

Scaling plant nitrogen use and uptake efficiencies in response to nutrient addition in peatlands

COLLEEN M. IVERSEN,¹ SCOTT D. BRIDGHAM,² AND LAURIE E. KELLOGG³

Department of Biological Sciences, University of Notre Dame, Notre Dame, Indiana 46556 USA

Abstract. Nitrogen (N) is the primary growth-limiting nutrient in many terrestrial ecosystems, and therefore plant production per unit N taken up (i.e., N use efficiency, NUE) is a fundamentally important component of ecosystem function. Nitrogen use efficiency comprises two components: N productivity (A_N , plant production per peak biomass N content) and the mean residence time of N in plant biomass (MRT_N). We utilized a five-year fertilization experiment to examine the manner in which increases in N and phosphorus (P) availability affected plant NUE at multiple biological scales (i.e., from leaf to community level). We fertilized a natural gradient of nutrient-limited peatland ecosystems in the Upper Peninsula of Michigan, USA, with 6 g N·m⁻²·yr⁻¹, 2 g P·m⁻²·yr⁻¹, or a combination of N and P. Our objectives were to determine how changes in carbon and N allocation within a plant to leaf and woody tissue and changes in species composition within a community, both above- and belowground, would affect (1) NUE; (2) the adaptive trade-off between the components of NUE; (3) the efficiency with which plants acquired N from the soil (N uptake efficiency); and (4) plant community production per unit soil N availability (N response efficiency, NRE). As expected, N and P addition generally increased aboveground production and N uptake. In particular, P availability strongly affected the way in which plants took up and used N. Nitrogen use efficiency response to nutrient addition was not straightforward. Nitrogen use efficiency differed between leaf and woody tissue, among species, and across the ombrotrophic–minerotrophic gradient because plants and communities were adapted to maximize either A_N or MRT_N , but not both concurrently. Increased N availability strongly decreased plant and community N uptake efficiency, while increased P availability increased N uptake efficiency, particularly in a nitrogen-fixing shrub. Nitrogen uptake efficiency was more important in controlling overall plant community response to soil N availability than was NUE, and above- and belowground community N uptake efficiencies responded to nutrient addition in a similar manner. Our results demonstrate that plants respond to nutrient availability at multiple biological scales, and we suggest that N uptake efficiency may be a more representative measurement of plant responses to nutrient availability gradients than plant NUE.

Key words: allocation; co-limitation; mean residence time; N limitation; nitrogen response efficiency; nitrogen uptake efficiency; nitrogen use efficiency; nutrient productivity; peatlands; P limitation; Upper Peninsula, Michigan, USA.

INTRODUCTION

Soil nitrogen (N) and phosphorus (P) availability often limit plant growth (Chapin 1980, Vitousek and Howarth 1991, Vitousek et al. 2002). Therefore, the amount of nutrients required to support plant growth may determine the competitive hierarchy of species within and among communities (Fargione and Tilman 2006). The classic test of nutrient limitation in a plant community is an increase in net primary production

(NPP) with the addition of a limiting nutrient (Chapin et al. 1986, Vitousek and Howarth 1991). However, in natural ecosystems, the relationship between plant growth and nutrient availability is not straightforward. This is because plants that have evolved under different nutrient regimes often vary in their ability to respond to increases in nutrient availability (Chapin 1980, Vitousek 1982, Chapin et al. 1986, Aerts and Chapin 2000). For example, plant communities occupying infertile habitats are often relatively unresponsive to nutrient addition due to sets of life-history traits that result in low productivity and long nutrient retention times in biomass. The converse is true of species characteristic of nutrient-rich sites (Chapin et al. 1986, Aerts and Chapin 2000).

One measure of plant adaptation to gradients of nutrient availability is nutrient use efficiency, or the amount of organic matter fixed in plant biomass per unit of nutrient taken up (Vitousek 1982, Garnier and

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¹ Present address: Environmental Sciences Division, Oak Ridge National Laboratory, Oak Ridge, Tennessee 37831 USA. E-mail: iversencm@ornl.gov

² Present address: Center for Ecology and Evolutionary Biology, University of Oregon, Eugene, Oregon 97403 USA.

³ Present address: University of Minnesota Law School, University of Minnesota, Minneapolis, Minnesota 55455 USA.

Aronson 1998, Pastor and Bridgham 1999, Aerts and Chapin 2000), and plant N use efficiency (NUE) has been the subject of many studies (among the recent studies are Silla and Escudero [2004], Lea and Azevedo [2006], and Norby and Iversen [2006]). Nitrogen use efficiency integrates plant physiological and morphological responses along nutrient availability gradients and is considered an index of a plant's capacity to utilize N as a limiting resource for growth. While there is an abundance of data on leaf-level NUE responses across nutrient availability gradients (Aerts and Chapin 2000), leaf NUE may not be representative of plant responses at larger spatial and temporal scales, as most communities are composed of plant species with different nutrient limitations (Koerselman and Meuleman 1996) and nutrient recycling strategies (Chapin 1980). The relative allocation of photosynthate and nutrients among plant tissues, above- and belowground, and among plant species with different life-history strategies will drive changes in NUE at scales of organization ranging from the leaf to the community level (Pastor and Bridgham 1999).

At the phenotypic level, nutrient addition often leads to a decline in plant NUE (Bridgham et al. 1995b) due to constraints on the growth of plants adapted to nutrient-poor conditions (Aerts and Chapin 2000). However, NUE rarely varies between infertile and nutrient-rich sites, because NUE implicitly embodies an adaptive trade-off between the two components of NUE: (1) production per unit N in the plant and (2) the ability of plants to retain and recycle nutrients internally (Berdendse and Aerts 1987).

The relationship between plant NUE and soil nutrient availability is further complicated by the fact that the NUE index does not explicitly consider the complex process of nutrient acquisition from the soil, which involves several physical, physiological, and symbiotic mechanisms (Garnier and Aronson 1998, Aerts and Chapin 2000, Evans 2001). In many cases, plant [N] is not well-correlated with indices of soil nutrient availability (i.e., nutrients that are readily utilized by growing plants; Bridgham et al. 2001, Meuleman et al. 2002). Thus, the mechanisms of plant adaptation and response to nutrient gradients may be better understood by measuring plant responses to soil nutrient availability such as plant N uptake or plant production per unit of N available in the soil (N uptake efficiency and N response efficiency, respectively). However, these metrics have received less attention to date (Shaver and Melillo 1984, Bridgham et al. 1995a, Pastor and Bridgham 1999, Hiremath and Ewel 2001, Covelo and Gallardo 2002, Finzi et al. 2002). Given the complexities of the processes regulating plant nutrient uptake, plant NUE and plant responses to soil nutrient availability may differ qualitatively across nutrient availability gradients (Bridgham et al. 1995b, Pastor and Bridgham 1999).

Peatlands provide an excellent system in which to examine the effects of nutrient loading on plant commu-

nity NUE and plant responses to soil nutrient availability under nutrient-limited conditions. Peatlands occur along a natural gradient of nutrient availability, ranging from N-poor bogs to relatively N-rich fens (Bridgham et al. 1996, 2001, Wheeler and Proctor 2000, Bragazza and Gerdol 2002), allowing us to quantify the relative importance of plant phenotypic plasticity for N uptake and use compared with species adaptation. Bogs are ombrotrophic systems that receive all water and associated ions from the atmosphere due to a deep accumulation of organic matter isolating them from groundwater and surface water inflows. These systems typically have low soil pH (≤ 4), alkalinity, concentrations of base cations, and N availability and are dominated by mosses in the genus *Sphagnum*, as well as ericaceous shrubs and black spruce (*Picea mariana* (Miller)). "Rich" fens are minerotrophic systems that receive significant inputs from groundwater, surface water, or both. They have surface water pH > 6 and higher alkalinity, concentrations of base cations, and N availability than bogs. Brown mosses, sedges of the genus *Carex*, and deciduous shrubs dominate the ground layer of rich fens. "Intermediate" fens are intermediate in terms of species composition and soil pH (4–5.5).

We examined vascular plant production and efficiency responses after five years of N and P addition in a bog (see Plate 1), intermediate fen, and rich fen in the Upper Peninsula of Michigan, USA. We tested three hypotheses. (1) Increased nutrient availability would increase above-ground production of plants with the physiological capacity to respond, and these plants would be more common in relatively N-rich fens. Conversely, nutrient addition would increase luxury uptake of nutrients of plants limited in their ability to invest newly acquired nutrients into growth or in plants limited by other nutrients. These plants would be more common in the relatively N-poor bog. Changes in the relationship between production and N acquisition would drive changes in NUE. (2) Increasing nutrient availability would increase plant production per unit N and decrease the mean residence time of nutrients in the plant, leading to small or no change in NUE. For this reason, plant nutrient efficiency expressed as N uptake efficiency and N response efficiency (NRE) would be more responsive to changes in nutrient availability than NUE. (3) Nitrogen use efficiency and N uptake efficiency would differ qualitatively at scales of individual plant tissues (i.e., leaves, wood, and roots), the whole plant, and community through differences in plant physiology, nutrient allocation, and species-specific traits and also differ across the ombrotrophic–minerotrophic gradient through changes in nutrient availability and community composition.

METHODS

Site description

Our experimental sites were located in Gogebic County (46° N, 89° W) in the Upper Peninsula of Michigan, USA, at the University of Notre Dame

Environmental Research Center (UNDERC). Dominant vegetation in the bog (pH = 3.8) included *Sphagnum* spp. mosses, ericaceous shrubs such as *Chamaedaphne calyculata* (L.) Moench, *Vaccinium oxycoccus* L., *Kalmia polifolia* Wangenh., *Ledum groenlandicum* Oeder, and *Andromeda polifolia* L. var. *glaucophylla* (Link) DC., as well as the sedge *Carex oligosperma* Michx and the forb *Scheuchzeria palustris* L. The dominant vegetation in the intermediate fen (pH = 4.9) was graminoids, including *Carex* spp. and *Calamagrostis canadensis* (Michx.) P. Beauv., deciduous shrubs *Alnus incana* (L.) Moench, ssp. *rugosa* (Du Roi) Clausen (henceforth *A. rugosa*), and *Photinia floribunda* (Lindl.) Robertson & Phipps, scattered ericaceous shrubs such as *Chamaedaphne calyculata* and *L. groenlandicum*, and *Sphagnum* spp. mosses. The vegetation in the rich fen (pH = 6.0) was also dominated by *Carex* spp., *Calamagrostis canadensis*, the shrubs *Spiraea alba* Du Roi, *A. rugosa*, and *Salix* spp., and scattered forbs such as *Comarum palustre* L., *Galium labradoricum* (Wieg.) Wieg., and *Campanula aparinoides* Pursh. See Appendix A for a complete list of the dominant species in each peatland that were used in the following analyses.

Four 32 × 32 m plots in each peatland received one of the following treatments annually from 1998 to 2002: no additions (control), 6 g N/m² in the form of urea (CO(NH₂)₂), 2 g P/m² as superphosphate (Ca(H₂PO₄)₂), or a combination of N and P. Nutrients were added with hand spreaders in early June of each year (Keller et al. 2006). Nutrient addition rates were chosen based upon previous fertilization studies in northern peatland ecosystems (cf. Chapin et al. 2003, 2004). Our goal was to alleviate potential nutrient limitation (cf. Chapin et al. 1986), and therefore the amount of N added was much greater than local atmospheric N deposition (~0.6 g N·m⁻²·yr⁻¹ as wet deposition of inorganic N in 2002; National Atmospheric Deposition Program 2003). Given that we only added fertilizer one time per season, we used a slow-release P fertilizer, which was only available as a Ca-phosphate. The addition of Ca had no measureable effect on peat pH in the phosphorus addition plots (L. E. Kellogg, unpublished data).

In 2002, five 1 × 1 m plots were randomly placed within each 32 × 32 m main plot for vegetation analysis. The intensive nature of the sampling required for this study precluded use of multiple sites of each peatland type, which limits our ability to generalize our results across the ombrotrophic–minerotrophic gradient in other peatlands. However, these sites are representative of others in this area that we have examined (Kellogg and Bridgham 2003, Kellogg 2004, Keller et al. 2006). We focused our efforts on examining changes in plant N economy (i.e., NUE, N uptake efficiency, and NRE) with nutrient addition because the ombrotrophic–minerotrophic gradient is coincident with a relatively clear N availability gradient, while changes in P

availability across the gradient are less straightforward (Bridgham et al. 2001).

NUE calculations

Vitousek (1982) defined NUE (in grams of new biomass per gram N uptake) in perennial plants as NPP (in grams of newly produced biomass per square meter per year) divided by the amount of N taken up by or lost from the plant (in grams of N uptake per square meter per year):

$$\text{NUE} = \text{NPP}/\text{N uptake}. \quad (1)$$

However, it is often more informative to look at the component parts of NUE (Berendse and Aerts 1987):

$$\text{NUE} = A_N \times \text{MRT}_N \quad (2)$$

where A_N is nutrient productivity, or NPP per peak biomass N content (in grams of new biomass per gram of N content per year), and MRT_N is the mean residence time of N in the plant (in years). We estimated A_N as the increase in biomass over the growing season (in grams of new biomass per square meter per year) divided by the nutrient content at peak standing crop (in grams of N content per square meter; cf. Berendse and Aerts 1987). It is difficult to calculate all of the components of MRT_N (e.g., nutrient resorption) for non-photosynthetic tissues of a plant. Therefore, we estimated MRT_N of perennial plant tissues as the turnover rate of the plant nutrient pool (cf. Berendse and Aerts 1987), which is equal to N mass at peak growing season (in grams of N content per square meter) divided by the N taken up in newly produced tissue (in grams of N uptake per square meter per year). The MRT_N of annual tissues (i.e., the aboveground portion of grasses and sedges and the leaves of deciduous shrubs) was defined as having a life span of one year, though deciduous plant tissues are produced solely during the growing season. An annual time step for MRT_N is most pertinent in examination of perennial plant response at the ecosystem level, and the timescale usually involved in NUE studies is a full growing season or more (Hirose and Monsi 1975, Garnier and Aronson 1998). Additionally, using a MRT_N of less than one year for aboveground plant tissue produced solely in the growing season would decrease NUE (Eq. 2), but would not change relative treatment responses within that tissue. Many of the graminoid species have perennial belowground tissues, and thus the MRT of the whole plant is typically greater than one year (Eckstein and Karlsson 1997, Eckstein et al. 1999). However, we were unable to separate belowground tissues by species with the in-growth core technique, so we only examined species-level N efficiency dynamics in aboveground tissues.

Patterns in leaf-level N efficiencies are not necessarily similar to whole-plant patterns (Aerts 1999, Aerts and Chapin 2000). One needs to consider the allocation of dry matter into leaves, stems, and roots as a function of nutrient availability, as all have very different nutrient

concentrations and residence times and therefore NUE. A logical extension of Eq. 2 to the whole plant and community is

$$\text{NUE}_{\text{community}} = \frac{\sum \text{NPP}_{ij}}{\sum \text{N content}_{ij}} \times \frac{\sum \text{N content}_{ij}}{\sum \text{N uptake}_{ij}} \quad (3)$$

where i is the i th species of n species in the community, and j is the j th part of the plant (e.g., leaves, wood, roots, etc.). The summation of the production, N uptake, and N content of individual organs within a species and of individual species within a community explicitly accounts for potential changes in allocation patterns within species and changes in species abundance in response to nutrient addition. The first component in the equation (NPP/N content) is equal to community-level A_N , while the second component (N content/N uptake) is equal to community-level MRT_N .

Others have further considered the relationship between NUE and soil nutrient availability (Shaver and Melillo 1984, Bridgman et al. 1995b, Pastor and Bridgman 1999):

$$\text{NRE} = \text{NUE} \times \text{N uptake efficiency} \quad (4)$$

or $\text{NPP}/\text{available N} = \text{NPP}/\text{N uptake} \times \text{N uptake}/\text{available N}$, where NRE is N response efficiency or NPP relative to the pool of available soil N (in grams of new biomass per gram of available N per year) and N uptake efficiency is the proportion of available soil N that is taken up by the plant (in grams of N uptake per gram of available N per year; cf. Pastor and Bridgman 1999). Nitrogen uptake efficiency will depend on allocation to belowground biomass, maximum uptake velocities of roots, and the physiological ability of plants to respond to pulses of nutrient availability.

Soil nutrient availability

Soil inorganic N and P availability were estimated from four 0–25 cm depth cores taken from each treatment in May 2002. While it would have been useful to make multiple measurements of nutrient availability throughout the growing season, this was not logistically feasible given the size of the study and available resources. Inorganic soil N availability was determined by extracting 7 g (wet mass) of root-free peat with 2 mol/L KCl (Olsen and Sommers 1982). Ammonium concentration was measured using the salicylate method (EPA Method 10-107-06-2-A), and $[\text{NO}_3^-]$ was measured with the cadmium reduction method (EPA Method 12-107-04-1-B) on a Lachat Quikchem 8000 Autoanalyzer (Lachat, Loveland, Colorado, USA). Total inorganic N availability was the sum of NH_4^+ and NO_3^- availability. Available soil PO_4 was determined using a dilute acid-fluoride (AF) extraction of 7 g (wet mass) of root-free peat (Olsen and Sommers 1982), with $[\text{PO}_4]$ measured using a modified Murphy and Riley method (Murphy and Riley 1962).

Aboveground vascular biomass and N content

Total aboveground biomass and NPP were determined by clipping and collecting vegetation from all nutrient addition plots in each peatland during the peak of the growing season in August 2002. All vegetation was clipped to the peat surface in each of four randomly placed 20×20 cm squares in five 1×1 m² plots for each fertilization treatment (20 plots per site). We determined annual production for the peatland vegetation as follows: graminoids were separated into living tissue produced during that growing season (biomass was equal to annual production for these species). By definition, graminoid MRT_N was set to one year, and NUE was simply the inverse of nutrient concentration. Evergreen shrubs were separated into new (<1-year), 1-year, and >2-year age classes for both leaf and woody tissue, and deciduous shrubs were separated into new and old woody biomass (age classes in woody biomass could not be distinguished). We did not account for increases in shrub stem diameter, which may result in an underestimation of annual production. Where possible, the mean leaf mass and number of leaves produced per year were used to determine increases in leaf biomass for 1-year and 2+year leaves of evergreen shrubs, while all deciduous leaves were considered new production ($\text{MRT}_N = 1$). All plant tissue was dried at 60°C for at least 48 h. Nitrogen concentrations were determined with a Costech Elemental Combustion System (Costech, Valencia, California, USA) on subsamples of species that comprised >2% of the aboveground production in each peatland (these species are listed in Appendix A). Tissue N content and N uptake were calculated as biomass \times mean tissue [N] or $\text{NPP} \times [\text{N}]$ of newly produced tissue, respectively.

We chose two dominant species from each peatland for a more in-depth analysis. No two species were dominant in all three sites, but the species chosen for individual analysis comprised half of the biomass by mass in the bog and intermediate fen and a quarter of the biomass in the species-rich fen. We focused on *Carex oligosperma* (a perennial sedge) and *Chamaedaphne calyculata* (an evergreen shrub) in the bog and on *Calamagrostis canadensis* (a perennial grass) and *Alnus rugosa* (a deciduous, N-fixing shrub) in the intermediate and rich fens. We chose not to include mosses, which were primarily *Sphagnum* spp., because *Sphagnum* often exhibits a toxic response to even moderate N additions (Lee et al. 1987, Aerts et al. 2001, Limpens et al. 2003, Chapin et al. 2004), which we also observed in these plots (Keller et al. 2006). We have found previously that *Sphagnum* species have a comparatively low NUE (relatively high nutrient concentrations and low photosynthetic capacity; Iversen 2004).

Belowground community biomass and production

Total plant belowground biomass was determined by collecting four replicate 6 cm diameter \times 25 cm deep

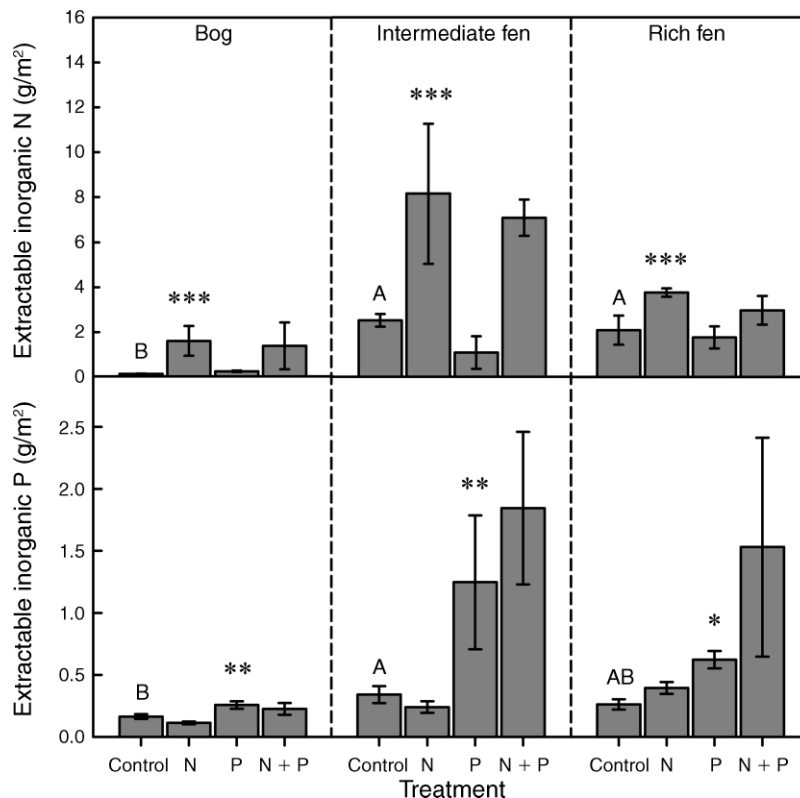


FIG. 1. Total available inorganic N and P to 25-cm depth in a bog, an intermediate fen, and a rich fen in the following treatments: Control, N addition (N), P addition (P), and combined N and P addition (N + P). The experimental sites were located in the Upper Peninsula of Michigan, USA, at the University of Notre Dame Environmental Research Center (UNDERC). Data are treatment means \pm SE, where $n = 4$ in all treatments. There were no significant interactions between N and P (i.e., all inorganic nutrient responses were additive). Letters above bars indicate significant differences in nutrient availability among sites before nutrient addition (i.e., in the control plots, $P < 0.05$).

† $P < 0.10$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

cores from each fertilization treatment in mid-June 2002. Fine roots (<1 mm diameter) were picked by hand from each core, and the peat and roots were dried separately at 60°C for at least 48 h. The bulk density and root biomass of each peat core were calculated on a dry-mass basis. Roots were finely ground (Udy Mill, Udy Corporation, Fort Collins, Colorado, USA), and total root N content (in grams per square meter) was determined by digestion with concentrated H₂SO₄ and 30% H₂O₂ (Lowther 1980) and colorimetric analysis using a Lachat Autoanalyzer for total N (EPA Method 10-107-06-2-A).

Net belowground community production was determined for each fertilization treatment using replicate 6 cm diameter root in-growth cores filled with homogenized, root-free peat from the same wetland type (cf. Weltzin et al. 2000). Four in-growth cores were placed in each fertilization treatment to 25 cm depth in mid-May 2002 (for a total of 16 cores per site). After the in-growth cores were removed in October 2002, new root growth was determined on a dry-mass basis as above, where live fine roots were separated by hand from the peat. Ground roots were analyzed on a Costech ECS 4010

Elemental Combustion System as above (see *Above-ground vascular biomass...*) to determine total N concentration in the new roots.

Statistical analysis

A two-way factorial analysis of variance (ANOVA) was used to test whether plant community production, N concentration and uptake, and efficiency parameters were significantly affected by N or P addition within a site (cf. Tank and Dodds 2003) using the SAS GLM procedure (SAS Institute, Cary, North Carolina, USA). We used the sampling plots ($n = 5$) within each control or nutrient addition treatment as the replicate in our statistical analyses. A significant main effect term in the ANOVA indicated a response to N or P irrespective of the other nutrient (for example, a response to N in both the N addition plots and the plots to which N was added in combination with P). A significant interaction term in the ANOVA indicated a nonadditive effect of the nutrients on one another (for example, a dampened response to N when N was added in combination with

TABLE 1. The effect of N and P addition on the aboveground biomass and annual production, tissue N concentration, and N uptake of the dominant vascular species in a bog, an intermediate fen, and a rich fen.

| Treatment | <i>n</i> | Biomass (g/m ²) | Biomass [N] (mg/g) | N content (g N/m ²) | Production (g·m ⁻² ·yr ⁻¹) | New tissue [N] (mg/g) | N uptake (g N·m ⁻² ·yr ⁻¹) |
|---------------------------------|----------|--------------------------------|-----------------------|------------------------------------|--|--------------------------|--|
| Bog | | | | | | | |
| <i>Carex oligosperma</i> | | | | | | | |
| Control | 5 | 27 ± 6 | 13.7 ± 0.5 | 0.4 ± 0.1 | 27 ± 6 | 13.7 ± 0.5 | 0.4 ± 0.1 |
| Nitrogen | 5 | 29 ± 18 | 14.8 ± 0.6 | 0.5 ± 0.3 | 29 ± 18 | 14.8 ± 0.6 | 0.5 ± 0.3 |
| Phosphorus | 5 | 44 ± 9* | 14.7 ± 0.5 | 0.7 ± 0.2* | 44 ± 9* | 14.7 ± 0.5 | 0.7 ± 0.2* |
| N + P | 5 | 99 ± 31 | 14.1 ± 0.9 | 1.5 ± 0.5 | 99 ± 31 | 14.1 ± 0.9 | 1.5 ± 0.5 |
| <i>Chamaedaphne calyculata</i> | | | | | | | |
| Control | 5 | 155 ± 30 | 9.5 ± 0.3 | 1.5 ± 0.3 | 30 ± 6 | 12.2 ± 0.3 | 0.4 ± 0.1 |
| Nitrogen | 5 | 317 ± 35*** | 9.3 ± 0.7 | 3.0 ± 0.4*** | 56 ± 11** | 13.1 ± 0.6 | 0.7 ± 0.2** |
| Phosphorus | 5 | 58 ± 9 | 11.7 ± 0.2** | 0.7 ± 0.1 | 21 ± 3 | 14.3 ± 0.3** | 0.3 ± 0.05 |
| N + P | 5 | 610 ± 111*** | 10.3 ± 0.6 | 6.2 ± 1.0*** | 86 ± 28 | 15.2 ± 0.9 | 1.3 ± 0.4 |
| Intermediate fen | | | | | | | |
| <i>Calamagrostis canadensis</i> | | | | | | | |
| Control | 2 | 12 ± 7 | 10.6 ± 1.8 | 0.1 ± 0.1 | 12 ± 7 | 10.6 ± 1.8 | 0.1 ± 0.1 |
| Nitrogen | 1 | 3 ± 3 | 18.6 | 0.05 ± 0.0 | 3 ± 3 | 18.6 | 0.05 ± 0.0 |
| Phosphorus | 1 | 8 ± 5 | 17.8 | 0.1 ± 0.1 | 8 ± 5 | 17.8 | 0.1 ± 0.1 |
| N + P | 4 | 121 ± 64 | 14.7 ± 0.8 | 1.6 ± 0.8 | 121 ± 64 | 14.7 ± 0.8 | 1.6 ± 0.8 |
| <i>Alnus rugosa</i> | | | | | | | |
| Control | 5 | 639 ± 330 | 12.1 ± 0.7 | 8.1 ± 4.5 | 162 ± 93 | 22.8 ± 0.5 | 3.7 ± 2.2 |
| Nitrogen | 4 | 658 ± 530 | 15.3 ± 0.9 | 11.5 ± 9.6 | 232 ± 188 | 23.3 ± 1.0 | 5.8 ± 4.9 |
| Phosphorus | 4 | 2541 ± 690** | 13.7 ± 0.9 | 34.3 ± 9.1*** | 776 ± 204** | 24.4 ± 1.1*** | 19.0 ± 5.2*** |
| N + P | 5 | 3622 ± 943 | 13.2 ± 1.0† | 50.7 ± 14.3 | 1031 ± 332 | 24.6 ± 1.0 | 24.9 ± 7.3 |
| Rich fen | | | | | | | |
| <i>Calamagrostis canadensis</i> | | | | | | | |
| Control | 2 | 5 ± 4 | 10.5 ± 0.8 | 0.1 ± 0.0 | 5 ± 4 | 10.5 ± 0.8 | 0.1 ± 0.0 |
| Nitrogen | 5 | 35 ± 11** | 13.0 ± 0.5 | 0.4 ± 0.1* | 35 ± 11** | 13.0 ± 0.5 | 0.4 ± 0.1* |
| Phosphorus | 5 | 77 ± 23*** | 13.2 ± 0.9† | 1.1 ± 0.3*** | 77 ± 23*** | 13.2 ± 0.9† | 1.1 ± 0.3*** |
| N + P | 5 | 140 ± 29 | 13.9 ± 1.0 | 1.9 ± 0.3 | 140 ± 29 | 13.9 ± 1.0 | 1.9 ± 0.3 |
| <i>Alnus rugosa</i> | | | | | | | |
| Control | 3 | 20 ± 14 | 17.9 ± 0.6 | 0.3 ± 0.2 | 11 ± 7 | 22.2 ± 1.4 | 0.2 ± 0.1 |
| Nitrogen | 4 | 21 ± 13 | 16.7 ± 1.4 | 0.4 ± 0.2 | 12 ± 7 | 22.2 ± 0.5 | 0.3 ± 0.2 |
| Phosphorus | 4 | 1438 ± 567** | 16.2 ± 1.0 | 22.1 ± 8.0*** | 476 ± 152** | 25.9 ± 1.3*** | 12.6 ± 4.2*** |
| N + P | 3 | 566 ± 388 | 14.8 ± 0.7 | 8.8 ± 6.2 | 154 ± 113 | 26.0 ± 0.9 | 4.2 ± 3.1 |

Notes: Biomass [N] is the mean tissue N concentration of the standing aboveground biomass weighted by the mass of tissue with a given [N], while new tissue [N] is the mean weighted tissue [N] of annually produced tissue. Sample size is *n* = 5 for biomass, N content, production, and N uptake; *n* given in the table is that of the [N] of tissue. Data shown in all tables are means ± SE in the following treatments: Control, N addition, P addition, and combined N and P addition (N + P). *Calamagrostis canadensis* occurred in only one plot in the N and P treatments in the intermediate fen, and there is no SE associated with these data. Asterisks next to the "N + P" treatment data signify a significant interaction between N and P. The experimental sites were located in the Upper Peninsula of Michigan, USA, at the University of Notre Dame Environmental Research Center (UNDERC).

† *P* < 0.10; * *P* < 0.05; ** *P* < 0.01; *** *P* < 0.001.

P). We considered differences significant at *P* < 0.10. To be concise in our presentation of the results, we typically only mention treatment effects that were significant at this probability level. The *F* statistics and *P* values for individual species and above- and belowground community responses are reported in Appendix B. All nonnormal data were log-transformed prior to analysis, and unless specifically mentioned, leaf and woody tissue responded to nutrient addition in a manner that was qualitatively similar to the overall plant response (see Appendix C for a detailed description of plant-level responses and Appendices D and E for tissue responses). Differences between sites were determined with a *t* test using the LSMEANS procedure in SAS, and site data

presented are averaged across treatments unless there was a significant site × treatment interaction.

RESULTS

Resource availability

Ammonium was the main form of available inorganic N in all sites; NO₃ averaged no more than 6% of extractable inorganic soil N and was usually below detection limits except in the rich fen. Nitrogen addition significantly increased total inorganic N availability in the three sites (*P* < 0.0001; Fig. 1). In the unfertilized control plots, total inorganic N availability was less in the bog than in the fens. Phosphorus addition increased PO₄ availability in all three sites (*P* < 0.05; Fig. 1).

TABLE 2. Aboveground efficiency metrics for dominant vascular species in response to nutrient addition in a bog, an intermediate fen, and a rich fen.

| Treatment | <i>n</i> | A_N (g new biomass· [g N content] ⁻¹ ·yr ⁻¹) | MRT _N (yr) | NUE (g new biomass/ g N uptake) | N uptake efficiency (g N uptake· [g N _{av}] ⁻¹ ·yr ⁻¹) | NRE (g new biomass· [g N _{av}] ⁻¹ ·yr ⁻¹) |
|---------------------------------|----------|---|--------------------------|---------------------------------------|---|--|
| Bog | | | | | | |
| <i>Carex oligosperma</i> | | | | | | |
| Control | 5 | 74 ± 3 | 1 | 74 ± 3 | 2.7 ± 0.6 | 214 ± 10 |
| Nitrogen | 5 | 68 ± 3 | 1 | 68 ± 3 | 0.3 ± 0.2*** | 35 ± 4*** |
| Phosphorus | 5 | 68 ± 2 | 1 | 68 ± 2 | 2.6 ± 0.6 | 83 ± 5† |
| N + P | 5 | 72 ± 4 | 1 | 72 ± 4 | 1.0 ± 0.4 | 62 ± 7† |
| <i>Chamaedaphne calyculata</i> | | | | | | |
| Control | 5 | 21 ± 4 | 4.3 ± 0.7 | 82 ± 2 | 2.6 ± 0.5 | 191 ± 10 |
| Nitrogen | 5 | 18 ± 2** | 4.4 ± 0.6** | 77 ± 3 | 0.5 ± 0.1*** | 18 ± 5*** |
| Phosphorus | 5 | 31 ± 2 | 2.3 ± 0.1 | 70 ± 1** | 1.2 ± 0.2 | 172 ± 9 |
| N + P | 5 | 13 ± 3* | 6.0 ± 1.2* | 67 ± 4 | 0.9 ± 0.3** | 72 ± 7* |
| Intermediate fen | | | | | | |
| <i>Calamagrostis canadensis</i> | | | | | | |
| Control | 2 | 97 ± 16 | 1 | 97 ± 16 | 0.1 ± 0.1 | 12 ± 1 |
| Nitrogen | 1 | 54 | 1 | 54 | 0.0 | 2 |
| Phosphorus | 1 | 56 | 1 | 56 | 0.2 | 13 |
| N + P | 4 | 69 ± 4 | 1 | 69 ± 4 | 0.3 ± 0.5 | 21 ± 5 |
| <i>Alnus rugosa</i> | | | | | | |
| Control | 5 | 19 ± 2 | 2.2 ± 0.3 | 44 ± 1 | 1.5 ± 1.4 | 65 ± 9 |
| Nitrogen | 4 | 21 ± 4 | 2.2 ± 0.4 | 43 ± 2 | 0.9 ± 1.2*** | 36 ± 8** |
| Phosphorus | 4 | 23 ± 1 | 1.8 ± 0.1 | 41 ± 2** | 22.0 ± 2.3*** | 897 ± 12*** |
| N + P | 5 | 18 ± 3 | 2.7 ± 0.7 | 41 ± 2 | 3.5 ± 1.5** | 146 ± 10 |
| Rich fen | | | | | | |
| <i>Calamagrostis canadensis</i> | | | | | | |
| Control | 2 | 96 ± 7 | 1 | 96 ± 7 | 0.1 ± 0.2 | 7 ± 2 |
| Nitrogen | 5 | 77 ± 3† | 1 | 77 ± 3† | 0.1 ± 0.3 | 9 ± 3 |
| Phosphorus | 5 | 77 ± 5† | 1 | 77 ± 5† | 0.6 ± 0.7** | 44 ± 5** |
| N + P | 5 | 73 ± 5 | 1 | 73 ± 5 | 0.6 ± 0.5 | 47 ± 5 |
| <i>Alnus rugosa</i> | | | | | | |
| Control | 3 | 31 ± 4 | 1.5 ± 0.1 | 45 ± 3 | 0.2 ± 0.4 | 8 ± 3 |
| Nitrogen | 4 | 28 ± 3* | 1.7 ± 0.2 | 45 ± 1 | 0.1 ± 0.3*** | 4 ± 2** |
| Phosphorus | 4 | 23 ± 2** | 1.7 ± 0.2 | 39 ± 2** | 9.0 ± 2.0*** | 340 ± 12*** |
| N + P | 3 | 16 ± 1 | 2.5 ± 0.3 | 39 ± 1 | 2.3 ± 1.7** | 87 ± 10 |

Notes: Abbreviations are: A_N , N productivity; MRT_N, mean residence time of N; NUE, N use efficiency; NRE, N response efficiency; N_{av}, available N. By definition, MRT_N = 1 for annually produced or deciduous tissues with a lifespan of ≤1 year and A_N = NUE. Other details are as in Table 1.

Differences in PO₄ availability along the ombrotrophic–minerotrophic gradient were not straightforward.

Representative vascular plant responses

In the interest of conciseness, we focus only on the key responses of the representative vascular plant species here. Detailed descriptions of the species-specific nutrient responses are in Appendix C. Nitrogen addition, P addition, or a combination of nutrients generally increased plant production and N uptake in the bog, the intermediate fen, and the rich fen (Table 1; see Appendix B for *F* statistics and *P* values). The responses of the shrub species (i.e., *Chamaedaphne calyculata* in the bog and *Alnus rugosa* in the fens) were driven by changes in the amount of wood or leaf tissue comprising the biomass of each shrub in a given nutrient treatment, as leaf and woody tissue differed in annual production, tissue [N], and N content (Appendix D).

Nutrient addition generally resulted in small declines in plant NUE (<15% relative to the control), because changes in NUE were dampened due to the compensating responses of A_N and MRT_N (Table 2). We observed much stronger effects of nutrient addition on plant N uptake efficiency and NRE. Nitrogen addition generally led to large declines in plant N uptake efficiency and NRE (>40% relative to the control). Interestingly, the converse was true for P addition, which generally increased the efficiency with which plants took up and used soil N for biomass production; N uptake efficiency and NRE were between two and 50 times greater after P addition in both of the fen species. The positive effects of P addition on plant production, N uptake, and N use were particularly striking for the N-fixing shrub, *A. rugosa*, in both the intermediate fen and the rich fen (Tables 1 and 2). In the two bog species, P addition compensated in part for declines in N uptake efficiency and NRE with N addition (Table 2).

TABLE 3. The effect of N and P addition on above- and belowground community biomass, production, tissue [N], and N uptake in a bog, an intermediate fen, and a rich fen.

| Treatment | n | Biomass | | Biomass [N] (mg/g) | Biomass N content (g N/m ²) |
|-------------------------|----|-------------------------|-----|-------------------------|--|
| | | (g/m ²) | (%) | | |
| Bog | | | | | |
| Aboveground | | | | | |
| Control | 5 | 227 ^C ± 27 | 89 | 10.9 ^B ± 0.4 | 2.4 ^C ± 0.2 |
| Nitrogen | 5 | 591 ± 40*** | 98 | 11.0 ± 0.5 | 6.5 ± 0.5*** |
| Phosphorus | 5 | 242 ± 18** | 86 | 12.3 ± 0.3† | 3.0 ± 0.2** |
| N + P | 5 | 1039 ± 138* | 97 | 11.3 ± 0.5 | 11.8 ± 1.7† |
| Belowground | 16 | 1736 ^A ± 267 | | 3.0 ^C ± 0.2 | 5.4 ^A ± 0.9 |
| Intermediate fen | | | | | |
| Aboveground | | | | | |
| Control | 5 | 1106 ^A ± 363 | 93 | 11.6 ^B ± 0.6 | 12.8 ^A ± 4.3 |
| Nitrogen | 5 | 1473 ± 579† | 97 | 14.8 ± 1.4† | 22.6 ± 10.1† |
| Phosphorus | 5 | 3693 ± 546*** | 99 | 11.7 ± 1.0 | 45.4 ± 8.8*** |
| N + P | 5 | 6476 ± 719 | 97 | 12.6 ± 1.1 | 79.4 ± 7.3 |
| Belowground | 16 | 1714 ^A ± 584 | | 8.5 ^A ± 0.7 | 12.8 ^A ± 3.8 |
| Rich fen | | | | | |
| Aboveground | | | | | |
| Control | 5 | 407 ^B ± 77 | 82 | 13.0 ^A ± 0.4 | 5.3 ^B ± 1.0 |
| Nitrogen | 5 | 468 ± 88 † | 83 | 13.0 ± 0.9** | 5.8 ± 0.9† |
| Phosphorus | 5 | 1896 ± 671*** | 88 | 15.4 ± 0.8 | 28.0 ± 8.9*** |
| N + P | 5 | 3508 ± 1203 | 88 | 10.8 ± 0.7** | 35.6 ± 11.0 |
| Belowground | 16 | 1954 ^A ± 410 | | 5.9 ^B ± 0.5 | 12.8 ^A ± 3.4 |

Notes: Percentages are the percentages of total aboveground biomass or production represented in the analysis. New-tissue [N] includes new roots (i.e., roots sampled from in-growth cores). Belowground treatments were combined within a site, where $n = 16$, except for standing crop [N] in the intermediate fen and new tissue [N] in the bog and rich fen, for which $n = 15$. Letters signify differences among sites ($P < 0.10$) in the control plots (Aboveground) or combined treatments (Belowground). Other details are as in Table 1.

Aboveground community responses

The production and N uptake responses of >82% of vascular plant biomass in each peatland were combined and examined at the community level. Before nutrient addition (i.e., in the control plots), aboveground biomass and N content differed along the ombrotrophic–minerotrophic gradient (Table 3). Aboveground community responses to nutrient addition also differed along the ombrotrophic–minerotrophic gradient, especially between the bog and the fens (Table 3; Figs. 2 and 3).

Bog.—Nitrogen and P addition each increased the aboveground biomass and N content of the vascular plant community in the bog (Table 3), and their effects were synergistic (see Appendix B for supporting statistics). Only P addition increased the average [N] of the bog community. Nitrogen and P addition each increased aboveground production and N uptake in the bog, but only N addition increased the [N] of newly produced plant tissue. Nitrogen addition decreased A_N , increased MRT_N , and decreased aboveground NUE of the bog community (Fig. 2). Nitrogen addition alone decreased community N uptake efficiency and NRE in the bog, though these responses were somewhat alleviated by the addition of P in combination with N (Fig. 3).

Intermediate and rich fens.—Nitrogen and P addition increased aboveground biomass and N content in the intermediate and rich fens, though the increase in biomass and N content was much greater with P addition (Table 3). Nitrogen addition increased the mean [N] of the aboveground community in the intermediate fen. Nutrient addition effects on mean [N] of the aboveground community in the rich fen were less straightforward. Phosphorus addition increased aboveground production, the [N] of newly produced tissue, and N uptake in the intermediate and rich fens (Table 3). Phosphorus addition decreased A_N in the intermediate and rich fens (Fig. 2). Nutrient addition had no effect on MRT_N in the intermediate fen, while P addition increased MRT_N in the rich fen. Phosphorus addition decreased NUE in the two fens, while N addition decreased NUE in the intermediate fen, but not in the rich fen. Phosphorus addition increased while N addition decreased community N uptake efficiency and NRE in the intermediate and rich fens (Fig. 3).

Belowground community responses

Nutrient addition did not affect root biomass, root production, mean root [N], N content, the [N] of newly produced root tissue, or root N uptake in any of the peatlands (results not shown; see supporting statistics in

TABLE 3. Extended.

| Production | | New-tissue [N] (mg/g) | N uptake (g N·m ⁻² ·yr ⁻¹) |
|--|-----|--------------------------|--|
| (g·m ⁻² ·yr ⁻¹) | (%) | | |
| 91 ^B ± 6 | 94 | 13.5 ^B ± 0.2 | 1.2 ^B ± 0.1 |
| 166 ± 14*** | 94 | 16.0 ± 0.6*** | 2.7 ± 0.3*** |
| 125 ± 8 ** | 90 | 14.4 ± 0.3 | 1.8 ± 0.1** |
| 313 ± 58 | 98 | 16.4 ± 0.4 | 5.1 ± 0.9 |
| 141 ^C ± 10 | | 10.7 ^B ± 0.4 | 1.5 ^C ± 0.1 |
| | | | |
| 350 ^A ± 81 | 88 | 17.3 ^A ± 1.2 | 6.4 ^A ± 2.0 |
| 696 ± 235 | 94 | 19.8 ± 0.8 | 14.5 ± 5.6 |
| 1019 ± 184 *** | 95 | 22.1 ± 1.4** | 23.6 ± 4.9*** |
| 1719 ± 269 | 96 | 22.8 ± 0.5 | 38.8 ± 5.5 |
| 592 ^B ± 76 | | 10.3 ^B ± 0.3 | 6.3 ^B ± 0.9 |
| | | | |
| 300 ^A ± 30 | 87 | 14.6 ^B ± 0.8 | 4.4 ^A ± 0.6 |
| 330 ± 80 | 82 | 13.9 ± 1.1 | 4.3 ± 0.8 |
| 829 ± 185 *** | 84 | 21.1 ± 2.1** | 17.9 ± 4.6*** |
| 981 ± 261 | 88 | 17.2 ± 1.3 | 18.1 ± 5.3 |
| 947 ^A ± 113 | | 14.4 ^A ± 0.3 | 14.0 ^A ± 1.9 |

Appendix B). Thus, we combined individual treatments to show the belowground response across sites; root biomass and N content were similar among the three peatlands, while root production and N uptake differed (Table 3).

Nutrient addition also had no effect on belowground A_N , MRT_N , or NUE (results not shown). However, when averaged across treatments, belowground A_N and MRT_N exhibited compensating responses along the ombrotrophic–minerotrophic gradient, resulting in dampened changes in NUE (Fig. 4). Nutrient addition affected belowground N uptake and N response efficiencies in a manner strikingly similar to the aboveground community in each peatland (Fig. 3).

DISCUSSION

We set out to determine the manner in which nutrient addition would affect plant production, N uptake, and N use across multiple biological scales ranging from the leaf to the community level in peatlands along an ombrotrophic–minerotrophic gradient. We found three important results: (1) species and community production and N uptake were strongly affected by soil P availability, (2) the trade-off between A_N and the mean residence time of N in plant tissue (MRT_N) dampened NUE responses to nutrient addition, and therefore plant and community N uptake efficiency responded to nutrient addition in a much more dynamic manner than NUE, and (3) plant responses to nutrient addition varied substantially across different biological scales. We discuss these findings below in the context of our initial hypotheses.

Plant production and N uptake

We hypothesized that increased nutrient availability would increase the aboveground production and N uptake of plants in relatively N-rich fens, while conversely increasing the luxury uptake of N of plants (nutrient uptake in excess of what is required for growth) in the relatively N-poor bog. We observed the classic response of plant nutrient limitation (Chapin et al. 1986): nutrient addition increased aboveground production in individual species and in the overall community. As we hypothesized, the absolute increase in biomass was greater for the species in the nutrient-rich fens than in the nutrient-poor bog (Tables 1 and 3). Depending on the species and site, plant growth and N uptake increased in response to N addition, P addition, or a combination of both nutrients. Phosphorus availability was important in limiting plant growth and N uptake across the ombrotrophic–minerotrophic gradient (Table 3); the importance of P as a factor limiting growth in peatlands has also been suggested by others (Bridgman et al. 1996, Koerselman and Meuleman 1996, Bedford et al. 1999, Chapin et al. 2004). In particular, the N-fixing shrub *A. rugosa* was strongly P-limited in both the intermediate and rich fens (Table 1). This is not surprising given that N fixers have been shown to increase growth and N fixation as a secondary effect of greater P uptake, and P addition has been found previously to have a positive effect on the percentage of N uptake derived from atmospheric fixation (Ekblad and HussDanell 1995).

In contrast to our hypothesis, N addition rarely resulted in luxury N uptake. While luxury nutrient uptake is often pronounced in plants that grow slowly (Chapin et al. 1986), our findings indicate that peatland plants adapted to nutrient-poor conditions retain enough phenotypic plasticity to take up N in proportion to their growth requirements. The only cases of luxury N uptake involved the addition of P (Table 1), again indicating the strong interaction between N and P availability. Plant functional group was also important in N dynamics, and leaf [N] followed the evergreen shrub \leq graminoids $<$ deciduous shrub trend, as shown previously (Aerts and Chapin 2000).

Surprisingly, belowground community production did not respond to nutrient addition. However, there may have been species-specific responses that we were unable to detect with root in-growth cores, which are a community-level measurement. Nutrient addition increased the ratio of aboveground to belowground biomass allocation within communities (Table 3) as would be generally predicted (Aerts and Chapin 2000). However, belowground production was much greater in the fens than the bog (Table 3), despite greater soil N availability in the fens (Fig. 1). This result is surprising given that theory predicts that suboptimal nutrient availability leads to increased biomass allocation to roots. This theory may not hold for several reasons: (1) greater biomass allocation to roots has been observed in

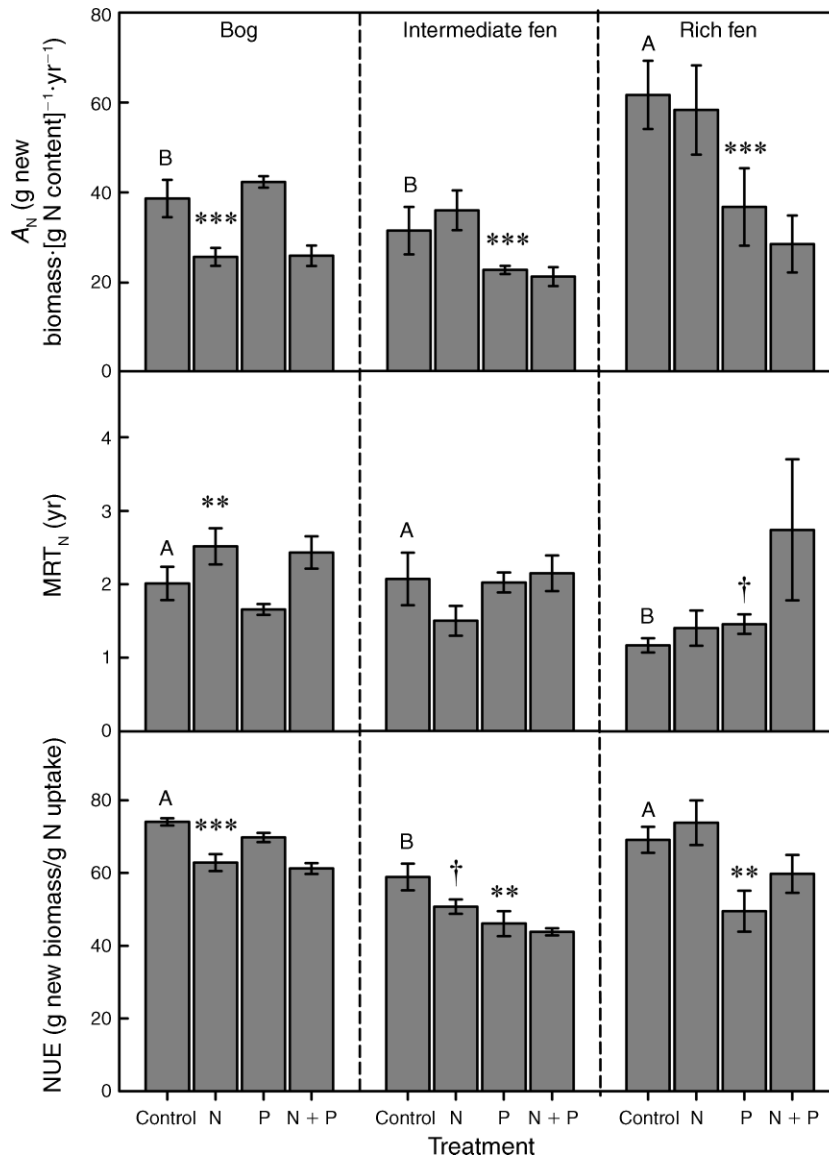


FIG. 2. Aboveground community N productivity (A_N), mean residence time of N (MRT_N), and N use efficiency (NUE). Data are treatment means \pm SE, where $n = 5$ for all treatments. $A_N \times MRT_N = NUE$. Other details are as in Fig. 1.

nutrient-rich compared to nutrient-poor sites in other field experiments (as reviewed in Aerts and Chapin 2000), (2) our results show the importance of P as a limiting nutrient, and differences in P availability were small and did not clearly follow the ombrotrophic–minerotrophic gradient, and (3) we did not consider the predominance of the nonvascular *Sphagnum* species in the bog.

Comparison of efficiency indices

We hypothesized that plant responses to gradients of soil nutrient availability expressed as N uptake efficiency and N response efficiency would be more responsive to changes in nutrient availability than NUE because NUE

is a ratio comprised of two conflicting processes selected to maximize nutrient use: plant productivity per unit N acquired (A_N) and the mean residence time of N in plant tissue (MRT_N) (Berendse and Aerts 1987). At small scales, A_N and MRT_N often respond to gradients of nutrient availability in opposing directions, resulting in dampened NUE responses (Aerts and Decaluwe 1994, Aerts and Chapin 2000).

We observed a trade-off between A_N and MRT_N at multiple biological scales, ranging from leaf to community level. The trade-off between A_N and MRT_N occurred across the ombrotrophic–minerotrophic gradient, and our study is the first to our knowledge to demonstrate this trade-off belowground. Before nutrient

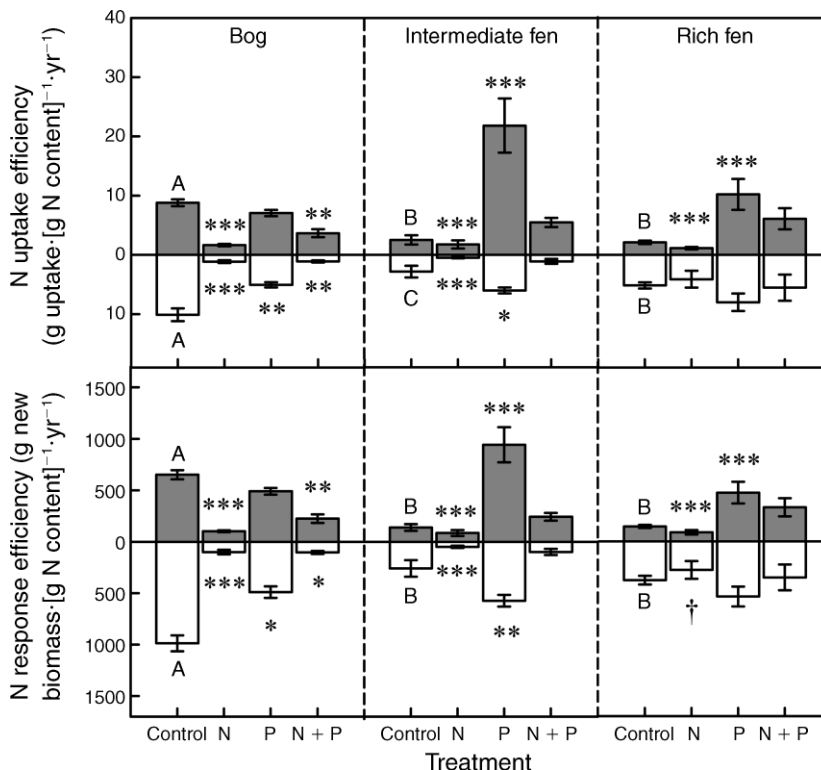


FIG. 3. Total above- and belowground N uptake efficiency and N response efficiency in a bog, an intermediate fen, and a rich fen. Above- and belowground responses are shown above and below the line, respectively, in each graph. Data are treatment means \pm SE, where $n=5$ for each treatment in the aboveground community and $n=4$ in each treatment in the belowground community, except in the N treatment in the bog and the combined N and P treatment in the rich fen, for which $n=3$. Other details are as in Fig. 1.

addition, the vascular plant community in the nutrient-poor bog was adapted to maximize MRT_N , while the plant communities in the relatively nutrient-rich fens were adapted to maximize A_N in both above- (Fig. 2) and belowground tissues (Fig. 4). The adaptive trade-off between A_N and MRT_N resulted in muted changes in NUE along the ombrotrophic–minerotrophic gradient.

We also examined the responses of A_N and MRT_N within communities due to nutrient addition. The addition of a limiting nutrient tended to decrease A_N and, conversely, increase MRT_N , thereby muting changes in NUE at the tissue, plant, and community scales (Table 2, Fig. 2, Appendix E). This response to nutrient addition within communities reflects both phenotypic responses of the species and changes in the relative abundances of the resident species (we saw few new species enter the plots over the length of the experiment). The directionality of the response in A_N and MRT_N is counterintuitive when considered in the context of plant adaptation, but is likely due to physiological constraints on plant growth, the importance of tissue [N] in controlling efficiency parameters (Aerts and Decaluwe 1994, Aerts and Chapin 2000, Meuleman et al. 2002), and the allocation of biomass among tissues and species with different A_N and MRT_N .

As we hypothesized, the apparently inherent trade-off between A_N and MRT_N makes the NUE index of limited usefulness in understanding the relationship between plant nutrient limitation and soil nutrient availability. In particular, the N uptake efficiency and NRE indices explicitly incorporate plant and community response to changes in soil nutrient availability (see *Methods*; Shaver and Melillo 1984, Bridgman et al. 1995b, Pastor and Bridgman 1999), while NUE does not. Given logistical constraints, we were only able to use a one-time measurement of extractable inorganic N and P concentrations in the soil as our metric of nutrient availability. However, we have extensively documented the increase in soil N availability along the ombrotrophic–minerotrophic gradient in other studies (Bridgman et al. 2001), including in the same sites in which this experiment was performed (Kellogg 2004). Thus we believe our estimates of soil nutrient availability are reasonable, especially given the large increases in extractable inorganic N and P we observed with nutrient addition, although this is an aspect of the study that could be improved upon in future research.

Nitrogen uptake efficiency showed a much more dynamic response to nutrient addition than did plant NUE. Though the magnitude of response differed by tissue, dominant species, and site, changes in N uptake

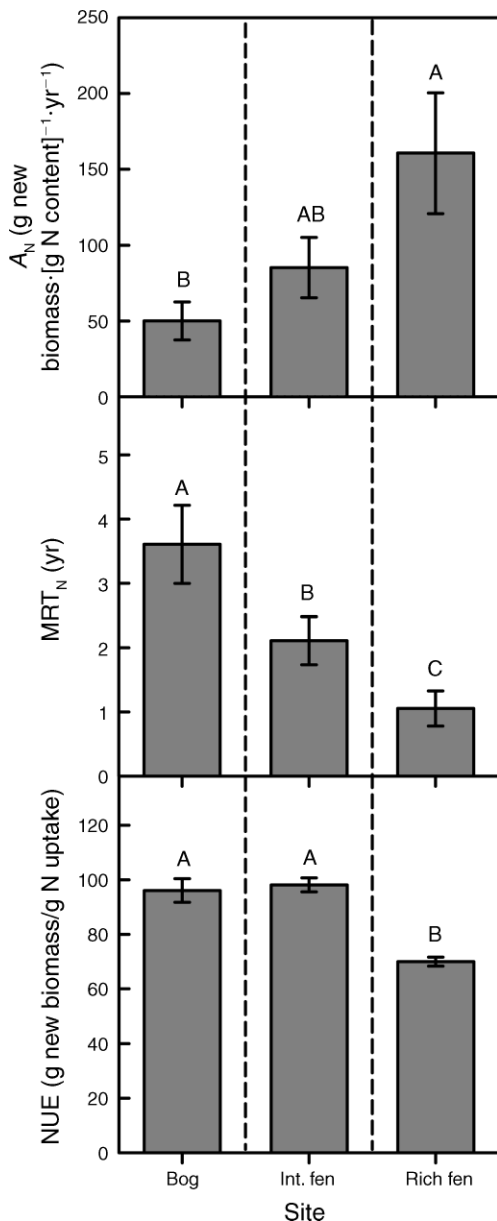


FIG. 4. Belowground community N productivity (A_N), mean residence time of N (MRT_N), and N use efficiency (NUE). Data are site means \pm SE in a bog, an intermediate (Int.) fen, and a rich fen; $n = 15$ in the bog, and $n = 16$ in the intermediate and rich fens. Letters above bars signify significant differences among sites ($P < 0.10$).

efficiency with fertilization were ubiquitous among the vascular species along the ombrotrophic–minerotrophic gradient (Table 2, Fig. 3). We commonly observed a decrease in N uptake efficiency with N addition because N uptake did not increase commensurate with increased N availability (Tables 1 and 3). In contrast, P addition facilitated an increase in N uptake efficiency, indicating that plants were more efficient in acquiring available N when fertilized with P. Ultimately, plant production per

unit of available N (NRE) was much more responsive to changes in N uptake efficiency than to changes in NUE (i.e., Eq. 4).

Changes in plant nutrient acquisition from the soil may have significant implications for nutrient cycling within an ecosystem. On one hand, decreased relative N uptake with N addition could mean greater N losses from the system as a whole, while on the other hand, P addition appears to increase the ability of plants to acquire N from the soil system. To our knowledge, only a handful of other studies have examined plant NRE (Shaver and Melillo 1984, Bridgham et al. 1995b, Hiremath and Ewel 2001, Covelo and Gallardo 2002, Finzi et al. 2002). Given its importance in our study, it is critical to see to what extent our results are representative of other ecosystems.

Scaling NUE and N uptake efficiency at multiple biological levels

We hypothesized that plant NUE and N uptake efficiency would differ at biological scales ranging from the leaf to the community level. While a number of authors have speculated that NUE could differ at different biological scales (as reviewed in Garnier and Aronson 1998, Aerts and Chapin 2000), ours is one of the few studies that have examined this important ecological phenomenon (Eckstein and Karlsson 1997, Hiremath and Ewel 2001, Silla and Escudero 2004). Plant efficiency responses to gradients of nutrient availability may vary across multiple biological scales for two reasons: (1) one of the main ways for plants to change their N efficiency is to alter the storage of C and nutrients in tissues with different nutrient concentrations and residence times (Vitousek 1982, Berendse and Aerts 1987, Bridgham et al. 1995b, Aerts and Chapin 2000) and (2) changes in plant community structure will change the N efficiency of a community to the extent that new species differ in their capacity for production and N acquisition (e.g., Pastor and Bridgham 1999).

In our study, N addition, P addition, and a combination of N and P addition often resulted in small declines in NUE at the scale of individual plant tissues, whole plants, and the entire community, presumably because of physiological constraints on plant production relative to nutrient uptake (cf. Aerts and Chapin 2000). However, as we hypothesized, different factors were important in shaping NUE response, depending on the biological scale. At the tissue level, NUE generally declined because tissue [N] increased with nutrient addition (Table 1, Appendices D and E). At the whole-plant level, NUE declined due to changes in C allocation. For example, nutrient addition increased the production of leaves relative to wood in the shrub species (Appendix D). As leaves had comparatively lower NUE relative to woody tissue (Appendix E), this resulted in declining NUE at the whole-plant level (Table 2). At the community level, changes in NUE were driven by changes in C and N allocation within plants



PLATE 1. A bog ecosystem that is part of a series of peatlands that span an ombrotrophic–minerotrophic gradient at the University of Notre Dame Environmental Research Center in the Upper Peninsula of Michigan, USA. Small, white PVC poles indicate sampling plots for vegetation analysis. Author C. Iversen is kneeling in the foreground. Photo credit: S. D. Bridgham.

and also changes in species abundance. For example, the increased dominance of *Alnus rugosa* in the P addition plots (Table 1) led to declining NUE in the fens (Fig. 2) because of the low NUE of the N-fixing shrub (Table 2). An increase in shrub dominance appears to be a common response to fertilization in peatland ecosystems (Thormann and Bayley 1997, Pastor and Bridgham 1999, Chapin et al. 2004).

While N uptake efficiency is also controlled in part by C allocation to tissue types with different nutrient concentrations, there is an additional layer of complexity associated with the processes controlling plant nutrient acquisition from the soil (Bridgham et al. 1995b, Pastor and Bridgham 1999). Even so, and in contrast to NUE, N uptake efficiency generally decreased in response to increased N availability at all biological scales (Table 2, Fig. 3, Appendix E). Further, the similarity in N uptake efficiency and NRE responses between the above- and belowground components of the plant communities (Fig. 3) may indicate a direct link between root uptake velocities and physiological capacity in controlling plant N acquisition and production (Aerts and Chapin 2000). The similarity in N uptake

efficiency and NRE responses at multiple biological scales contrasts with the complexity of plant NUE responses and confirms the relatively straightforward application of these indices in examining plant responses to nutrient availability gradients.

Conclusions

Our study tested the usefulness of the NUE index by scaling plant NUE responses to nutrient addition from the leaf to the community level and across a natural gradient of soil nutrient availability. We found that P availability had large effects on plant production and N uptake and may exert strong controls over plant N use across nutrient availability gradients. Nitrogen use efficiency generally declined in response to nutrient addition as would be expected, but NUE differed at levels of biological organization ranging from individual plant tissues to the whole plant to the above- and belowground components of the entire community. It was not possible to scale to community-level NUE from leaf- or species-level dynamics alone, and the many previous NUE studies that have focused on foliage may not be predictive of ecosystem-scale responses. We found a trade-off between A_N and MRT_N at multiple

levels of biological organization, including the below-ground component, suggesting that A_N and MRT_N cannot be maximized at the same time. Because of the trade-off between A_N and MRT_N , NUE may not be an effective index to examine plant responses to nutrient availability gradients. Nitrogen uptake efficiency was much more responsive to changing nutrient availability than was NUE in both individual plants and the entire community, and the large changes in N uptake efficiency drove large changes in NRE. Moreover, these responses were strikingly similar above- and belowground. Because of inherent trade-offs in the plant life-history traits that maximize either A_N or the MRT_N , it may be much more useful in the future for researchers to focus on plant and community N uptake efficiency and NRE instead of NUE.

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APPENDIX A

List of dominant vascular species in the bog, the intermediate fen, and the rich fen (*Ecological Archives* E091-051-A1).

APPENDIX B

ANOVA tables of species and community responses to nutrient addition in the bog, the intermediate fen, and the rich fen (*Ecological Archives* E091-051-A2).

APPENDIX C

Detailed description of plant-level production and N efficiency responses of representative vascular species to nutrient addition in the bog, the intermediate fen, and the rich fen (*Ecological Archives* E091-051-A3).

APPENDIX D

Biomass, production, and N uptake in leaves and wood of dominant shrub species in response to nutrient addition in the bog, the intermediate fen, and the rich fen (*Ecological Archives* E091-051-A4).

APPENDIX E

Nitrogen use efficiency and N response efficiency in leaves and wood of dominant shrub species in response to nutrient addition in the bog, the intermediate fen, and the rich fen (*Ecological Archives* E091-051-A5).