Reports

Is the growth of temperate forest trees enhanced along an ambient nitrogen deposition gradient?

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Abstract. The extent to which atmospheric N deposition is enhancing primary production and CO_2 sequestration along the ambient N deposition gradients found within many regional temperate forest ecosystems remains unknown. We used tree diameter measurements from 1984 and 2004, allometric equations, and estimates of wet N deposition from 32 permanent plots located along an ambient N deposition gradient in the Adirondack Park, New York, USA, to determine the effects of N deposition on the basal area and woody biomass increments (BAI and WBI, respectively) of individual stems from all the major tree species. Nitrogen deposition had either a neutral or positive effect on BAI and WBI, with the positive effects especially apparent within the smaller size classes of several species. The nature of these growth responses suggests that other co-varying factors (e.g., temperature, tropospheric ozone, soil acidification) may be partially counteracting the species-dependent fertilization effect of N deposition that was suggested by recent foliar N data across this gradient. Nevertheless, in documenting a fertilization effect from chronic, low-level, ambient rates of N deposition, this study underscores the need for more research on how N deposition is affecting rates of primary production, CO_2 sequestration, and even vegetation dynamics in many forests worldwide.

Key words: Adirondack Mountains; balsam fir; nitrogen deposition gradient; red maple; red spruce; tree growth.

INTRODUCTION

Globally, nitrogen is a key growth-limiting nutrient in terrestrial ecosystems (Vitousek and Howarth 1991, LeBauer and Treseder 2008), and fertilization with N alone has long been known to increase aboveground productivity in temperate forests (Miller 1981). Accordingly, there is interest in determining the extent to which elevated levels of fossil fuel combustion, and the associated atmospheric emission and deposition of anthropogenic N onto temperate forests may be alleviating this nutrient limitation and enhancing vegetation growth and CO_2 sequestration (Vitousek et al. 1997, de Vries et al. 2006, Magnani et al. 2007). Despite the obvious mechanism and potential importance of N deposition within the ecology of temperate forests, there is still limited knowledge regarding the extent to which the current rates of atmospheric N deposition are affecting tree growth and vegetation dynamics within temperate forest ecosystems.

Most investigations of N and forest vegetation growth have relied upon experimental high-dose treatments over short time periods (e.g., <15 years) and are therefore inherently limited in their ability characterize the long-term and broad spatial-scale vegetation responses to chronic low-level N deposition. Further, these short-term experimental N addition studies have demonstrated that vegetation responses are variable and change over time. One recent meta-analysis found that, in the short-term, most forests increase biomass under increased N input conditions (LeBauer and Treseder 2008). However, some experimental N addition studies indicate that very high doses of N deposition lead to either slower rates of biomass production (Hyvönen et al. 2008), or both mortality and increased growth of surviving trees (Wallace et al. 2007). Moreover, in longer-term studies, decreased growth has been linked to the process of nitrogen saturation (Aber et al. 1998). For instance, Magill et al. (2004) used data from a long-term (15 years) N fertilization experiment to find that the cumulative effects of N deposition on temperate forest biomass production can be negative.

Ambient N deposition gradients provide an opportunity to examine the cumulative long-term effects of chronic N deposition on terrestrial ecosystems across broad spatial scales and under ambient rates of deposition. A recent investigation of temperate forests spanning a non-contiguous gradient of N deposition in Western Europe and North America indicated that net forest productivity was enhanced in locations with elevated N deposition (Magnani et al. 2007). Though subsequent investigations suggested that the influence of N deposition on forest C sequestration was overesti-

mated by Magnani et al. (2007), they also concluded that ambient rates of N deposition are still likely to be increasing forest growth and C sequestration (de Vries et al. 2008, Sutton et al. 2008).

Recent investigations in forests of the northeastern United States have described ambient atmospheric N deposition gradients at regional scales (Ollinger et al. 1993, Ito et al. 2002). While the ranges of these northeastern U.S. gradients are smaller than those occurring in Europe and globally (Gundersen et al. 1998, Magnani et al. 2007), recent studies indicate that even these low-level northeastern U.S. gradients are affecting regional patterns of N availability (see summary by Aber et al. 2003). For instance, forest floor N concentrations have been shown to parallel N deposition gradients in red spruce stands from the western Adirondack Mountains, New York to eastern Maine (McNulty et al. 1991). Similarly, another study showed that eight canopy species increased foliar N concentrations along an N deposition gradient within the Adirondack Park, New York (McNeil et al. 2007). Further, the same study showed that broadleaf deciduous and less shade tolerant tree species (e.g., *Betula alleghaniensis*) have comparatively larger increases in foliar N along the N deposition gradient than either needleleaf evergreen (e.g., *Picea rubens*) or more shade-tolerant species (e.g., *Fagus grandifolia*), possibly because these species tend to allocate more leaf N to RuBisCO (ribulose-1,5-bisphosphate carboxylase/oxy-genase) and thus may receive a greater photosynthetic gain per unit N invested (McNeil et al. 2007). Since foliar N is strongly related to rates of photosynthesis and primary productivity (Evans 1989, Smith et al. 2002), these foliar N trends suggest that N deposition could be causing a general growth enhancement across the Adirondack N deposition gradient, as well as a preferential growth enhancement in broadleaf deciduous and less shade tolerant species. Accordingly, Elvir et al. (2006) suggested that higher foliar N concentrations in *Acer saccharum* in N-amended plots at Bear Brook, Maine contributed to higher photosynthetic rates in that species. Collectively, studies conducted across ambient N deposition gradients in temperate forests of the northeastern U.S. provide: (1) strong evidence that the chronic, low-levels of N deposition are affecting ecosystem N availability and (2) a direct and spatially consistent mechanism (increased foliar N) for stimulating enhanced growth.

This study makes use of a unique set of long-term vegetation growth measurements collected across the well-characterized N deposition gradient within the Adirondack Park (Fig. 1). Specifically, we combine modeled estimates of wet N deposition with measurements of the diameter growth and woody biomass increment between 1984 and 2004 of all the major species in 32 northern hardwood or spruce-fir stands located along the N deposition gradient. Drawing from these data, we use univariate linear regression to address
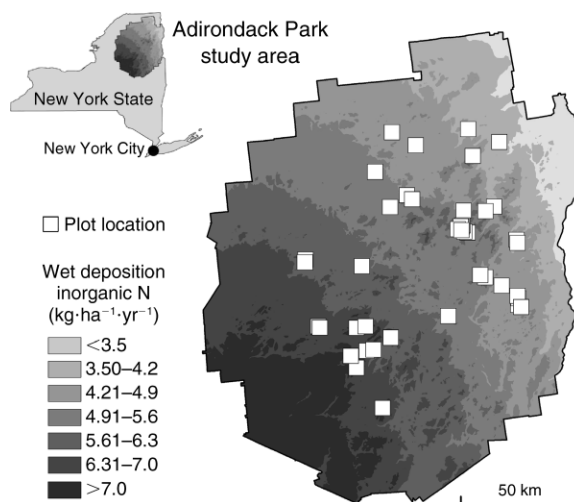

FIG. 1. Locations of the 32 study plots across the Adirondack Park N deposition gradient.

two primary questions: (1) Is the growth and woody biomass accumulation of individual trees greater in areas receiving higher rates of N deposition? and (2) Is this enhanced growth uniform across species and size classes? Based on the strong and species-specific foliar N responses to the same Adirondack Park N deposition gradient (McNeil et al. 2007), we hypothesized that the spatial pattern within the growth data would not only evidence a fertilization effect (i.e., increased growth) along the N deposition gradient, but that this effect would also be stronger in broadleaf deciduous and less shade tolerant species.

METHODS

Study area and plot descriptions

The 32 permanent vegetation plots used in this investigation (Andersen 1988, Bedison et al. 2007) are located within the 2.5 million hectare Adirondack Park, New York and represent northern hardwood and subalpine spruce–fir forests of the region (Fig. 1). Accordingly, plots were divided into two distinct forest types; northern hardwood and spruce–fir. Northern hardwood forests are characterized by American beech (*Fagus grandifolia* Ehrh.), sugar maple (*Acer saccharum* Marsh.), red maple (*Acer rubrum* L.), and yellow birch (*Betula alleghaniensis* Britton) with important associated conifers of red spruce (*Picea rubens* Sarg.) and balsam fir (*Abies balsamea* (L.) Mill.). Subalpine spruce-fir forest plots are dominated by red spruce, balsam fir and paper birch (*Betula papyrifera* var. *cordifolia* (Marsh.) Regel) and are generally found at elevations ≥ 800 m in this network of plots (Bedison et al. 2007).

These plots provide a rare opportunity to partially isolate the effect of N deposition from the confounding effects of disturbance history because they all were in "more or less original and undisturbed forested areas" in

1930–1932 (Heimburger 1933) and have been protected as state-owned "wild forests" or "wilderness" since that time. A previous analysis of the recent vegetation dynamics in our study plots (Bedison et al. 2007) revealed that the overall growth (i.e., growth of live stems + ingrowth − mortality) has been stable, if not declining (but in a not statistically significant trend) over our study period (1984–2004) in both northern hardwood and spruce–fir plots. Importantly, we found that variability in these plot-based measures of mortality, ingrowth, or overall growth was not related to the N deposition gradient. Thus, for purposes of our study, we could consider vegetation dynamics such as mortality as random stochastic processes that are unlikely to affect patterns among N deposition and the growth of live stems.

Growth and biomass measurements

We converted diameter at breast height (dbh) vegetation measurements of live stems ≥ 2.0 cm dbh in 1984 and 2004 into basal area. We also estimated live woody biomass using species-specific allometric equations and dbh measurements of individual stems (Appendix A). We calculated the basal area increment (BAI, m^2/yr) and woody biomass increment (WBI, kg/yr) of individual stems as an annual average from the growth measured over the 20-year interval between 1984 and 2004 and results for both measures are presented accordingly.

N deposition

We used an existing multiple regression model (Ito et al. 2002, McNeil et al. 2007) and the plot coordinates of latitude, longitude, and elevation to estimate the total inorganic N in wet deposition at all plot locations. While this N deposition model provides well-validated and temporally consistent estimates of spatial variability in wet N deposition during the 20-year time interval of our study, it does not assess the spatial pattern of N inputs from dry, cloud water, and fog forms of N deposition (Ito et al. 2002, McNeil et al. 2007). Recent and ongoing studies in the northeastern United States indicate that these additional forms of atmospheric N deposition typically make a relatively small contribution to total N deposition (15–30% of wet deposition) at lower elevations and are likely to have largely coincident spatial patterns with wet N deposition (Weathers et al. 2006; K. Weathers, *personal communication*). Nevertheless, due to the strong elevation gradient of N deposition in the Adirondacks (e.g., Miller 1993), the contribution of dry, cloud-water, and fog forms of N deposition can be greater at higher elevations, windward aspects, and in needleleaf evergreen forests, causing total N deposition in the region to be as high as ~30 kg N ha^{-1} yr^{-1} (Miller 1993, Weathers et al. 2006).

Statistical analysis

We used univariate linear regression to test the hypothesis that increased N deposition would predict increased BAI and WBI. We note that BAI and WBI are not independent measures of growth, but we report them both for completeness. To meet the requirements of normality, BAI and WBI data were log_{10}-transformed. Since an analysis of variance (ANOVA) revealed that forest type, species, size class, and their interactions were significant effects ($P < 0.0001$) within the BAI and WBI data, we repeated the regression analyses after stratifying the data by forest type, species, and size class. We did not analyze species that were not well represented (e.g., $N \leq 30$ stems) or that were not distributed along a sufficient portion of the N deposition gradient. To assess species-specific differences in the relative magnitude of growth response to N deposition, we normalized the linear regression slope (m) by the mean growth rate (either BAI or WBI), which yielded a unitless index of growth response that accounts for general differences in species growth rates. We used JMP (v 7.0.1, SAS Institute, Cary, North Carolina, USA) for all statistical analyses and evaluated statistical significance at $P \leq 0.05$.

RESULTS

All the results from the regression analyses on the pooled and stratified data were either positive or statistically non-significant, suggesting that the gradient of N deposition either had a positive or neutral effect on growth. Considering all stems in all size classes, the BAI ($P < 0.0001$, $R^2 = 0.01$, $N = 1070$) was slightly higher in areas receiving higher rates of N deposition, but this small effect achieved statistical significance primarily through large sample size. Nevertheless, regressions of all stems in size classes 1 and 2 also revealed a significant effect of N deposition on growth (Table 1). The corresponding WBI results from Table 1 are reported in Appendix B. Moreover, regression analyses of all stems stratified by forest type revealed similar trends (Table 1). Furthermore, stratifying the data by forest type and size class, regression analyses revealed that stems from size classes 1 and 2 within spruce–fir plots had higher BAI and WBI in areas of high N deposition (Table 1). Likewise, the BAI and WBI of all small saplings (i.e., size class 1) in northern hardwood plots were higher in areas of high N deposition (Table 1).

Regression analyses stratified by species revealed some stronger relationships, particularly in balsam fir, red maple, and red spruce. The strongest relationship occurred in the small size class of red maple, with the N deposition gradient explaining roughly 40% of spatial variability in growth (Table 1). A similar positive relationship occurred across all size classes for red maple, but was strongly driven by proportionately larger sample sizes within the smallest size class. Also, this relationship was partially influenced by trees from one high deposition plot that had a relatively open canopy (Table 1, Appendix C). Finally, the smallest size class of red spruce stems within northern hardwood forests had higher BAI and WBI in areas of higher N deposition. Comparison of the growth response indices revealed

TABLE 1. Stratified basal area increment (BAI, m^2/yr) response of tree species to atmospheric nitrogen deposition (kg·ha^{-1}·yr^{-1}).

Species	Size class†	Forest type	N	Mean response (m^2/yr)	P	R^2	m	Growth response index‡
All	1	all	638	6.3×10^{-5}	<0.0001	0.04	0.11	3
All	2	all	206	1.6×10^{-4}	0.02	0.02	0.11	3
All	all	NH	727	1.3×10^{-4}	0.02	0.01	0.06	2
All	all	SF	385	1.3×10^{-4}	0.04	0.01	0.09	2
All	1	SF	182	7.9×10^{-5}	0.0004	0.07	0.25	6
All	2	SF	110	1.6×10^{-4}	0.02	0.05	0.17	4
All	1	NH	455	6.3×10^{-5}	0.0003	0.03	0.09	2
Acer rubrum	1	NH	39	5.0×10^{-5}	0.0002	0.31	0.42	10
Acer rubrum	all	NH	56	7.9×10^{-5}	<0.0001	0.28	0.42	10
Abies balsamea	1	SF	118	7.9×10^{-5}	<0.0001	0.17	0.43	10
Abies balsamea	1	all§	168	6.3×10^{-5}	<0.0001	0.20	0.28	7
Abies balsamea	all	all	302	1.0×10^{-4}	<0.0001	0.06	0.18	5
Picea rubens	1	NH	55	9.1×10^{-5}	<0.0001	0.29	0.69	17

Notes: Regressions were performed on log$_{10}$-transformed data; slope m is shown. Abbreviations are northern hardwood, NH and spruce–fir, SF.

† Size classes are defined as: 1, 2.0–9.9; 2, 10.0–14.9; 3, 15.0–19.9; 4, 20.0–24.9; 5, 25.0–29.9; 6, ≥30.0 cm dbh.

‡ Calculated as the ratio of the slope to the absolute value of the log of the mean response, multiplied by 100.

§ Balsam fir stems in both northern hardwood (NH) and spruce–fir plots.

that the generalist, broadleaf deciduous species of red maple was the most responsive species while the needleleaf evergreen species were relatively less responsive, though the large response of *P. rubens* in northern hardwood plots is difficult to explain (Table 1).

DISCUSSION

Interpretation of any gradient-based study must be carried out with caution, as responses observed along a measured gradient can be influenced by one or more co-varying environmental factors. While it is difficult, if not impossible to address all these environmental factors, we did use a robust dataset of ancillary GIS data (described in McNeil 2006) to find that neither the individual nor combined spatial patterns of soil type, bedrock geology, or species composition explained the growth responses we observed along the N deposition gradient. Similarly, these growth responses were not explained by single geographic variables (e.g., altitude, latitude) that can be related to variation in other environmental factors (e.g., photosynthetically active radiation [PAR]). The Adirondack Park N deposition gradient does share a coincident spatial pattern with a gradient of precipitation. While we considered that the precipitation gradient could directly cause a physiological growth response, estimates from an independent precipitation model (DAYMET; Thornton et al. 1997), indicated that precipitation alone could not explain the results presented here. This is not surprising given the mesic endpoints of the precipitation gradient (range of 961–1575 mm/yr in the sample plots).

While we did not find any covarying environmental factors that could explain the growth responses along the N deposition gradient, there are several factors that could partially counteract a growth response to N deposition. First, since higher elevations receive increased N deposition but are also subjected to colder

temperatures that could slow growth, temperature may counteract a fertilization effect along this component of the Adirondack N deposition gradient. Second, the spatial pattern of tropospheric ozone is oftentimes coincident with N deposition, and ozone can adversely affect forest growth in northeastern forests (Ollinger et al. 2002). Third, although comparison of foliar N, soil, and surface water data from across the Adirondack Park deposition gradient suggests that these forests are generally within the earlier "fertilization" stage of the process of N saturation (McNeil et al. 2007), growth could be adversely affected by N deposition itself if the 80+ year-old forests in our study plots were at more advanced stages of N saturation. Finally, there is a strong potential that forest growth could be adversely affected by ongoing increases in soil acidity, and especially by the resultant loss of soil base cations occurring along the largely coincident nitrate (NO_3^-) and sulfate (SO_4^{2-}) acidic deposition gradients in the Adirondack Park (Friedland and Miller 1999, Nellemann and Thomsen 2001, Sullivan et al. 2006). Indeed, the possibility that temperature, ozone, N saturation and especially the sustained loss of base cations have partially counteracted an N fertilization effect across the Adirondack atmospheric deposition gradient is in strong agreement with two salient aspects of our results: (1) the preponderance of statistically insignificant results, and (2) the species-specific nature of the observed growth responses along the N deposition gradient. In particular, it is very notable that we observed significant growth responses in three species (red maple, red spruce, and balsam fir) that are better adapted to the increasingly acidic and base-poor soil conditions occurring in the elevated atmospheric deposition environments throughout this region (Canham et al. 2006, Sullivan et al. 2006).

While we formulated our hypotheses based on previous measurements of increased foliar N across the

Reports

Reports

N deposition gradient (McNeil et al. 2007), our results underscore the need to consider the simultaneous effects of multiple agents of global change (e.g., SO_4^{2-} deposition, state of N saturation, tropospheric ozone, climate) in projecting growth responses to N deposition. Moreover, our results suggest that growth responses can be species-specific and may be modulated by the overall suite of adaptive traits inherent to each species. For instance, in light of the foliar N response of sugar maple to the Adirondack N deposition gradient (McNeil et al. 2007) and the observed increases in sugar maple growth along an N deposition gradient in the Southern Appalachians (Boggs et al. 2005), it is surprising that sugar maple did not have a significant growth response. Since sugar maple is known to be most competitive in base cation-rich environments (Canham et al. 2006), it may be that this species is poorly adapted to the relatively N rich, but base cation poor environments that are increasing in the Adirondack Park in response to acidic deposition (Sullivan et al. 2006). Similarly, previous studies have found that red spruce growth and health at higher elevations in the Adirondack Mountains are affected by base cation leaching (Shortle and Smith 1988) and winter injury induced by acidic precipitation (Vann et al. 1992). However, our results indicate that red spruce in lower elevation northern hardwood plots responded positively to N deposition. Finally, based on its limited foliar N response to N deposition (McNeil et al. 2007), we did not expect such a strong growth response in balsam fir. This discrepancy could be due to the different sampling locations of the growth and foliar N surveys. In particular, much of the balsam fir growth data were from high-elevation plots. These plots receive proportionally greater contributions of cloud-water and dry forms of N deposition, yet our results were largely unaffected when we supplemented the wet deposition model estimates with measurements of cloud-water and dry forms of N deposition determined by Miller (1993) at Whiteface Mountain, New York. Nevertheless, canopy openings caused by spruce mortality in these high-elevation SF sites (Bedison et al. 2007) could have also spurred accelerated balsam fir growth.

Due to the preponderance of species that had no significant relationship, our results can only provide minimal support for the hypothesis that the growth response would be larger in less shade tolerant and broadleaf deciduous species (Table 1). However, the species-specific nature of growth response was apparent (Table 1). Thus, more detailed studies are needed not only to provide direct observation of the effect of N deposition on species-specific rates of RuBisCO allocation and photosynthetic production, but also to identify the specific pathways whereby enhanced N deposition is translated into increased foliar N, photosynthate production, and finally vegetative growth.

Regardless of mechanism, the species-specific nature of growth response has important implications for future stand composition and ecosystem functioning of Adirondack forests, especially insofar as species shifts may affect future patterns of nutrient cycling (Lovett et al. 2004). In particular, our results should be considered alongside other studies suggesting that elevated N deposition may enhance seedling survival (Sefcik et al. 2007), lead to competitive exclusion of characteristic species by more nitrophilic vegetation (Bobbink et al. 1998), and affect species dominance and overall biodiversity (Vitousek et al. 1997). Further, the influence of deposition on red maple growth may be yet another anthropogenic perturbation (e.g., fire suppression, logging, land clearing) that is contributing to the proliferation of this "super-generalist" species in some forests (Abrams 1998).

We show here that long-term growth measurements can serve as a valuable ecological record. However, the error inherent in making repeated dbh measurements may have introduced enough noise to confound effects of N deposition, especially in larger size classes. Moreover, increased partitioning to belowground carbon allocation with increased stand age has been shown in some forests and may exacerbate decreases in aboveground woody net primary production (NPP, Ryan et al. 2004). Similarly, Litton et al. (2007) concluded that partitioning of C to wood is low and to belowground biomass is high in low-resource availability conditions, conditions which are typical of low nutrient status Adirondack soils. Together, the effects of ontogeny and C allocation strategies may have further confounded the use of the diameter measurements to evaluate the effects of N deposition in larger size class stems. More precise dendrological and belowground measurements of growth over longer time intervals are likely needed to detect the effect of N deposition in larger individuals.

The low R^2 values reported here must also be interpreted in light of the ubiquitous fact that, in addition to N deposition, there are numerous other factors affecting tree growth. As found by Magnani et al. (2007), one important factor is disturbance history. Indeed, the fact that we were able to detect any growth response to N deposition may be because all of our plots were in "more or less original and undisturbed forested areas" in 1930–1932 (Heimburger 1933) and have been protected as state-owned "wild forests" or "wilderness" since that time.

This study adds important evidence from the northeastern United States to the few investigations conducted in southern U.S. and European temperate forests that have utilized ambient conditions and in situ measurements to report enhanced growth of temperate forest vegetation along regional gradients of N deposition (e.g., Nellemann and Thomsen 2001, Boggs et al. 2005). Ambient gradients of N deposition not only provide realistic conditions and remove confounding influences introduced in short-term high-dose N addition investigations, but since the rate of N addition is more

important than the accumulated amount of N (Högberg et al. 2006), gradient-based studies can also provide a more acute understanding of the ecophysiological responses of forest vegetation to typically low-level, ambient rates of N deposition that now occur in many forests worldwide (Galloway 1998). In addition to the aforementioned possible effects on vegetation dynamics, increased growth along ambient gradients of N deposition may have important implications for the global carbon cycle. We suggest that longer-term or more precise data (e.g., from dendrological studies) may extend our sapling-based evidence and reveal that plot-level growth and CO_2 sequestration may also be enhanced along this ambient, low-level, regional N deposition gradient.

Conclusions

We show that the growth and biomass accumulation of individual trees within a number of size classes and within several tree species is enhanced along an ambient gradient of N deposition in the Adirondack Mountains, New York. These results signify the need for much future research, but from the present study, we find that (1) the present rates of elevated N deposition in the Adirondack Park are enhancing growth and thus may be enhancing NPP and CO_2 sequestration in the region, (2) the effects of N deposition on growth should be assessed in the context of other covarying environmental factors, and (3) future investigations should study and consider the implications of species-specific responses of forest vegetation to N deposition. In particular, future research could benefit by increasing the spatial and temporal resolution of measurements along existing N deposition gradients and by establishing more precise methodologies to measure vegetation growth response.

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Reports

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APPENDIX A

A table listing the allometric equations used in woody biomass increments calculation (*Ecological Archives* E090-122-A1).

APPENDIX B

A table listing the woody biomass increments response to N deposition (*Ecological Archives* E090-122-A2).

APPENDIX C

Figures showing basal area increment response of tree species between 1984 and 2004 along the nitrogen deposition gradient (*Ecological Archives* E090-122-A3).