



Temperature and leaf form drive contrasting sensitivity to nitrogen deposition across European forests

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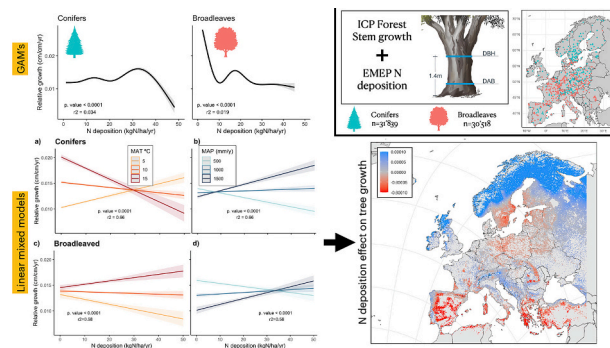
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HIGHLIGHTS

- N deposition effect in forests growth is strongly modulated by the leaf form (conifers vs broadleaves), showing contrasting saturation levels.
- We also highlight the important role of temperature, which strongly interacts with the effect of N deposition on tree growth
- We provide maps showing the effect of N deposition according to its interaction with temperature, precipitation, and leaf form stand density.

GRAPHICAL ABSTRACT



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ABSTRACT

Raised emissions of biologically reactive nitrogen (N) have intensified N deposition, enhancing tree productivity globally. Nonetheless, the drivers of forest sensitivity to N deposition remain unknown. We used stem growth data from 62,000 trees across Europe combined with N deposition data to track the effects of air temperature and precipitation on tree growth's sensitivity to N deposition and how it varied depending on leaf form over the past 30 years. Overall, N deposition enhanced conifer growth (until $30 \text{ kg N ha}^{-1} \text{ yr}^{-1}$) while decreasing growth for broadleaved angiosperms. Lower temperatures led to higher growth sensitivity to N deposition in conifers potentially exacerbated by N limitation. In contrast, higher temperatures stimulated growth sensitivity to N deposition for broadleaves. Higher precipitation equally increased N deposition sensitivity in all leaf forms. We conclude that air temperature and leaf form are decisive in disentangling the effect of N deposition in European forests, which provides crucial information to better predict the contribution of N deposition to land carbon sink enhancement.

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1. Introduction

Since the industrial revolution, nitrogen (N) deposition has risen worldwide (from ~30 to ~80 Tg N/year since 1850; Kanakidou et al., 2016), profoundly altering terrestrial ecosystems with substantial effects on global biogeochemical fluxes, plant growth, and biodiversity (Elser et al., 2010; Battye et al., 2017; Penuelas et al., 2020; Gundersen et al., 1998; Bobbink et al., 2010; Bobbink et al., 2022). This increase in N is thought to have boosted the global carbon (C) land sink by 0.2–0.74 PgC/yr (Townsend et al., 1996; Magnani et al., 2007; Zaehle, 2013; Wang et al., 2017), primarily through enhanced plant productivity in the Northern Hemisphere (Lebauer and Treseder, 2008; Fisher et al., 2012). Even though N deposition has decreased in Europe in the last 30 years (Ackerman et al., 2019), forests have shown limited response to this decrease (Schmitz et al., 2019), and there are still regions exceeding the critical N loads (Bobbink et al., 2022). While N deposition is generally expected to stimulate plant growth, previous work highlighted growth inhibition when deposition exceeded critical thresholds (Flechard et al., 2020; Etzold et al., 2020), thereby casting some doubt on how forests will respond in the future. Similarly, the impacts of N deposition on growth likely vary with plant functional characteristics and local environmental conditions (Horn et al., 2019). Despite major ramifications for forest C sequestration, the effects of rising air temperature and changes in precipitation on the sensitivity to growth in responses to N deposition at broad scales remain unresolved.

The effects of plant N absorption, air temperature, and water availability (i.e., precipitation) on tree growth are strongly intertwined, meaning that global warming and precipitation changes should be major drivers of how future N deposition will impact growth in forests (Gessler et al., 2017; Peñuelas et al., 2017). Nitrogen deposition fractions are mainly inorganic (Cape et al., 2012) and highly soluble in water. When deposited, N compounds are passively absorbed by plant roots during water uptake (Muratore et al., 2021). Therefore, water availability potentially increases N absorption with warming-enhanced evapotranspiration (Grossiord et al., 2020). Leaves can also take up N compounds, a process that is strongly correlated with stomata opening and stomatal conductance, which in turn correlates with air temperature and water availability (Gessler et al., 2000; Tomaszewski and Sievering, 2007; Guerrieri et al., 2024). Moreover, up to a given threshold, high temperature and precipitation increase biomass production (Lin et al., 2010; Wu et al., 2011; Wang et al., 2018; Zhou et al., 2022), and therefore plant N demand. Yet, when N demand exceeds N availability, N limitation occurs with various consequences for plant functions, including reduced growth (Etzold et al., 2020). Globally, N availability also increases with temperature, which favors N-fixation and N cycling (Cleveland et al., 2013; Deng et al., 2018; Salazar et al., 2020), with lower rates of these processes leading to N limitations for vegetation in colder areas (Du et al., 2020). Thus, N deposition should stimulate growth in N-deficient areas that are not co-limited by other nutrients, while N deposition above a certain threshold could inhibit growth due to soil acidification and nutrient imbalances when the N demand is satisfied (Aber et al., 1998; Etzold et al., 2020; Ferretti et al., 2014; Rehman et al., 2022). The role of temperature and precipitation in determining the effect of N deposition on growth will also vary depending on site N availability (Zhou et al., 2022). Nonetheless, the strength of this feedback varies between species and functional groups (Xia and Wan, 2008).

Trees can be classified by leaf form as either broadleaved or needle-leaved, which in Europe correlates with broadleaved and conifers, and in the case of the forests studied here, also denotes angiosperms and gymnosperms. In this study, needle-leaved conifers will be referred to as 'conifers' and broadleaved-angiosperms will be referred to as 'broadleaves'. Trees with these leaf forms exhibit contrasting characteristics, including genetic differences, elemental composition, functional/physiological traits, and resource-use strategies (Díaz et al., 2016; Vallicrosa et al., 2022). Needle-leaves are usually fast-growing species when resources are abundant (Rees et al., 2001), whereas broadleaves are more

competitive under resource-poor conditions (Grime, 1979; Tilman, 1988). Therefore, the geographic distribution of needle-leaves and broadleaves is affected by climate, soil conditions, and is further influenced by management, leading to irregular distributions throughout the globe (Woodward and Williams, 1987; Ma et al., 2023). Globally, higher latitudes are strongly dominated by needle-leaved trees, whereas lower latitudes tend to be more broad-leaved-dominated (Ma et al., 2023). In comparison to broad-leaved trees, needle-leaved species often show more conservative strategies (Flo et al., 2021) with lower water use (Augusto et al., 2015) and photosynthetic rates (Lusk et al., 2003). Such physiological differences can be explained by the typically lower stomatal conductance (Lin et al., 2015) and higher hydraulic safety margins (Choat et al., 2012) found in northern-hemisphere conifers compared to broad-leaved trees. Differences in physiological characteristics and contrasting global distributions are bound to differentially affect the sensitivity of conifers and broadleaves to N deposition. Yet, no study to date has addressed their varying sensitivity at a large and comprehensive scale.

Here we utilized data from European-wide forest growth monitoring carried out from 1995 to 2019 on 650 plots of the International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests operating under the UNECE Convention on Long-range Transboundary Air Pollution (ICP Forests) Level II plot network across 21 countries and coupled with European Monitoring and Evaluation Programme (EMEP) v5.0 N deposition data. We tested i) whether N deposition differently affects growth between leaf forms (conifers vs. broadleaves) at the continental level, ii) whether N deposition interacts with air temperature and precipitation to affect tree growth and iii) the potential role of N-limitation on i and ii. In our approach we use general additive models (GAMs) and linear mixed models with interactive variables to model the effect of leaf form and climate on N deposition sensitivity as well as to visualize its spatially explicit domain in Europe. Our findings will help to disentangle the contribution of N deposition to plant growth, potentially anticipate N deposition effects in a hotter climate, and therefore better calculate the land C sink.

We hypothesize that i) the effect of N deposition on tree growth should be differential depending on leaf form, since conifers and broadleaves are known to have contrasting resource use strategies. Thus, conifers are expected to transform high levels of N deposition into growth, whereas broadleaves, are expected to show lower saturation points leading to lower growth enhancement with N deposition. In turn, we hypothesize that ii) the N deposition effect on tree growth should differ depending on temperature and precipitation regimes since these two environmental variables affect N availability, plant growth, and, therefore, N demand. Plants absorb N in a water solution; hence, more water availability and more water uptake driven by higher temperature should increase N uptake and promote further growth. Finally, we expect that iii) conifers, which are more abundant in N-limited environments, would increase their growth with higher N deposition, seeing their N limitation relieved, while broadleaves growing in more N-saturated regions would show less growth enhancement and potentially even growth depression.

2. Methods

2.1. Data acquisition

We used stem diameter growth data from the ICP Forests monitoring network between 1995 and 2019. The ICP Forests survey 'growth' provides information about plant traits collected using harmonized methods at individual trees and plot levels among European countries. In this study, we used data on stem growth at the individual tree level (downloaded on 18.10.2023). The growth survey assessed the change in diameter at breast height (DBH) for trees taller than 130 cm at irregular year intervals ranging from one-, to twenty-year intervals (median = 5, mean = 4.5) contained in plots of at least 0.25 ha. Tree's DBH vary from

0.6 to 130 cm, with 1 to 640 individuals sampled per plot. Further details for the sampling can be found in the ICP forests manuals (<http://icp-forests.net/page/icp-forests-manual>), 'part V' (Dobbertin et al., 2020). We homogenized the growth coming from irregular time windows by calculating the yearly growth per period, assuming constant growth between the initial and final years of one inventory period. We obtained the modeled spatial-explicit mean annual temperature (MAT) and mean annual precipitation (MAP) data for the same period (1995–2019) from CRU TS v4.05 of the Climatic Research Unit of the University of East Anglia with a spatial resolution of 0.5° (Harris et al., 2020).

Annual data for N ($\text{NO}_3^- + \text{NH}_4^+$, dry and wet) atmospheric deposition were downloaded from the EMEP v5.0 (Crippa et al., 2021) map with a spatial resolution of $0.1 \times 0.1^\circ$ for longitude and latitude, which estimates regional atmospheric dispersion and deposition of acidifying and eutrophication compounds of N over Europe. This model, and therefore map, is created with ground-based observations and provides an accuracy between predicted and observed values of above an R^2 of 0.7 in all the considered N deposition fractions (<https://aeroyal.met.no/pages/overall/?project=emep&experiment=2023-reporting¶meter=concnh4&station=ALL&statistic=R&time=2021&frequency=yearly#>)

(Marchetto et al., 2021). By summarizing the reduced and oxidized compounds of N deposition, we obtained the total N deposition in $\text{kg N ha}^{-1} \text{ yr}^{-1}$. Further, we calculated the accumulated N deposition in a moving 5-year window from 1991 to 2019. For example, the 5-year accumulated N deposition of 1995 is the sum of the yearly total N deposition from 1991, 1992, 1993, 1994, and 1995. We matched the final year of the yearly growth value with the final year of the 5-year accumulated N deposition, corresponding to the median of the time span windows, and adapted the window to the time span of each year series. After, we converted the 5-year values into annual values for clarity and to facilitate comparison with other studies. The higher levels of N deposition in Europe are historically found in central Europe; and we find the lowest levels of N deposition in colder temperatures in Northern Europe (Figs. S1, S2).

We extracted N limitation from Du et al., 2020. This data was upscaled by using N and P reabsorption efficiency worldwide, including sites in Europe, and providing a range from approximately -1 for strong prevailing of P limitation and approximately 1 for strong prevailing of N limitation, if any. Thus, we reclassified the map excluding values lower than 0, only focusing on areas where Du et al. (2020) suggest a potential N limitation as the prevailing case. After, we extracted the corresponding MAT, MAP, N deposition, and N limitation data for each tree using the plot coordinates and the function *extract* from the *raster* R package.

2.2. Data pruning

We first calculated the stem relative growth rate per tree (cm of diameter increase per year per cm of stem diameter) to avoid, as far as possible, the inherent differences in scale between small and large trees so that their performances can be compared on an equitable basis (Hunt, 1990, p. 6). We then subset the trees with more than one recording through the time scale. Non-positive values and values above the 0.99 quantiles were considered unrealistic and, therefore, excluded. The database was further separated by leaf form, having 95'102 observations of 30'518 broadleaved trees comprehending 35 species and 97'553 observations of 31'839 coniferous trees comprehending 17 species. Thus, we have used data from 62'349 trees (192'655 observations in total) located in 405 different plots distributed among 21 countries (Fig. S3) and covering samplings from 1995 to 2019.

2.3. Statistical analysis

In each subset separated by leaf form, we calculated generalized

additive models (GAM) using the R package *mgcv* (Wood, 2011). GAM models are useful to describe the shape of data distributions allowing to visually compare non-linear trends. Considering relative stem growth as the dependent variable, 5-year accumulated N deposition as the independent variable with 6 knots, and thin plate splines (Wood, 2003) as well as latitude as random effects. The reference year, used in our plots and analysis, is the end of the 5-year period and the latitude is the finest provided by the ICP forest inventory. We plotted the results using the function *plotGAM* in the *voxel* R package (García de la Garza et al., 2018). We followed the same procedure to study the four most abundant species in our dataset per leaf form, being *Picea abies*, *Pinus sylvestris*, *Abies alba*, and *Pinus pinaster* for conifers and *Fagus sylvatica*, *Carpinus betulus*, *Quercus petraea*, and *Quercus coccifera* for broadleaves.

In addition, we calculated linear mixed models using the *lmer* function in *lme4* (Bates et al., 2015) and *lmerTest* (Kuznetsova et al., 2017) R packages in each subset. Relative stem growth, which followed a gamma distribution, was considered the dependent variable, and mean annual temperature (MAT), mean annual precipitation (MAP), sampling year, and 5-year N deposition (Ndep) as independent variables considering the interaction between MAT and Ndep, and MAP and Ndep. By including the sampling year, we control for the potential temporal correlation. We considered the tree as a random factor to compare each tree's growth record with its previous measurements, controlling for the potential differences due to tree age. Residuals in both models followed a normal distribution. For further verification, the same models have run with the dependent variable log-transformed with comparable results (Table S1). Additionally, we calculated the relative importance of each variable in the models using the function *domin* of the *domir* R package (Luchman, 2024). We repeated the same model structure to examine the four most abundant species per leaf form in conifers and broadleaves separately (see above). Additional variables such as total soil N, N limitation, or aridity were considered but discarded due to cross-correlation with MAT and MAP (Fig. S4). We plotted the interactions between MAT, MAP, and Ndep of the linear mixed model by using the function *plot_model* from the R package *sjPlot* (Lüdtke, 2023) and setting three fixed interaction levels for MAT (5, 10, and 15°C) and MAP (500, 1000, and 1500 mm/yr).

To assess the temperature effect on N limitation, we separated broadleaves and conifers by MAT in four groups each: $< 5^\circ\text{C}$, between 5 and 10°C , between 10 and 15°C and $> 15^\circ\text{C}$, with 21'525, 46'167, 28'493 and 800 observations in conifers and 3'776, 22'958, 61'867 and 6'488 in broadleaves respectively. We generated boxplots describing the N limitation by group using *ggplot* and the MAT group on the x-axis and N limitation on the y-axis.

2.4. Mapping

We used the conifer and broadleaved density map provided by Ma et al., 2023 to map the interaction between N deposition, MAT, and MAP for the different leaf forms. We summed the map categories 'needle-leaves evergreen' and 'needle-leaves deciduous' to obtain the percentage of basal area occupied by needle-leaves (referred as conifers in this study) and repeated the process for broadleaves. We used the coefficients of the trained conifers and broadleaved linear mixed model to provide a spatially explicit representation of the interaction between MAT, MAP, and N deposition. Thus, we represent the slope of the relationship in each value of MAT and MAP for the two leaf forms. Finally, we aggregate the interactions in conifers, multiplied by the percentage of the basal area occupied by conifers, repeated the process with broadleaves, and obtained a final map where we see the effect of N deposition in Europe depending on the leaf form and interactions with temperature and precipitation. We plotted the resulting map of the N deposition effect on growth with *ggplot* (Wickham, 2016) and used the country boundaries from Natural Earth (<https://www.naturalearthdata.com/downloads/>).

3. Results

Conifer and broadleaved trees exhibited contrasting relative stem growth responses to N deposition. Overall, N deposition was shown to have a positive effect on relative stem growth in conifers and a negative effect in broadleaves. Conifers showed a slightly oscillating increasing pattern between relative stem growth and N deposition, which peaked around 30 kg N/ha/yr, and decreased sharply beyond this value. This peak value is also followed by *Picea abies* and *Pinus sylvestris*, which are the species with sufficiently high N deposition values to be representative (Fig. S4). In contrast, broadleaved trees had an overall decreasing nonlinear relationship of relative stem growth and N deposition, with a small increase at around 18 kg N/ha/yr, stabilizing around 26 kg N/ha/yr (Fig. 1), both with a significance <0.0001 . *Fagus sylvatica*, *Quercus petraea*, and *Quercus coccifera* also presented general decreases of growth with N deposition, whereas *Carpinus betulus* showed a pattern similar to conifers (Fig. S5). Since the r^2 is very low when describing conifers and broadleaves (0.034 and 0.019), the strength of the analysis is to visually show the contrasting responses to N deposition without further predictive power. For further confirmation of the contrasting responses to N deposition between leaf forms, a similar pattern was also found in the linear model, where N deposition positively correlated with relative stem growth in conifers ($7.22e-05$, p -value = 0.02, r^2 = 0.66) and negatively correlated in broadleaves ($-3.20e-04$, p -value <0.0001 , r^2 = 0.58) (Table S1).

We built a linear mixed model to describe relative tree growth, with mean annual temperature (MAT) and mean annual precipitation (MAP) interacting with N deposition, using the tree as a random factor. The r^2 of the model describing conifers' growth response to N deposition, MAT, and MAP was 0.66, and the model describing broadleaves' was 0.58. The direction of the interaction between N deposition and MAT was opposite between leaf forms (Fig. 2a–c, Table S1), which further confirms the contrasting responses to N deposition shown in Fig. 1. N deposition positively correlated with relative stem growth in conifers ($7.22e-05$, p -value = 0.02) and negatively correlated in broadleaves ($-3.20e-04$, p -value <0.0001) (Table S1). Conifers showed a negative interaction with temperature, with higher N deposition in colder areas associated with enhanced growth (i.e., reflecting stronger sensitivity to N deposition). Contrastingly, broadleaves showed higher growth sensitivity to N deposition in hotter areas. Interestingly, above a MAT of 9 °C, N input has a negative effect on relative growth in conifers (Fig. 2a), while in broadleaves below a MAT of 11 °C, the interaction between N deposition and temperature shifts from positive to negative (i.e., lower sensitivity to N deposition at colder temperatures). The interaction between N deposition and MAP is positive in both leaf forms, showing higher growth sensitivity to N deposition with rising MAP (Fig. 2b–d, Table S1). According to N deposition's variable importance, N deposition explained around 20 % of the variability explained by the model in both cases (0.20 in conifers and 0.23 in broadleaves), temperature explained 37 % of the variability in conifers and 20 % of the variability in broadleaves, whereas precipitation explained 18 % in conifers and 15 % in broadleaves (Table S2). In general, the responses vary among different species (Table S3).

To test if the contrasting interactions between temperature and N deposition for broadleaves and conifers are due to differences in spatial distribution of each group (Figs. S3 and S6), we repeated the same analysis only in mixed plots where broadleaves and conifers co-occur. Most of the mixed plots are found in central Europe, corresponding with the area that has received higher levels of N deposition in the last 30 years (Batool et al., 2022; Fig. S1). Interestingly, the results showed comparable trends in conifers between the two datasets, both for MAT and MAP, as well as a similar interaction between N deposition and MAT for broadleaves (Fig. S7), suggesting that their contrasting N sensitivity is not driven by differences in their spatial distribution, but leaf form identity. In contrast, the interaction between MAP and N deposition in broadleaves showed a negative interaction with growth in mixed plots

(Fig. S7, Table S4).

MAT was shown to correlate with N limitation (Fig. S8), so both variables cannot coexist in the same linear model. To further explore if N deposition alleviates N limitation in colder areas, and thus, helping to understand the interaction between N deposition and MAT, we assessed N limitation patterns across Europe. We extracted the N limitation values from Du et al., 2020, which are expressed from 0 (no N limitation) to 1 (maximum N limitation). We found that N limitation in conifers increased with reduced MAT, with trees growing in colder areas ($\text{MAT} < 5^\circ\text{C}$) showing the highest N limitation (Fig. 3). Conversely, N limitation in broadleaves did not appear to be influenced by temperature. These results suggest that the effect of temperature on growth sensitivity to N deposition could be driven by the strong N limitation experienced by conifers in the northern latitude regions that they dominate (Fig. S6).

When combining the relative proportion of land cover occupied by the two leaf forms (Fig. S6) and the combined growth sensitivity to N deposition as a function of MAT and MAP (Fig. S9), we found contrasting effects throughout European forests (Fig. 4). The proportion of land occupied by conifers and broadleaves in Europe is extracted from Ma et al., 2023, mixed with the results shown in Fig. S9. In general, in forests in southern latitudes around the Mediterranean Sea we found a strong negative effect of N deposition on growth, potentially explained by the low MAP. In contrast, northern latitudes, and mountain ridges such as the Alps or the Carpathians showed a positive effect of N deposition on growth, potentially due to a combination of the high abundance of conifers, their high sensitivity to N deposition in cold temperatures and the generally low N deposition values in these regions. Relatively southern areas like the North-west of the Iberian Peninsula and the northeast of the Adriatic Sea also show positive effects of N deposition, correlated with high MAP.

4. Discussion

4.1. N deposition effect

Our results show contrasting impacts of N deposition on tree growth based on tree leaf form and climatic conditions, shown by the non-linear (GAM) model and the linear mixed-effects model. In conifers, N deposition represents 20 % of the relative stem growth variability described by the linear model and positively affects stem growth, until at around 30 kg N/ha/yr. The same tipping point was previously described by Etzold et al., 2020 but was instead generalized across European forests without consideration of leaf form. Our results suggest that this finding was likely driven solely by conifers. Far from being a generalized pattern, our results show the opposite trend in broadleaves, which decrease their growth with N deposition. There, N deposition explains 23 % of the growth variability described by the linear model. Similar patterns have been seen in three of the four most represented broadleaved species in our dataset (*Fagus sylvatica*, *Quercus petraea*, and *Quercus coccifera*). The slight rebound in growth response to N deposition at about 18 kg N/ha/yr for broadleaves can be attributed to beech (*Fagus sylvatica*), a highly abundant tree that was found to have a significant tipping point response here and in previous studies (Etzold et al., 2020). Indeed, beech trees make up 43 % of the total observations for broadleaves in the ICP forest database, indicating that this species is a major contributor to the observed pattern. Similarly, the pronounced initial relative growth decrease in response to N deposition seems to be led by *Quercus petraea* and follows more moderate decreasing patterns in the rest of the species. These contrasting responses between leaf forms suggest differences in the nutritional status of conifers and broadleaves that could respond to differences in N availability. Previous research in central Europe determined that conifer species (i.e. *Picea abies*) were generally found in N-limited conditions (lower nutritional optimum), thereby potentially benefiting more strongly from N additions. On the other hand, broadleaves (i.e., *Fagus sylvatica* and *Quercus* spp.) were

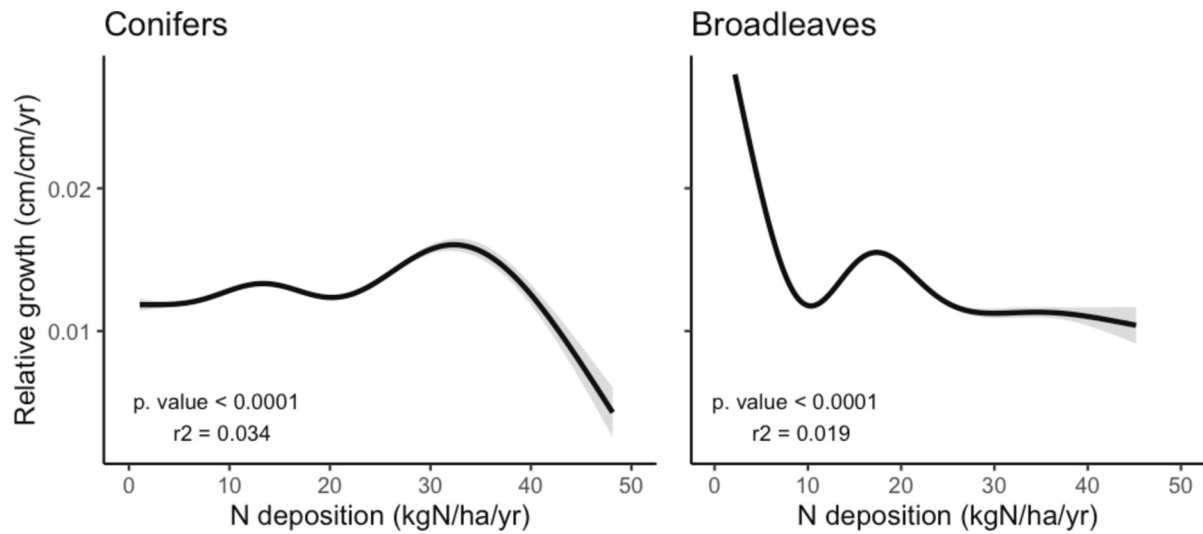


Fig. 1. Non-linear N deposition effects on relative stem growth by leaf form. Results of the generalized additive models (GAMs) describing the relative stem growth response to nitrogen (N) deposition in kg N/ha/yr for conifer and broadleaved trees. Latitude is considered a random factor. N deposition values extracted from EMEP modeled total N deposition. Tree growth data span from 1995 to 2019.

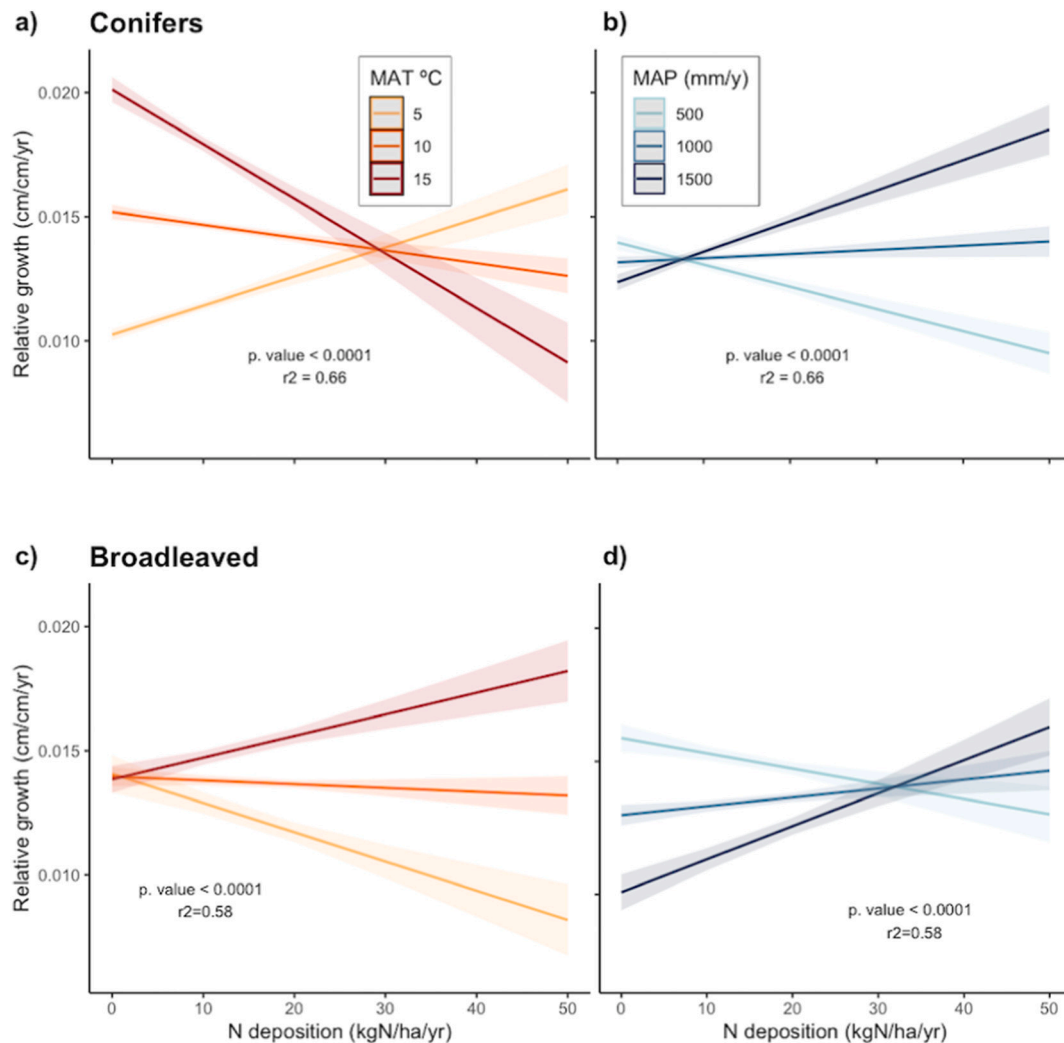


Fig. 2. Growth sensitivity to N deposition depends on temperature and precipitation. Interaction between mean annual temperature (MAT) and mean annual precipitation (MAP) on the relative growth with nitrogen (N) deposition in conifers (a, b) and broadleaved trees (c, d) in Europe. The P-value of each variable is displayed, as well as the r² of each model.

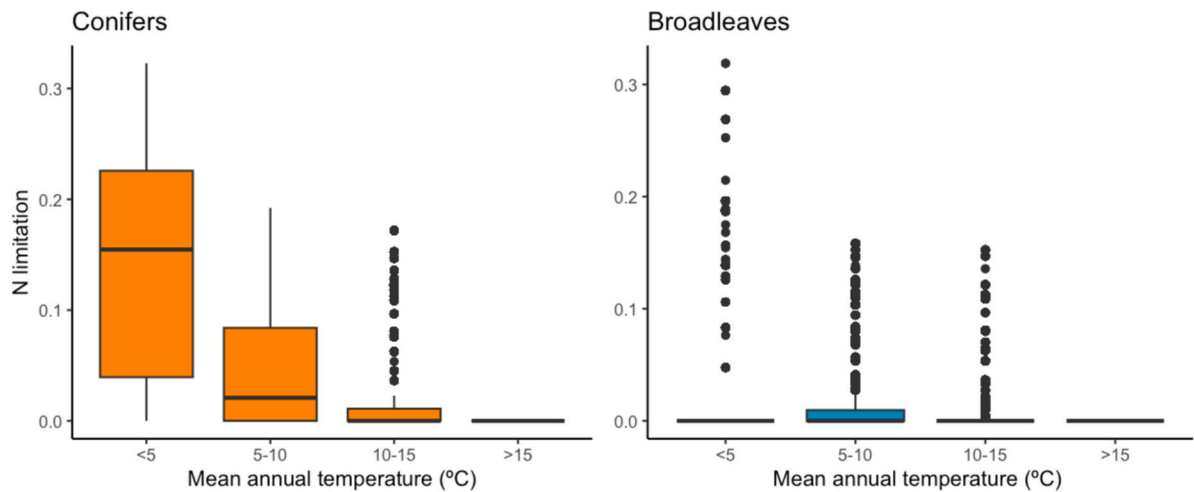


Fig. 3. N limitation patterns depending on temperature by leaf form. Mean tree nitrogen (N) limitation as a function of the mean annual temperature (°C) for conifers and broadleaves. Boxes represent trees living below 5°, between 5 and 10, 10 and 15, and over 15 °C. N limitation values were extracted from [Du et al., 2020](#) and comprehended standardized values from 0 (no N limitation) to 1 (maximum N limitation).

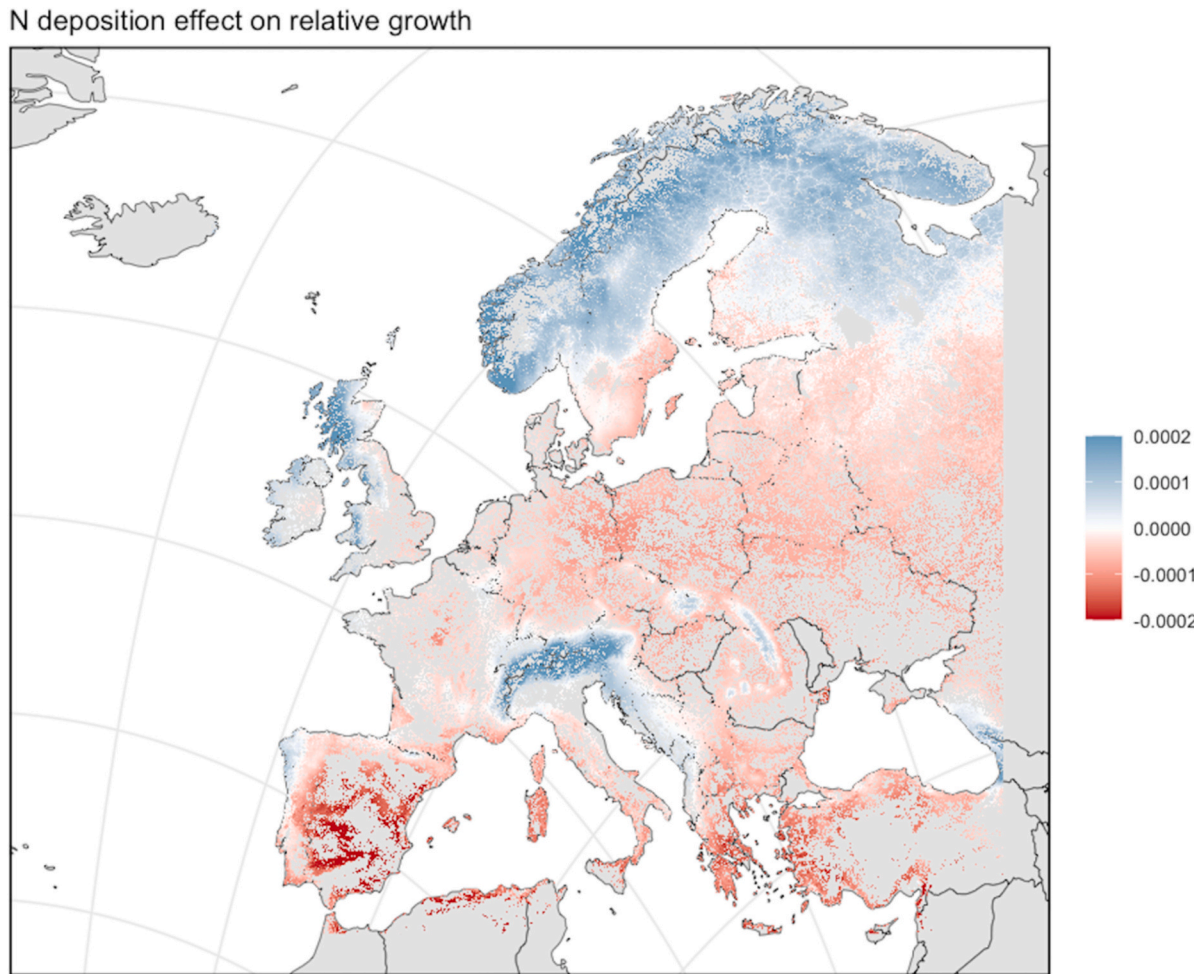


Fig. 4. Growth sensitivity to N deposition. Combined temperature and precipitation effects on the growth sensitivity of forests to N deposition. The effect of leaf form and interactions with mean annual temperature and mean annual precipitation is considered, based on the results of the linear mixed model. Blue colors describe a positive effect on relative stem growth, and red colors describe negative responses to N addition in cm/cm/yr per kg of N/ha/yr.

slightly above their nutritional optimum, showing signs of N saturation ([Mellert and Göttlein, 2012](#); [Jonard et al., 2015](#)). Thus, a decline of growth as a response to N deposition for broadleaves matches with a

potential saturation of those species but we suggest interpreting the sharp decrease below 8 kg N/ha/yr in *Quercus petraea* carefully.

4.2. The role of temperature, precipitation, and N limitation

MAT was shown to play an important role in driving the effects of N deposition on growth, which differentially affected trees based on leaf forms. Conifers showed a more substantial growth response (i.e., stronger sensitivity) to N deposition in cold temperatures, which also corresponds to N-limited areas for trees (Du et al., 2020; Vallicrosa et al., 2022). Thus, the addition of extra N provided from atmospheric deposition potentially enhanced growth while contributing to alleviating the N limitation. In contrast, broadleaves are generally less abundant in northern latitudes and mountain ranges and, therefore, practically unaffected by temperature-driven N limitation. Despite the general negative effect of N deposition on broadleaves growth, N deposition still brought modest positive effects for broadleaves in warm and southern latitudes, where extra N supply might help broadleaves to overcome the antagonistic effects of drought (Grossiord et al., 2018; Schönbeck et al., 2021; Vallicrosa et al., 2021; Wang et al., 2023). Moderate growth enhancement in such conditions could be partially associated with increased uptake of N driven by higher evaporative demand and water loss during warm and wet periods. Indeed, plants' N uptake is positively correlated with increasing water uptake since soil available N is dissolved in water and incorporated by simple diffusion during the process of obtaining water (Muratore et al., 2021). Consequently, higher precipitation also drives increased growth sensitivity to N deposition in both leaf forms, leading overall to higher sensitivity to N deposition in wetter and colder regions at higher latitudes and lower growth gains in the southernmost regions of Europe where MAP is low. Nonetheless, in areas with a strong N deposition such as central Europe, high levels of MAP still decrease growth in broadleaves, which are expected to be already N-saturated.

Since conifers are more likely to live in cold N-limited environments and have been shown to benefit more from N deposition, it would be reasonable to assume that contrasting sensitivities between leaf forms are purely due to differences in distribution. Nonetheless, the results remained comparable when training the model only with mixed plots (containing both conifers and broadleaves). We cannot deny the N limitation relief by N deposition in cold environments. However, our results suggest that the differences between leaf forms are inherent to their resource-use strategies. In Europe, conifers are usually fast-growing species when resources are abundant (Rees et al., 2001), whereas broadleaves are more competitive under resource-poor conditions (Grime, 1979; Tilman, 1988). Thus, N saturation levels are expected to differ between conifers and broadleaves, as this study suggested. Even though in less intensity, different species in the same leaf form group have shown to have different ecological requirements and, therefore, resource-use strategies. In this study, we seek to find continental large-scale patterns. Still, the species-specific variability range could also affect the N deposition effect and interaction between temperature and precipitation on a more local scale, depending on the specific species composition.

Overall, evidence points towards N deposition, temperature, and precipitation as relevant factors controlling plant growth at global and continental scales (Lebauer and Treseder, 2008; Wang et al., 2019; Etzold et al., 2020). Nonetheless, other factors such as forest management and stand structure (i.e. age distribution) could explain part of the tree growth variability our models are not explaining. Despite a decreasing trend of N deposition in Europe since the 1990s (Waldner et al., 2014; Banzhaf et al., 2015), wide areas persistently remain above the critical loads (around 10–15 kg N ha⁻¹ yr⁻¹ in most European forests) being still a reason for ecological concern (Bobbink et al., 2022; Crippa et al., 2021). Since preindustrial times, global surface temperatures have increased by an average of ~1.1 °C whereas, in Europe, the average global surface temperature increase has already surpassed 2 °C (EUCRA, 2024). In addition, precipitation regimes have changed regionally across Europe, showing more extreme events such as longer droughts and torrential rains (André et al., 2024). Thus, exploring the

interactions between rainfall and temperature on N deposition and plant productivity in Europe is becoming increasingly relevant. We, therefore, suggest that future models should incorporate the interactive effects of MAT, MAP, and N deposition to better predict the global C sink. Nonetheless, future research is needed to test whether these conclusions hold in other regions, and ecosystems, thereby allowing for increased predictive accuracy of the global C cycle.

4.3. Methodological biases

This study focuses on understanding the impacts of N deposition on European tree growth over the last three decades and the N loads we studied model real field values. Thus, we acknowledge that N deposition levels have historically been especially higher in temperate latitudes, reducing the sample size of higher N deposition levels in extremely cold or hot environments (Fig. S6). This environmental bias could impact the accuracy of assessing high N deposition loads in extreme environmental conditions. Even though we describe the effect of N deposition using also non-linear models, we do not include the N saturation effect in our maps showing the interaction with temperature and precipitation, since we used linear approaches, and our goal was to emphasize the interactive effect of climate and leaf form. For our analyses, we used modeled N deposition values, which include an associated error with real ground values (lower than 30 %). Even though these mismatches have been associated mainly with canopy retention and pixel generalization (Marchetto et al., 2021), they still need to be acknowledged as potentially affecting our results.

5. Conclusion

Following our initial hypothesis, our work emphasizes strong contrasting growth sensitivities to N deposition between tree leaf forms. N deposition generally increases conifer's growth until a tipping point is reached at 30 kg N/ha/yr. Contrastingly, N deposition systematically reduces stem growth in broadleaves. These leaf-form-specific responses further interact with temperature and precipitation, with conifers living in colder, wetter, and N-limited areas benefiting the most from N deposition. In contrast, the moderately positive interaction between temperature and N deposition for broadleaves suggests that atmospheric N deposition could help mitigate the impact of climate change (i.e. drought) in southern and hotter latitudes. On the other hand, the interaction between N deposition and precipitation exists, but remains positive regardless of the leaf form. Our results suggest that conifers and broadleaves are currently in different nutritional status, potentially due to contrasting spatial distribution, contrasting nutritional needs and, therefore, N saturation levels. Conifers, with their dominance in N-limited areas and, in addition to their fast-growing strategy, have greater potential to benefit from higher N deposition levels. Based on our results, we believe that inclusion of temperature, and leaf form is crucial to accurately assess how N deposition will contribute to the future of the land C sink.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2024.176904>.

CRediT authorship contribution statement

Helena Vallicrosa: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Kate M. Johnson:** Writing – review & editing, Validation, Supervision, Conceptualization. **Arthur Gessler:** Writing – review & editing, Validation. **Sophia Etzold:** Writing – review & editing, Validation. **Marco Ferretti:** Writing – review & editing, Supervision. **Peter Waldner:** Writing – review & editing, Validation. **Charlotte Grossiord:** Writing – review & editing, Validation, Supervision, Resources, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

We declare no competing interests.

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Data availability

The data used to perform this research is available under request at <http://icp-forests.net/>. The generated code is openly available at: <https://github.com/helenavallicrosa/Ndep.EuropeanForests>.

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