# Long-term responses of aquatic macrophyte diversity and community structure to variation in nitrogen loading

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## Abstract

In a chain of small lakes in southeastern Michigan, USA, macrophyte community dynamics have shown a strong relationship to variations in nitrogen (nitrate and ammonia) loading that appear to correlate with variations in regional annual precipitation. We examined the community structures of two of these lakes 9 years after a drought in 1987–1988 which had temporarily reduced nutrient loading in the system, and during which the macrophytes in normally more eutrophic Shoe Lake had shifted from a *Ceratophyllum*-dominated community of low diversity to a more diverse community similar to that in less productive East Graham Lake downstream. With a return to the normal precipitation rates and associated nitrogen loading, the macrophytes in Shoe Lake returned to a community dominated by the non-rooted species *Ceratophyllum demersum*. However, overall species diversity remained relatively high in Shoe Lake after the drought event.
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## 1. Introduction

Nitrogen loading, especially in nitrogen limited aquatic environments, is of increasing concern because of its effects on the diversity, community structure, and overall health of the systems (Vitousek et al., 1997; Paerl, 1997; Bedford et al., 1999; Goldman, 2000; Sala et al., 2000). Annual wet deposition of dissolved inorganic nitrogen (DIN) from anthropogenic inputs is estimated to be 10 times higher than normal background levels for the eastern and

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mid-western regions of the United States and 100 times higher than background levels in heavily impacted European locations (reviewed in Vitousek et al., 1997). Although most freshwater aquatic systems are naturally phosphate limited, eutrophication from anthropogenic phosphorus inputs often causes many of these systems to become nitrogen limited. Under these conditions, elevated nitrogen deposition can bring such systems to higher levels of eutrophication, dramatically affecting the community structure, dynamics, and diversity of these communities (Schindler et al., 1990; Vitousek et al., 1997; Peterson et al., 2001). To address the question of how the performance of previously N-limited organisms and ecosystems is affected by inputs of nitrogen that have become larger than normal for their evolutionary background (Vitousek et al., 1997), site-specific analyses of non-point loading associated with eutrophication are needed (Carpenter et al., 1998). For example, Valiela et al. (2000) illustrated the local effects of nitrogen loading on estuarine plant communities.

Over the past two decades, we have studied aquatic plant diversity and community structure in a chain of small lakes in southeastern Michigan, which is within the region of northeastern US where atmospheric nitrogen deposition has been the highest in North America (Charles, 1991). A gradient of DIN concentrations exists in the surface water along this lake chain, and overall nitrogen levels fluctuate with major changes in annual precipitation. Earlier (Hough et al., 1989) we documented a relatively stable situation in which the most N-enriched of the lakes (Shoe Lake) was dominated by non-rooted macrophytes, phytoplankton, and periphyton with low diversity in rooted macrophytes. Later (Hough et al., 1991), we reported a relatively rapid shift in this community during a 2 year drought which lowered the loading rates and availability of DIN; non-rooted plants and phytoplankton declined markedly, and the rooted plant community increased in diversity to more closely resemble the N-limited lake (East Graham Lake) downstream.

Our hypothesis that high nitrogen loading and availability maintains low diversity in macrophyte communities primarily because of dominance by enhanced non-rooted plants and their shading effects (Hough et al. (1989, 1991)) suggested the prediction that, in the decade following the drought event, the previously N-enriched community structure would return in this system. Here, we report the outcome of this prediction, having carried out a reexamination of these macrophyte communities.

## 2. Study site and methods

The chain of small hard-water kettle lakes lies along the west branch of Stoney Creek located in the Bald Mountain State Recreation Area in southeastern Michigan USA (Fig. 1). From its source at the outflow of Bunny Run Lake in the village of Lake Orion, Stoney Creek flows eastward for ≈1 km through a wetland and meadow into Shoe Lake, followed closely by West Graham Lake and East Graham Lake. Below the Bald Mountain Recreational Area, the creek flows through additional lakes before it enters the Clinton River, a major tributary of Lake St. Clair in the Great Lakes.

Nutrient levels in the headwaters of this chain at Bunny Run Lake are moderate, and become enriched along the stream, especially with inorganic nitrogen, resulting in the highest levels at the Shoe Lake inflow (Fig. 2). This enrichment appears to be largely from precipitation runoff, as (1) there is no habitation or agriculture along this narrow watershed
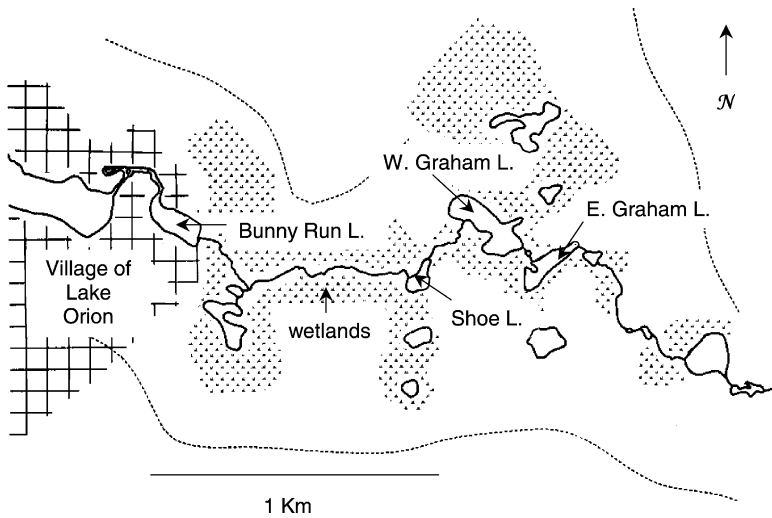
Fig. 1. Stoney Creek (West Branch) chain of lakes, Oakland County, MI, USA. Stream flow is from west to east.

below the outflow of Bunny Run Lake, and (2) nitrate and ammonia nitrogen concentrations in local precipitation generally are much higher than in the surface waters, by factors of three to eight-fold in 1985–1986 (Allenson, 1992) and by factors of 5 to >10 fold in 1997 (Montante, unpublished data). However, while this N-enrichment is readily apparent along the long stretch of stream from Bunny Run Lake to Shoe Lake, and sometimes in the short stretch between Shoe Lake and West Graham Lake (Fig. 2), the enrichment appears to be
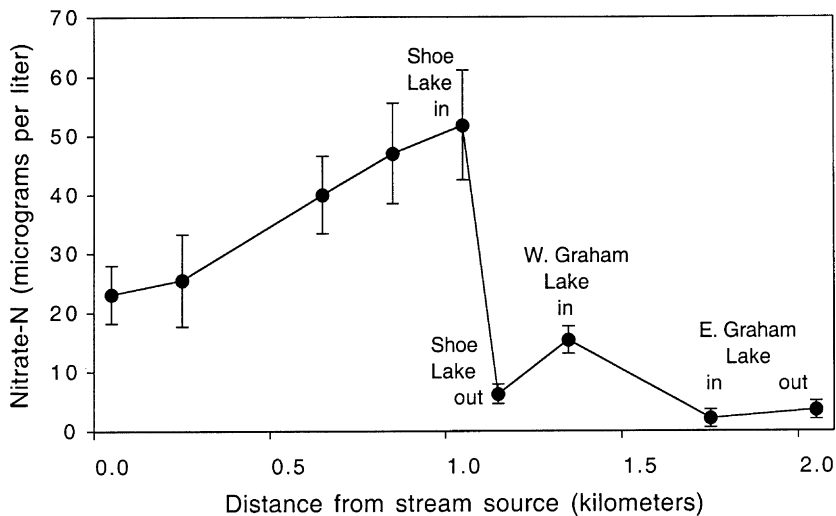


Fig. 2. Nitrate nitrogen concentrations along upper Stoney Creek and its chain of lakes during a year of normal annual precipitation. Mean ± S.D. of all biweekly measurements over the summer of 1984. From Allenson (1992).

reversed within the close succession of lakes including Shoe Lake and the Graham Lakes, presumably because the rate of removal in the lakes is more rapid than the enrichment rate.

Shoe Lake (1.9 ha surface area; 5.5 m maximum depth) is normally moderately eutrophic with abundant phytoplankton, periphyton, and non-rooted macrophytes but with a poorly developed rooted submersed macrophyte community that is light limited (Hough et al., 1989). After flowing through Shoe Lake, the water at its outflow is markedly lower in total DIN. DIN is kept very low in West Graham Lake and in the closely adjacent East Graham Lake (4.5 ha surface area; 11 m maximum depth). As a consequence, the phytoplankton, periphyton, and non-rooted macrophyte communities are N-limited in East Graham Lake (determined experimentally by Hough et al., 1989; Hough and Thompson, 1996), and the rooted macrophyte community is much more productive and diverse than in Shoe Lake.

Drought conditions began in the upper central USA in 1987, and became severe in 1988 with precipitation and surface flow generally reduced to 30% below normal. Stream discharge rates at the inflow of Shoe Lake during 1988 were 70% below those in 1986. Flow rates returned to normal after 1988.

During several different years over the past two decades, we monitored limnological conditions in this system every 3 weeks during the spring and summer using standard methods according to Wetzel and Likens (1991) as described in Hough et al. (1989). Macrophytes were collected from both Shoe Lake and East Graham Lake in mid-summer of 1979, 1988, and 1996. Transects perpendicular to the shore were spaced 15 m apart around the perimeter of the lake, similar to the method of Dubois et al. (1984). Along the transect, samples were taken using a 6-pronged macrophyte hook at depths of 0.25, 0.5, 1, 1.5, 2, and 2.5 m. Plants were identified according to Crow and Hellquist (2000a,b) and Gleason and Cronquist (1991). From the species frequency data for each lake in each year, we calculated the Shannon diversity (Zar, 1995). We also calculated indexes of dissimilarity and similarity of community structures in paired comparisons among lakes and years. In addition to the Bray–Curtis distance index that is commonly used in ecological studies (Zar, 1995), we also calculated chord distance index (CRD, one of the relative Euclidean distance group; Ludwig and Reynolds, 1988). CRD is an especially useful dissimilarity index for quantitative abundance data because with squared functions it puts more emphasis on relative proportions of species than on absolute quantities (Zar, 1995), which we believe is an important factor in our study. Finally, while our data were not appropriate for multivariate analyses, we calculated Pearson correlation coefficients as an index of similarity of community structures in paired comparisons, which enabled us to test for statistical significance of differences among multiple *r*-values (Zar, 1995).

## 3. Results

DIN and total phosphorus concentrations at the inflow and outflow of Shoe Lake generally have remained relatively consistent over time as shown by the 1982–1986 and 1996 data (Table 1). However, at the Shoe Lake inflow in 1988 the DIN concentrations were about 40% lower than in previous years, and at the Shoe Lake outflow DIN was virtually zero in 1988. Moreover, reduced stream discharge rates had resulted in an 80% reduction of both nitrogen and phosphorus loading rates at the Shoe Lake inflow (from 733 g N per day and

Table 1

Concentrations (mean ± S.D.) of total phosphorus and total dissolved inorganic nitrogen in stream water at Shoe Lake during summer

|  | Phosphorus[a] $\mu$g l$^{-1}$ | | | Nitrogen[b] $\mu$g l$^{-1}$ | |
| --- | --- | --- | --- | --- | --- |
|  | Inflow | Outflow | | Inflow | Outflow |
| 1982 | 26 (3.7) | 23 (4.1) | | 85 (14) | 25 (5.0) |
| 1984 | 19 (6.1) | 12 (2.8) | | 74 (28) | 18 (15) |
| 1986 | 25 (15) | 20 (2.5) | | 87 (19) | 29 (15) |
| 1988 | 20 (5.6) | 17 (3.4) | | **49** (25) | **<1*** |
| 1996 | 14 (6.3) | 14 (6.9) | | 98 (27) | 33 (24) |

Data for years prior to 1996 appeared originally in Hough et al. (1989, 1991).

[a] Phosphorus concentrations at the inflow did not differ significantly among years (Kruskal–Wallis test, $P > 0.5$); concentrations at the outflow also did not differ among years (Kruskal–Wallis test, $P > 0.1$); concentrations in all years at the outflow were significantly lower than at the inflow (*t*-test, $P < 0.001$).

[b] Nitrogen concentrations at the inflow differed significantly among years (ANOVA, $P < 0.05$), with 1988 being different from all other years ($P < 0.01$); concentrations at the outflow differed significantly among years (ANOVA, $P < 0.05$), with 1988 being different from all other years ($P < 0.05$); concentrations in all years at the outflow were significantly lower than at the inflow (*t*-test, $P > 0.001$).

* Below detection limits.

211 g P per day in 1986 to 122 g N per day and 50 g P per day in 1988). By 1996, loading rates of both nutrients (1117 g N per day and 160 g P per day) had returned to levels similar to those in 1986.

In 1996, the majority of macrophyte species in Shoe Lake that were dominant in pre-drought years had returned to pre-drought levels of abundance (Table 2). Most notably, sample frequencies of *Ceratophyllum demersum* and *Utricularia vulgaris* were reduced by 63 and 39 $\Delta F$ (%), respectively in the drought of 1988, but since then they have increased to levels similar to or above pre-drought levels. *Najas flexilis* followed a similar pattern, whereby its frequency was reduced by 92 $\Delta F$ (%) during the drought but rebounded afterwards to 170 $\Delta F$ (%) of pre-drought levels. *Myriophyllum verticillatum*, which had decreased by 54 $\Delta F$ (%) during the drought, also returned but only to 60 $\Delta F$ (%) of its pre-drought frequency. Some species including *Chara vulgaris* and *Myriophyllum sibiricum* increased in frequency during the drought and then returned to lower levels. *M. sibiricum*, rare in pre-drought years, disappeared in 1996, while *C. vulgaris* retained a substantial part of the foothold gained in 1988 and remained present at 128 $\Delta F$ (%) of its 1979 frequency.

In general, by 1996 the macrophyte community structure in Shoe Lake appeared to be returning to one similar to that seen before the 1988 drought. Pearson correlation coefficients of the Shoe Lake communities among years suggest that the 1996 Shoe Lake community was most like that in 1979, and the chord distance (dissimilarity) was least for 1996 versus 1979 (Table 3). In comparing the two lakes, the 1988 Shoe Lake community was most similar to the East Graham Lake communities of 1979 and 1988. However, after the Shannon diversity index and species richness rose in Shoe Lake during the drought years (Table 2), they remained high since the drought.

In contrast to Shoe Lake, overall diversity in East Graham Lake was high and relatively stable throughout the two decades. However, some specific aspects of community structure

Table 2
Species frequencies (percentage of all samples in each lake containing each species[a])

| | Shoe Lake | | | East Graham Lake | | |
|---|---|---|---|---|---|---|
| | 1979 | 1988 | 1996 | 1979 | 1988 | 1996 |
| **Non-rooted; submersed leaves** | | | | | | |
| *Ceratophyllum demersum* L. | 91 | 34 | 84 | 30 | 4 | 32 |
| *Utricularia vulgaris* L. | 49 | 30 | 53 | 15 | 18 | 55 |
| **Rooted; submersed leaves** | | | | | | |
| *Elodea canadensis* (Michx.) Planchon | 6 | 17 | 40 | 20 | 8 | 32 |
| *Myriophyllum sibiricum* Komarov[b] | 3 | 22 | 0 | 54 | 36 | 11 |
| *Myriophyllum verticillatum* L. | 35 | 16 | 21 | 0 | 1.5 | 35 |
| *Najas flexilis* (Willd.) Rostk. and Schmidt | 26 | 2 | 44 | 12 | 26 | 37 |
| *Potamogeton illinoensis* Morong | 8 | 0 | 0.88 | 24 | 17 | 0.6 |
| *Potamogeton filiformis* Pers.[c] | 2.6 | 4.4 | 0.44 | 1 | 4.6 | 2.1 |
| *Potamogeton foliosus* Raf. | 0 | 25 | 1.3 | 0 | 2.2 | 4.3 |
| *Potamogeton pectinatus* L.[d] | 0 | 0 | 2.6 | 28 | 13 | 30 |
| *Potamogeton pusillus* L. | 0 | 22 | 31 | 0 | 5.2 | 37 |
| *Potamogeton zosteriformis* Fern. | 36 | 24 | 35 | 39 | 12 | 32 |
| *Scirpus subterminalis* Torr. | 0 | 2 | 0 | 4 | 10 | 14 |
| **Rooted; submersed and floating leaves** | | | | | | |
| *Potamogeton amplifolius* Tuckerm. | 0 | 0 | 0 | 11 | 0.2 | 1.4 |
| *Potamogeton natans* L. | 18 | 10 | 35 | 1 | 9 | 17 |
| *Potamogeton nodosus* Poir. | 0 | 5.5 | 8.8 | 0 | 3.5 | 0 |
| **Rooted; floating or emergent leaves** | | | | | | |
| *Brasenia schreberi* J.F. Gmel. | 0 | 0 | 0 | 4 | 7 | 8.2 |
| *Eleocharis equisetoides* (Ell.) Torr. | 0 | 0 | 0.44 | 3 | 2.4 | 4.1 |
| *Nuphar variegata* Engelm. ex Durand | 2 | 10 | 12 | 5 | 8 | 13 |
| *Nymphaea odorata* Ait.[e] | 13 | 25 | 28 | 10 | 23 | 19 |
| *Pontederia cordata* L. | 1 | 3 | 21 | 2 | 5 | 10 |
| **Rhizoidal macroalgae** | | | | | | |
| *Chara vulgaris* L. | 25 | 55 | 32 | 56 | 75 | 53 |
| *Nitella flexilis* (L.) Ag. | 0.6 | 2.3 | 0.44 | 14 | 6 | 0 |
| Species richness (*S*) | 15 | 18 | 22 | 21 | 25 | 24 |
| Shannon diversity (*H′*) | 2.15 | 2.57 | 2.58 | 2.53 | 2.72 | 2.84 |

Species richness $S$ = total number of species present; Shannon diversity $H' = -\Sigma p_i \ln p_i$. Data for years prior to 1996 appeared originally in Hough et al. (1989, 1991).

[a] Additional rare species included *Vallisneria americana* Michx. (1.8% SL'96, 0.3% EGL'79), *Utricularia intermedia* Hayne (0.3% EGL'79), *Potamogeton alpinus* Balb. (18% EGL'88, 19% EGL'96), *Zosterella dubia* (Jacq.) Small (formerly *Heteranthera dubia* (Jacq.) MacM. (Fassett, 1957)) (10% SL'96, 11% EGL'96), *Ranunculus longirostris* Godr. (3.9% SL'96, 0.7% EGL'96), *Potamogeton gramineus* L. (3.9% EGL'88).

[b] Formerly *Myriophyllum exalbescens* Fernald (Fassett, 1957).

[c] Recently renamed *Stuckenia filiformis* (Pers.) Börner (Crow and Hellquist, 2000a,b).

[d] Recently renamed *Stuckenia pectinata* (L.) Börner (Crow and Hellquist, 2000a,b).

[e] Formerly *Nymphaea tuberosa* Paine (Fassett, 1957).

Table 3
Coefficients of dissimilarity (B–C, CRD) and similarity (*r*) of community structures (from species frequencies in Table 2) among lakes and years (S: Shoe Lake; EG: East Graham Lake)

|  | S 96 vs. EG 79 | S 79 vs. EG 79 | S 79 vs. S 88 | S 96 vs. S 88 | S 88 vs. EG 79 | S 88 vs. EG 88 | S 96 vs. EG 96 | S 79 vs. S 96 |
|---|---|---|---|---|---|---|---|---|
| B–C | 0.58 | 0.53 | 0.45 | 0.40 | 0.41 | 0.41 | 0.27 | 0.28 |
| CRD | 0.94 | 0.94 | 0.76 | 0.67 | 0.70 | 0.68 | 0.55 | 0.46 |
| *r* | **0.23** | **0.27** | 0.50* | 0.52* | 0.61** | 0.61** | 0.71** | **0.84**** |

B–C: Bray–Curtis dissimilarity index; CRD: chord distance; *r*: Pearson correlation coefficient.
  * *r*-values individually significant at 0.05 level (2-tailed), but not significant in a table-wide sequential Bonferroni test (Rice, 1989).
  ** *r*-values significant at 0.01 level (2-tailed). Bold data denote that, in multiple comparisons of *r* (Zar, 1995), 0.84 is significantly different (0.05 level) from both 0.23 and 0.27.

did change over the years in East Graham Lake. *C. demersum* experienced the same pattern of decline during the drought and later resurgence as it did in Shoe Lake (Table 2), as did *Potamogeton zosteriformis*, *Potamogeton pectinatus*, and *Elodea canadensis*. A temporary increase in *C. vulgaris* during the drought years occurred in both lakes. Also, several species became much more abundant in 1996 than in either of the two previous decades.

## 4. Discussion

During the drought of 1988, the increase in the overall diversity of Shoe Lake macrophytes was a result of a decline in the dominant non-rooted macrophytes, and an increase in the more diverse benthic macrophyte community due to increased light availability (Hough et al., 1991). Similar drought effects during that period were reported elsewhere, including a temporary reversal in the trend of declining transparency of Lake Tahoe (Goldman, 2000), and an expansion of the distribution of submersed macrophytes in the Choptank river (Stevenson et al., 1993). In 1996, nutrient levels in Shoe Lake were comparable to the pre-drought years and correlated with a general reversal of many of the drought induced trends in the macrophyte community. Non-rooted macrophytes such as *Ceratophyllum* and *Utricularia* are dependent on available nitrogen in the water column (Best, 1980; Goulder and Boatman, 1971). These species had declined along with the nitrogen levels during the 1988 drought, as did phytoplankton chlorophyll *a* and epiphytic algae, and this allowed increased light penetration into the portion of the littoral zone occupied by the rooted macrophytes. As predicted, after the 1988 drought the non-rooted macrophytes returned to frequencies approaching or exceeding pre-drought levels, most likely because of the return of higher N-levels.

While most rooted macrophytes in Shoe Lake had increased in frequency with greater light availability during the drought, two rooted species that conversely had declined markedly at that time are *Najas flexilis* and *Myriophyllum verticillatum*. These two differ from most of the other species in that they both require free $CO_2$ as a carbon source, whereas their competitors can use bicarbonate. Bicarbonate use generally is advantageous in hardwater lakes, but less so under the limiting light conditions in Shoe Lake prior to

the drought, because the energy needed for active transport of bicarbonate requires higher photosynthetic rates (reviewed in Hough and Fornwall, 1988). Therefore, *N. flexilis* and *M. verticillatum* appear to have been able to compete well prior to 1988, but less so during the drought because the increase in light availability was favorable to the bicarbonate users (as demonstrated experimentally by Hough and Fornwall, 1988) including *M. sibiricum* and *C. vulgaris*, which increased during the drought. In 1996, the return of both of the free $CO_2$ requiring species to greater abundance, and the decline of both of the known bicarbonate users, was consistent with a predicted influence of a return to pre-drought levels of available light and the interaction of carbon source physiology.

While most macrophyte species returned to pre-drought abundance levels as predicted, the continuation of the elevated diversity in Shoe Lake after the drought was unexpected. Several factors contributed to the continuing high diversity in Shoe Lake, including colonization by previously absent species, increases in some previously rare species, and an overall shift to a more uniform frequency distribution. First, colonization by new species and an increase in previously rare species elevated the diversity (for example, without the newly introduced species such as *Ranunculus longirostris*, *Zosterella dubia*, *Eleocharis equisetoides*, *Vallisneria americana*, and *Potamogeton pectinatus* in 1996, the diversity would have been 2.40 rather than 2.58). Both cases may reflect the ability of certain species to quickly invade areas vacated by *C. demersum* during the drought. Second, the abundance of floating leaved or emergent plants including *Nuphar variegata*, *Nymphaea odorata* and *Pontederia cordata* increased both during and after the drought. Once established, these surface-leaved and emergent plants are less susceptible to shading by *Ceratophyllum*. Sýkora (1979) also noted that emergents proliferated in response to drought conditions, and were able to retain and expand on the foothold gained during the drought. Third, the high level of diversity maintained after 8 years suggests that, in disturbed systems, general community diversity may be more stable than are specific aspects of community structure. Finally, the climatic warming trend in the recent decades may be influencing the communities in all of the lakes; diversity appears to be increasing slightly in East Graham Lake as well. However, if N-loading remains relatively high, we expect that continued dominance and shading by *Ceratophyllum*, phytoplankton and periphyton will eventually reduce the macrophyte diversity again in Shoe Lake.

In conclusion, our observations here, along with the previous observations and experiments (Hough and Fornwall, 1988; Hough et al., 1991) over the past two decades in a relatively small and well defined watershed illustrate the sensitivity of freshwater macrophyte communities to the effects of variations in nutrient loading, particularly as influenced by atmospheric deposition of nitrogen compounds. Further work is needed here to quantify the sources of the nutrient loading and to determine the relative roles of the different pathways of nitrogen metabolism in the community.

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