Nitrogen concentrations in boreal and temperate tree tissues vary with tree age/size, growth rate and climate

Martin Thurner[1,2], Kailiang Yu[23], Stefano Manzoni[3,4,5], Anatoly Prokushkin[56], Melanie A. Thurner[67,2], Zhiqiang Wang[7,8,9], Thomas Hickler[1,109]

5   [1]Senckenberg Biodiversity and Climate Research Centre (SBiK-F), Senckenberg Gesellschaft für Naturforschung, Frankfurt am Main, Germany
[2]Karlsruhe Institute of Technology (KIT), KIT-Campus Alpin, Institute of Meteorology and Climate Research - Atmospheric Environmental Research (IMK-IFU), Garmisch-Partenkirchen, Germany
[23]High Meadows Environmental Institute, Princeton University, Princeton, New Jersey, USA
10 [34]Department of Physical Geography, Stockholm University, Stockholm, Sweden
[45]Bolin Centre for Climate Research, Stockholm, Sweden
[56]V.N. Sukachev Institute of Forest SB RAS, Krasnoyarsk, Russia
[67]Universität Hamburg, Hamburg, Germany
[78]Sichuan Zoige Alpine Wetland Ecosystem National Observation and Research Station, Southwest Minzu University,
15 Chengdu, China.
[89]Institute of Qinghai-Tibetan Plateau, Southwest Minzu University, Chengdu, China.
[910]Goethe University Frankfurt, Frankfurt am Main, Germany

Correspondence to: Martin Thurner (~~martinthurner87@googlemail.com~~martin.thurner@kit.edu)

Abstract. ~~Nitrogen (N) concentration in tree tissues controls p~~Photosynthesis, growth and plant maintenance respiration are
20 closely related to tree tissue nitrogen (N) concentrations. While earlier studies of ~~its~~ the variation in tissue N concentrations
and underlying controls have mostly focused on leaves, here we identify the large-scale controls of N concentration in other
tree compartments for the first time. This is achieved by constructing and analysing ~~an unprecedented~~a novel database of N
concentrations in stems, roots and branches covering all common Northern hemisphere boreal and temperate tree genera,
combined with data for leaves mostly from existing databases. This database allows us to explore the large-scale abiotic
25 (climate, soil N concentration) and biotic controls (tree age/size, leaf type, growth rate) of tree tissue N concentration. We
find that N concentrations decrease with increasing tree age (or size) and are significantly higher in deciduous compared to
evergreen trees in all tissues. Low growth rates or unfavorable climate conditions (very cold or dry climate) significantly
decrease leaf (the latter only for needleleaf deciduous and needleleaf evergreen trees), but not stem N concentration,
indicating their effects on N allocation. Plant traits and environmental conditions together explain very large parts of the
30 variation in tissue N concentrations. These results suggest that changes in the distribution of tree age/size, species, and
extreme climate, induced by climate change, forest management or disturbances, will have substantial consequences for the
carbon (C) sequestration potential of boreal and temperate forests by altering tissue N concentrations. We expect that the
expansion of tree species better adapted to dry conditions in European temperate forests will result in a higher N
concentration in all tree tissues and elevated N allocation fractions to stems, which might lead to higher productivity, but

35 also higher maintenance respiration. The identified relationships need to be represented in dynamic global vegetation models (DGVMs) to estimate future effects of N limitation on the C cycle.

1 Introduction

Nitrogen (N) acquired by plants is incorporated into amino acids and thus proteins and enzymes, nucleic acids, and chlorophyll and as such it is critical for photosynthesis and plant growth. Since leaf N concentration is strongly related to
40 carboxylation capacity (Dong et al., 2022), increases in leaf N concentration are associated to higher photosynthetic rates, especially in N-limited ecosystems (Wright et al., 2004). Most terrestrial ecosystems are affected by N limitation (LeBauer & Treseder, 2008), resulting in a reduced response of photosynthesis and growth to global warming and increasing atmospheric carbon dioxide (CO_2; Luo et al., 2004; Reich et al., 2006a; Terrer et al., 2019; Kou-Giesbrecht et al., 2023). N limitation is particularly relevant in northern boreal and temperate ecosystems (Du et al., 2020). At the same time, increased
45 N concentrations in leaves, but also in other tissues (branches, stems, roots), directly translate into higher maintenance respiration (R_m) rates (Ryan, 1991; Reich et al., 2006b). Accordingly, Nnot only plant growth and litter decomposition (Parton et al. 2007), but also respiration is directly related to the vegetation N content (Reich et al., 2006b), since maintenance respiration (R_m, (respiratory costs that plants have to invest to maintain a healthy state) supports protein repair and replacement, and most plant organic N is in proteins (Ryan, 1991). Moreover, also litter decomposition is driven by the
50 plant tissue N content (Parton et al., 2007).

These relationships are represented in dynamic global vegetation models (DGVMs), but how tissue N content is prescribed or modelled differs between models, which indicates high uncertainty (Kou-Giesbrecht et al., 2023). Tissue-specific N concentrations are either prescribed and more or less specific for certain plant functional types (PFTs) or they change in relation to environmental factors (Meyerholt & Zaehle, 2015). A common approach is to optimize leaf N concentration for
55 maximum net carbon gain (e.g. in Lund-Potsdam-Jena (LPJ) type of models (Haxeltine & Prentice, 1996; Sitch et al., 2003), and wood and fine root N concentrations are usually simply assumed to vary proportionally with leaf N concentration (Meyerholt & Zaehle, 2015).

Despite the potential role of N concentration across plant tissues, previous studies have largely focused on global biogeographic understanding of leaf N concentration (Butler et al., 2017; Moreno-Martinez et al., 2018). These studies are
60 facilitated by extensive leaf N concentration data from databases like TRY (Kattge et al., 2020). However, extrapolation to whole plants has been hampered by relatively sparse data on tissue N concentration in other tree compartments (i.e., branches, stems, and roots). While numerous N concentration measurements are available for fine roots (Iversen et al., 2017; Wang et al., 2019; 2021), N concentration data representative for the entire root system including coarse roots are comparatively sparse due to the complexity of such measurements. To address this knowledge gap, and since our study aims
65 to facilitate large-scale estimates of tissue N contents and R_m in boreal and temperate forests in future studies, here we focus on total root N concentrations. Such estimates of tissue N contents and R_m are dependent on remote sensing biomass data

and measurements of biomass allometry, which (in contrast to measurements of N concentrations) more frequently include total root biomass but rarely fine root biomass separately (Thurner et al., 2014; 2019; Schepaschenko et al., 2017). Estimates of root N concentrations, root N contents and root respiration are important, for instance, for improving estimates of the land C sink in C budgets (Friedlingstein et al., 2023).

N concentrations are highly variable among tissues and are an order of magnitude lower in structural compartments (i.e., branches, stems, and coarse roots) compared to leaves. Hence, information on distinct N concentrations for all living tree compartments (leaves, branches, stem sapwood, roots) and underlying environmental controls is required to better constrain the influence of N limitation on the response of the vegetation C cycle to environmental changes. ~~Such information will also allow inferring whole tree R_m by concomitant use of available data on the biomass of these compartments (Thurner et al., 2014; 2019).~~ Although the influence of many environmental and biological factors on tree tissue N concentration has been identified in certain experiments or stands, it has not been determined at global scale. The combined effects of tree species identity and their growth rates, climatic conditions, soil N availability, and tree size/age on N concentrations in leaves, but especially stems, roots and branches remain largely unexplored across boreal and temperate forest ecosystems. Here we compile an extensive database of N concentration measurements in boreal and temperate tree stems, roots and branches from the literature and own measurements in regions where other data is sparse (Siberia), in addition to measurements for leaves that are to a large extent available from TRY. Especially with regard to stem, root and branch N concentrations, our database is ~~of unprecedented comprehensiveness~~ novel since it integrates numerous studies that focused on selected species and forest stands. Moreover, we collect information on simultaneously measured environmental controls (tree species, climate, tree size/age, soil N concentration). These data allow investigating the controls of N concentration in tree compartments other than leaves for the first time across the entire northern hemisphere boreal and temperate forests.

We use our compiled N concentration database to test the following hypotheses:

1. Tissue N concentration decreases with tree age/size.

N concentration has been reported to decrease in stem and branch segments (Bosc et al., 2003; Feng et al., 2008) and also in roots (Ceccon et al., 2016) of increasing age or increasing diameter (Ceschia et al., 2002), but only for single trees or stands and selected tree species. Other studies of certain needleleaf evergreen species at the stand scale, however, found N concentrations in stems and bark, but not branches and foliage, to decrease with stand age (Sprugel, 1984; Ranger et al., 1995; Ponette et al., 2001). Accordingly, the generality of this relationship has yet not been confirmed for all common boreal and temperate tree genera at global scale. Possible underlying mechanisms are a) a decline in photosynthetic capacity with increasing tree age/size and associated decline in required N to support photosynthesis (Yoder et al. 1994; Steppe et al. 2011), b) a decreasing share of tissues with high N concentrations~~living cells~~ in older trees due to the ~~(~~conversion of living cells in the sapwood to heartwood and due to N retranslocation (Augusto et al., 2008; Thurner et al., 2019), and c) a

100 depletion of soil N during early growth stages or a stabilisation of N in organic matter (especially in boreal forests), which limits growth in mature forests (Norby et al. 2010).

2. Deciduous trees have higher tissue N concentrations than evergreen trees.

105 Both leaf and woody tissue N concentrations differ strongly between tree species (e.g. Martin et al., 2015). Leaf N concentration is much higher in deciduous than in evergreen broadleaf and needleleaf trees, since trees with thin, short-living leaves have higher N concentrations and in general also higher growth rates to support photosynthesis of foliage with shorter lifespan (Chapin et al., 1993; Reich et al., 1992; Reich, 2014; Schulze et al., 1994). Similar relationships have been observed between fine root N concentration and fine root longevity (Withington et al., 2006). Fast-growing, deciduous species also
110 have a greater capacity to acquire nutrients or usually live in nutrient-rich areas (Lambers & Poorter, 1992). For these reasons, deciduous trees are supposed to exhibit higher N concentrations compared to evergreen trees not only in their living tissue, but also in their structural woody components. However, the significance of the difference in branch, stem and coarse root N concentration between deciduous and evergreen boreal and temperate trees still has to be demonstrated based on an extensive database. An earlier study by Meerts (2002), for instance, relied on solely nine samples of sap- and heartwood N
115 concentration in Gymnosperms. In addition, little is known about tissue N concentrations in needleleaf deciduous trees (i.e. larch (*Larix*)).

3. Trees that are slow-growing or growing under unfavorable climatic conditions (very cold or dry climate) allocate a lower share of N to their leaves and a higher share of N to their stems compared to trees that are fast-growing or
120 growing under favorable conditions.

Fast-growing species have been found to allocate relatively more N to their leaves and less N to their stems compared to slow-growing species (Poorter et al., 1990), due to their different defense and allocation strategies. However, these observations were based on a greenhouse experiment considering only non-woody herbaceous species, and thus still need to
125 be verified for boreal and temperate tree species at global scale. Plants face a trade-off when investing resources into growth or defense (Bazzaz et al., 1987; Herms & Mattson, 1992), and because N is critically involved in defense mechanisms (Ullmann-Zeunert et al., 2013), their N economy is central in this trade-off. Specifically, N is required for chemical defense against herbivores and pathogens through N-based secondary metabolites, for instance alkaloids (Herms & Mattson, 1992). However, how defense mechanisms are controlled by N is yet not fully understood (Sun et al., 2020), because research
130 having mostly focussed on herbivory and pathogens, but less on defense against environmental stresses (Loehle, 1988). While in fast-growing species higher rates of photosynthesis and thus growth require more N to be allocated to their leaves, it has been suggested that slow-growing species tend to allocate relatively more N to their stems to support defense mechanisms (Loehle, 1988). In addition to being the result of a growth-defense trade-off, relatively more N might as well be

stored in reserves in stems of slow-growing compared to fast-growing trees due to a relative oversupply of N as they grow in
135   ecosystems limited by other resources (Chapin et al., 1990), including low temperatures, water or light.

Climatic conditions affect tissue N via species sorting, but also acclimation mechanisms. Unfavourable climatic conditions (very cold or dry climate) favor tree species with slow growth and high investment into defense against cold stress and drought, respectively (Chapin, 1991), leading to relatively lower N concentrations in leaves and higher N concentrations in stems.

140   Up to now, the effects of temperature and water availability on N allocation have rarely been analysed at global scale. Although leaf N concentration is not strongly related to mean annual temperature (MAT; Laughlin et al., 2011), it tends to decrease with decreasing MAT in the high-latitudes (Reich & Oleksyn, 2004). This relationship might be due to different interacting effects of acclimation and adaptation of plant physiology to temperature on the one hand, but also to gradients in soil nutrient availability on the other hand (Reich & Oleksyn, 2004). In contrast, according to Tang et al. (2018), the N
145   concentration not only in leaves, but also in stems and roots decreases with increasing MAT and mean annual precipitation (MAP) across all ecosystems in China. In general, they found that the N concentration in stems and roots is more strongly related to abiotic factors than leaf N concentration. These contrasting results motivate a more complete analysis at the global scale.

150   4.   Tissue N concentration increases with soil N concentration.

In addition, tissue N concentrations vary with soil N, because higher N availability in the soil supports higher levels of N uptake. However, the relationship between soil N and the N concentration in structural tree compartments (i.e., branches, stems, and coarse roots) remains rarely investigated, and available studies have been limited to single or a few field sites or
155   forest stands and a selection of tree species. For instance, higher soil N has been observed to result in elevated N concentrations in all tree tissues in *Populus* trees grown in a field experiment (Pregitzer et al., 1995).

This relationship has been studied more extensively for leaves and fine roots. Fine root N concentration has been found to be correlated with soil nitrate availability in US temperate forests (Hendricks et al., 2000) and negatively correlated with soil C:N ratio in boreal and temperate forests in Europe (Ostonen et al., 2017). In contrast, Tateno & Takeda (2010) reported
160   decreasing leaf, but surprisingly not fine root, N concentrations with decreasing soil N availability in a temperate deciduous forest in Japan. In permafrost regions, foliar N concentration has been reported to decrease with decreasing active layer thickness and consequently less available nutrients (Prokushkin et al., 2018). These partly contradictory results and the scarcity of studies on structural tree compartments show that further investigation of the relationship between tree tissue and soil N concentration considering all common boreal and temperate tree genera at global scale is required.

165

        5.   Both plant traits and environmental conditions are important controls of tissue N concentrations and together
            explain large parts of the variation therein.

As discussed above, tree tissue N concentrations have been shown to be related to different plant traits and environmental conditions. However, previous studies have usually focused on single factors, but have not comprehensively studied effects and interactions of multiple controls for tissues other than leaves (e.g. Reich & Oleksyn, 2004) and fine roots (e.g. Yuan et al., 2011; Wang et al., 2020). For the first time we investigate here the relationships between N concentrations in branches, stems and (coarse) roots and plant traits (tree age/size, leaf type, growth rate) as well as environmental conditions (temperature, water availability, soil nutrient availability) across the entire Northern Hemisphere boreal and temperate forests.

2 Materials and Methods

2.1 ~~An unprecedented~~A novel database of N concentration measurements in tree tissues

We collect ~~an unprecedented~~a novel database of N concentration measurements in stems (i.e., trunks), roots and branches of northern hemisphere boreal and temperate trees by an extensive literature research. For this task, we search Web of Science for stem, root and branch nitrogen concentrations for all common boreal and temperate tree genera (for search criteria see Supporting Information S1). To a lesser extent, we also collect leaf N concentration measurements from the literature, because numerous measurements of leaf N concentration are already available from the TRY database (Kattge et al., 2020). Since measurements are rare in Russian boreal forests, we include own measurements for *Larix gmelinii* in the central part of the Nizhnyaya Tunguska River basin in Central Siberia (ca. 64° N 100° E; Larjavaara et al., 2017; Prokushkin et al., 2018). Moreover, data sources from the Russian and Chinese literature, the TRY database (Kattge et al., 2020) and the biomass and allometry database (BAAD; Falster et al., 2015) are considered.

Only measurements of N concentration under natural conditions (no greenhouses, no trees grown in pots, no fertilizer, and no other experiments) are included in the database. In addition, we only include studies with explicit information on the measurement location and the investigated tree species. We only analyse measurements of total root N concentration, but do not include measurements of N concentration specifically for fine roots. In cases where separate measurements are available for (stem) sapwood and heartwood, we include only N concentrations of sapwood. Replicate measurements, if available from the studies, are retained. All tissue N concentrations are expressed in g N / g dry weight. In total, the compiled database investigated here comprises 1048 stem, 267 root, 599 branch, and 5944 leaf N concentration measurements. A list of the data sources is found in Supporting Information S2. While almost all of the stem (911 collected from literature, 1 own, 52 from TRY, 84 from BAAD), root (266 collected from literature, 1 own) and branch (all collected from literature) N concentration measurements have been collected from in total 192 studies from the literature, leaf N concentration measurements are to a large extent available from existing databases (188 collected from literature, 5 own, 5522 from TRY, 229 from BAAD). The spatial distribution of N concentration measurements applied in this study is shown in Fig. 1.

200
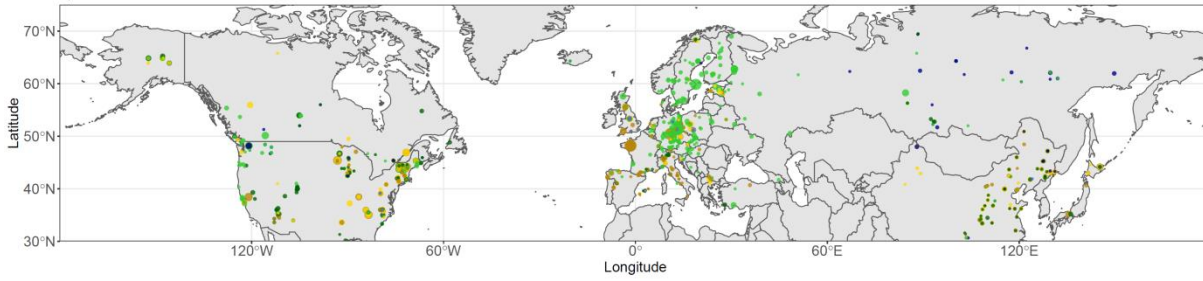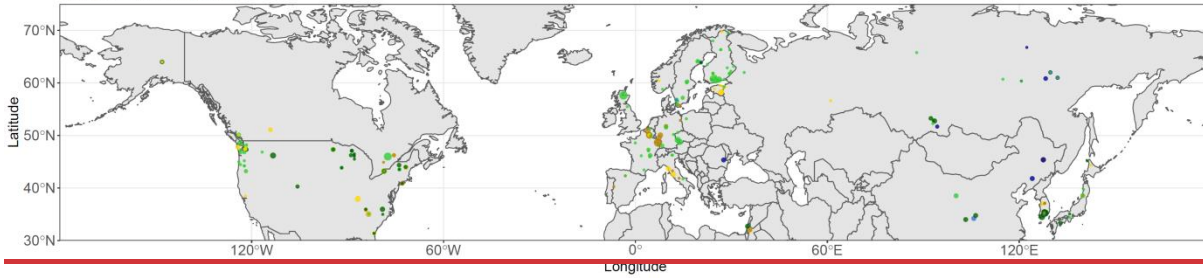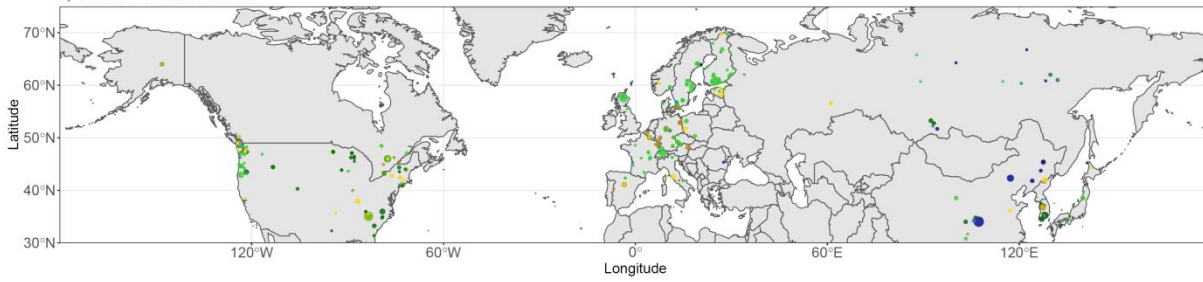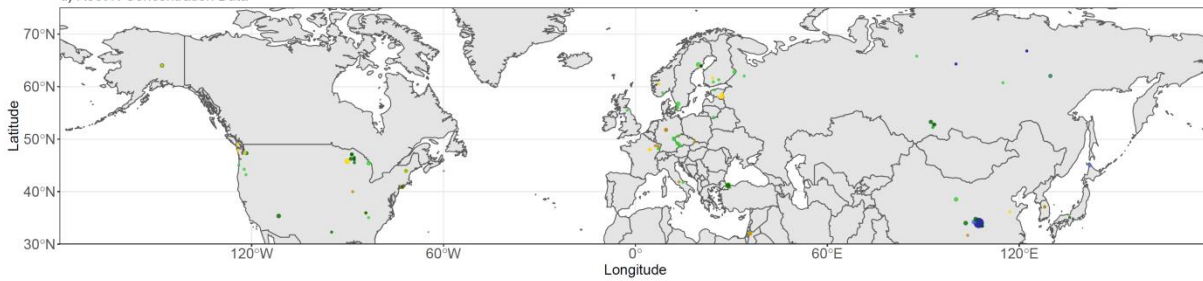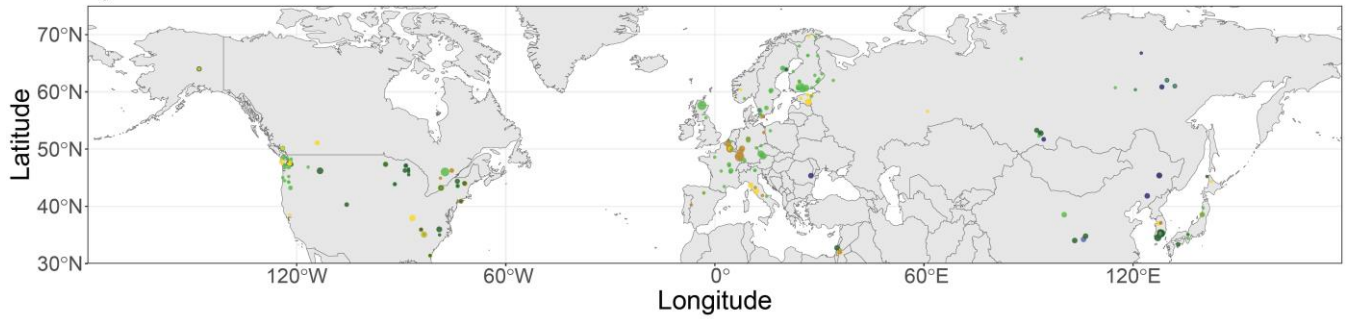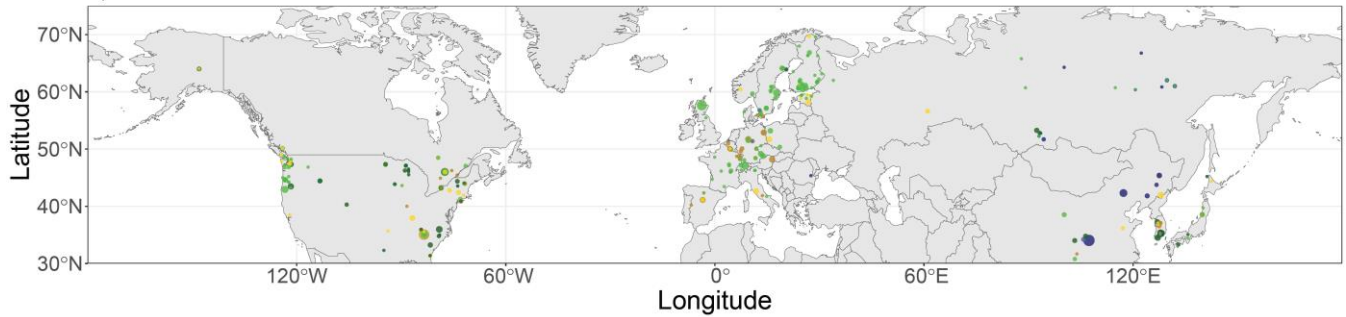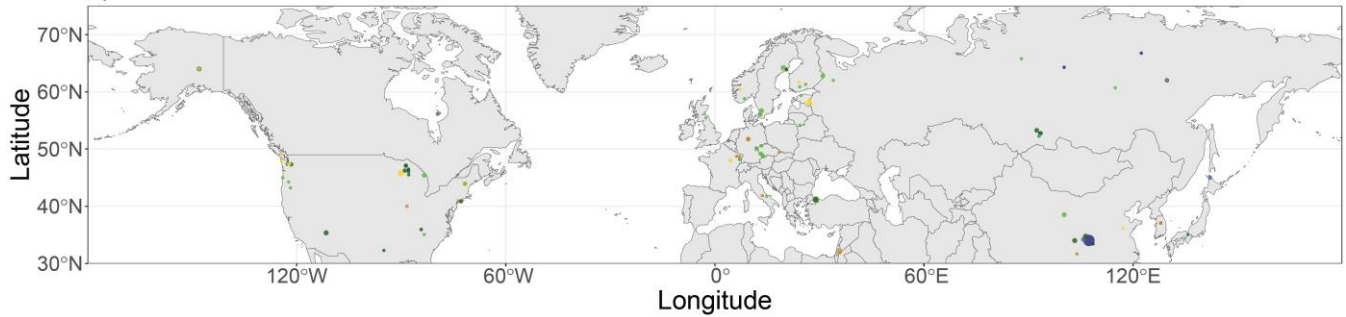
Figure 1: Spatial distribution of N concentration measurements applied in this study in a) leaves, b) branches, c) stems, and d) roots of boreal and temperate tree species, grouped according to their leaf type (BD: broadleaf deciduous, ND: needleleaf deciduous, NE: needleleaf evergreen) and growth rate. n denotes the number of measurements.

2.2 Explanatory variables

To explain the variation in tree tissue N concentrations, we consider the following explanatory variables: tree species grouped according to growth / leaf type classes, mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm), tree height (m), and soil total N concentration (g N / g dry weight). Additional analyses also include tree age (years) and compartment biomass per area (kg dry weight / m^2 ground). The choice of this selection of variables is motivated by their hypothesised control on tissue N concentration (see Introduction) and the availability of corresponding measurements from studies contained in the compiled database. In addition, spatially extensive information is available for most of these variables, which will allow to derive spatial products of tissue N concentration in subsequent studies. The relatively low sample numbers of many species, especially in case of root, but also branch and stem N concentration, prevent an analysis of the large-scale controls of tissue N concentrations at species level. Therefore, we aggregate species by leaf types and analyse these relationships for different leaf types separately. Furthermore, we investigate the influence of variations in tissue N concentrations with season and needle age on our results.

Information on MAT, MAP, soil N concentration, tree height, age, and biomass is extracted from the respective studies, when available. Growth / leaf type classes categorise tree species according to their growth rate (fast-growing, slow-/medium-growing) and leaf type (BD: broadleaf deciduous, ND: needleleaf deciduous, NE: needleleaf evergreen). By combining these two characteristics, we classify species into six growth / leaf type classes. We exclude data without information on tree species as well as broadleaf evergreen trees from the analysis since available measurements for this leaf type are scarce. Due to missing information on actual growth rates of the species at the specific measurement sites, we assign their typical growth rate (slow/medium: <= 60.96 cm/year; fast: > 60.96 cm/year; threshold corresponds to 2 feet/year) to each investigated tree species based on our expert judgement and an online research (see Supporting Information S3). In addition, we classify MAT (MAT < 0 °C vs. MAT >= 0 °C) and MAP (MAP < 500 mm vs. MAP >= 500 mm) into climatic classes to separate very cold and dry conditions from more favourable climatic conditions for plant growth. As an alternative measure of dryness, we calculate the aridity index (AI = MAP / potential evapotranspiration) from CHELSA Version 2.1 long-term climate data at the study locations (1981-2010; 30 arcsec resolution; Brun et al., 2022), as information on potential evapotranspiration is usually not available from the compiled studies. Similarly, we separate dry (AI < 0.65) from humid (AI >= 0.65) conditions following the UNEP classification (UNEP , 1992).

2.3 Regression analysis and generalized additive models

We apply linear regression and also partial regression (because of its ability to account for interaction effects between explanatory variables) to explore how the variation in tree tissue N concentration can be explained by the above mentioned explanatory variables. The low susceptibility of partial regression analysis to overfitting allows for a high confidence in the detected relationships. Measurements of tree age and soil N concentration are relatively sparse, thus reducing the available data for partial regression analyses with each included explanatory variable. Thus, we perform the partial regressions by controlling for only one explanatory variable at a time. Model accuracy is quantified in terms of modelling efficiency (MEF; Nash & Sutcliffe, 1970), pairwise partial correlations and the p-values of the partial regressions. Significance of differences in N concentration between tree tissues, growth / leaf type classes and climatic classes is quantified by the p-values of pairwise t-tests. Although the distributions of tissue N concentrations are positively skewed and thus deviate from a normal distribution (as evident in Q-Q plots in Fig. S5~~3~~ and S6~~4~~ in Supporting Information S1~~0~~), t-tests are applied here since they are relatively robust to deviations from normality, especially for large sample sizes (e.g. Fagerland, 2012).

In addition, we apply generalized additive models (GAMs) to investigate how much of the variation in tree tissue N concentration can be explained by the selected explanatory variables and to gain additional insights into the relative importance of different individual controls and their interactions. GAMs are employed because of their ability to account for non-linear relationships and interaction effects between explanatory variables and to include numerical as well as factorial variables (Hastie & Tibshirani, 1990; Wood, 2006). A total of 17 model setups are implemented for each tree tissue N concentration, using different combinations of explanatory variables, and considering either plant trait variables (leaf type, growth rate, tree age/height/biomass), environmental condition variables (MAT, MAP, soil N concentration), or both (see Supporting Information S4). For each of the implemented GAM setups with two or more variables, we compare models with and without interaction terms and select as the best model either the model with the lowest Akaike information criterion (AIC_{min}) or a simpler model if AIC values differ by at most two units following Burnham & Anderson (2004). Due to the relative sparseness of measurements of tree age (and tree height and biomass) and soil N concentration, we can include only one of these variables in a GAM at a time. For their application in the GAMs, MAT and MAP are derived from CHELSA Version 2.1 long-term climate data at the study locations (1981-2010; 30 arcsec resolution; Brun et al., 2022) when not available from the compiled studies in order to increase the sample size of GAMs considering these variables. Model predictive power is quantified in terms of MEF (Nash & Sutcliffe, 1970).

3 Results

Tree tissue N concentration is highest in leaves (median = 0.0167 gN g^{-1}, see Table S5 in Supporting Information S5), followed by roots (median = 0.0060 gN g^{-1}, Table S8) and branches (median = 0.0035 gN g^{-1}, Table S6), and much lower in stems (median = 0.0010 gN g^{-1}, Table S7). The differences in N concentration between these compartments are highly significant (see p-values of pairwise t-tests in Supporting Information S6).

There are strong differences in N concentrations between different tree species in all tissues (see Fig. S1 and Tables S10 –
265   S13 in Supporting Information S7). Especially in leaves, ~~broadleaf deciduous~~BD species (e.g. different species of Acer,
Betula, Fagus, Fraxinus, Populus and Quercus) have higher levels of N concentrations than ~~needleleaf evergreen~~NE species
(e.g. different species of Abies, Picea, Pinus). In some cases, even different species of the same genus exhibit strongly
different tissue N concentrations. However, these differences between species are also influenced by other controls and
might be due to differences in specific growing conditions and sometimes low sample numbers.

270   **3.1 Relationship between tissue N concentrations and tree age, height and tissue biomass**

We find that tree tissue N concentration decreases with tree age as well as tree height and compartment biomass in leaves,
branches, stems and roots (Fig. 2). This negative correlation (with MEFs up to 0.302) is evident in most cases (and in many
cases significant at the 5% level) when looking at leaf types (~~broadleaf deciduous, needleleaf deciduous, needleleaf~~
~~evergreen~~BD, ND, NE) separately. Note that we do not correct for heteroscedasticity occurring in some of the linear
275   relationships identified in Fig. 2 (cf. Fig. S7~~5~~ in Supporting Information S12~~1~~) since one major reason for heteroscedasticity
in these linear models is their non-consideration of other important explanatory variables (see below). When accounting for
the influence of other explanatory variables (MAT, MAP, soil N concentration), the partial correlation analysis reveals that
N concentration is in most cases negatively correlated to tree age for all investigated tree tissues (leaves, branches, stems,
roots) and leaf types (Table S14 in Supporting Information S8). These negative correlations are sometimes, but not always
280   significant due to few available measurements in some cases. Note that the partial correlation can be analysed only for a
subset of the data, since measurements of the included explanatory variables are not available for all measurements of tissue
N concentration. Especially measurements of tree age and soil N concentration are relatively sparse.
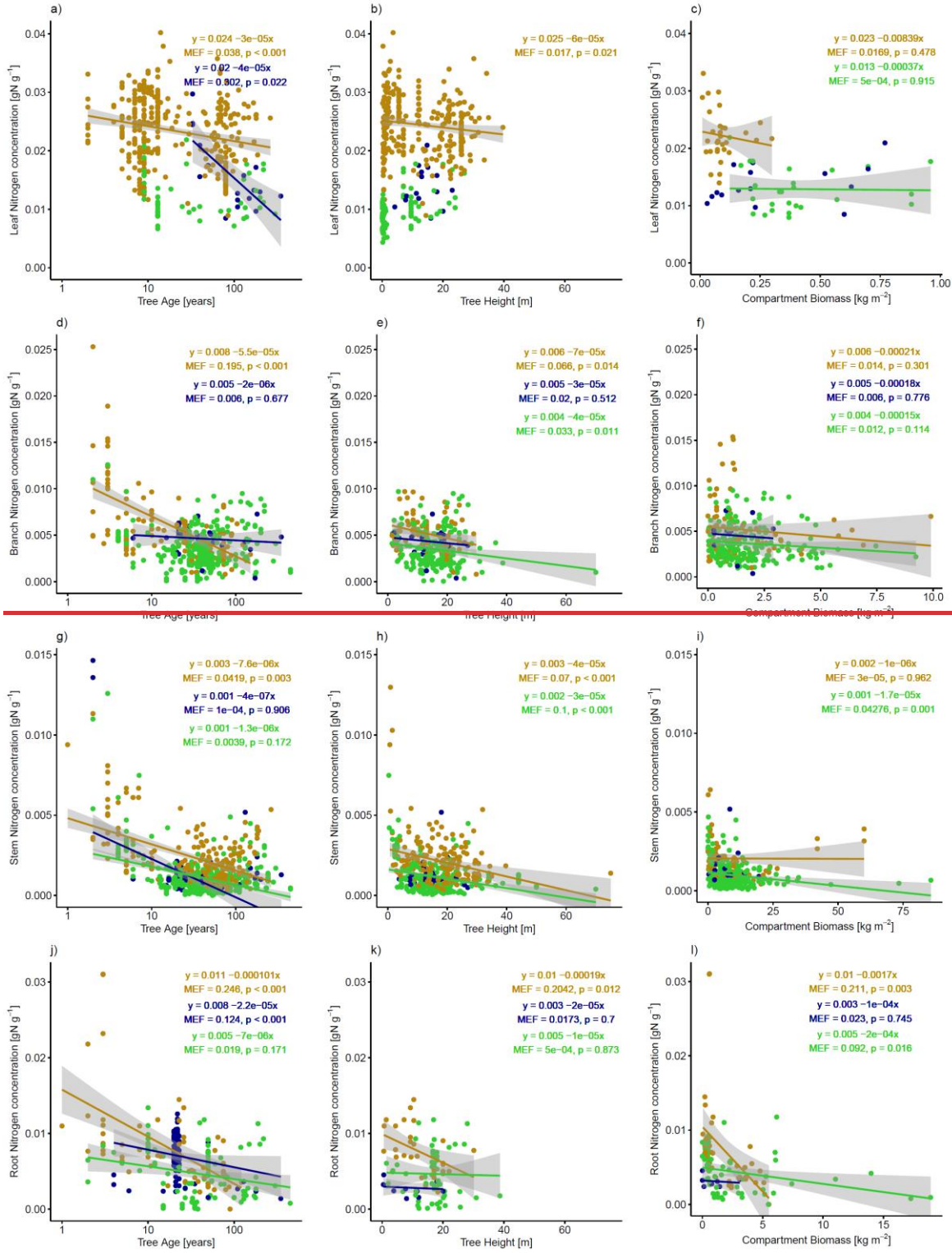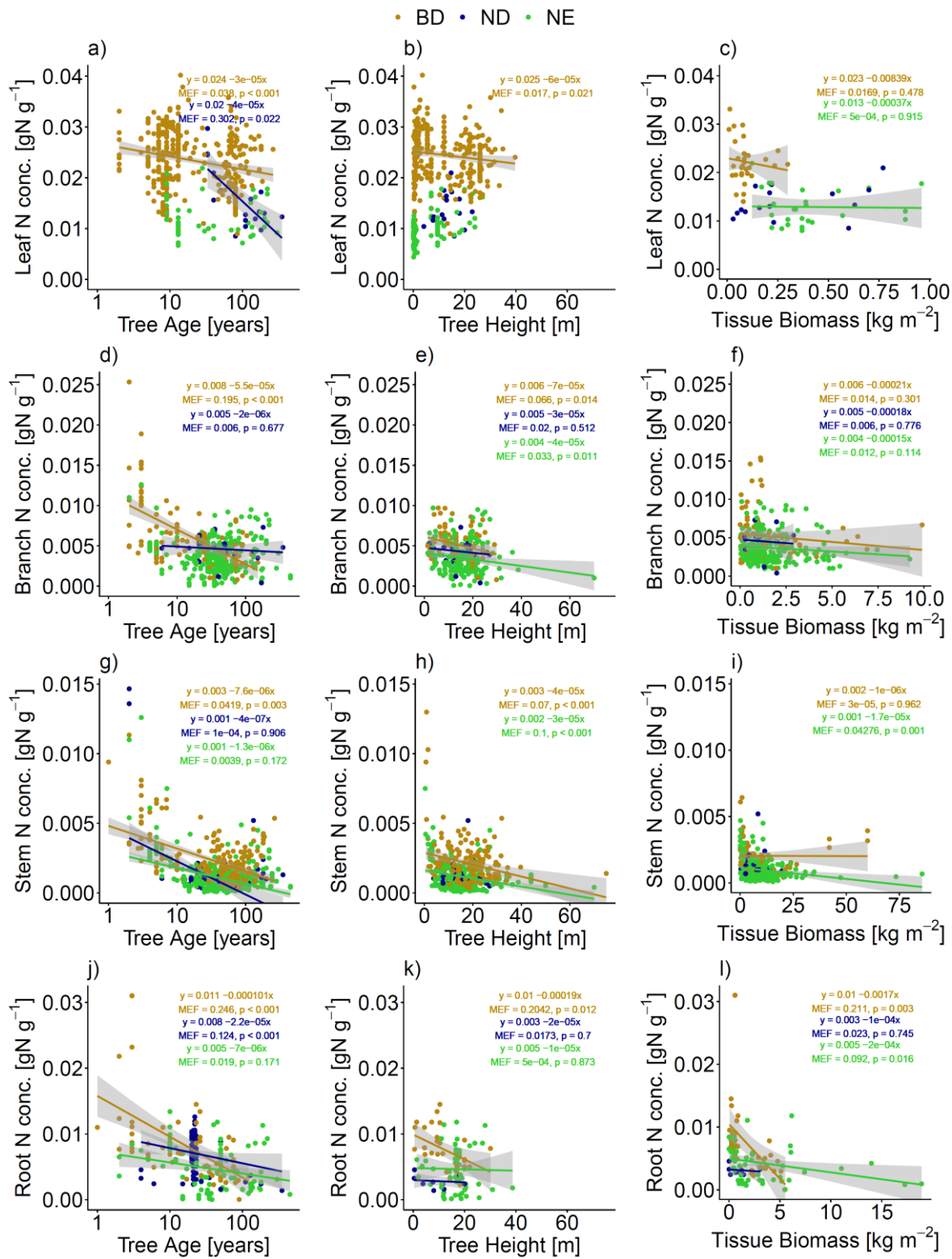
Figure 2: The relationship between a-c) leaf, d-f) branch, g-i) stem, and j-l) root N concentration and tree age, tree height, and compartment biomass. Linear models have been fitted for leaf types (broadleaf deciduous, BD; needleleaf deciduous, ND; needleleaf evergreen, NE) separately and only in case of negative correlation. The strength of the linear relationships is quantified by their modelling efficiency (MEF) and their significance is quantified by the p-value. 95 % confidence intervals are shown in grey.

3.2 Relationships between tissue N concentrations and leaf type, season and needle age

In addition to tree age/size, we find that tree tissue N concentration is also related to leaf type (broadleaf deciduous, needleleaf deciduous, needleleaf evergreenBD, ND, NE; Fig. 3). Compared to needleleaf evergreenNE trees, broadleaf deciduousBD trees have significantly higher N concentrations in leaves (median = 0.0222 gN g^{-1} vs. 0.0124 gN g^{-1}, Table S5), branches (median = 0.0042 gN g^{-1} vs. 0.0030 gN g^{-1}, Table S6), stems (median = 0.0017 gN g^{-1} vs. 0.0008 gN g^{-1},Table S7), and roots (median = 0.0064 gN g^{-1} vs. 0.0038 gN g^{-1}, Table S8; p-values and pairwise t-tests for these comparisons are reported in Table 1). Needleleaf deciduousND trees on average show intermediate levels of N concentration in their leaves (median = 0.0185 gN g^{-1}) and stems (median = 0.0010 gN g^{-1}), but high levels in their branches (median = 0.0049 gN g^{-1}) and roots (median = 0.0071 gN g^{-1}).

Among other things, variations in tissue N concentrations with season and needle age could potentially affect our results. However, the vast majority of measurements included in the compiled database have been taken during the summer season (June – September). In addition, we do not find significantly (at the 5% level) lower leaf N concentrations outside the summer season or with increasing needle age in additional analyses, which are however based on limited data for which information on measurement time and needle age are available (see Fig. S2 and S3 in Supporting Information S9).
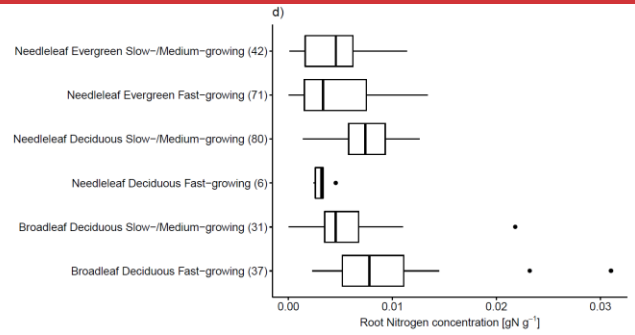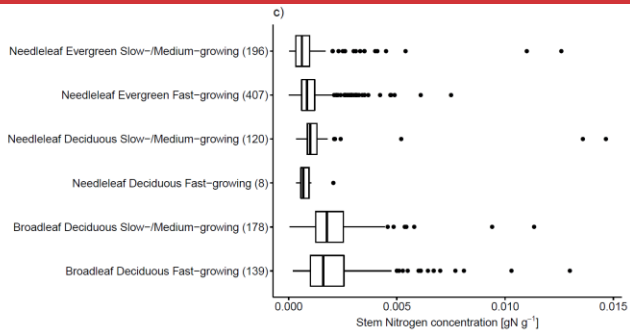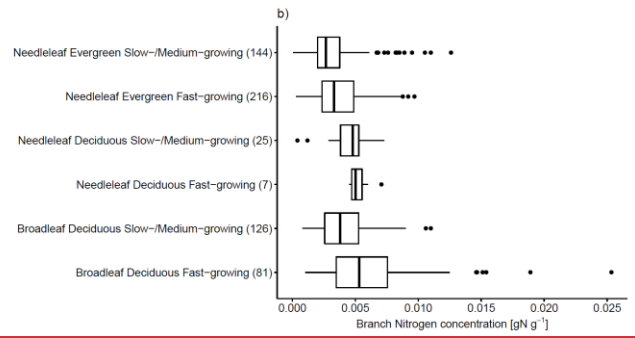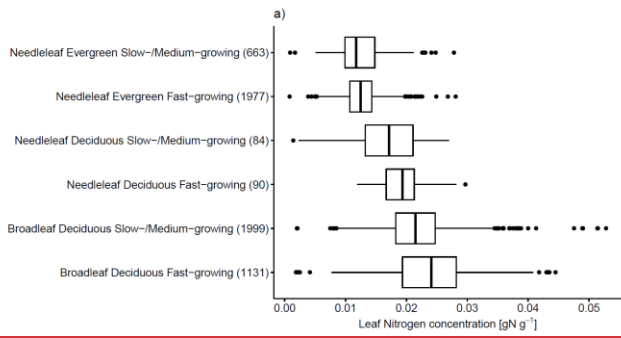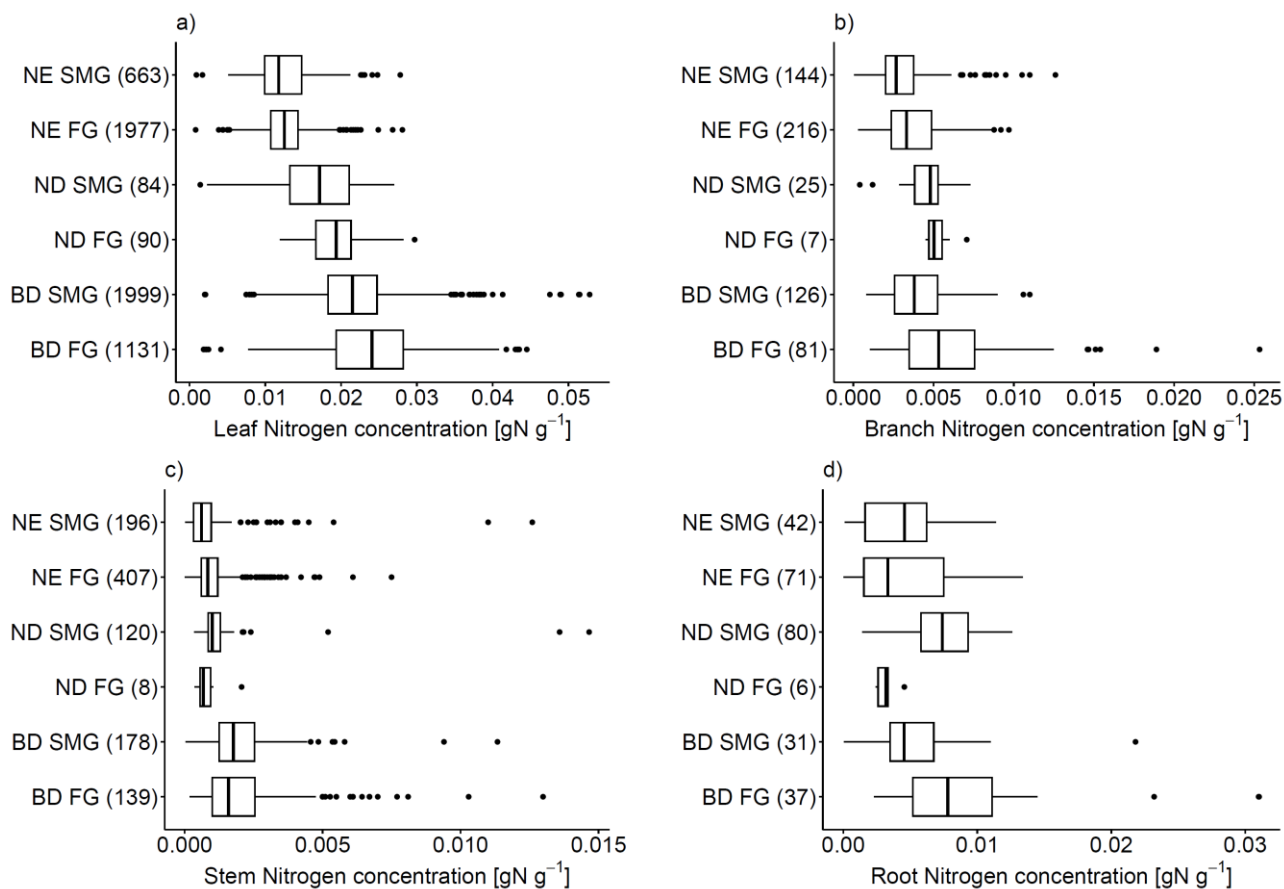
Figure 3: N concentration in a) leaves, b) branches, c) stems, and d) roots of boreal and temperate tree species, grouped according to their leaf type (BD: broadleaf deciduous, ND: needleleaf deciduous, NE: needleleaf evergreen) and growth rate (SMG: slow-/medium-growing, FG: fast-growing). The number of observations in each growth / leaf type class is stated in brackets. The box-whisker plots show the median and the interquartile range of values. The whiskers extend up to the most extreme data point which is no more than 1.5 times the interquartile range away from the box. Outliers are drawn as points.

Table 1: Significance of differences in leaf, branch, stem, and root N between leaf types and growth classes, quantified by the respective p-values of pairwise t-tests (BD = broadleaf deciduous, ND = needleleaf deciduous, NE = needleleaf evergreen, SMG = slow-/medium-growing, FG = fast-growing).

p-value	Leaf N	Branch N	Stem N	Root N
All BD vs. All ND	$< 2*10^{-16}$	0.428	$4.2*10^{-9}$	0.300
All BD vs. All NE	$< 2*10^{-16}$	$2.3*10^{-11}$	$< 2*10^{-16}$	$6.3*10^{-7}$
All ND vs. All NE	$< 2*10^{-16}$	0.026	0.054	$1.7*10^{-5}$
All SMG vs. All FG	$< 2*10^{-16}$	$8.3*10^{-4}$	0.500	0.740

BD SMG vs. BD FG	$< 2*10^{-16}$	$1.1*10^{-9}$	0.970	$4.7*10^{-4}$
ND SMG vs. ND FG	0.005	0.815	1	0.081
NE SMG vs. NE FG	0.066	0.646	0.970	1

3.3 Relationship between tissue N concentrations and tree growth rate and climate

320 Tissue N concentration varies systematically with tree growth rate (fast-growing, slow-/medium-growing; Fig. 3). However, the identified relationships are sometimes different among tree compartments. Leaf and branch N concentration tends to be higher in fast-growing than in slow-/medium-growing tree species across all leaf types (Tables S5 and S6). In contrast, only ~~needleleaf evergreen~~NE stem N concentration shows this behaviour, while fast-growing trees exhibit a lower stem N concentration than slow-/medium-growing trees in ~~broadleaf deciduous~~BD and ~~needleleaf deciduous~~ND trees (Table S7). In

325 roots, in turn, fast-growing trees show a higher N concentration compared to slow-/medium-growing trees in case of ~~broadleaf deciduous~~BD trees, but a lower N concentration in ~~needleleaf evergreen~~NE and ~~needleleaf deciduous~~ND trees (Table S8). However, these findings are not always significant (Table 1), and the results for branch, stem and root N concentration of fast-growing ~~needleleaf deciduous~~ND trees are to be interpreted with care due to very few values available. The leaf N concentration of ~~needleleaf deciduous~~ND and ~~needleleaf evergreen~~NE trees is significantly lower under very cold

330 climate conditions (MAT < 0°C) compared to more favourable conditions (MAT >= 0°C). Similar differences are observed for root N concentration of ~~needleleaf deciduous~~ND trees (Fig. 4; Table 2). In contrast, branch and stem N concentration of ~~needleleaf evergreen~~NE trees is significantly higher under very cold compared to more favourable climate. Similarly, for these leaf types, leaf and root N concentrations are significantly lower, but branch and stem N concentrations are significantly higher under dry climate conditions (MAP < 500 mm) compared to more favourable conditions (MAP >= 500

335 mm; Fig. 4; Table 2). When considering an alternative dryness indicator (AI; see Methods section), we also observe a significantly lower leaf N concentration of ~~needleleaf deciduous~~ND and ~~needleleaf evergreen~~NE trees under dry (AI < 0.65) compared to more favourable (AI >=0.65) conditions, but opposite patterns for ~~broadleaf deciduous~~BD trees (see Fig. S~~4~~2 in Supporting Information S~~10~~9; Table 2). Root N concentration is significantly lower not only for ~~needleleaf deciduous~~ND, but also ~~needleleaf evergreen~~NE trees, whereas branch N concentration is significantly higher for ~~broadleaf deciduous~~BD

340 trees when AI < 0.65. Note that in some cases, few available measurements of tissue N concentrations of specific leaf types under extreme climate hamper the detection of significant differences.
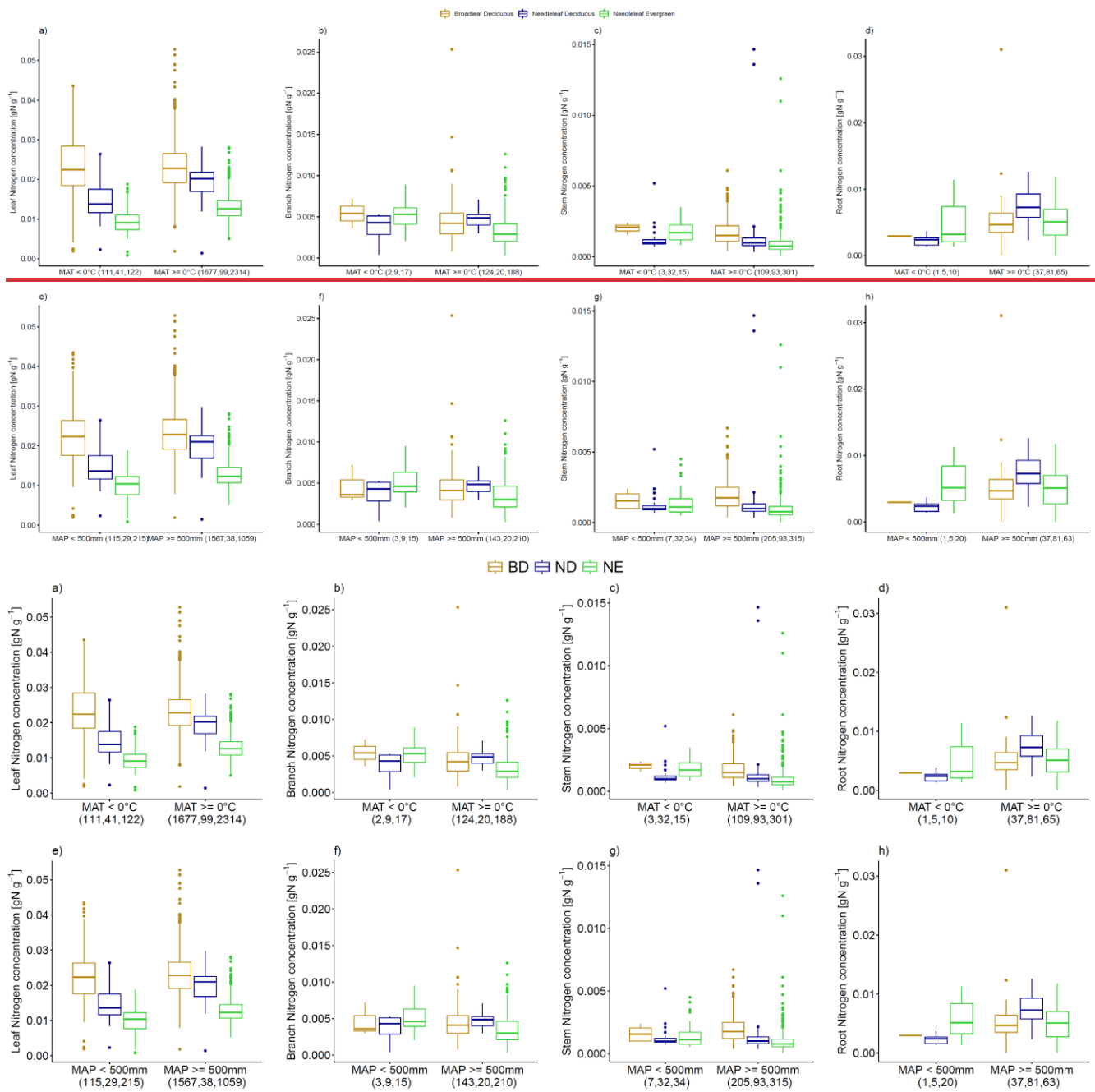
Figure 4: The variation in leaf, branch, stem, and root N concentration for a-d) mean annual temperature (MAT) classes (MAT < 0°C vs. MAT >= 0°C) and e-h) mean annual precipitation sum (MAP) classes (MAP < 500mm vs. MAP >= 500mm) and for leaf types (**BD:** broadleaf deciduous, **ND:** needleleaf deciduous, **NE:** needleleaf evergreen) separately. The number of observations in each climatic class and for each leaf type is stated in brackets. The box-whisker plots show the median and the interquartile range of values. The whiskers extend up to the most extreme data point which is no more than 1.5 times the interquartile range away from the box. Outliers are drawn as points.

Table 2: Significance of differences in leaf, branch, stem, and root N between climatic classes and for leaf types (BD: broadleaf deciduous, ND: needleleaf deciduous, NE: needleleaf evergreen) separately, quantified by the respective p-values of pairwise t-tests (MAT = mean annual temperature, MAP = mean annual precipitation sum, AI = aridity index). In some cases, not enough measurements are available (–).

p-value	Leaf N	Branch N	Stem N	Root N
MAT < 0°C vs. MAT >= 0°C; BD	0.820	0.680	0.800	–
MAT < 0°C vs. MAT >= 0°C; ND	$1.0*10^{-9}$	0.034	0.820	$2.3*10^{-5}$
MAT < 0°C vs. MAT >= 0°C; NE	$< 2*10^{-16}$	$1.9*10^{-4}$	0.012	0.750
MAP < 500 mm vs. MAP >= 500 mm; BD	0.360	0.950	0.340	–
MAP < 500 mm vs. MAP >= 500 mm; ND	$5.8*10^{-4}$	0.034	0.820	$2.3*10^{-5}$
MAP < 500 mm vs. MAP >= 500 mm; NE	$< 2*10^{-16}$	0.002	0.024	0.230
AI < 0.65 vs. AI >= 0.65; BD	$1.3*10^{-7}$	$3.0*10^{-6}$	–	0.100
AI < 0.65 vs. AI >= 0.65; ND	$4.7*10^{-4}$	0.980	0.730	0.017
AI < 0.65 vs. AI >= 0.65; NE	$2.4*10^{-4}$	0.930	0.430	0.024

Accordingly, the partial correlation analysis (Table S14 in Supporting Information S8) shows that leaf N concentration is significantly positively correlated with MAT when controlled for tree age and MAP for ~~needleleaf evergreen~~NE trees, whereas root N concentration is significantly positively correlated with MAT when controlled for MAP and soil N concentration for ~~broadleaf deciduous~~BD trees and when controlled for tree age for ~~needleleaf deciduous~~ND trees. Branch and stem N concentrations are significantly negatively correlated with MAT when controlled for tree age and MAP for ~~needleleaf evergreen~~NE trees. In addition, stem N concentration of ~~needleleaf deciduous~~ND trees is significantly negatively correlated with MAT when controlled for soil N concentration. However, for ~~broadleaf deciduous~~BD trees there are opposite patterns for certain control variables (consistent significant negative correlation between leaf N concentration of ~~broadleaf deciduous~~BD trees and MAT; significant positive correlation for ~~broadleaf deciduous~~BD trees between their branch N concentration and MAT when controlled for MAP and soil N concentration and their stem N concentration and MAT when controlled for tree age and MAP).

With regard to MAP, we find significant positive correlations with leaf N concentration of ~~needleleaf deciduous~~ND trees when controlled for tree age and MAT and of ~~needleleaf evergreen~~NE trees when controlled for MAT. Similarly, root N concentration of ~~needleleaf deciduous~~ND trees is consistently significantly positively correlated with MAP. Negative correlations between branch N concentration and MAP are significant for ~~broadleaf deciduous~~BD trees when controlled for tree age and MAT, and for ~~needleleaf evergreen~~NE trees across all control variables. Stem N concentration and MAP are most often negatively correlated, but only in few cases significantly. Again, there are in some cases also opposite patterns for certain control variables and leaf types (significant negative correlation between leaf N concentration of ~~broadleaf~~

375 ~~deciduous~~BD trees and MAP when controlled for MAT and soil N concentration; significant positive correlation between branch N concentration of ~~needleleaf deciduous~~ND trees and MAP when controlled for MAT; significant negative correlation between root N concentration of ~~broadleaf deciduous~~BD trees and MAP when controlled for MAT and soil N concentration).

3.4 Relationship between tissue and soil N concentrations

380 Tissue N concentrations increase with increasing soil N concentration (MEF up to 0.084) in some cases when looking at leaf types separately (Fig. 5). The strongest relationships (in terms of MEF) are detected for root N concentrations of ~~broadleaf deciduous~~BD and ~~needleleaf evergreen~~NE trees (not significant at the 5% level) and stem N concentration of ~~needleleaf evergreen~~NE trees (significant at the 5% level). Note again that we do not correct for heteroscedasticity occurring in some of the linear models in Fig. 5 (cf. Fig. S8~~6~~ in Supporting Information S12~~1~~) because it can be explained by their non-

385 consideration of other important explanatory variables. When accounting for the influence of other explanatory variables in the partial correlation analyses (Table S14 in Supporting Information S8), we detect a significant positive correlation between root and soil N concentration when controlled for tree age and MAP for ~~broadleaf deciduous~~BD trees, and between stem and soil N concentration when controlled for tree age for ~~needleleaf evergreen~~NE trees. In most cases, there is no significant correlation, but for ~~needleleaf deciduous~~ND trees, the partial correlation analysis shows even significant negative

390 correlations between stem and soil N concentration when controlled for MAT and between root and soil N concentration when controlled for tree age and MAT.
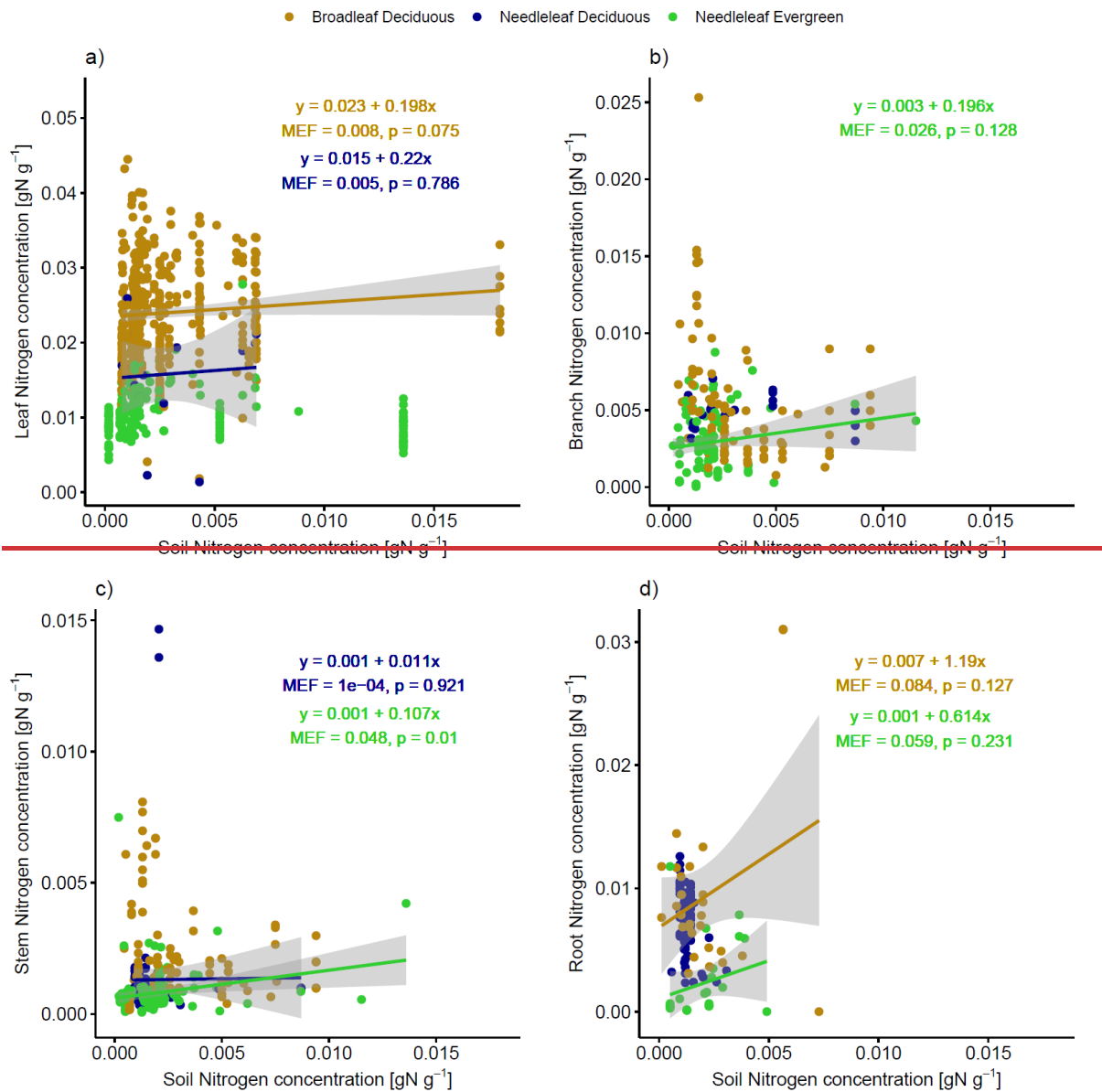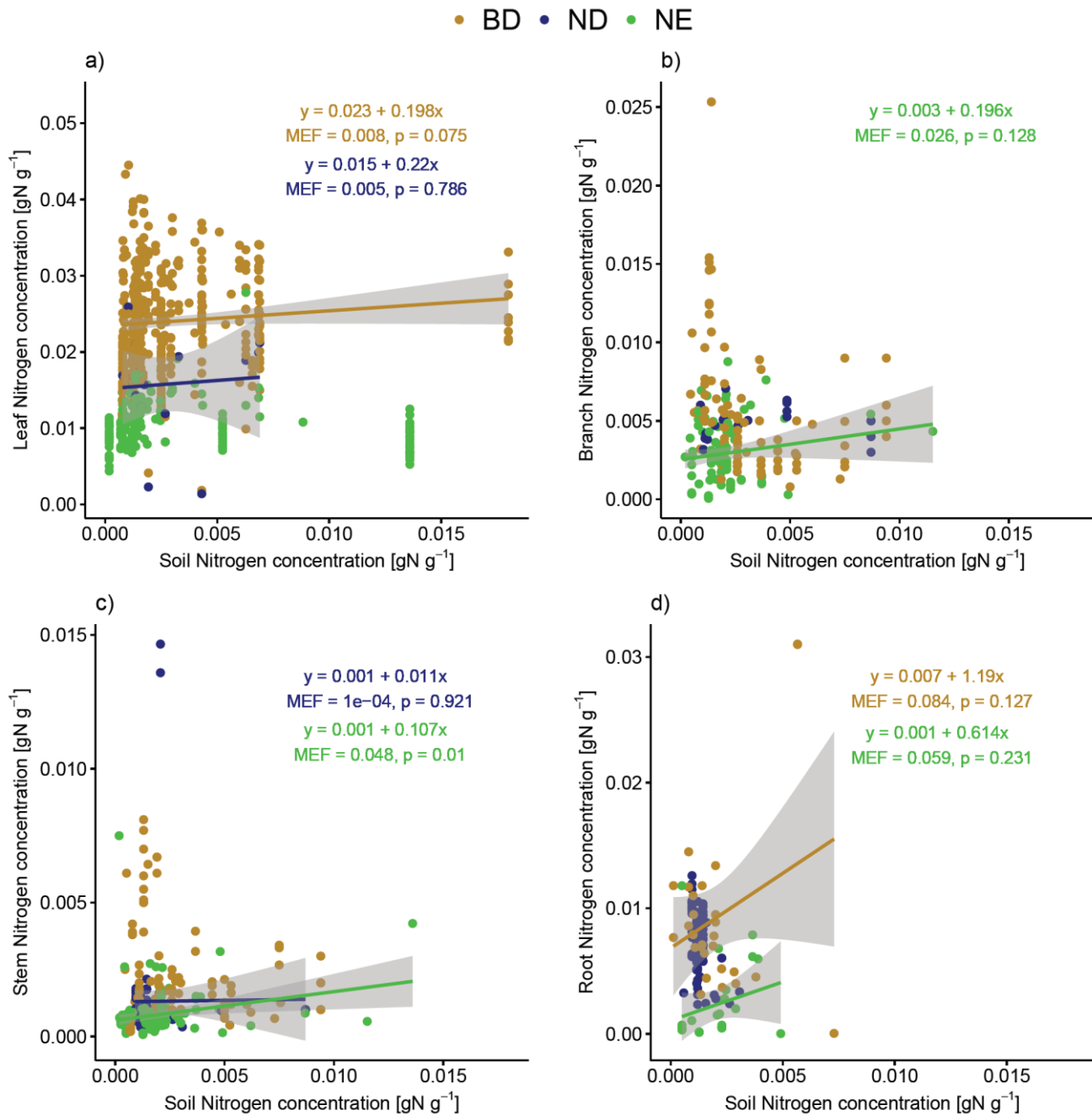
Figure 5: The relationship between a) leaf, b) branch, c) stem, and d) root N concentration and soil N concentration. Linear models have been fitted for leaf types (**BD:** broadleaf deciduous, **ND:** needleleaf deciduous, **NE:** needleleaf evergreen) separately and only in case of positive correlation. The strength of the linear relationships is quantified by their modelling efficiency (MEF) and their significance is quantified by the p-value. 95 % confidence intervals are shown in grey.

3.5 Generalized additive model (GAM) results

The GAMs that considered together multiple of the explanatory variables investigated here and their interactions can explain very large parts of the variation in tree tissue N concentrations. MEFs reach values up to 0.779 for leaves (considering leaf type, compartment biomass, MAT, and MAP), 0.702 for branches (considering leaf type, compartment biomass, MAT, and MAP), 0.922 for stems (considering leaf type, MAT, MAP, and soil N concentration), and 0.928 for roots (considering leaf type, compartment biomass, MAT, and MAP) (Fig. 6 and Tables S1 – S4 in Supporting Information S4). While GAMs considering only plant trait variables (GAMs 1 – 9) show a better performance compared to GAMs considering only environmental condition variables (GAMs 10 – 12) for leaf (MEF = 0.772 vs. MEF = 0.516; number of available measurements n = 73 vs. n = 624) and stem (MEF = 0.605 vs. MEF = 0.488; n = 823 vs. n = 323) N concentrations, the opposite is the case for branch (MEF = 0.402 vs. MEF = 0.692; n = 437 vs. n = 201) and root (MEF = 0.568 vs. MEF = 0.862; n = 98 vs. n = 136) N concentrations when comparing the best models of these different setups (GAMs 1 – 9 vs. GAMs 10 – 12) in terms of their MEF. Single variables in general explain relatively small fractions of the variation in tree tissue N concentrations (MEF < 0.3), with the exception of leaf type (MEF = 0.51), tree height (MEF = 0.336) and compartment biomass (MEF = 0.368) for leaves, climate variables (MAT and MAP; MEF = 0.428) for branches, tree age (MEF = 0.366) and height (MEF = 0.315) for stems, and climate variables (MEF = 0.352) and soil N concentration (MEF = 0.552) for roots. Note that comparisons of the individual GAMs have to be interpreted with care due to differences in the available number of measurements for each explanatory variable. Accordingly, the different GAMs rely on different sample sizes.
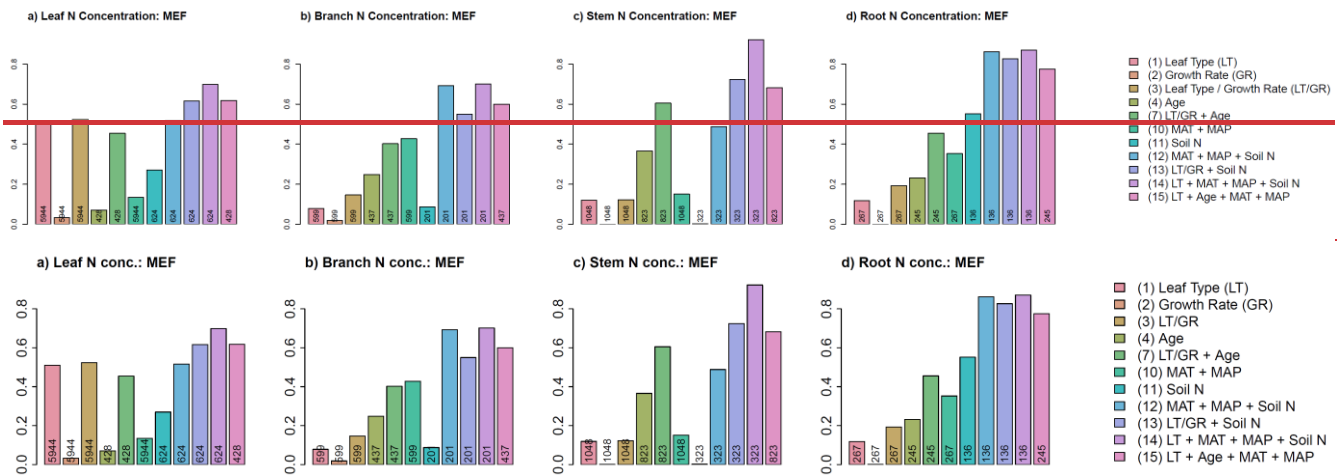
Figure 6: Modelling efficiencies (MEFs) of a selection of 11 of the in total 17 applied generalized additive models (GAMs) for modelling a) leaf, b) branch, c) stem, and d) root N concentration using different combinations of explanatory variables. GAMs (1) – (4), (7), and (10) – (15) as described in the Supporting Information S4 are shown. Numbers in each bar indicate the number of available measurements for each GAM. For values of the MEFs for all the GAMs implemented for each tissue, refer to Tables S1 – S4.

4 Discussion

At global scale, when incorporating measurements from the entire northern hemisphere boreal and temperate forests, we find that tissue N concentration decreases consistently (and in many cases significantly at the 5% level) with tree age/size in leaves, branches, stems and roots (in agreement with Hypothesis 1). This relationship is especially evident for relatively young and small trees, before it levels out for more mature trees. This finding is in accordance with N concentrations in stem, branch (Bosc et al., 2003) and root (Ceccon et al., 2016) segments of different age observed in individual trees. In contrast to earlier studies at stand scale (Sprugel, 1984; Ranger et al., 1995; Ponette et al., 2001), N concentration decreases with tree age/size in all compartments and not only in stems. Thus, at global scale, reductions in tree age (by forest management or disturbances) would result in general in higher N concentrations in all tissues of boreal and temperate trees. This finding is in line with different mechanisms that can explain the decline in tissue N concentration with tree age/size, including a decline in photosynthetic capacity (Yoder et al. 1994; Steppe et al. 2011), a decreasing share of tissues with high N concentrations (Augusto et al., 2008; living cells (Thurner et al., 2019), and a depletion of soil N (Norby et al. 2010).

While broadleaf deciduousBD trees exhibit significantly higher N concentrations than needleleaf evergreenNE trees in all tissues (in agreement with Hypothesis 2), the N concentrations in leaves, branches and roots (but not stems) of needleleaf deciduousND trees are significantly higher compared to needleleaf evergreenNE trees. The observed relation between leaf lifespan and tissue N concentration based on our global database confirms earlier results from smaller datasets for leaves (Chapin et al., 1993; Reich et al., 1992; Reich, 2014; Schulze et al., 1994) and structural woody components (Meerts, 2002). Note, however, that Meerts (2002) discussed that his sample size was too low for drawing definite conclusions. The higher tissue N concentrations of broadleaf deciduousBD trees can be explained by a higher proportion of living parenchyma cells in Angiosperms compared to Gymnosperms (Merrill et al., 1966), but they are also influenced by environmental effects, as evergreen trees often grow in harsher environments with low N availability. Accordingly, the lower N concentration of needle-leaved trees is generally thought to be part of a more nutrient conserving strategy.

Other studies have rarely covered needleleaf deciduousND trees (i.e. larch (*Larix*) species prevalent in boreal forests mainly in Siberia, but also in North America and in high alpine regions). In these regions in general characterized by N limitation (Schulze et al., 1995; Beer et al., 2007; Du et al., 2020), *Larix* species allocate little N to stems, but relatively more N to their needles compared to needleleaf evergreenNE trees, in order to support photosynthesis of their short-lived foliage. This is likely due to their high N resorption efficiency allowing them to use N resorbed from senescing leaves at the beginning of the next growing season when the soil is still frozen (Prokushkin et al., 2018). In boreal forests in Eastern Siberia, climate change may lead to a replacement of *Larix* by pine (*Pinus*; Shuman et al., 2011), which may result in decreased levels of N concentration in tree tissues (except in stems) according to our findings. In contrast, in temperate forests in Central Europe spruce (*Picea*) and *Pinus* (amongst others) are expected to be replaced by oak (*Quercus*; Hanewinkel et al., 2013), leading to

increased N concentrations in tree tissues. It should be noted that changes in tissue-level N concentrations do not necessarily match trends in the total N stock in vegetation, as the proportion and turnover times of various tissues will also vary as

460 species change.

Moreover, we find that low growth rates or unfavorable climatic conditions (very cold or dry climate) significantly decrease leaf (the latter only in case of ~~needleleaf deciduous~~ND and ~~needleleaf evergreen~~NE trees), but not stem N concentration, indicating that growth conditions affect N allocation (in agreement with Hypothesis 3). This finding can be explained by the higher investment of trees into defense mechanisms (Loehle, 1988; Chapin, 1991) or alternatively accumulation of N in

465 reserves (Chapin et al., 1990) in the stem under unfavorable growth conditions, whereas trees allocate more N to leaves in order to support higher growth rates under favorable conditions (growth-defense trade-off; Bazzaz et al., 1987; Herms & Mattson, 1992). This result is also in line with observations by Poorter et al. (1990) who demonstrated that fast-growing species allocate relatively more N to their leaves and less N to their stems compared to slow-growing species. However, while their results were based on a greenhouse experiment considering only non-woody herbaceous species, we show here

470 that this relationship is also applicable to boreal and temperate tree species at large spatial scales. Our observation of lower leaf N concentrations of ~~needleleaf deciduous~~ND and ~~needleleaf evergreen~~NE trees under very cold temperatures is also in accordance with a decrease in leaf N with decreasing MAT in the high-latitudes detected by Reich & Oleksyn (2004). However, while Tang et al. (2018) found that N concentration in leaves, stems and roots decreases with increasing temperature and precipitation across all ecosystems in China, we find a consistently significant negative correlation only

475 between leaf N concentration of ~~broadleaf deciduous~~BD trees and MAT as well as between branch N concentration of ~~needleleaf evergreen~~NE trees and MAP based on our database integrating over the entire northern boreal and temperate forests. The decrease in leaf N concentration of ~~broadleaf deciduous~~BD trees with increasing temperature has also been observed by Yin (1993) and discussed by Haxeltine & Prentice (1996), but, according to our results, does not apply to ~~needleleaf deciduous~~ND and ~~needleleaf evergreen~~NE trees. As noted above, these trends in N concentrations do not

480 necessarily translate into trends in whole-plant N requirements. In fact, unfavorable conditions decrease overall plant growth, so that higher N concentrations do not imply that slow-growing species have higher N requirements than fast-growing ones.

Extrapolating from the relation between unfavorable growth conditions and tree tissue N concentrations that we observe, an increase of MAT caused by climate change may on the one hand reduce the requirement of adaptation to cold stress and also the limitation of growth by low temperatures in boreal regions. This would result in relatively higher allocation of N to

485 leaves than to stems. On the other hand, drier conditions in certain temperate regions will both require intensified defense against drought stress and increase the water-limitation of growth, which could lead to opposite effects on N allocation. In turn, water limitation might increase leaf N concentrations to improve photosynthetic capacity when stomatal closure limits CO_2 uptake (Wright et al. 2001), however, this mechanism is not reflected in our finding of lower leaf N concentration of ~~needleleaf deciduous~~ND and ~~needleleaf evergreen~~NE trees in dry conditions. In addition, changes in the distribution of tree

490 species with diverging growth rates may have important consequences on N allocation to leaves and stems in boreal and temperate forests.

Regarding branch (significant decrease for low growth rates; for ~~needleleaf evergreen~~NE trees significant increase under very cold and dry climate) and root (no consistent effect of growth rates; for ~~needleleaf deciduous~~ND trees significant decrease under very cold and dry climate) N concentration, growth rates and unfavorable climate show some opposite or no consistent effects. Interpretability of results for these compartments is hampered by the, despite our efforts, relatively low number of available measurements of branch and (total) root N concentrations, especially under extreme climatic conditions. Disentangling the controls of N allocation to branches and roots under unfavorable growth conditions will require further measurement campaigns.

In addition, we observe an increase in root N concentrations of ~~broadleaf deciduous~~BD and ~~needleleaf evergreen~~NE trees (not significant at the 5% level) and in stem N concentration of ~~needleleaf evergreen~~NE trees (significant at the 5% level) with soil N concentration. Although there is a positive correlation also for some other tissues and leaf types, we do not find a consistent significant increase in tissue N with soil N concentration across the boreal and temperate forest regions (contrary to Hypothesis 4). Thus, at such spatial scales and integrating over all common boreal and temperate tree species, we cannot confirm observations from field experiments of increases in N concentrations of all tissues of *Populus* trees with higher soil N availability (Pregitzer et al., 1995). The N limitation in boreal forests estimated by, for instance, Du et al. (2020) may not be strong enough to be reflected in tissue N concentrations of boreal (and also temperate) trees, except maybe in root N concentrations of ~~broadleaf deciduous~~BD and ~~needleleaf evergreen~~NE trees and stem N concentration of ~~needleleaf evergreen~~NE trees, which indeed seem to be limited by soil N availability. Consequently, increased N deposition (Schwede et al., 2018) may lead to elevated N concentrations in roots and stems of these leaf types, but not necessarily other tissues and leaf types in boreal and temperate forests. However, we note that our findings are based on relationships between tree tissue N concentrations and total soil N concentration instead of plant-available soil N. For instance, in permafrost regions plant-available soil N might be low despite sufficient total soil N concentration levels (Prokushkin et al., 2018). Although plant-available soil N could thus be an important explanatory variable of tree tissue N concentrations, we had to rely on total soil N concentration measurements since they are more widely available from the studies contained in our database.

The GAMs that considered together multiple explanatory variables and their interactions can explain very large fractions of the variation in tree tissue N concentration, strongly improving predictions compared to univariate models. Both plant traits and environmental conditions are important controls of tissue N concentrations (in agreement with Hypothesis 5), with plant traits (leaf type, growth rate, tree age/height/biomass) explaining larger fractions of the variation in leaf and stem, but not branch and root N concentrations compared to environmental conditions (MAT, MAP, soil N concentration). These findings support the hypothesis that leaf and stem N concentrations are considerably influenced by plant strategies related to ecological trade-offs (growth-defense trade-off). In contrast, the spatial distributions of branch and (coarse) root N concentrations at biome scale in boreal and temperate forests seem to be more strongly determined by gradients in climate and soil conditions. Until now, it has not been possible to investigate these relationships for branch, stem and root N concentrations at biome scale. Current theory on the global relationships between plant traits and environmental conditions

(e.g. Bruelheide et al., 2018; Joswig et al., 2022; Maynard et al., 2022) is based on plant traits which have been more extensively available.

Based on limited data on measurement time and needle age, we do not detect significantly lower leaf N concentrations outside the summer season or with increasing needle age. To further improve the robustness of the results of this study, additional efforts in future field measurement campaigns are required, including:

a) additional measurements of N concentration in currently underrepresented regions (high latitudes except Scandinavia, Mediterranean regions) and PFTs (broadleaf evergreen trees),

b) more simultaneous measurements of N concentration in different tree tissues and in general more measurements of underrepresented tissues (branches, roots),

c) more simultaneous measurements of explanatory variables (especially of tree age, height and biomass and soil N concentration, but also simultaneous measurements of actual tree growth rates at the specific sites, of plant-available soil N, of other nutrients, or of different plant nutrient-acquisition strategies for instance by different types of mycorrhizal fungi (e.g. Thurner et al., 2024)),

d) improved coverage of other potential confounding factors (e.g. season (e.g. Vose & Ryan, 2002; Damesin, 2003), including differences between green and senesced plant material, for instance due to N resorption and translocation from senescing leaves (e.g. Vergutz et al., 2012); variation within tree stems (e.g. Pruyn et al., 2005; Merrill & Cowling, 1966; Schowalter & Morrell, 2002), between branch and root orders (e.g. Mei et al., 2015; Liu et al., 2016), across canopy height (Meir et al., 2002), with leaf age (e.g. Oren et al. 1988) and across soil horizons (e.g. Oren et al. 1988); N deposition (e.g. Magill et al., 1997)), and

e) more standardized measurement procedures (e.g. concerning sampling of tree tissues).

Our findings have important implications for the coupling of the C and N cycles in vegetation. For instance, changes in climate are expected to lead to the expansion of tree species better adapted to dry conditions in large parts of European temperate forests (e.g., *Quercus* species; Hanewinkel et al., 2013), which replace (amongst others) needleleaf evergreenNE with broadleaf deciduousBD trees, exhibit relatively low growth rates, initially are of younger age, and meet soil conditions affected by increased N deposition (Schwede et al., 2018). In this example, as a result of these species shifts,changes we would expect a higher N concentration in all tree tissues and elevated N allocation fractions to stems. An increased leaf N concentration willThis might, in turn, supportlead to higher photosynthesis (especially in N-limited ecosystems)productivity, but higher tissue N concentrations would result also in higher R_m and the elevated N allocation fraction to stems might lead to a reduced C use efficiency (CUE; Manzoni et al., 2018) due to elevated (stem sapwood) $R_m$maintenance respiration (Thurner et al., 2019). However, depending on the interplay of changes in the controls of tree tissue N concentration and other processes, the resulting net effects on N and C cycles remain largely unknown and require further investigation. In particular, our analyses do not cover effects of increasing atmospheric CO_2.

The found relationships (except for differences in tissue N concentration between leaf types) are not represented in current DGVMs, which usually assume fixed ratios between leaf, wood and fine root N concentrations (Meyerholt & Zaehle, 2015).

560   Unrealistic representations of tissue N concentrations in DGVMs and other carbon cycle models could be quite crucial because future predictions of climate impacts and carbon cycle changes by these models heavily depend on CO_2 fertilization effects and the extent to which they are constrained by N limitation (Hickler et al., 2015; Aurora et al., 2020; Kou-Giesbrecht et al., 2023). Not considering the decrease in tissue N concentration with tree age, for example, implies that the effects of forest management and disturbances on the coupling of the C and N cycles cannot be realistically reproduced by DGVMs.

565   Differences in tissue N concentrations between pioneer and late-successional trees could be incorporated by DGVMs that distinguish these growth types, such as LPJ-GUESS (Hickler et al., 2012). Moreover, the difference in the relationship between leaf N concentration and temperature that we observe here between different leaf types reveals a potential shortcoming in current DGVM parameterizations (cf. Haxeltine & Prentice, 1996). In addition to their critical importance for the improvement of N allocation in DGVMs, the identified relationships, together with available data on tree tissue biomass

570   (Thurner et al., 2014; 2019), will also be the basis for spatially extensive mapping of tissue N concentration and content and highly novel spatial estimates of plant respiration in boreal and temperate forests in future studies.

5 Conclusions

Here, for the first time we identified the large-scale abiotic and biotic controls of tree tissue N concentrations based on ~~an unprecedented~~a novel database of N concentrations in stems, roots and branches of all common Northern hemisphere boreal

575   and temperate tree genera that we compiled. In conclusion, our findings emphasize that N concentrations in boreal and temperate trees at large spatial scales consistently decrease with tree age/size and are significantly higher in deciduous compared to evergreen trees in all tissues (leaves, branches, stems, roots), but increase with soil N concentration only in roots of ~~broadleaf deciduous~~BD and ~~needleleaf evergreen~~NE trees. Low growth rates or unfavorable climatic conditions are found to decrease leaf (the latter only in case of ~~needleleaf deciduous~~ND and ~~needleleaf evergreen~~NE trees), but not stem N

580   concentration, indicating that growth conditions affect N allocation. Both plant traits and environmental conditions are important controls of tissue N concentrations and together explain very large parts of the variation therein. These relationships have considerable implications for the coupling of the C and N cycles in vegetation, since ~~tissue N concentrations determine~~ photosynthesis, growth and plant respiration as well as litter decomposition are closely related to tissue N concentrations. Thus, changes in the distribution of tree age/size, tree species, and extreme climate, induced by

585   climate change, forest management or disturbances, may have substantial consequences for the C sequestration potential of boreal and temperate forests by their effects on tree tissue N concentrations. The identified relationships are only poorly represented in current DGVMs and need to be represented in order to realistically estimate future effects of N limitation on the C cycle.

Data availability

590 The "Nitrogen concentrations in boreal and temperate tree tissues" dataset is available from the Dryad repository (https://datadryad.org/stash/share/oiP-1kVy0Qv6Sq651nOAHaoihC_dnKahn-SIUxlVPg8).

Author contribution

MT designed the study with input from KY, SM, MAT and TH. MT collated measurements from the literature and compiled the tree tissue N concentration database with contributions from KY, AP and ZW. AP contributed own measurements. MT
595 analysed the data and mainly wrote the manuscript. All authors contributed to the interpretation of results and writing of the manuscript.

Competing interests

The authors declare that they have no conflict of interest.

Acknowledgements

600 Martin Thurner has received funding from the European Union's Horizon 2020 research and innovation programme under the Marie Sklodowska-Curie grant agreement No 891402. Stefano Manzoni acknowledges support from the Swedish Research Council (2020-03910) and Formas (2021-02121). We sincerely thank the TRY initiative on plant traits (http://www.try-db.org) for contributing to leaf N and the Biomass And Allometry Database (BAAD; https://github.com/dfalster/baad) for contributing to leaf and stem N concentration data used in this study. The TRY initiative
605 and database is hosted, developed and maintained by J. Kattge and G. Boenisch (Max Planck Institute for Biogeochemistry, Jena, Germany). The BAAD is hosted, developed and maintained by D. Falster (University of New South Wales, Sydney, Australia).

References

Arora VK, Katavouta A, Williams RG, Jones CD, Brovkin V, Friedlingstein P, Schwinger J, Bopp L, Boucher O, Cadule P,
610 et al. 2020. Carbon–concentration and carbon–climate feedbacks in CMIP6 models and their comparison to CMIP5 models. Biogeosciences 17(16): 4173-4222.

Augusto L, Meredieu C, Bert D, Trichet P, Porté A, Bosc A, Lagane F, Loustau D, Pellerin S, Danjon F, et al. 2008. Improving models of forest nutrient export with equations that predict the nutrient concentration of tree compartments. Annals of Forest Science 65: 808.

615 Bazzaz FA, Chiariello NR, Coley PD, Pitelka LF. 1987. Allocating Resources to Reproduction and Defense: New assessments of the costs and benefits of allocation patterns in plants are relating ecological roles to resource use. BioScience 37(1): 58-67.

Beer C, Lucht W, Gerten D, Thonicke K, Schmullius C. 2007. Effects of soil freezing and thawing on vegetation carbon density in Siberia: A modeling analysis with the Lund-Potsdam-Jena Dynamic Global Vegetation Model (LPJ-DGVM).

620 Global Biogeochemical Cycles 21(1).

Bosc A, De Grandcourt A, Loustau D. 2003. Variability of stem and branch maintenance respiration in a Pinus pinaster tree. Tree Physiology 23(4): 227-236.

Brun P, Zimmermann NE, Hari C, Pellissier L, Karger DN. 2022. Global climate-related predictors at kilometer resolution for the past and future. Earth System Science Data 14(12): 5573-5603.

625 Burnham KP, Anderson DR 2004. Multimodel Inference: Understanding AIC and BIC in Model Selection. Sociological Methods & Research 33(2): 261-304.

Butler EE, Datta A, Flores-Moreno H, Chen M, Wythers KR, Fazayeli F, Banerjee A, Atkin OK, Kattge J, Amiaud B, et al. 2017. Mapping local and global variability in plant trait distributions. Proc Natl Acad Sci U S A 114(51): E10937-E10946.

Bruelheide H, Dengler J, Purschke O et al. 2018. Global trait–environment relationships of plant communities. Nat Ecol

630 Evol 2, 1906–1917.

Ceccon C, Tagliavini M, Schmitt AO, Eissenstat DM. 2016. Untangling the effects of root age and tissue nitrogen on root respiration in Populus tremuloides at different nitrogen supply. Tree Physiol 36(5): 618-627.

Ceschia E, Damesin C, Lebaube S, Pontailler J-Y, Dufrene E. 2002. Spatial and seasonal variations in stem respiration of beech trees (Fagus sylvatica). Annals of Forest Science 59(8): 801-812.

635 Chapin FS. 1991. Integrated Responses of Plants to Stress: A centralized system of physiological responses. BioScience 41(1): 29-36.

Chapin FS, Autumn K, Pugnaire F. 1993. Evolution of Suites of Traits in Response to Environmental Stress. The American Naturalist 142: S78-S92.

Chapin FS, Schulze E-D, Mooney HA. 1990. The Ecology and Economics of Storage in Plants. Annual Review of Ecology

640 and Systematics 21: 423-447.

Damesin C. 2003. Respiration and photosynthesis characteristics of current-year stems of Fagus sylvatica: from the seasonal pattern to an annual balance. New Phytol 158(3): 465-475.

Dong N, Prentice IC, Wright I, Wang H, Atkin OK, Bloomfield KJ, Domingues TF, Gleason SM, Maire V, Onoda Y, et al. 2022. Leaf nitrogen from the perspective of optimal plant function. Journal of Ecology 110: 2585–2602.

645 Du E, Terrer C, Pellegrini AFA, Ahlström A, van Lissa CJ, Zhao X, Xia N, Wu X, Jackson RB. 2020. Global patterns of terrestrial nitrogen and phosphorus limitation. Nature Geoscience 13(3): 221-226.

Fagerland MW 2012. t-tests, non-parametric tests, and large studies – a paradox of statistical practice? BMC Medical Research Methodology 12, 78.

Falster DS, Duursma RA, Ishihara MI, Barneche DR, FitzJohn RG, Vårhammar A, Aiba M, Ando M, Anten N, Aspinwall
650 MJ, et al. 2015. BAAD: a biomass and allometry database for woody plants. Ecology 96(5): 1445.

Feng Z, Brumme R, Xu YJ, Lamersdorf N. 2008. Tracing the fate of mineral N compounds under high ambient N deposition in a Norway spruce forest at Solling/Germany. Forest Ecology and Management 255(7): 2061-2073.

Friedlingstein P, O'Sullivan M, Jones MW, Andrew RM, Bakker DCE, Hauck J, Landschützer P, Le Quéré C, Luijkx IT, Peters GP, et. al. 2023. Global Carbon Budget 2023, Earth Syst. Sci. Data 15(12): 5301–5369.

655 Hanewinkel M, Cullmann DA, Schelhaas M-J, Nabuurs G-J, Zimmermann NE. 2013. Climate change may cause severe loss in the economic value of European forest land. Nature Climate Change 3(3): 203-207.

Hastie TJ, Tibshirani RJ 1990. Generalized additive models. Chapman & Hall/CRC, Boca Raton, FL.

Haxeltine A, Prentice IC. 1996. A General Model for the Light-Use Efficiency of Primary Production. Functional Ecology 10(5): 551-561.

660 Hendricks JJ, Aber JD, Nadelhoffer KJ, Hallett RD. 2000. Nitrogen Controls on Fine Root Substrate Quality in Temperate Forest Ecosystems. Ecosystems 3(1): 57-69.

Herms DA, Mattson WJ. 1992. The Dilemma of Plants: To Grow or Defend. The Quarterly Review of Biology 67(3): 283-335.

Hickler T, Rammig A, Werner C. 2015. Modelling CO2 Impacts on Forest Productivity. Current Forestry Reports 1(2): 69-
665 80.

Hickler T, Vohland K, Feehan J, Miller PA, Smith B, Costa L, Giesecke T, Fronzek S, Carter TR, Cramer W, et al. 2012. Projecting the future distribution of European potential natural vegetation zones with a generalized, tree species-based dynamic vegetation model. Global Ecology and Biogeography 21(1): 50-63.

Iversen CM, McCormack ML, Powell AS, Blackwood CB, Freschet GT, Kattge J, Roumet C, Stover DB, Soudzilovskaia
670 NA, Valverde-Barrantes OJ, et al. 2017. A global Fine-Root Ecology Database to address below-ground challenges in plant ecology. New Phytologist 215(1): 15-26.

Joswig JS, Wirth C, Schuman MC et al. 2022. Climatic and soil factors explain the two-dimensional spectrum of global plant trait variation. Nat Ecol Evol 6, 36–50.

Kattge J, Bonisch G, Diaz S, Lavorel S, Prentice IC, Leadley P, Tautenhahn S, Werner GDA, Aakala T, Abedi M, et al.
675 2020. TRY plant trait database - enhanced coverage and open access. Glob Chang Biol 26(1): 119-188.

Kou-Giesbrecht S, Arora VK, Seiler C, Arneth A, Falk S, Jain AK, Joos F, Kennedy D, Knauer J, Sitch S, et al. 2023. Evaluating nitrogen cycling in terrestrial biosphere models: a disconnect between the carbon and nitrogen cycles. Earth System Dynamics 14(4): 767-795.

Lambers H, Poorter H 1992. Inherent Variation in Growth Rate Between Higher Plants: A Search for Physiological Causes and Ecological Consequences. Advances in Ecological Research Volume 23, 187-261.

Larjavaara M, Berninger F, Palviainen M, Prokushkin A, Wallenius T. 2017. Post-fire carbon and nitrogen accumulation and succession in Central Siberia. Sci Rep 7(1): 12776.

Laughlin DC, Fulé PZ, Huffman DW, Crouse J, Laliberté E. 2011. Climatic constraints on trait-based forest assembly. Journal of Ecology 99(6): 1489-1499.

LeBauer DS, Treseder KK. 2008. Nitrogen limitation of net primary productivity in terrestrial ecosystems is globally distributed. Ecology 89(2): 371-379.

Liu B, He J, Zeng F, Lei J, Arndt SK. 2016. Life span and structure of ephemeral root modules of different functional groups from a desert system. New Phytol 211(1): 103-112.

Loehle C. 1988. Tree life history strategies: the role of defenses. Canadian Journal of Forest Research 18(2): 209-222.

Luo Y, Su B, Currie WS, Dukes JS, Finzi A, Hartwig U, Hungate B, McMurtrie RE, Oren R, Parton WJ, et al. 2004. Progressive Nitrogen Limitation of Ecosystem Responses to Rising Atmospheric Carbon Dioxide. BioScience 54(8): 731-739.

Magill AH, Aber JD, Hendricks JJ, Bowden RD, Melillo JM, Steudler PA. 1997. Biogeochemical Response of Forest Ecosystems to Simulated Chronic Nitrogen Deposition. Ecological Applications 7(2): 402-415.

Manzoni S, Čapek P, Porada P, Thurner M, Winterdahl M, Beer C, Brüchert V, Frouz J, Herrmann AM, Lindahl BD, et al. 2018. Reviews and syntheses: Carbon use efficiency from organisms to ecosystems – definitions, theories, and empirical evidence, Biogeosciences 15(19): 5929–5949.

Martin AR, Gezahegn S, Thomas SC. 2015. Variation in carbon and nitrogen concentration among major woody tissue types in temperate trees. Canadian Journal of Forest Research 45(6): 744-757.

Maynard DS, Bialic-Murphy L, Zohner CM et al. 2022. Global relationships in tree functional traits. Nat Commun 13, 3185.

Meerts P. 2002. Mineral nutrient concentrations in sapwood and heartwood: a literature review. Annals of Forest Science 59(7): 713-722.

Mei L, Xiong Y, Gu J, Wang Z, Guo D. 2015. Whole-tree dynamics of non-structural carbohydrate and nitrogen pools across different seasons and in response to girdling in two temperate trees. Oecologia 177(2): 333-344.

Meir P, Kruijt B, Broadmeadow M, Barbosa E, Kull O, Carswell F, Nobre A, Jarvis PG. 2002. Acclimation of photosynthetic capacity to irradiance in tree canopies in relation to leaf nitrogen concentration and leaf mass per unit area. Plant, Cell & Environment 25(3): 343-357.

Merrill W, Cowling EB. 1966. Role of nitrogen in wood deterioration: amounts and distribution of nitrogen in tree stems. Canadian Journal of Botany 44(11): 1555-1580.

Meyerholt J, Zaehle S. 2015. The role of stoichiometric flexibility in modelling forest ecosystem responses to nitrogen fertilization. New Phytol 208(4): 1042-1055.

Moreno-Martínez Á, Camps-Valls G, Kattge J, Robinson N, Reichstein M, van Bodegom P, Kramer K, Cornelissen JHC, Reich P, Bahn M, et al. 2018. A methodology to derive global maps of leaf traits using remote sensing and climate data. Remote Sensing of Environment 218: 69-88.

715 Nash JE, Sutcliffe JV. 1970. River flow forecasting through conceptual models part I - a discussion of principles. Journal of Hydrology 10: 282-290.

Norby RJ, Warren JM, Iversen CM, Medlyn BE, McMurtrie RE. 2010. CO2 enhancement of forest productivity constrained by limited nitrogen availability. Proc Natl Acad Sci U S A 107(45): 19368-19373.

Oren R, Werk KS, Schulze ED, Meyer J, Schneider BU, Schramel P. 1988. Performance of Two Picea abies (L.) Karst.

720 Stands at Different Stages of Decline. VI. Nutrient Concentration. Oecologia 77(2): 151-162.

Ostonen I, Truu M, Helmisaari HS, Lukac M, Borken W, Vanguelova E, Godbold DL, Lohmus K, Zang U, Tedersoo L, et al. 2017. Adaptive root foraging strategies along a boreal-temperate forest gradient. New Phytol 215(3): 977-991.

Parton W, Silver WL, Burke IC, Grassens L, Harmon ME, Currie WS, King JY, Adair EC, Brandt LA, Hart SC, et al. 2007. Global-scale similarities in nitrogen release patterns during long-term decomposition. Science 315(5810): 361-364.

725 Ponette Q, Ranger J, Ottorini J-M, Ulrich E. 2001. Aboveground biomass and nutrient content of five Douglas-fir stands in France. Forest Ecology and Management 142(1): 109-127.

Poorter H, Remkes C, Lambers H. 1990. Carbon and Nitrogen Economy of 24 Wild Species Differing in Relative Growth Rate. Plant Physiology 94(2): 621-627.

Pregitzer KS, Zak DR, Curtis PS, Kubiske ME, Teeri JA, Vogel CS. 1995. Atmospheric CO2, soil nitrogen and turnover of 730 fine roots. New Phytologist 129(4): 579-585.

Prokushkin A, Hagedorn F, Pokrovsky O, Viers J, Kirdyanov A, Masyagina O, Prokushkina M, McDowell W. 2018. Permafrost Regime Affects the Nutritional Status and Productivity of Larches in Central Siberia. Forests 9(6).

Pruyn ML, Gartner BL, Harmon ME. 2005. Storage versus substrate limitation to bole respiratory potential in two coniferous tree species of contrasting sapwood width. J Exp Bot 56(420): 2637-2649.

735 Ranger J, Marques R, Colin-Belgrand M, Flammang N, Gelhaye D. 1995. The dynamics of biomass and nutrient accumulation in a Douglas-fir (Pseudotsuga menziesii Franco) stand studied using a chronosequence approach. Forest Ecology and Management 72(2): 167-183.

Reich PB, Cornelissen H. 2014. The world-wide 'fast-slow' plant economics spectrum: a traits manifesto. Journal of Ecology 102(2): 275-301.

740 Reich PB, Hobbie SE, Lee T, Ellsworth DS, West JB, Tilman D, Knops JM, Naeem S, Trost J. 2006a. Nitrogen limitation constrains sustainability of ecosystem response to CO2. Nature 440(7086): 922-925.

Reich PB, Oleksyn J. 2004. Global patterns of plant leaf N and P in relation to temperature and latitude. Proceedings of the National Academy of Sciences 101(30): 11001-11006.

Reich PB, Tjoelker MG, Machado JL, Oleksyn J. 2006b. Universal scaling of respiratory metabolism, size and nitrogen in 745 plants. Nature 439(7075): 457-461.

Reich PB, Walters MB, Ellsworth DS. 1992. Leaf Life-Span in Relation to Leaf, Plant, and Stand Characteristics among Diverse Ecosystems. Ecological Monographs 62(3): 365-392.

Ryan MG. 1991. Effects of Climate Change on Plant Respiration. Ecological Applications 1(2): 157-167.

Schowalter TD, Morrell JJ. 2002. Nutritional Quality of Douglas-Fir Wood: Effect of Vertical and Horizontal Position on Nutrient Levels. Wood and Fiber Science 34(1): 158-164.

Schulze ED, Schulze W, Koch H, Arneth A, Bauer G, Kelliher FM, Hollinger DY, Vygodskaya NN, Kusnetsova WA, Sogatchev A, et al. 1995. Aboveground biomass and nitrogen nutrition in a chronosequence of pristine Dahurian Larix stands in eastern Siberia. Canadian Journal of Forest Research 25(6): 943-960.

Schulze E-D, Kelliher FM, Körner C, Lloyd J, Leuning R. 1994. Relationships among maximum stomatal conductance, ecosystem surface conductance, carbon assimilation rate, and plant nitrogen nutrition: a global ecology scaling exercise. Annual Review of Ecology and Systematics 25(1): 629-662.

Schwede DB, Simpson D, Tan J, Fu JS, Dentener F, Du E, deVries W. 2018. Spatial variation of modelled total, dry and wet nitrogen deposition to forests at global scale. Environ Pollut 243(Pt B): 1287-1301.

Shuman JK, Shugart HH, O'Halloran TL. 2011. Sensitivity of Siberian larch forests to climate change. Global Change Biology 17(7): 2370-2384.

Sitch S, Smith B, Prentice IC, Arneth A, Bondeau A, Cramer W, Kaplan JO, Levis S, Lucht W, Sykes MT, et al. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. Global Change Biology 9: 161-185.

Sprugel DG. 1984. Density, Biomass, Productivity, and Nutrient-Cycling Changes During Stand Development in Wave-Regenerated Balsam Fir Forests. Ecological Monographs 54(2): 165-186.

Steppe K, Niinemets Ü, Teskey RO 2011. Tree Size- and Age-Related Changes in Leaf Physiology and Their Influence on Carbon Gain. Size- and Age-Related Changes in Tree Structure and Function, 235-253.

Sun Y, Wang M, Mur LAJ, Shen Q, Guo S. 2020. Unravelling the Roles of Nitrogen Nutrition in Plant Disease Defences. Int J Mol Sci 21(2).

Tang Z, Xu W, Zhou G, Bai Y, Li J, Tang X, Chen D, Liu Q, Ma W, Xiong G, et al. 2018. Patterns of plant carbon, nitrogen, and phosphorus concentration in relation to productivity in China's terrestrial ecosystems. Proc Natl Acad Sci U S A 115(16): 4033-4038.

Tateno R, Takeda H. 2010. Nitrogen uptake and nitrogen use efficiency above and below ground along a topographic gradient of soil nitrogen availability. Oecologia 163(3): 793-804.

Terrer C, Jackson RB, Prentice IC, Keenan TF, Kaiser C, Vicca S, Fisher JB, Reich PB, Stocker BD, Hungate BA, et al. 2019. Nitrogen and phosphorus constrain the CO2 fertilization of global plant biomass. Nature Climate Change 9(9): 684-689.

Thurner M, Beer C, Crowther T, Falster D, Manzoni S, Prokushkin A, Schulze ED, Gillespie T. 2019. Sapwood biomass carbon in northern boreal and temperate forests. Global Ecology and Biogeography 28(5): 640-660.

780 Thurner M, Beer C, Santoro M, Carvalhais N, Wutzler T, Schepaschenko D, Shvidenko A, Kompter E, Ahrens B, Levick SR, et al. 2014. Carbon stock and density of northern boreal and temperate forests. Global Ecology and Biogeography 23(3): 297-310.

Thurner MA, Caldararu S, Engel J, Rammig A, Zaehle S. 2024. Modelled forest ecosystem carbon-nitrogen dynamics with integrated mycorrhizal processes under elevated CO_2. Biogeosciences 21, 1391-1410.

785 Ullmann-Zeunert L, Stanton MA, Wielsch N, Bartram S, Hummert C, Svatos A, Baldwin IT, Groten K. 2013. Quantification of growth-defense trade-offs in a common currency: nitrogen required for phenolamide biosynthesis is not derived from ribulose-1,5-bisphosphate carboxylase/oxygenase turnover. Plant J 75(3): 417-429.

UNEP. 1992. Middleton N, Thomas DSG, eds. World Atlas of Desertification. United Nations Environment Programme. London: Edward Arnold.

790 Vergutz L, Manzoni S, Porporato A, Novais RF, Jackson RB. 2012. Global resorption efficiencies and concentrations of carbon and nutrients in leaves of terrestrial plants. Ecological Monographs 82(2): 205-220.

Vose JM, Ryan MG. 2002. Seasonal respiration of foliage, fine roots, and woody tissues in relation to growth, tissue N, and photosynthesis. Global Change Biology 8(2): 182-193.

Wang Z, Huang H, Yao B, Deng J, Ma Z, Niklas KJ. 2021. Divergent scaling of fine-root nitrogen and phosphorus in
795 different root diameters, orders and functional categories: A meta-analysis. Forest Ecology and Management 495.

Wang Z, Lv S, Song H, et al. 2020. Plant type dominates fine-root C:N:P stoichiometry across China: A meta-analysis. Journal of Biogeography 47: 1019-1029.

Wang Z, Yu K, Lv S, Niklas KJ, Mipam TD, Crowther TW, Umaña MN, Zhao Q, Huang H, Reich PB, et al. 2019. The scaling of fine root nitrogen versus phosphorus in terrestrial plants: A global synthesis. Functional Ecology 33(11): 2081-
800 2094.

Withington JM, Reich PB, Oleksyn J, Eissenstat DM. 2006. Comparisons of Structure and Life Span in Roots and Leaves among Temperate Trees. Ecological Monographs 76(3): 381-397.

Wood SN 2006. Generalized additive models: an introduction with R. Chapman & Hall/CRC Press, Boca Raton, FL.

Wright IJ, Reich PB, Westoby M. 2001. Strategy shifts in leaf physiology, structure and nutrient content between species of
805 high- and low-rainfall and high- and low-nutrient habitats. Functional Ecology 15(4): 423-434.

Wright I, Reich P, Westoby M, Ackerly DD, Baruch Z, Bongers F, Cavender-Bares J, Chapin T, Cornelissen JHC, Diemer M, et al. 2004. The worldwide leaf economics spectrum. Nature 428: 821–827.

Yin X. 1993. Variation in foliar nitrogen concentration by forest type and climatic gradients in North America. Canadian Journal of Forest Research 23(8): 1587-1602.

810 Yoder BJ, Ryan MG, Waring RH, Schoettle AW, Kaufmann MR. 1994. Evidence of Reduced Photosynthetic Rates in Old Trees. Forest Science 40(3): 513-527.

Yuan Z, Chen H, Reich P 2011. Global-scale latitudinal patterns of plant fine-root nitrogen and phosphorus. Nature Communications 2: 344.

Supporting Information