrical stainless steel mesh cage imbedded within an otherwise undisturbed lichen cushion (approx. 25 mm in diameter and 80 mm in height). Opaque plastic beads were placed in the bottom of the mesh cages to a depth of 20–40 mm to provide a uniform substratum permeable to water and to raise lichen apices to the same level as those in the surrounding lichen cushion. In addition to this study of the growth of *C. portentosa* in its original habitat, a further 48 samples of the same species were collected at site 32, treated in a similar manner as above and transplanted to the other four heathland sites (12 replicate samples at each site; Fig. 1). The growth of native lichen (treated as above) at site 32 served as a control for transplanted material. The oven dry mass of both native and transplanted thalli was measured after 1 year's growth in the field (M_1).

Mean relative growth rate was calculated following Hunt (1990):

$$\mathrm{RGR} = (\log_e M_1 - \log_e M_0)/(t_1 - t_0)$$

$$(\mathrm{mg\ mg^{-1}\ year^{-1}})$$

2.2. Total N determination

The transplanted lichen samples were rehydrated overnight in water-saturated air (over water in a desiccator) at 5°C, sprayed with deionised water and two horizontal strata were cut with a razor blade for subsequent chemical analysis: the apical 5 mm (apices) and a stratum between 40–50 mm (base) down from the top. These sub-sam-

Fig. 1. The location of the study sites.

ples were then oven-dried at 80°C, weighed and digested in 2.2 ml mixture of H_2O_2 and H_2SO_4 (1:1.2; v:v) after Allen (1989). The digest was analysed for total N ($[N]_{apices}$, $[N]_{base}$) following the indophenol blue method (Allen, 1989) to yield concentrations of total N in the thallus apices ($[N]_{apices}$) and bases ($[N]_{base}$). Hyvärinen (1997) has previously measured $[N]_{apices}$ and $[N]_{base}$ in *C. portentosa* at each of the five heathland sites and, for comparative purposes, these values have been used for the native lichens in the present study.

2.3. N uptake

Apparent nitrogen uptake was estimated from data on growth and N concentration; it was estimated following two different approaches:

2.3.1. Minimum apparent uptake (D^{N}_{min})

$$D^{N}_{min} = \Delta M^{*}[N]_{base} \qquad (1)$$

where:

$\Delta M = M_1 - M_0 =$ dry mass increment (mg)

This model is based on the observed steep vertical gradient in $[N]_{lichen}$ (Hyvärinen, 1997) such that $[N]_{apices} > > [N]_{apices}$; it assumes that N is recycled in the lichen thallus and that the growth-lead demand for N is partially met by the upward translocation of N from the transition zone between the living top and basal necromass. A precondition for Eq. (1) is that the lichen is in a steady state and that the only output for N is in accumulating necromass (Crittenden, 1991).

Table 1
Locations of study sites in relation to corresponding rain gauges in the UK Acid Deposition Monitoring Network

Site no.	Name of site	Grid reference	Distance between ss and rg (km)	Discrepancy in altitudes between ss and rg (m)[a]
15	Kirkby Moor	TF 223626	20.1	−27
17	Allerthorpe Common	SE 766482	10.5	7
24	Drowning Flow	NY 761976	7.5	170
28	Claish Moss	NM 713675	8.0	−20
32	Halsary	ND 195493	7.2	−8
Mean			10.7	46.4[b]

Site numbers follow Stedman (1993). ss, study site; rg, rain gauge.

[a] Positive values indicate that study site is located at higher altitude than a rain gauge and vice versa.

[b] Of absolute values.

2.3.2. Maximum apparent N uptake ($D^{\mathrm{N}}_{\mathrm{max}}$)

$$D^{\mathrm{N}}_{\mathrm{max}} = \Delta M^{*}[\mathrm{N}]_{\mathrm{apices}} \quad (2)$$

Eq. (2) calculates N uptake for apical growth without the implicit assumption of N translocation from the older parts; the question of the fate of N in lower strata is left open and all new growth takes place in the apices. Standardised $D^{\mathrm{N}}_{\mathrm{min}}$ and $D^{\mathrm{N}}_{\mathrm{max}}$ values were calculated by using the same start mass for all lichens (= the mean start mass of lichens transplanted). This facilitates investigation of the effects of lichen morphology (e.g. density of podetia) on N taken up per unit area.

2.4. Data on precipitation and air chemistry

Data on precipitation acidity and total wet deposited N ($\mathrm{NH_4^+} + \mathrm{NO_3^-}$) were provided by the National Environmental Technology Centre (NETCEN, AEA Technology; Stedman, 1993; Stedman et al., 1993): these were based on the analysis of weekly bulk samples of precipitation collected at stations in close proximity to the study sites (Table 1). These raw data were used to calculate total wet N depositions during the lichen growth period. An area of 4 cm^2 was used when estimating the maximum atmospheric wet N supply per lichen sample.

2.5. Data analysis

Relationships between lichen growth, N content, apparent N uptake and atmospheric N input were analysed using standard parametric tests. Non-parametric tests were applied if the prerequisites regarding the distribution normality or variance homogeneity were not met even after transformations. Differences in site mean RGR values between native and transplanted lichens were analysed by the paired t-test, and inter-site differences by the Kruskall–Wallis test (e.g. Zar, 1996) followed by Dunn's (Dunn, 1964) multiple a posteriori test. One-way ANOVA after $\log_{10}(x+1)$ and $1/\sqrt{x}$ transformations followed by Tukey HSD a posteriori test was employed for analysis of differences in apparent N uptake between sites. Furthermore, Dunnet's a priori t-test (Zar, 1996) and one-way ANOVA were used to analyse differences in thallus N concentration between transplants and experimental material at site 32, the site from which the transplanted thalli originated.

3. Results

Of the 12 replicate lichen samples of both types placed in the field to grow, between four and 12 samples from each site were recovered intact (see

Fig. 2). Damage, where it occurred, was largely owing to trampling by livestock. Lichens harvested from all sites generally appeared healthy although the basal parts of some thalli from sites 15 and 17 showed early signs of necrosis and some specimens at sites 32 and 25 had initiated fruiting body formation. Mean start biomass for all lichen transplants was approx. 160 mg and the mean end biomass was approx. 200 mg; values for native lichens were approx. 125 and 175 mg, respectively. This produced a mean increase in biomass of approx. 20–60% depending on the site and the origin of the podetia. Accordingly, mean RGR per year at the different sites varied between 0.13 and 0.43 (Fig. 2). Mean RGR values for transplanted lichens were significantly lower than those for the native material (Fig. 2). The performance of lichen transplants varied significantly between sites: the highest RGR was observed at site 28 (Fig. 2). In contrast, differences between sites in the RGR of native lichen were not statistically significant. However, this may be due to the poor power (0.44) of one-way ANOVA and the associated high risk of type II error caused by the unexpectedly high loss of replicates at some sites rather than the null hypothesis being valid.

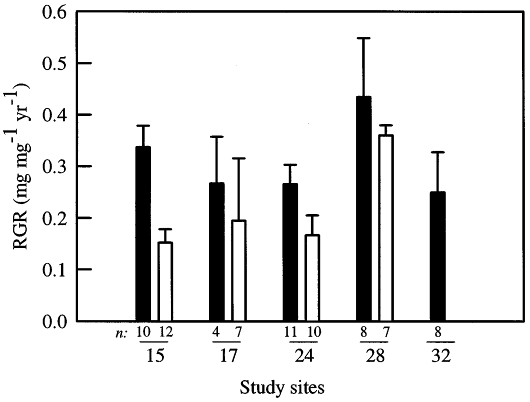

Fig. 2. Relative growth rates of *C. portentosa* at the study sites. ■, native lichens; □, lichens transplanted from site 32 (mean values for each site ± 1 S.E.). Paired t-test for the differences between site mean RGRs of native and transplanted lichens: $t = -4.19$, df $= 3$, $P = 0.025$. Inter-site comparisons of RGRs: native material, ns; transplants, Kruskall–Wallis $\chi^2 = 16.52$, df $= 4$; $P = 0.002$ (no tied ranks), Dunn's (Dunn, 1964) multiple a posteriori test: 15 vs. 28, 24 vs. 28 different at $P < 0.05$.

Inter-site differences in total wet N deposition during the study year were considerably smaller than differences in mean concentrations of nitrogenous ions (especially NH_4^+) in precipitation (Fig. 3a,b). The pattern of N delivery varied markedly between the five locations in two ways. First, the greater the total wet N load the higher the concentration ratio of $NH_4^+ : NO_3^-$ in the precipitation (Fig. 3b). Second, precipitation depth at site 28 was more than three times that at the other sites (Fig. 3e) and, accordingly, at this site both NH_4^+ and NO_3^- were deposited either always in very low concentrations or, alternatively, rainfall episodes of high N concentration were infrequent (Fig. 3a). Site-specific acid deposition load followed largely a similar rainfall dependent pattern as N deposition. Accordingly, in spite of fairly low precipitation acidity observed at site 28 its acid deposition equalled that of site 17 where mean rainfall acidity was three times higher (Fig. 3c,d). There was also inter-site variation in the seasonal distribution of rainfall: at sites 15,17 and 24 approx. 30% of the annual precipitation was delivered during the second and third quarters of the study year, whereas approx. 40% of the total year's precipitation was received at the two other sites during the same half-year period (Fig. 3e).

After 1 year's growth, both $[\mathrm{N}]_{\mathrm{apices}}$ and $[\mathrm{N}]_{\mathrm{base}}$ in transplanted *C. portentosa* had increased compared to material grown at site 32 (mean $[\mathrm{N}]_{\mathrm{apices}} = 8.77$ mg g^{-1}, S.D. 1.88; mean $[\mathrm{N}]_{\mathrm{base}} = 1.77$ mg g^{-1}, S.D. 0.38) with the exception of lichen transplanted to site 28 (Table 2). A statistically significant rise in $[\mathrm{N}]_{\mathrm{apices}}$ was encountered at sites 15, 17 and 24 whereas $[\mathrm{N}]_{\mathrm{base}}$ was markedly higher only at sites 15 and 17. However, the percentage increase in $[\mathrm{N}]_{\mathrm{base}}$ was greater than that in $[\mathrm{N}]_{\mathrm{apices}}$ at these two sites (Table 2). Interestingly, in spite of the higher N load at site 28 compared to site 32, $[\mathrm{N}]_{\mathrm{apices}}$ was slightly lower at site 28 indicating either greater growth dilution or less efficient capture of N from precipitation at this site.

Since transplanted lichen material was initially uniform there were no differences between standardised and non-standardised estimates of N uptake and only non-standardised values are reported (Fig. 4a). In contrast, lichens native to the sites exhibited clear inter-site differences in this respect: differences between standardised and non-standardised values were greatest at sites 17, 24 and 28 (Fig. 4b,c). This was because at these three sites the mean start masses of lichen podetia were smaller (approx. 96, 127 and 102 mg, respectively) than that of lichens at site 32 selected as a standard (approx. 160 mg).

There were only minor differences between sites in $D_{\mathrm{max}}^{\mathrm{N}}$ and $D_{\mathrm{min}}^{\mathrm{N}}$ for transplanted lichens (Fig. 4a). Higher N concentration in transplanted lichens at sites with high N deposition was countered by lower growth rates to such an extent that estimated N uptake was broadly similar at all sites. Conversely, there were clear differences between sites in N uptake in native lichens: the highest standardised and non-standardised $D_{\mathrm{max}}^{\mathrm{N}}$ and $D_{\mathrm{min}}^{\mathrm{N}}$ values were evident at sites 15 and 17. In general, estimated wet deposited N probably exceeded $D_{\mathrm{min}}^{\mathrm{N}}$ for transplanted lichens at all sites whereas it was roughly equal to $D_{\mathrm{min}}^{\mathrm{N}}$ at the original habitat for these podetia (site 32 in Fig. 4a). $D_{\mathrm{max}}^{\mathrm{N}}$ for both native and transplanted material was clearly higher at all sites than site specific wet deposited N. For podetia native to sites wet deposited N supply seemed inadequate to meet $D_{\mathrm{min}}^{\mathrm{N}}$ at site 15 and perhaps at site 17, whereas at the other sites $D_{\mathrm{min}}^{\mathrm{N}}$ was met (Fig. 4b). The standardised $D_{\mathrm{min}}^{\mathrm{N}}$ values showed, however, that if the start mass of lichens at site 28 had been similar to site 32 $D_{\mathrm{min}}^{\mathrm{N}}$ would not have been met by wet N deposition (Fig. 4c).

4. Discussion

Growth in *Cladonia portentosa* was comparatively vigorous and readily measurable over the timescale of a year. However, RGR values recorded by Kärenlampi (1971) and Kytöviita (1993) for *C. stellaris*, *C. rangiferina* and *C. mitis*

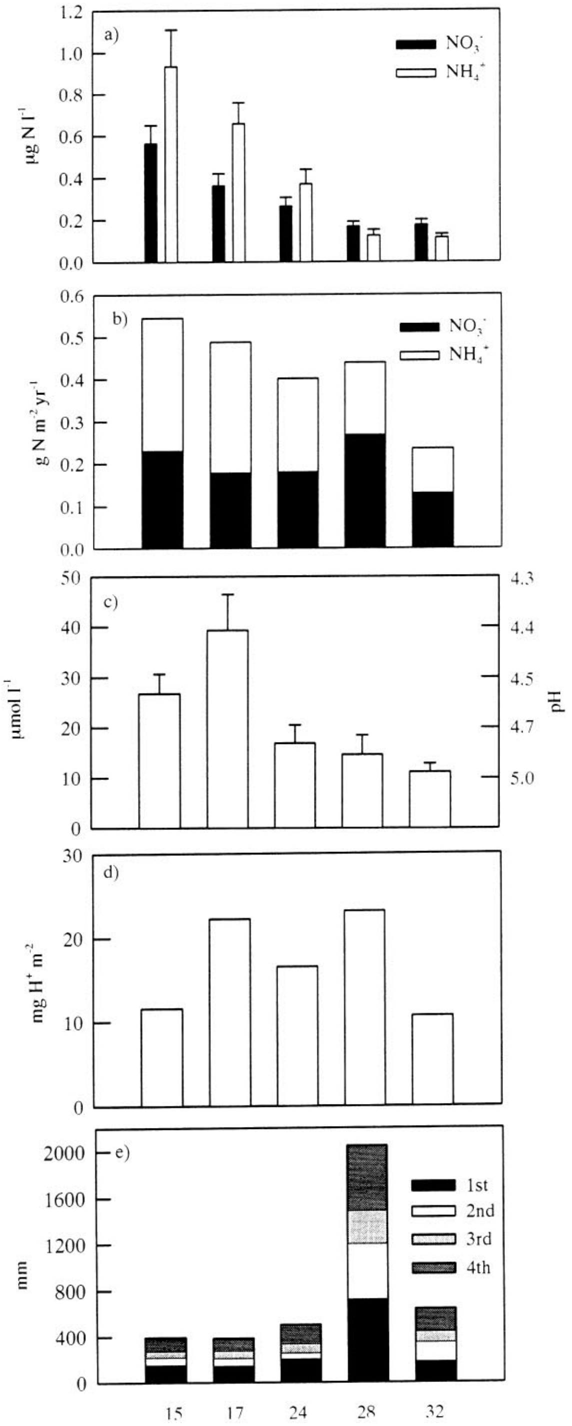

Fig. 3.

Fig. 3. (see left) Precipitation data for the five study sites during the 1 year growth period. (a) Mean weekly concentrations of NO_3^- and NH_4^+ ($\pm$S.E.), (b) total wet N deposition, (c) mean weekly precipitation acidity ($\pm$S.E.), (d) total acid deposition and (e) total precipitation. Each segment in bars in (e) represents one quarter of the study year starting from the bottom (i.e. 1st = 11 Nov to 10 Feb, 2nd = 11 Feb to 10 May, 3rd = 11 May to 10 Aug, 4th = 11 Aug to 10 Nov).

Table 2
One-way ANOVA on inter-site differences in (a) $[N]_{apices}$ and (b) $[N]_{base}$ in transplanted *Cladonia portentosa* thalli

(a) $[N]_{apices}$

Source of variation	SS	df	MS	*F*	*P*
Between sites	143.86	4	35.97	5.38	0.002
Within sites	240.54	36			
Total	384.40	40			
Site no. (x)	Mean difference (mg g^{-1}) $[N]_x$–$[N]_{32}$	S.E.	*q*	*P* (one-tailed)	
15	2.76	0.58	4.73	0.048	
17	5.32	0.97	5.50	0.003	
24	2.83	0.56	5.07	0.039	
28	−0.63	0.64	0.98	0.924	

(b) $[N]_{base}$

Source of variation	SS	df	MS	*F*	*P*
Between sites	14.90	4	3.73	11.00	0.000
Within sites	12.20	36			
Total	27.10	40			
Site no. (*x*)	Mean difference (mg g^{-1}) $[N]_x$–$[N]_{32}$	S.E.	*q*	*P* (one-tailed)	
15	1.21	0.13	9.10	0.000	
17	1.74	0.22	7.89	0.000	
24	0.47	0.13	3.76	0.131	
28	−0.006	0.14	0.01	0.812	

Dunnet's *t*-test is used a priori to analyse whether mean lichen N concentration at a site is significantly higher compared to the native habitat (site 32). Dunnet's *t*-test was performed according to Zar (1996).

growing in subarctic woodlands during the summer were approx. 1.5–4 times higher than those observed here. The lower annual mean RGR values in *C. portentosa* compared to summer mean values in lichens growing in the Subarctic probably reflects less favourable conditions at the temperate heathland sites. The highest values of RGR were observed at a high rainfall site raising the possibility that water availability could be growth-limiting for this species. It is well known that green algal lichens have the capacity to rehydrate using atmospheric water vapour (e.g. Butin, 1954; Lange and Bertsch, 1965) and thus are not entirely dependent on rainfall for water supply. Nonetheless, Kärenlampi (1971) demonstrated a positive correlation between summer rainfall and RGR in mat-forming lichens of the genera *Cladonia* and *Stereocaulon* in subarctic woodland, and Crittenden et al. (1994), working with some of the same species, also recorded higher RGR in a wet compared to a dry year. This is in accordance with the observation of Bruns-Strenge and Lange (1991) that dew, mist and rain were the main sources of hydration for *C. portentosa* at a coastal site. Thus, it seems reasonable to suggest that the better growth of *C. portentosa* at site 28 might reflect longer periods with moisture conditions suitable for physiological activity here than at other sites. Armstrong (1993) hypothesised that periods of maximum growth in foliose lichens would be those in which rainfall and maximum insolation coincided. Should this apply to *C. portentosa* the growth attainment at the three southernmost sites during 1995 should have been poorer than average since the annual precipitation was not only lower than long-term means (Campbell et al., 1994) but its proportion received during summer was smaller than at the other sites (Fig. 3e).

The minor regional differences in RGR observed here suggest that the modified chemical characteristics of *C. portentosa* recorded by us (Hyvärinen and Crittenden, 1996; Hyvärinen, 1997) at N-polluted sites were probably not associated with impaired growth. Even at sites 15 and 17, where rainfall quality is probably amongst the poorest in British heathlands (Stedman et al., 1993), the mean RGR of native material was comparable to that at site 32 which was subjected to a broadly similar amount of precipitation but considerably lower depositions of NH_4^+, NO_3^- and H^+. In contrast, there was an indication that transplanted lichens from site 32 did not grow as well at the southern sites despite being subject to higher NH_4^+ and NO_3^- depositions. This points to the potential importance of adaptation to local environmental conditions and accords with the observation of Press et al. (1986) that *Sphagnum cuspidatum* transplanted from an unpolluted area to a site with high N deposition showed reduced growth together with increased tissue N concentration after a period of 6 months. There is some evidence that the growth of *Cladonia* spp. responds positively to nutrient addition (Crittenden et al., 1994) but intraspecific differences and adaptive traits in N (and P) utilisation by lichens are virtually unexplored.

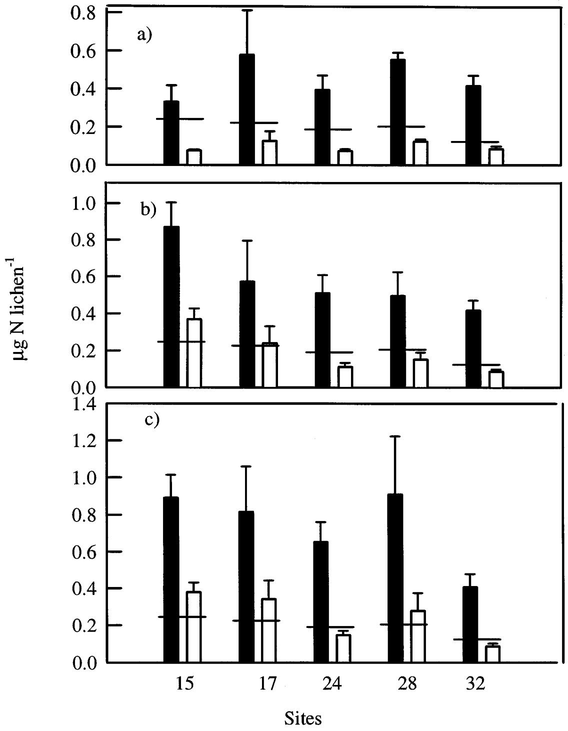

Fig. 4. Nitrogen uptake in (a) lichens transplanted from site 32 (including native material grown at site 32), (b) lichens native to their sites and (c) as in (b) but values standardised to the start mass of 160 mg. ■, D^N_{max}; □, D^N_{min}, (mean values ± 1 S.E.). Site-specific total wet deposited N is denoted by horizontal lines. Inter-site comparisons: (a) D^N_{max} and D^N_{min} both ns; (b) D^N_{max} ns, D^N_{min} one-way ANOVA after $\log_{10}(x+1)$ transformation, $F=5.19$, $P=0.002$, Tukey HSD a posteriori: 15 vs. 24 and 15 vs. 32 different at $P<0.05$; (c) D^N_{max} ns, D^N_{min} one-way ANOVA after $1/\sqrt{x}$ transformation, $F=4.78$, $P=0.003$, Tukey HSD a posteriori: 15 vs. 32 and 17 vs. 32 different at $P<0.05$; df = 4 in all cases.

The results of an earlier study (Hyvärinen, 1997) of regional variation in both $[N]_{apices}$ and $[N]_{base}$ in *C. portentosa* in the British heathlands showed that they both were positively correlated with total N deposition but, of the two parameters, $[N]_{base}$ varied more widely and was the better correlate. It was suggested that in N-polluted regions, higher atmospheric loads of NH_4^+ and NO_3^- might perturb internal N cycling and lead to a more pronounced increase in $[N]_{base}$ than in $[N]_{apices}$. In the present work, total thallus N concentration was found to have increased markedly in *C. portentosa* transplanted to sites with higher N loads but the change was proportionally greater in $[N]_{base}$ than $[N]_{apices}$ (Table 2). This finding is entirely consistent with our earlier results. In the present study, any possibility that underlying soil influences the N content of the basal parts of the lichen can be excluded since podetia were completely isolated from the natural substratum. Values of D^N_{min} and D^N_{max} calculated for the transplanted lichens (Fig. 4a) suggest that wet deposited N supply alone approached a supra-optimal level for *C. portentosa* (i.e. N supply approaches D^N_{max}) at site 15 while at all sites the N supply exceeded D^N_{min}. Dry deposition of N, for which unfortunately there are no accurate estimates available, may account for up to one half of total N deposition at the most N-polluted sites (INDITE, 1994) increasing the likelihood that N supply at site 15 exceeded D^N_{max}; under these circumstances the sink strength for N in the lichen apices could have approached zero.

At the remotest sites (24, 28 and 32; Fig. 4b), where dry deposited N can be assumed to be a minor factor (cf. Singles et al., 1998), $D^{\mathrm{N}}_{\mathrm{min}}$ values roughly equalled measured wet deposition. Since regional variation in N deposition is strongly positively correlated with $[\mathrm{N}]_{\mathrm{base}}$ in *C. portentosa* (Hyvärinen, 1997), it is tempting to speculate that $D^{\mathrm{N}}_{\mathrm{min}}$ might approach an exact expression for total N deposition, perhaps being equalled by $[\mathrm{N}]_{\mathrm{base}}$ where growth increments do not show significant regional variation. The divergence between standardised and non-standardised (Fig. 4b,c) $D^{\mathrm{N}}_{\mathrm{min}}$ and $D^{\mathrm{N}}_{\mathrm{max}}$ values suggested that there were differences between sites in the morphology of the native lichens. For example, casual observation suggested that there were between-site differences in the density of podetial branching within the lichen cushions. Therefore, if $D^{\mathrm{N}}_{\mathrm{min}}$ was to be used to predict N deposition per unit area then it would be more appropriate to use non-standardised values.

According to Crittenden (1991) accumulation of necromass in mat-forming lichens facilitates lichen dominance by serving as a means to suppress the establishment and growth of vascular plants. Since decomposition rates of detritus produced by photosynthetic organisms are largely explained by differences in the C, N and P content (Enrique et al., 1993), it would not be surprising if elevated decomposition rates of necromass and thus reduced competitive ability were encountered in lichens from nitrogen-polluted areas where $[\mathrm{N}]_{\mathrm{base}}$ is greatly increased. However, this mechanism will accelerate lichen decomposition only if lichen growth, and thus decomposition of basal parts, are not limited by other key nutrients such as phosphorus. It has been experimentally verified that *C. portentosa* can intercept phosphate very efficiently from simulated rainwater (Hyvärinen and Crittenden, 1998) but there is a dearth of information on the levels of P deposition in British heathlands. Should such data become available in the future the question of potential nutrient limitation in *C. portentosa* could be revisited. Also the role recycling of phosphorus from the old parts of thallus in order to fund the growth of apices deserves attention in this context.

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