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Separation of effects of moderate N deposition from natural change in ground vegetation of forests and bogs

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ABSTRACT

The effect of moderate rates of nitrogen deposition on ground floor vegetation is poorly predicted by uncontrolled surveys or fertilization experiments using high rates of nitrogen (N) addition. We compared the temporal trends of ground floor vegetation in permanent plots with moderate (7–13 kg·ha^{-1}·yr^{-1}) and lower bulk N deposition (4–6 kg·ha^{-1}·yr^{-1}) in southern Sweden during 1982–1998. We examined whether trends differed between growth forms (vascular plants and bryophytes) and vegetation types (three types of coniferous forest, deciduous forest, and bog). Trends of site-standardized cover and richness varied among growth forms, vegetation types, and deposition regions. Cover in spruce forests decreased at the same rate with both moderate and low deposition. In pine forests cover decreased faster with moderate deposition and in bogs cover decreased faster with low deposition. Cover of bryophytes in spruce forests increased at the same rate with both moderate and low deposition. In pine forests cover decreased faster with moderate deposition and in bogs and deciduous forests there was a strong non-linear increase with moderate deposition. The trend of number of vascular plants was constant with moderate and decreased with low deposition. We found no trend in the number of bryophyte species. We propose that the decrease of cover and number with low deposition was related to normal ecosystem development (increased shading), suggesting that N deposition maintained or increased the competitiveness of some species in the moderate-deposition region. Deposition had no consistent negative effect on vegetation suggesting that it is less important than normal successional processes.

KEY WORDS

Nitrogen deposition; vascular plants; bryophytes; species richness; succession; understorey

INTRODUCTION

While rates of acid deposition in western Europe decreased by 34% from 1980 to 1995 due to the control of sulphur emissions (Berge et al., 1999), rates of N deposition have since remained fairly constant (Berge et al., 1999). Since most temperate terrestrial ecosystems are N-limited (Jefferies and Maron, 1997, Lee, 1998), N deposition now represents a larger threat to natural communities than acidification. In the second half of the last century, the abundance of fast-growing, weedy species typical of fertile soils increased, while species characteristic of infertile soils decreased in industrialized regions of Central Europe (Bobbink et al., 1998) where rates of N deposition are high (20–40 $kg\cdot ha^{-1}\cdot yr^{-1}$ in 1996, Berge et al., 1999). Fertilization experiments suggest that many of the observed changes in ground layer vegetation can be attributed to N addition (Hofmann et al., 1990, van Dobben et al., 1999, Nordin et al., 2005) and that effects are strongest in the least fertile habitats (Hofmann et al., 1990, Gilliam, 2006).

These experiments involved high doses of N applied in long intervals (Hofmann et al., 1990, Rühling and Tyler, 1991, Tyler et al., 1992, Hallbacken and Zhang, 1998, Rainey et al., 1999, van Dobben et al., 1999, Nordin et al., 2006) and rarely applied treatments corresponding to the repeated low-concentration deposition by precipitation and sedimentation. In contrast, experiments involving moderate rates of N application resulted in only weak responses of forest floor species (Kellner and Redbo-Torstensson, 1995). Similarly, a review of N deposition effects on forests in southern Sweden (Binkley and Högberg, 1997) concluded that moderate rates of N deposition (5–20 $kg\cdot ha^{-1}\cdot yr^{-1}$) have increased the productivity of trees, but showed equivocal evidence that deposition has affected the understory.

An alternative to experimental N application is a survey of unmanipulated vegetation and deposition levels. In this approach, deposition rates are realistic and results may be more relevant. Surveys may compare differences in time and in space. Many conclude that the abundance and composition of the ground vegetation in forests exposed to moderate rates has changed as compared to earlier times or remote areas like northern Sweden (1–3 kg N $ha^{-1} \cdot yr^{-1}$) that are considered pristine (Falkengren-Grerup and Eriksson, 1990, Liu and Bråkenhielm, 1996, Diekmann et al., 1999, Strengbom et al., 2003, Bernhardt, 2005). Surveys have the disadvantage that co-varying factors, e.g. temperature, precipitation, canopy density, or site fertility, cannot be easily distinguished from temporal or spatial patterns of deposition. For example, species richness of the understorey of coniferous forests decreases weakly from north to south with increasing deposition (Bråkenhielm and Qinghong, 1995, Liu and Bråkenhielm, 1996), but the temporal trends of richness, evenness, and diversity of vegetation are not consistent among sites (Liu and Bråkenhielm, 1996). The effect of increasing deposition rates along the latitudinal gradient may be obscured by co-variation with tree productivity and canopy shading which may have eliminated some understorey species (Thomas et al., 1999). In addition, the lumping of different forest types and growth forms may increase variability and prevent the detection of contrasting trends.

In our analysis of survey data of ground floor vegetation in southern Sweden spanning 16 years we reduce the risk of confounding ~~of~~ deposition with latitude and climate inherent in country-wide studies (Liu and Bråkenhielm, 1996, Strengbom et al., 2003) by using the west–east gradient of deposition in this region. In contrast to Liu and Bråkenhielm (1996) who used repeated-measures analysis of variance to assess temporal variability, we use a regression approach. In our study we emphasize temporal trends and compare the change of species richness and cover between sites with higher and lower deposition. We control for differences in initial conditions by standardizing observed cover and richness for each site. Specifically, we test the hypotheses that (1) vegetation trends are absent in the late-successional ecosystems receiving less than the recently proposed critical load of N (6 kg ha^{-1} yr^{-1}, Nordin et al., 2005), while (2) species richness and cover of species tolerant of low N supply decrease and nitrophilous species increase in ecosystems receiving more than the critical load. In addition, we test (3) whether the trends differ among five vegetation types and two growth forms.

METHODS

Location and selection of sites

Ground floor vegetation was surveyed from 1982 to 1998 in nine undisturbed, protected reference plots (Fig. 1, Table 1) designated for monitoring programmes (Bråkenhielm, 1994, Kleemola and Forsius, 2000). The plots were sampled in different years, more frequently in the beginning than towards the end. The data is available via the internet from the Institute of Environmental Assessment, Swedish University of Agriculture (http://www.ma.slu.se, "Intensive plots: understorey vegetation"). In order to avoid post-fire effects and a strong N-S gradient in climate and vegetation, we considered plots only in unburned forests in the temperate vegetation zone, south of 60°N. To increase the temporal comparability of the vegetation change, we restricted the data set further to plots monitored from 1983±2 to 1996±2. The plots are located at five sites: Aneboda (57° 7' N, 14° 33' E), Dalby (55° 41' N, 13° 20' E), Berg (57° 4' N, 12° 47' E), Norra Kvill (57° 46' N, 15° 36' E), Tresticklan (58° 28 N, 11° 48' E), and Tyresta (59° 11' N, 18° 16' E).

Figure 1

Table 1

The nine plots represent five vegetation types: blueberry (*Vaccinium myrtillus*)-spruce (*Picea abies*) forest, herb-spruce forest, pine (*Pinus sylvestris*) forest, mixed deciduous forest, and bog (Table 1). Nomenclature of vegetation types follows Nordiska Ministerrådet (1984), nomenclature of species follows Rothmaler (1984, 1988). The mean acidity of the humus layer in the coniferous forests ranged between $\mathrm{pH_{aq}}$ 3.9 and $\mathrm{pH_{aq}}$ 4.3 (1990–1992) and was $\mathrm{pH_{aq}}$ 6.8 (1986) in the deciduous forest (L. Bringmark, unpublished data). The western sites of each vegetation type and the deciduous forest received on average >7 kg N $\mathrm{ha^{-1}}$ $\mathrm{yr^{-1}}$, whereas the eastern sites received on average <7 kg N $\mathrm{ha^{-1}}$ $\mathrm{yr^{-1}}$ bulk deposition (Fig. 1). We refer to the western sites as moderate-deposition sites, because the deposition rates are just above the suggested critical loads for bogs (5–10 kg N $\mathrm{ha^{-1}}$ $\mathrm{yr^{-1}}$, Bobbink et al., 2003) and boreal forests (6 kg N $\mathrm{ha^{-1}}$ $\mathrm{yr^{-1}}$, Nordin et al., 2005). The eastern sites we refer to as low-deposition sites.

Environmental variables

Bulk deposition and precipitation were measured annually from 1983–1996 in large forest gaps or in fields near each site by IVL Svenska Miljöinstitutet AB, Stockholm, for the Swedish Environmental Protection Agency. We obtained temperature data from the Swedish Meteorological and Hydrological Institute, Norrköping, from the stations that were closest to each site and that had ~~the~~ almost continuous records for 1983–1996.

Vegetation observations

At each site, one 40 m × 40 m plot was established in vegetation typical of a larger area, usually a watershed. If there was a larger portion of a different vegetation type at the same site, a second plot was established. Each plot was divided into 20 m × 20 m units, 10 m × 10 m subplots, and 0.5 m × 0.5 m quadrats. Using the same randomized pattern for each unit, two quadrats and five spare quadrats were selected in each subplot (32 quadrats/plot). Quadrats that included >10 % surface area unsuitable for vascular plant growth (boulders, trees, logs, etc.) or that were destroyed during the observation period by, e.g., trampling, were replaced with spare quadrats. In the pine forests, there was only one quadrat per subplot (16 quadrats/plot). In the low-deposition blueberry-spruce forest, lack of suitable space restricted plot size to 20 m × 20 m. There, two quadrats per subplot were used from 1982 to 1984 (8 quadrats/plot) and four from 1985 to 1996 (16 quadrats/plot).

Surveys were conducted during summer. Cover of vascular plants, bryophytes, and lichens in the quadrats was visually estimated in percentages. All field assistants were experienced in species identification and their cover estimates calibrated by the same person to produce comparable values. Species lists were established for each quadrat and used in each survey to maximize consistency among years and persons. Species richness refers to the number of species in all quadrats in each plot. We calculated mean cover for each species across all quadrats of a plot, whether individuals were present or not, and then summed the means for each plot for total cover. Thus, we did not correct total cover for overlapping plants.

Species richness and total cover in the first years of observation differed among plots, reflecting different site conditions (including climate) and site history. Moreover, a small absolute change in plots with low richness or cover is more significant than the same change in plots with high richness or cover. Therefore, we standardized species richness and expressed it as a percentage of cumulative richness (i.e., the number of species observed in one plot over the whole monitoring period). We standardized cover by expressing it as a percentage of the initial cover in each plot (i.e., total cover in the first year of observation = 100 %). Changes of standardized richness and cover are expressed as percentage points per year (pp/yr).

The cover and number of vascular species in the deciduous forest was monitored in spring and summer. Initially, both aspects were monitored in the same year, later alternating every two or three years. We merged these observations by taking the maximum cover of each species in each quadrat from spring and the corresponding observation from the previous summer before calculating the richness or cover for the whole plot.

We used tree basal area to detect drastic changes in canopy shading of the plots. Diameter at breast height (1.3 m) of each live tree was measured to the nearest cm in each plot. Basal area of each tree was calculated assuming a circular stem cross-section and summed over the plot area for each species. Measurements were repeated after about 5 years and in some sites again after 10 and 15 years.

Statistical analyses

The trends (linear temporal change) of richness and cover were compared between plots with low and high deposition, between growth forms (vascular plants and bryophytes), and between vegetation types using analyses of covariance (ANCOVAs). Deciduous forest occurred only in the high-deposition region and was excluded from ANCOVAs to keep the design balanced. The fully factorial ANCOVAs included the fixed-effect factors deposition region, growth form, and vegetation type, with time as covariate. We removed interactions not including time from the model when they were not significant at the 20% level. Statistics were calculated with JMP 4.0.1–4 (SAS Institute, Cary, NC, U.S.A.).

Significant serial correlation (autocorrelation) of residuals in regressions invalidates common statistical tests. We found no serial correlation between adjacent residuals using parametric (Pearson's r) and non-parametric tests (Kendall's τ).

We do not present results for lichens because they were rare in most plots (cover sum <2% in all plots except the low-deposition pine forest where cover sum was on average 11% across years with no significant temporal trend). Changes of tree basal areas were not compared statistically because measurements had been repeated only once or twice during the study period.

RESULTS

Deposition, precipitation, temperature, basal area

Bulk deposition of nitrogen (NO_3-N + NH_4-N) consisted of nitrate-N and ammonium-N in nearly equal proportions. Bulk deposition of N and acid compounds (H^+) generally decreased from the second half of the 1980s to 1996 (Fig. 2). The decrease of N deposition at individual sites, however, was significant only for the low-deposition sites. Acidic deposition decreased significantly at all sites except the high-deposition pine forest (Tresticklan). Annual precipitation at or near the high-deposition sites (870 mm) was higher than at the low-deposition sites (604 mm; $F_{1,75} = 64.7$, $P < 0.001$). The average precipitation volume did not change over time in either type of sites. Annual mean temperatures did not differ significantly between sites in the high and the low-deposition region.

Fig. 2

Changes in tree basal area were generally small, except for a strong increase in the high-deposition pine forest from 29 m^2/ha in 1989 to 35 m^2/ha in 1994 and a decrease in the low-deposition blueberry-spruce forest from 31 m^2/ha in 1982 to 22 m^2/ha in 1987 due to the fall of three trees killed by insects.

Cover

Trends of cover differed between growth forms and deposition region depending on vegetation type (Fig. 3, Fig. 4; growth form × vegetation × time: $F_{3,100} = 5.68$, $P = 0.001$;

deposition × vegetation × time: $F_{3,100} = 3.37$, $P = 0.02$). Therefore, we analyzed the trends separately for each vegetation type. In both types of spruce forests, cover of vascular plants decreased (Fig. 3) while that of bryophytes increased (Fig. 4; growth form × time: blueberry-spruce: $F_{1,30} = 25.9$, $P < 0.001$; herb-spruce: $F_{1,28} = 28.9$, $P < 0.001$). The trends did not differ between moderate and low deposition regions, suggesting that deposition had no effect on species in spruce forests. For pine forests, trends did not differ between growth forms, but cover decreased faster in the moderate (–4.7 pp/yr; Fig. 3, Fig. 4) than in the low-deposition region (–2.1 pp/yr; region × time: $F_{1,28} = 5.89$, $P = 0.02$). For bogs, cover of vascular plants decreased while cover of bryophytes increased (Fig. 4; growth form × time: $F_{1,18} = 16.9$, $P = 0.001$). The decrease of vascular plant cover was faster in the low (–4.7 pp/yr) than in the moderate-deposition sites (–1.6 pp/yr; region × time: $F_{1,8} = 27.1$, $P = 0.001$; Fig. 4) whereas the (linear) increase of bryophytes (3.4 pp/yr) did not differ between deposition categories (Fig. 4). In the deciduous forest the decrease of cover of vascular plants was not significant (Fig. 3), while the cover of the two bryophytes increased strongly from 0.5 % to 11 % (Fig. 4).

Figures 3 and 4

The dominant vascular species at most sites was *Vaccinium myrtillus* (blueberry), although lacking in the quadrats of the blueberry-spruce forest and the bog of the high-deposition sites and the deciduous forest. Due to its low abundance in the high-deposition herb-spruce forests (a national survey showed that this is a general pattern; Strengbom et al., 2003), we could compare the trends of *V. myrtillus* only for pine forests. Its decrease (–2.2 pp/yr) did not differ significantly between deposition regions. The inclusion of all dwarf shrubs allowed a meaningful comparison for pine forests and bogs. Dwarf shrubs, too, decreased at the same rate in pine forests in both regions. In bogs, cover of dwarf shrubs decreased significantly in the low-deposition site but showed no significant trend in the moderate-deposition site (deposition × time: $F_{1,8} = 29.7$, $P < 0.001$; Fig. 3).

In short, the cover of vascular plants decreased over time while that of bryophytes increased in all but the pine forests plots where the cover of bryophytes also decreased. Cover of vascular plants in bogs decreased faster in the low than in the moderate-deposition region, whereas in pine forests cover of vascular plants and bryophytes decreased faster in the moderate than in the low-deposition sites.

Species richness

Trends of species richness differed between vascular plants and bryophytes (growth form × deposition × time: $F_{1,107} = 4.50$, $P = 0.04$). Therefore, we analyzed the trends separately for each growth form. Richness of vascular plant species was constant in the moderate-deposition sites but decreased in the low-deposition sites (–2.7 pp/yr; Fig. 5; deposition × year: $F_{1,57} = 7.56$, $P = 0.008$). The rates of decrease did not differ among vegetation types. Species richness of bryophytes showed no significant trends over time (Fig. 6). In the deciduous forest there were only two moss species, the second found only in the last year. In summary, richness of vascular plant species decreased more slowly at higher rates of deposition, whereas richness of bryophytes showed no trend.

Figures 5 and 6

DISCUSSION

Cover

The cover of vascular plants generally decreased at all sites (Fig. 3), whereas the cover of bryophytes generally increased except in the pine forests (Fig. 4), where bryophyte cover also decreased. The rates of decrease did not differ between deposition regions in the spruce forests, were higher in the moderate-deposition site of the pine forests, but lower in the moderate-deposition site of the bogs. These trends do not confirm our hypothesis that higher rates of N deposition increase cover of vascular plants. Rather, the general decrease of cover of vascular plants suggests that some other environmental factor changed simultaneously in both deposition regions. Changes of cover reflect mostly the trends of the dominant species. The dominant vascular species, *Vaccinium myrtillus*, decreased at similar rates in both deposition regions. *V. myrtillus* decreases when soil N content is >1.3% (Mäkipää, 1999), but the nitrogen content of the humus layer in our forest plots (1.12–1.28 %, L. Bringmark, unpublished data) was below this threshold. However, the biomass of *V. myrtillus* also declines rapidly when light levels reduce its rate of photosynthesis below c. 20 % (Väisänen et al., 1977), a likely value in our forested plots (Kellomäki et al., 1977a). Thus, the generally observed lower cover of *Vaccinium* species in moderate-deposition forests (Strengbom et al., 2003) may not be a direct effect of increased deposition. Apparently, *Vaccinium* species can tolerate higher N deposition rates than commonly thought. This was also shown experimentally. *V. mayrtillus* and *V. vitis-idae* showed little response to fertilization with up to 50 kg N ha^{-1} yr^{-1} for four years (Nordin et al., 2006). We suggest that the decrease of *Vaccinium* species is more in line with an increase of shading with forest stand age. The increase of shading was apparently not strong enough to be reflected in a significant increase of tree basal area.

In the deciduous forest, the strong decrease of the shade-tolerant *Mercurialis perennis* (Ellenberg, 1986) was balanced by an increase of the nitrophilous, but light-indifferent *Aegopodium podagraria*. Therefore, there was no over all change. *Mercurialis*' decrease may be related to higher light levels due to the death of old trees in the plot. In other deciduous forests in the moderate-deposition region, cover of most species increased from c. 1950 to 1985 (Falkengren-Grerup, 1989). Species responses were interpreted as being mostly related to soil pH and not N, based on the species' indicator values and similar changes in vegetation along soil acidity gradients caused by stemflow (Falkengren-Grerup, 1989). The effect of increased tree production and shading, however, could not be excluded.

The increase of bryophyte cover in all plots except pine forest (Fig. 4) indicates that conditions for bryophyte growth improved. Most forest floor bryophytes are adapted to low light levels (Kellomäki et al., 1977b), This suggests reduced competition by vascular plants, which decreased in cover. Furthermore, the expansion of bryophyte cover, most of which are sensitive to acid rain and fertilization (Nygaard and Abrahamsen, 1991, Mäkipää, 1995, van Dobben et al., 1999), indicates that N deposition did not contribute strongly to the observed changes in vegetation cover. In pine forests, however, cover of bryophytes decreased and they did so faster in the moderate than in the low-deposition region (Fig. 4). The simultaneous decrease of bryophytes in both deposition regions suggests again that deposition alone was not responsible for the decline but may have sped up the decline in the moderate deposition pine forest. The decline in pine forest is neither in line with reduced light, as bryophytes in other sites apparently did not react negatively to increased shading. Comparison of the pine plot with the blueberry-spruce plot in the same low-deposition site, where bryophytes did not decrease, suggests that the decrease in the pine forests is linked to the tree species, but we are unable to deduce the responsible mechanism based on the available information.

In summary, higher rates of N deposition seem to have had little immediate effect on the cover of the forest understorey.

Richness

Change of vegetation cover represents mostly the dynamics of dominant and tolerant species. Our analysis of cover trends did not reveal any significant effect of N deposition. More subtle effects of N deposition may be detected by changes in the species richness, which represents mostly the response of rare and potentially sensitive species. Species richness of vascular plants generally decreased in the low-deposition sites and showed no trend in the moderate-deposition sites (Fig. 5). This was contrary to our expectations. We had assumed that species richness in the late-successional, low-deposition sites was stable. We had further expected that low rates of fertilization by N deposition would either allow more species to grow in the N-limited forests and richness would rise or that higher rates of deposition would allow nitrophilous species to out-compete species tolerant of low-fertile soils and richness would be lowered. The lack of a significant decrease in the moderate-deposition plots could be explained by arguing that species that are less tolerant or less competitive at high rates of N or acid deposition may have been lost from the plots before our study started (Nordin et al., 2005), whereas this process may still be continuing in the low-deposition region. This reasoning would agree with the generally lower number of species in the moderate-deposition spruce forests but not with the decrease of species richness in the low-deposition pine forest and bog, where the number of species was also low from the start of our study. Our results are more consistent with the hypothesis proposed in the preceding section that the environment in the late-successional forests is still changing in a way that is relevant to the ground vegetation. The species most likely to be lost from a site are those with low abundance because they are not well adapted to site conditions, i.e. lower light conditions according to our previous argument. Consequently, the lack of trend of species richness in the moderate-deposition sites suggests that higher N availability might partially compensate reduced growth due to shading. This would also explain the variation of species richness in the high-deposition sites as an effect of the annual variability of deposition (Fig. 2).

Trends of bryophyte richness did not differ between deposition regions (Fig. 6) but varied strongly across time in both regions. The lack of trend in bryophytes is surprising because bryophytes are usually considered more sensitive to high rates of N and acid deposition than vascular plants (Mäkipää, 1995). We conclude that the rates of deposition were not high enough to significantly affect the richness of bryophytes of the sites, although variation in deposition may have influenced the abundance and thus detectability of rare species causing the observed variability of species richness.

In summary, our results indicate that moderate rates of N deposition do not affect the richness of the ground vegetation negatively. We suggest that moderate rates of N deposition prevent the decrease of species richness of vascular plants by improving the competitive ability of rarer species as shading in maturing forests increases.

Deposition and ground vegetation.

In European regions with high rates of N deposition, and in fertilization experiments, the dominance of the ground vegetation shifts from low herbs and dwarf shrubs to fast growing, tall grasses and herbs (Bobbink et al., 1998). This appears to contrast with our results. N addition at our sites, however, was a fifth to a tenth of that used in most fertilization experiments (e.g., Kellner and Mårshagen, 1991, Mäkipää, 1994, van Dobben et al., 1999) and much lower than the rates in the Netherlands, where the most dramatic changes have been documented (Bobbink et al., 1998). Binkley and Högberg (1997), reviewing the effect of deposition on Swedish forests, pointed out that many studies that purported finding effects of deposition did not consider normal trends in forest stand development or other biotic influences, e.g., the tremendous increase of roe deer (*Capreolus capreolus*) and elk (*Alces*

alces) populations. These authors concluded that there was no evidence that N deposition had reduced the productivity of trees in Swedish forests. Our study indicates that there are no negative effects of moderate deposition on the understorey vegetation in southern Sweden either and thus supports Binkley and Högberg (1997). Canopy retention of N by coniferous trees is high (Piirainen et al., 1998, Klopatek et al., 2006) and the retained N is not necessarily returned to the soil with litter in regions with moderate N deposition (Köchy and Wilson, 2001, Klopatek et al., 2006) so that the amount of N deposited onto the ground vegetation is much smaller than that measured in open areas. N deposition in coniferous forests by throughfall is 63% of open field deposition in near-by sites (throughfall = 0.04 + 0.63 · bulk deposition, $R^2 = 0.63$; data obtained from Throughfall Monitoring Network, IVL Svenska Miljöinstitutet AB, Göteborg, Sweden). In the deciduous forest, however, throughfall deposition of N is on average 16 kg ha^{-1} higher than in the open field (SE = 1.2 kg ha^{-1}, $n = 7$). Total deposition to the open bogs is presumably higher than bulk deposition because dry and wet depositions are not intercepted by a dense tree canopy. But even in the open, moderate-deposition bog in our study, the strongest response was the increase of *Sphagnum magellanicum*. In contrast, in boreal northern Sweden, vegetation may be more sensitive to additional stress by elevated deposition, showing stronger or even negative effects (Nordin et al., 2005, Högberg et al., 2006), for which we found no support in our data from southern Sweden. Therefore, we disagree with the interpretation of a national survey (Strengbom et al., 2003, Nordin et al., 2005) that the lower abundance of *Vaccinium* species in the southern regions with higher deposition is caused by N deposition. Consequently, our results neither provide support for lowering the critical load for the ground floor vegetation in temperate forests and bogs to 6 kg ha^{-1} yr^{-1} as has been proposed for boreal forests (Nordin et al., 2005).

In conclusion, vegetation responses in the same vegetation type were generally similar in moderate (7–13 kg ha^{-1} yr^{-1}) and low (4–6 kg ha^{-1} yr^{-1}) deposition sites in southern Sweden when initial differences were accounted for. Most trends that were significant concerned vascular plants, were negative, and were stronger in low-deposition sites. Trends did not agree with expected across-the-board direct effects of N deposition. Effects differed between growth forms and among species and general trends were more likely a response to increased tree canopy shading.

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Table 1. Plot descriptions.

Vegetation type	blueberry-spruce forest		herb-spruce forest		pine forest		bog		deciduous forest
deposition category	low	high	low	high	low	high	low	high	high
site	Norra Kvill	Aneboda	Tyresta	Berg	Norra Kvill	Tresticklan	Tyresta	Berg	Dalby
cumulative richness									
vascular species	11	5	42	15	7	10	8	13	11
bryophytes	18	24	29	32	8	11	11	19	2
cover sum (first year of observation)									
vascular species	1.4	6.7	19.7	9.8	18.9	36.7	81.1	32.0	153.3
bryophytes	52.4	54.3	2.4	6.1	66.5	71.4	34.0	25.2	0.1
Basal area (m^2/ha)									
Picea abies	26	21	18	32	4				
Pinus sylvestris		14	9	13	24	29	24		
other trees (mostly deciduous)			12			1			37
mean cover (%)									
Vaccinium myrtillus	1		12		17	22	50		
Vaccinium vitis-idaea			2		3	9	3		
Calamagrostis arundinacea			9						
Pteridium aquilinum			4						
Deschampsia flexuosa		3		3					
Melampyrum pratense	1		1						
Melampyrum sylvaticum	1		1						
Pinus sylvestris		1		1				1	
Oxalis acetosella			1	1					
Dryopteris dilatata				1					
Molinia caerulea						3			
Ledum palustre							11		
Vaccinium uliginosum						2	8		
Rubus chamaemorus							3	2	
Calluna vulgaris						1		17	
Eriophorum vaginatum								7	
Erica tetralix								2	
Vaccinium oxycoccus								1	
Mercurialis perennis									71
Anemone nemorosa									28
Anemone ranunculoides									27
Aegopodium podagraria									18
Ranunculus ficaria									15
Pleurozium schreberi	31	8	2	1	29	27	20		
Dicranum polysetum	10	2	1		25	19	15		
Hylocomium splendens	10	2	2		2	4	1		
Dicranum scoparium	6	2	2		1				
Dicranum fuscescens	3	2			2				
Ptilium crista-castrensis	2	2		3		2			
Brachythecium starkei	3								
Dicranum majus		50	2						
Polytrichum formosum				8					
Sphagnum magellanicum								30	
Sphagnum rubellum								5	
Sphagnum tenellum								8	
Odontoschisma sphagni								5	
Eurhynchium praelongum									4
Cladina rangiferina					9		1		

FIGURE CAPTIONS

Fig. 1. Interpolated bulk nitrogen deposition (kg·ha-1·yr-1) in southern Sweden (1983-1996) and location of sites. White areas are outside the measuring network.

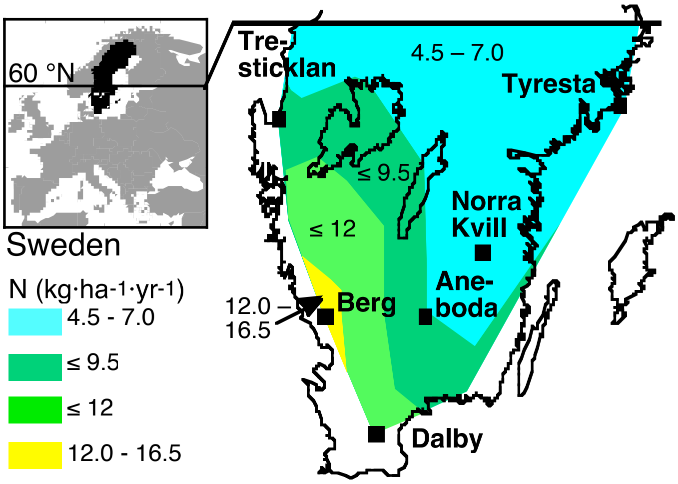
Fig. 2. Bulk nitrogen and acid deposition and precipitation during the study period at the six sites. N deposition decreased significantly in the low-deposition sites, acidic deposition decreased significantly at all sites except Tresticklan, there was no significant trend of precipitation.

Fig. 3. Total cover of vascular plants in high (—●—) and low-deposition plots (– –○– –). Lines indicate regressions compared with ANCOVA.

Fig. 4. Cover of bryophytes in high (—●—) and low-deposition plots (– –○– –). Lines indicate regressions compared with ANCOVA.

Fig. 5. Number of species (richness) of vascular plants in high (●) and low-deposition plots (– –○– –). The number of species is expressed as percentage of each plot's cumulative richness (Tab. 1). Lines indicate regressions compared with ANCOVA.

Fig. 6. Number of species (richness) of bryophytes in high (●) and low-deposition plots (○). The number of species is expressed as percentage of each plot's cumulative richness (Tab. 1). There were no significant linear regressions.



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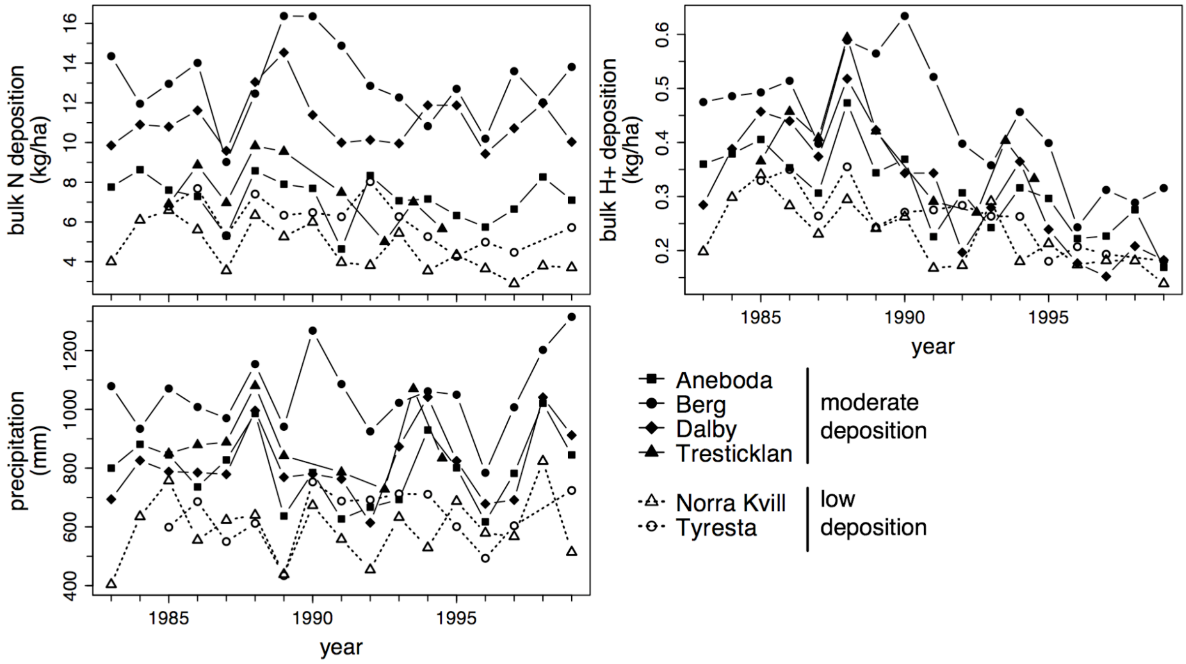

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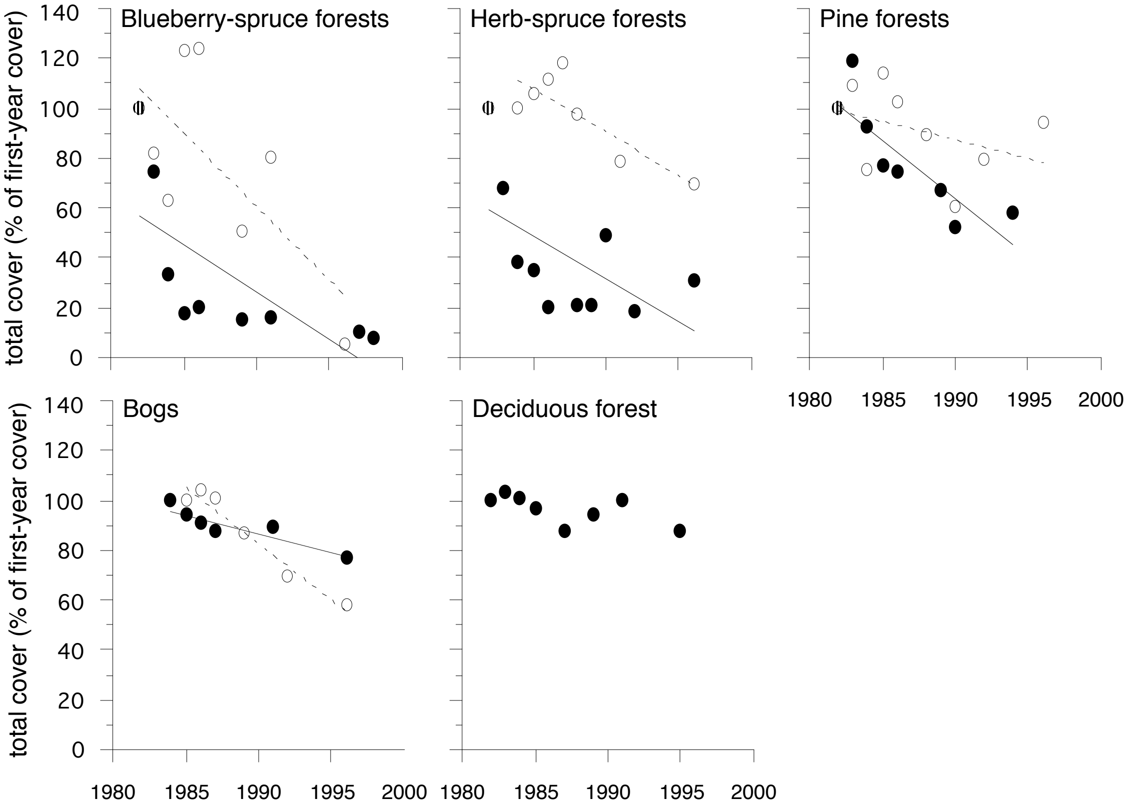

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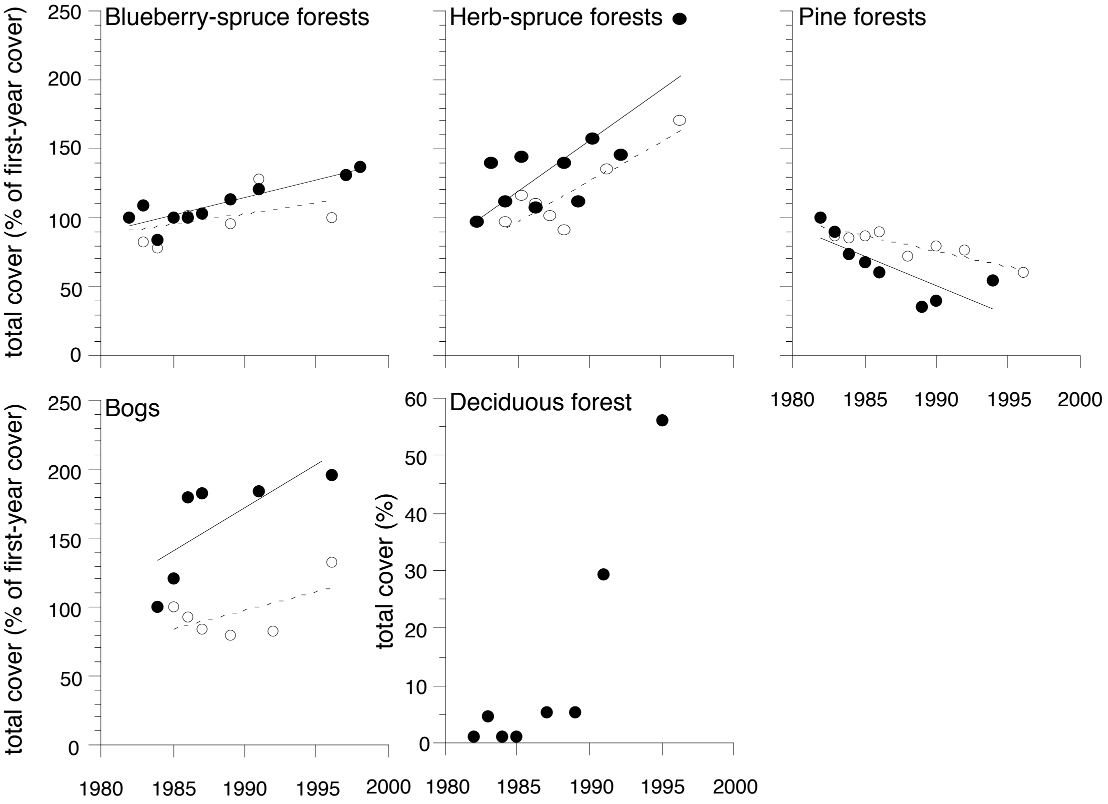
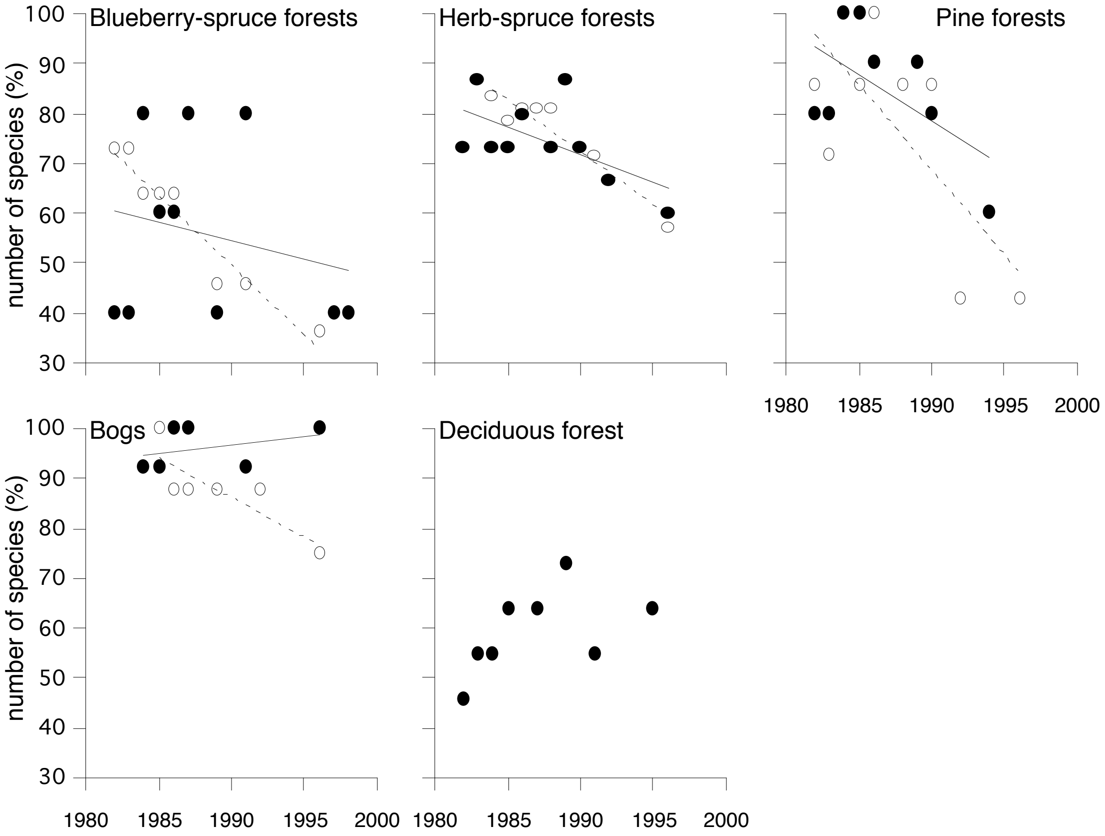


Fig. 4. Cover of bryophytes in high (—●—) and low-deposition plots (– –○– –). Lines indicate regressions compared with ANCOVA. Note that total cover in the deciduous forest is not scaled to initial cover.



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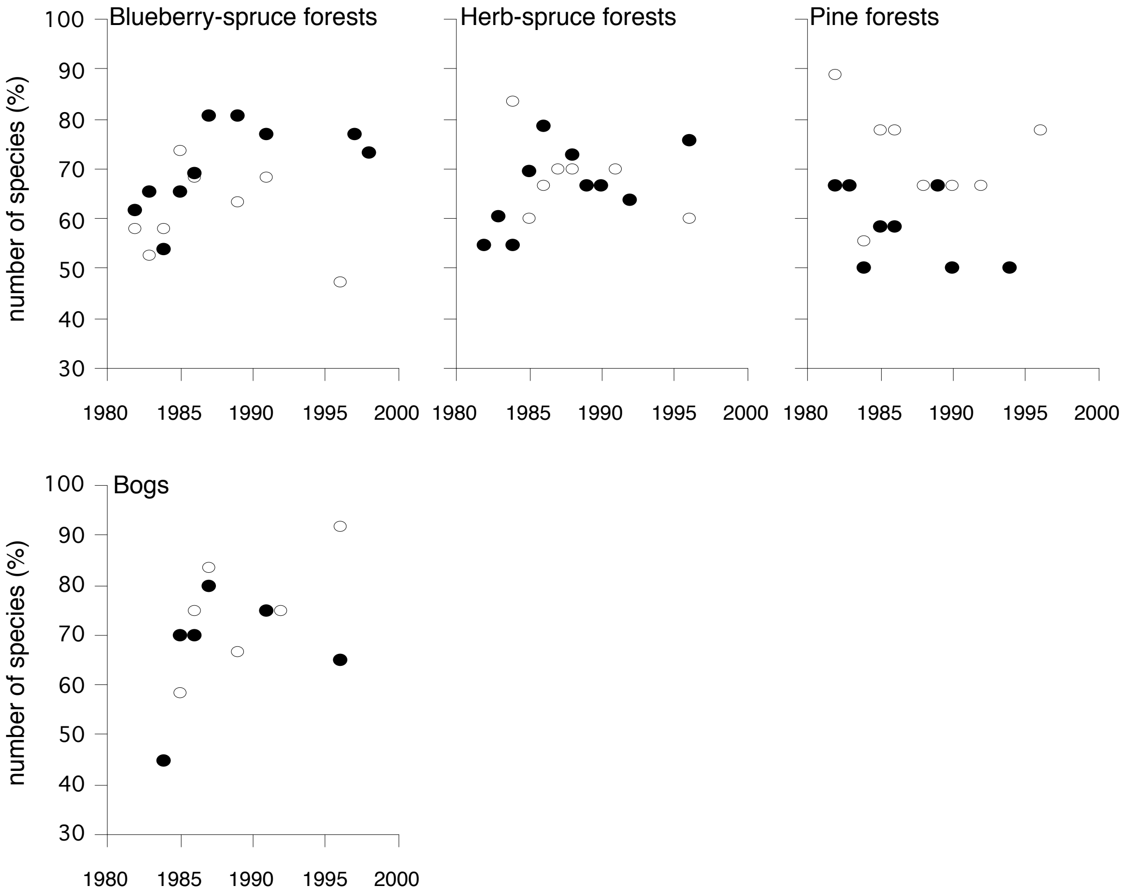

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