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

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Abstract. Nitrogen (N) concentration in tree tissues controls photosynthesis, growth and plant maintenance respiration. While earlier studies of its variation 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 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 (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 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 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

35 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. 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 (CO₂; 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). Not only plant

40 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).

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

45 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 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).

50 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 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 measurements are available for fine roots (Iversen et al., 2017; Wang et al.,

55 2019; 2021), N concentration data representative for the entire root system including coarse roots are comparatively sparse due to the complexity of such measurements. 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

60 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

65 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. 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 living cells in older trees (conversion of sapwood to heartwood; Thurner et al., 2019), and c) a 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.

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 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 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 growing under favorable conditions.

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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 be verified for boreal and temperate tree species at global scale. Plants face a trade-off when investing resources into growth

110 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 having mostly focussed on herbivory and pathogens, but less on defense against environmental stresses (Loehle, 1988).

115 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 ecosystems limited by other resources (Chapin et al., 1990), including low temperatures, water or light.

120 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.

Up to now, the effects of temperature and water availability on N allocation have rarely been analysed at global scale.

125 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 concentration not only in leaves, but also in stems and roots decreases with increasing MAT and mean annual precipitation

130 (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.

4. Tissue N concentration increases with soil N concentration.

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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 forest stands and a selection of tree species. For instance, higher soil N has been observed to result in elevated N

140 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 decreasing leaf, but surprisingly not fine root, N concentrations with decreasing soil N availability in a temperate deciduous

145 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.

150   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

155 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.

160 **2 Materials and Methods**

2.1 An unprecedented database of N concentration measurements in tree tissues

We collect an unprecedented 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

165 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
170 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
175 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
180 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.
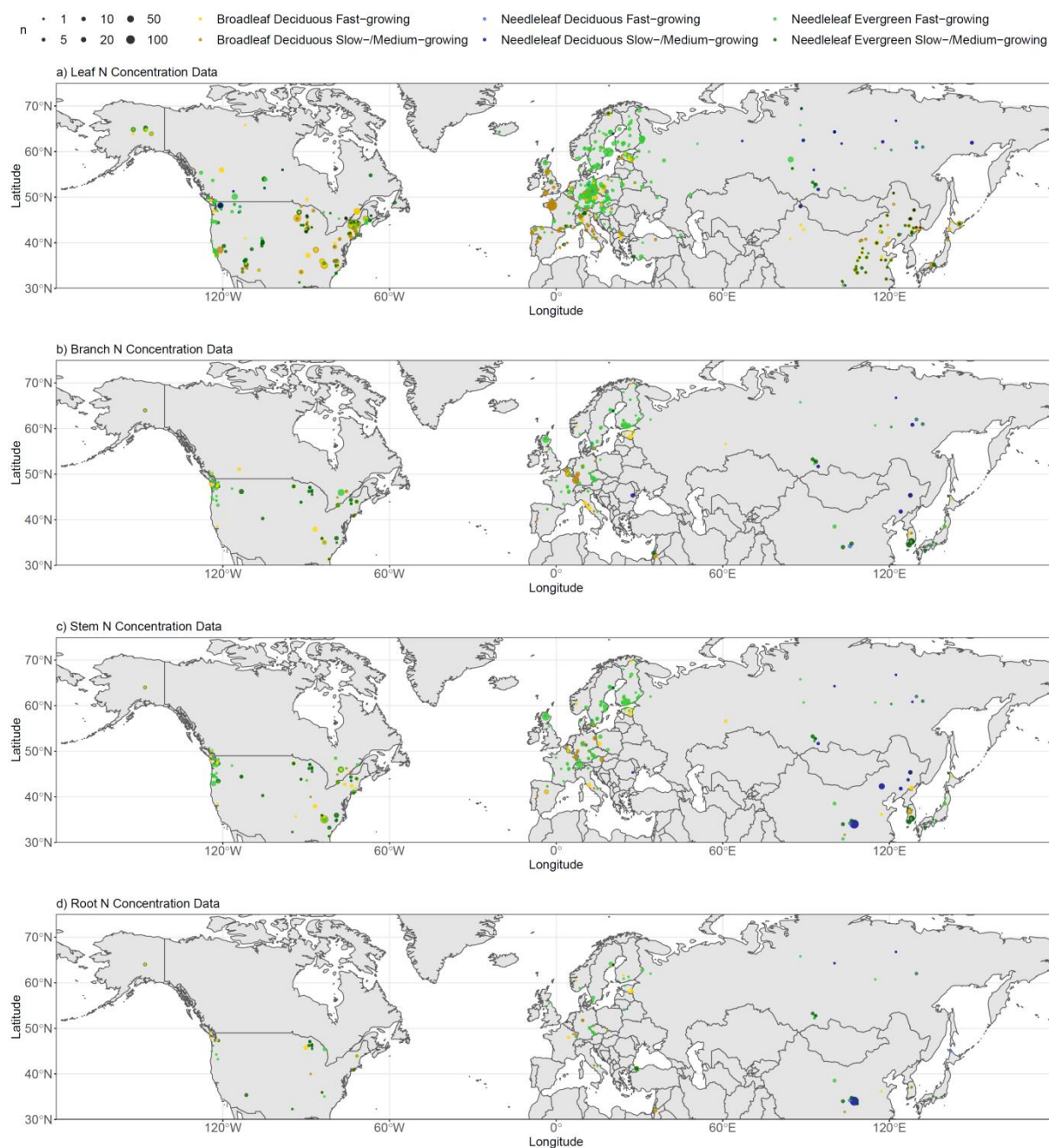
Figure 1: Spatial distribution of N concentration measurements applied in this study in a) leaves, b) branches, c) stems, and d) roots of boreal and temperate tree species, grouped according to their leaf type and growth rate. n denotes the number of measurements.

2.2 Explanatory variables

190   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

195   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.

200   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 (broadleaf deciduous, needleleaf deciduous, 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

205   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

210   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

215   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

220   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. S3 and S4 in Supporting Information S10), t-tests are applied here since they are
225   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
230   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
235   (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
240   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
245   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 – S13 in Supporting Information S7). Especially in leaves, broadleaf deciduous species (e.g. different species of Acer, Betula, Fagus, Fraxinus, Populus and Quercus) have higher levels of N concentrations than needleleaf evergreen species (e.g. different species of Abies, Picea, Pinus). In some cases, even different species of the same genus exhibit strongly different
250   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.

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) separately. Note that we do not correct for heteroscedasticity occurring in some of the linear relationships identified in Fig. 2 (cf. Fig. S5 in Supporting Information S11) 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 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.
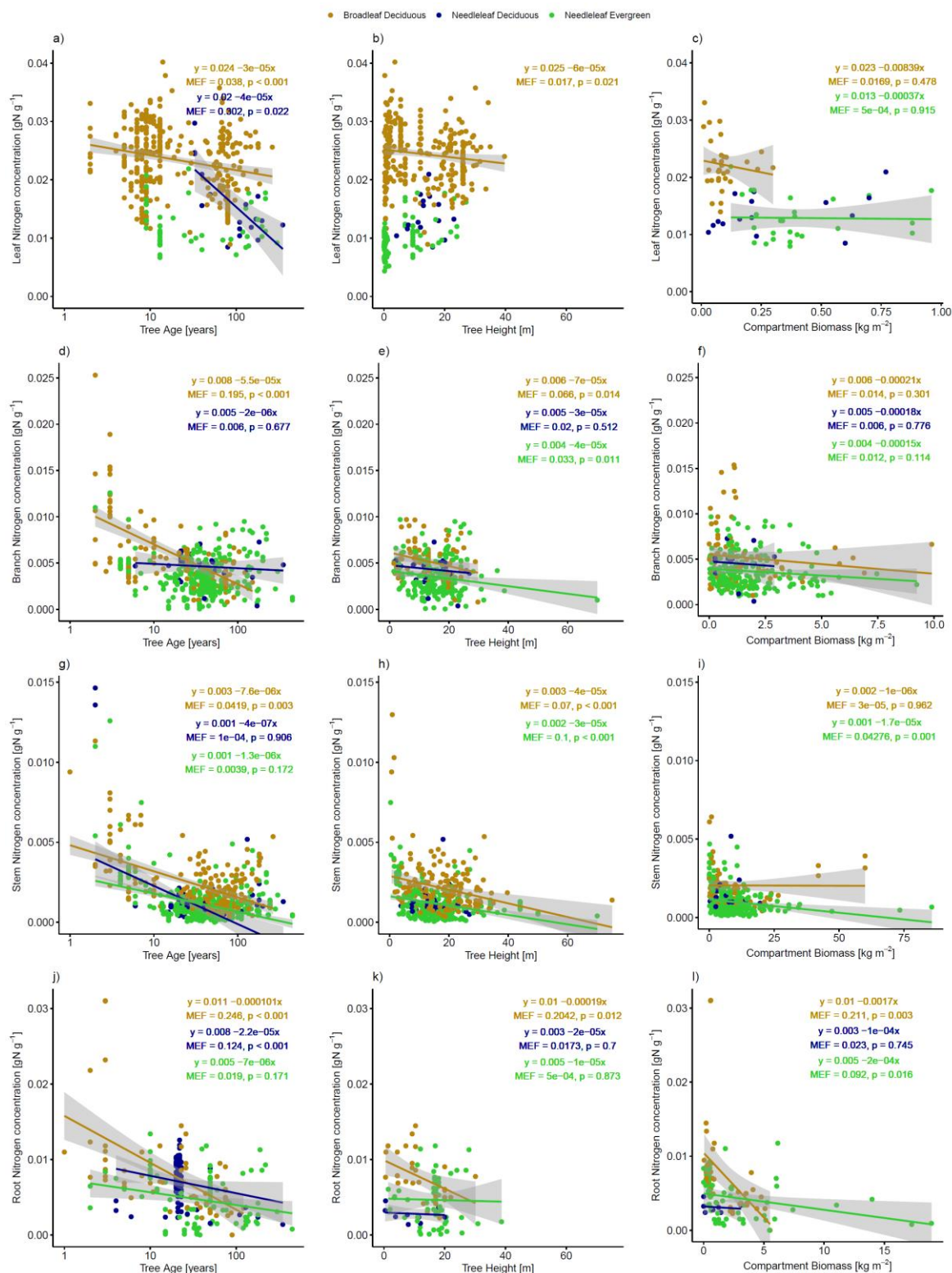
Figure 2: The relationship between a-c) leaf, d-f) branch, g-i) stem, and j-l) root N concentration and tree age, tree height, and compartment biomass. Linear models have been fitted for leaf types (broadleaf deciduous, needleleaf deciduous, needleleaf evergreen) separately and only in case of negative 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 Relationship between tissue N concentrations and leaf type

In addition to tree age/size, we find that tree tissue N concentration is also related to leaf type (broadleaf deciduous, needleleaf deciduous, needleleaf evergreen; Fig. 3). Compared to needleleaf evergreen trees, broadleaf deciduous 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 deciduous 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}).
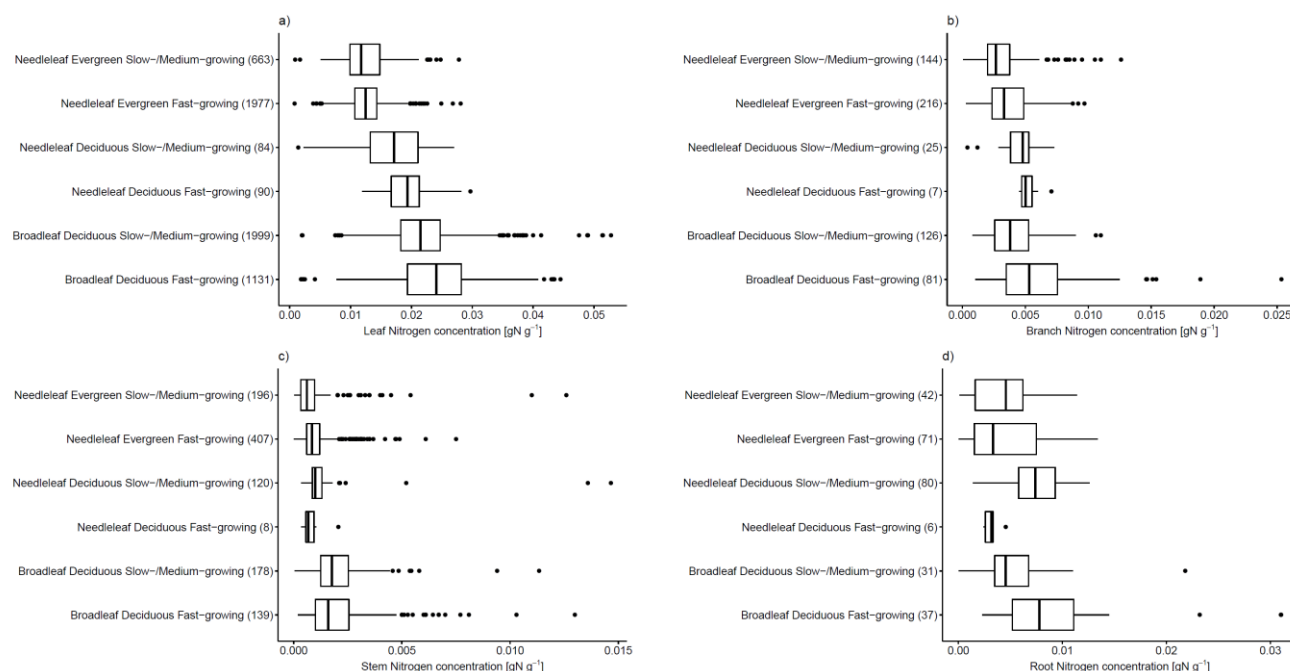
Figure 3: N concentration in a) leaves, b) branches, c) stems, and d) roots of boreal and temperate tree species, grouped according to their leaf type and growth rate. The number of observations in each growth / leaf type class is stated in brackets. The box-whisker plots show the median and the interquartile 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

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 stem N concentration shows this behaviour, while fast-growing trees exhibit a lower stem N concentration than slow-/medium-growing trees in broadleaf deciduous and needleleaf deciduous trees (Table S7). In roots, in turn, fast-growing trees show a higher N concentration compared to slow-/medium-growing trees in case of broadleaf deciduous trees, but a lower N concentration in needleleaf evergreen and needleleaf deciduous 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 trees are to be interpreted with care due to very few values available.

The leaf N concentration of needleleaf deciduous and needleleaf evergreen trees is significantly lower under very cold climate conditions (MAT < 0°C) compared to more favourable conditions (MAT >= 0°C). Similar differences are observed for root N concentration of needleleaf deciduous trees (Fig. 4; Table 2). In contrast, branch and stem N concentration of needleleaf evergreen 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 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 and needleleaf evergreen trees under dry (AI < 0.65) compared to more

favourable (AI >=0.65) conditions, but opposite patterns for broadleaf deciduous trees (see Fig. S2 in Supporting Information S9; Table 2). Root N concentration is significantly lower not only for needleleaf deciduous, but also needleleaf evergreen trees, whereas branch N concentration is significantly higher for broadleaf deciduous trees when AI < 0.65. Note that in some cases, few available measurements of tissue N concentrations of specific leaf types under extreme climate

315 hamper the detection of significant differences.
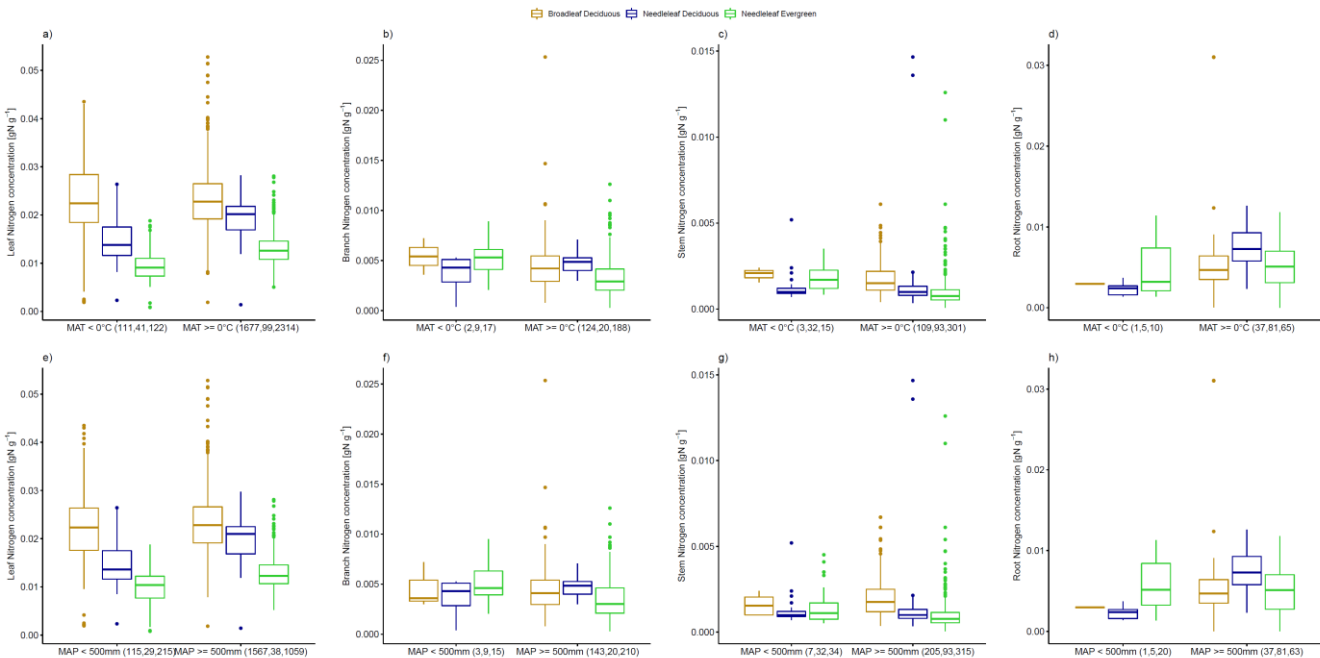
Figure 4: The variation in leaf, branch, stem, and root N concentration for a-d) mean annual temperature (MAT) classes (MAT <
0°C vs. MAT >= 0°C) and e-h) mean annual precipitation sum (MAP) classes (MAP < 500mm vs. MAP >= 500mm) and for leaf
320 **types (broadleaf deciduous, needleleaf deciduous, needleleaf 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.

325 **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

330 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 trees, whereas root N concentration is significantly positively correlated with MAT when controlled for MAP and soil N concentration for broadleaf deciduous trees and when controlled for tree age for needleleaf deciduous trees. Branch and stem N concentrations are significantly negatively correlated with MAT when controlled for tree age and MAP for needleleaf evergreen trees. In
335 addition, stem N concentration of needleleaf deciduous trees is significantly negatively correlated with MAT when controlled for soil N concentration. However, for broadleaf deciduous trees there are opposite patterns for certain control variables (consistent significant negative correlation between leaf N concentration of broadleaf deciduous trees and MAT; significant positive correlation for broadleaf deciduous 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
340 MAP).

With regard to MAP, we find significant positive correlations with leaf N concentration of needleleaf deciduous trees when controlled for tree age and MAT and of needleleaf evergreen trees when controlled for MAT. Similarly, root N concentration of needleleaf deciduous trees is consistently significantly positively correlated with MAP. Negative correlations between branch N concentration and MAP are significant for broadleaf deciduous trees when controlled for tree age and MAT, and
345 for needleleaf evergreen 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 deciduous trees and MAP when controlled for MAT and soil N concentration; significant positive correlation between branch N concentration of needleleaf deciduous trees and MAP when controlled for MAT; significant negative correlation between root N
350 concentration of broadleaf deciduous trees and MAP when controlled for MAT and soil N concentration).

3.4 Relationship between tissue and soil N concentrations

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 and needleleaf evergreen trees (not significant at the 5% level) and stem N concentration of needleleaf evergreen

355 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. S6 in Supporting Information S11) because it can be explained by their non-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 trees, and between stem and soil N

360 concentration when controlled for tree age for needleleaf evergreen trees. In most cases, there is no significant correlation, but for needleleaf deciduous trees, the partial correlation analysis shows even significant negative 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.
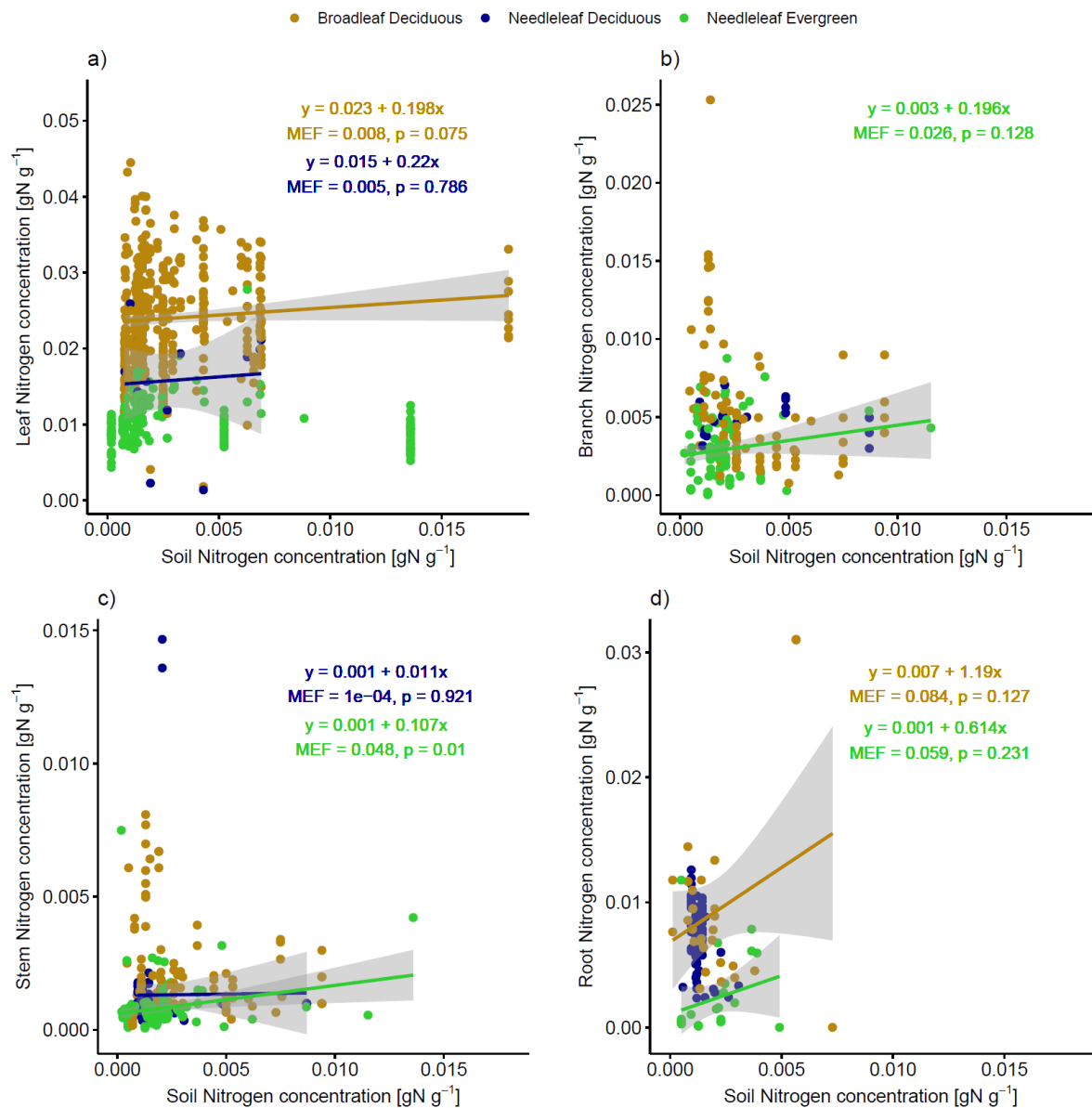
Figure 5: The relationship between a) leaf, b) branch, c) stem, and d) root N concentration and soil N concentration. Linear models have been fitted for leaf types (broadleaf deciduous, needleleaf deciduous, needleleaf evergreen) separately and only in case of positive correlation. The strength of the 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.
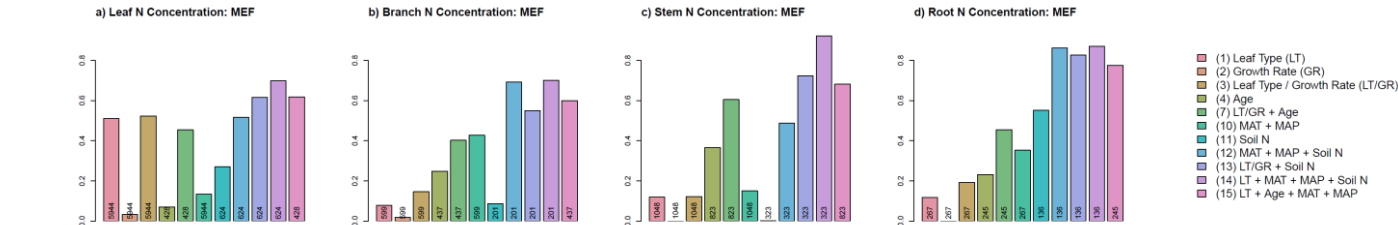
Figure 6: Modelling efficiencies (MEFs) of a selection of 11 of the in total 17 applied generalized additive models (GAMs) for modelling a) leaf, b) branch, c) stem, and d) root N concentration using different combinations of explanatory variables. GAMs (1) – (4), (7), and (10) – (15) as described in 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 living cells (Thurner et al., 2019), and a depletion of soil N (Norby et al. 2010).

While broadleaf deciduous trees exhibit significantly higher N concentrations than needleleaf evergreen trees in all tissues (in agreement with Hypothesis 2), the N concentrations in leaves, branches and roots (but not stems) of needleleaf deciduous trees are significantly higher compared to needleleaf evergreen 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 deciduous 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 deciduous 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 evergreen 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 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 and needleleaf evergreen 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 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 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 and needleleaf evergreen 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 between leaf N concentration of broadleaf deciduous trees and MAT as well as between branch N concentration of needleleaf evergreen 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 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 and needleleaf evergreen trees. As noted above, these trends in N concentrations do not 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 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 and needleleaf evergreen trees in dry conditions. In addition, changes in the distribution of tree 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 trees significant increase under very cold and dry climate) and root (no consistent effect of growth rates; for needleleaf deciduous trees significant decrease under very cold and dry climate) N concentration, growth rates and unfavorable climate show some opposite or no consistent
465   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 and needleleaf evergreen trees (not
470   significant at the 5% level) and in stem N concentration of needleleaf evergreen 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
475   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 and needleleaf evergreen trees and stem N concentration of needleleaf evergreen 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
480   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.

485   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
490   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

495 (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.

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
500   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-
505   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) 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,
510   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).

515 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 (*Quercus* species; Hanewinkel et al., 2013), which replace (amongst others) needleleaf evergreen with broadleaf deciduous 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 changes we would expect a higher N
520 concentration in all tree tissues and elevated N allocation fractions to stems. This might, in turn, lead to higher productivity, but also (stem sapwood) 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
525 DGVMs, which usually assume fixed ratios between leaf, wood and fine root N concentrations (Meyerholt & Zaehle, 2015). 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
530   forest management and disturbances on the coupling of the C and N cycles cannot be realistically reproduced by DGVMs.
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
535   the improvement of N allocation in DGVMs, the identified relationships, together with available data on tree tissue biomass
(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
540   unprecedented database of N concentrations in stems, roots and branches of all common Northern hemisphere boreal 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 and needleleaf evergreen trees. Low growth rates or unfavorable climatic conditions are found to decrease leaf
545   (the latter only in case of needleleaf deciduous and needleleaf evergreen trees), but not stem N 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. Thus, changes in the distribution of tree age/size, tree species,
550   and extreme climate, induced by 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

555   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
560 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

565 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
570 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).

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Supporting Information

S1   Web of Science search criteria

S2   Data sources

S3   Classification of tree species into Growth / Leaf type classes

S4   Generalized additive models

S5   N concentration summary statistics

S6   Significance of differences between leaf, branch, stem, and root N concentration

S7   Differences between tree species

S8   Partial correlations

S9   Aridity Index

S10   Q-Q plots

S11   Residual plots