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Large differences in plant nitrogen supply in German and Swedish forests – Implications for management

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ABSTRACT

In European forests, plant N supply varies from regions where N deposition is negligible and a low natural N supply limits production to regions where high N deposition adds to a high natural N supply. Here, we ask if the differences in N supply are too large to make one system of management for wood production, continuous–cover forestry or rotational forestry, optimal across these conditions.

We analyzed the C/N ratio in c. 8400 samples of surficial soil layers along a 2400 km long transect through Sweden and Germany to obtain a quantitative description of differences in plant N supply. We discuss the differences in relation to forest management, especially evidence that soil C/N ratios below 25 are associated with higher N supply, risks of leaching of nitrate, and gaseous losses of N_2O, whereas ratios above 25 are associated with a tighter N cycle and an N limitation to tree growth.

The percent soil with C/N ratios above 25 declines from 91 in N. Norrland in Sweden to 26 in Germany. Simultaneously, mor soils (with a distinct organic layer on top of the mineral soil) decline from 95% to 16%, while mull soils (in which organic matter and mineral particles are mixed) increase from 1% to 40%. However, low C/N ratios also occur in the north, where we find the largest width in C/N ratios from 16 in mull soils to 36 in mor soils, which compares with a variation in Germany from 17 to 27. Soils under conifers generally have higher C/N ratios than soils under broadleaves, but our survey data cannot support that the trees are the sole cause of this pattern. Very low C/N ratios occur in conifer–dominated forests in the north.

The high incidence (74%) of C/N ratios below 25 indicates that forest management in Germany should use methods, which minimize the risk of N losses. Continuous–cover forestry may fulfill that objective. In the north with 9% of the soils below this threshold, risks of N losses are small. There, rotational forestry involving clear–felling alleviates the competition for soil N from larger trees allowing successful regeneration of tree seedlings. From the perspective of interactions between plant N supply and management of forests for wood production, no single management system seems optimal along this large gradient. We propose that research on forest management systems should address the importance of N supply.

1. Introduction

The supply of nitrogen commonly limits plant production and determines the overall structure and function of many forest ecosystems (Vitousek and Howarth, 1991). For example, in Norway, Sweden and Finland, countries in the boreal zone, hundreds of fertilizer trials have demonstrated a widespread N limitation to forest tree growth (Nilsen, 2001; Nohrstedt, 2001; Saarsalmi and Mälkönen, 2001). In contrast, in densely populated areas in the temperate zone, where the natural soil N supply was already higher, anthropogenic N deposition has caused additional eutrophication of forests (e.g., de Vries et al., 2014). In Germany, there were reports of positive responses of tree growth to N fertilization up until the 1980ś (Kenk and Fischer, 1988). These responses may still occur, at least locally, but now many authors are concerned that the combined N deposition and natural N supply is in excess of plant demand and may affect tree health and water quality adversely (e.g., de Vries et al., 2014; Bolte et al., 2019). Hence, forest policy and forest management need to consider aspects on plant N

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supply and risks of N losses.

An important aspect of forest management is the method of tree regeneration. Tree seedlings compete with each other and with surrounding trees for scarce resources (Coomes and Grubb, 2000). This is obvious in N–poor boreal forest, where natural regeneration inside forests and close to forest edges is sparse as compared to away from edges in clearings (Aaltonen, 1919; Kuuluvainen and Ylläsjärvi, 2011; Ruuska et al., 2008; Axelsson et al., 2014). For example, Ruuska et al. (2008) found that seedling growth increased 10 times when moving 20 m away from the forest edge. Experiments with trenching under intact forest canopies (Romell and Malmström, 1945) and tree–girdling (Axelsson et al., 2014) in N–poor forests suggest that this effect is due to reduced below–ground competition rather than reduced competition for light. Foresters in northern Europe demonstrated a century ago that clear–felling (sometimes followed by prescribed burning) provided better conditions for growth of tree seedlings as compared to regeneration in stands with selective felling systems (Lundmark et al., 2017; Cogos et al., 2020). Hence, rotational silviculture based on clear–felling attained dominance in northern Europe around the 1950s–1960s.

The higher N supply in Central Europe (e.g., Persson et al. 2000) can be explained by a warmer climate, a longer vegetation period, the fact that accumulation of N in the soil has occurred during a longer period after the latest glaciation and possibly by the mineralogy of soils and bedrock. To this anthropogenic deposition has added N at high rates for almost a century. Today, the deposition of inorganic N is around 20 kg ha^{-1} yr^{-1} in Germany (Wellbrock et al., 2019b), which is 10 times above the N deposition in northern Sweden (Andersson et al., 2018; Ferm et al., 2019). Decisions and innovations to reduce emissions have led to declines in N deposition (Lajtha and Jones, 2013; Ferm et al., 2019), but the high levels are still of concern in the context of forest management (e.g., Bolte et al., 2019; Flechard et al., 2020). For example, forest harvests cause additional leaching of N and emission of the potent greenhouse gas N_2O, especially where the plant N supply is high.

Moreover, other values than wood production are increasingly appreciated, e.g., recreational values and preservation of the biota in old forests, which has led to a questioning of the widespread use of rotational silviculture in northern Europe (Siiskonen, 2013; Mårald et al., 2017). Selective felling methods, often referred to as continuous–cover –forestry (Pommerening and Murphy, 2004), have been more common in Central Europe. German authorities recommend them, for example. Selective felling is expected to cause less N leaching from forests as compared to clear–felling (Gundersen et al., 2006).

The debate about choice of forest management systems is intense nationally, e.g., in Sweden (Mårald et al., 2017), but also at the level of the European Union (EU), which may take decisions to standardize forestry across the union. We submit that the supply of N to plants is pivotal in this context, although largely overlooked in todaýs discussions about choice of management systems, which tend to focus most on recreational values and biodiversity issues. An important question is if any of continuous–cover–forestry or rotational forestry works better in terms of forest regeneration, wood production, N retention and management of water quality across the range in plant N supply in the EU member states (Fig. 1).

Thus, we ask if differences in N supply across Europe are significant enough to question the practice of one single silvicultural method. To answer this question, we make use of data on soils along a gradient through Sweden in the north to Germany in the south, two countries with uniquely detailed forest soil surveys. Hence, we encompass the

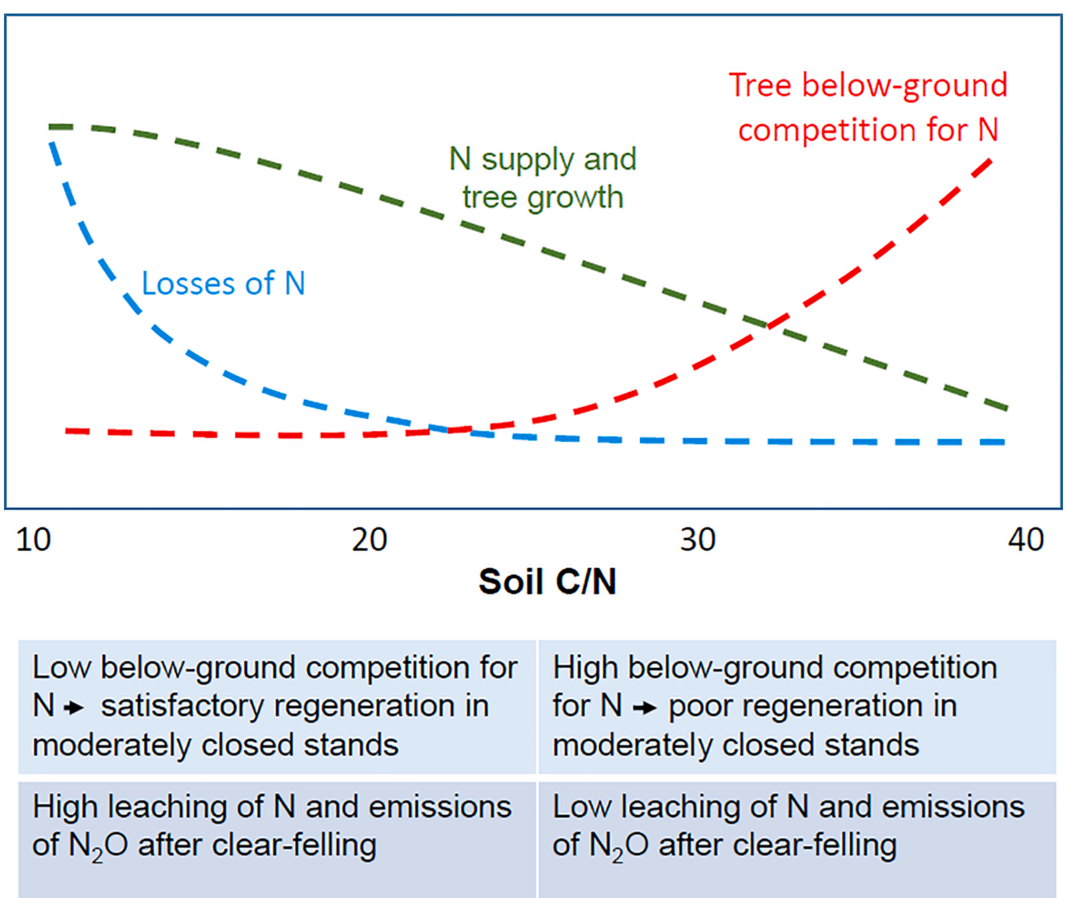

Fig. 1. Conceptual depiction of relations among N supply and loss, tree growth and potential for tree below–ground competition for N in temperate and boreal forests.

N–poor boreal forests of north Europe, where rotational forestry is commonly practiced, as well as the N–richer temperate forests of Central Europe, where selective felling systems are common. With data on soil N supply as background, we discuss the implications of our findings for forest policy and management, especially the choice of silvicultural method. We also pay attention to the possibility that tree species composition can cause differences in N supply (Vesterdal et al., 2008; Cools et al, 2014; Binkley and Fisher, 2020).

2. Materials and methods

We used data on soils from the detailed national forest soil inventories conducted in Sweden 2003–2012 (Nilsson et al., 2015; Stendahl et al., 2017) and in Germany 2006–2008 (Höhle et al., 2016; Wellbrock et al., 2019a). These data come from forest land as defined according to FAO. The data from Sweden refers to productive forests, i.e. forests with a production > 1 m^3 of wood ha^{-1} yr^{-1}; forestry is not allowed on less productive forest land. The total data set used consists of samples from c. 6600 and c. 1800 plots in Sweden and Germany, respectively. We studied data on C and N from analyses made on elemental analyzers, which are used in both countries (Nilsson et al., 2015; Höhle et al., 2016).

We organized the material such that our data described a gradient from north to south, with four regions of Sweden: northern Norrland, southern Norrland, Svealand and Götaland followed by Germany in the south. This gradient included forests from 69°N. to 47°N. (Fig. 2), a distance of c. 2440 km. In terms of area, Sweden has 28 Mha of forests, with 9.7, 6.9, 6.0 and 5.4 Mha in N. Norrland, S. Norrland, Svealand and Götaland, respectively. Germany has 10.3 Mha of forests.

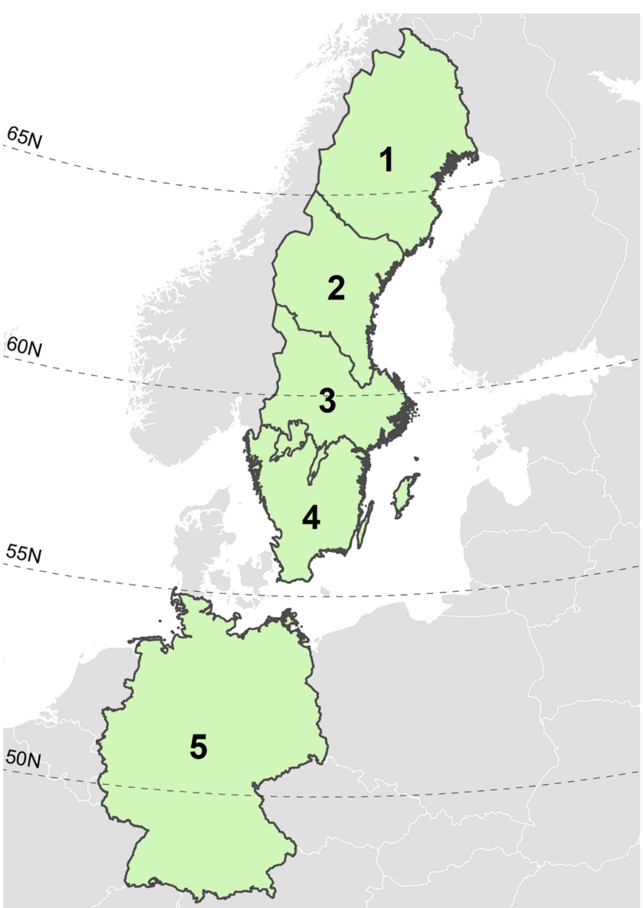

Fig. 2. The gradient from 69 °N to 47 °N; 1, N. Norrland; 2, S. Norrland; 3, Svealand; 4, Götaland (1–4 are parts of Sweden) and 5, Germany. The two larger islands in the Baltic Sea (Gotland and Öland) belong to region Götaland.

We studied forests on mineral soil, and thus excluded forests on peat soils, i.e. soils with an organic topsoil of > 0.3 m depth (in Germany, the percent C in peat also needs to be > 12), but also peat–like mor (with a mor–layer < 0.3 m thick) in Sweden and similar soils in Germany. Peat soils occupy, 14 and 3% in Sweden and Germany, respectively, and peat–like mor adds another 10% of soils in Sweden, but are less important in Germany. Forest soils on peat are less often subject to forest operations than the much more common mineral soils. We excluded the wetter soils, peat and peat–like mor, because anoxic conditions may confound the interpretation of the role of N supply.

We used data on the biologically active surficial soil layers, which are rich in fine roots of trees. These layers are the focal site of the interaction between decomposition of organic matter and the subsequent N uptake by mycorrhizal tree roots (Lindahl et al. 2007). The character of these layers vary from almost totally organic mor–layers (i.e. with 40–45% C) on top of the mineral soil to mull soils, where the organic matter is mixed with mineral soil particles and the organic matter is typically below 20% of the dry weight (thus, with a % C below 10). For this latter type of soil, we used data from the 0–5 cm depth of the mineral horizon in Germany, but 0–10 cm in Sweden. This difference does not affect our major results and conclusions for the following reasons. First, because the organic matter in the mull is commonly mixed to a depth well below both 0–5 and 0–10 cm. Second, because our major finding is that soils in Germany provide a higher N supply than soils in Sweden, while the focus on 0–5 cm would potentially lead to comparably higher C/N ratios for German mull soils.

Soil inventory staff classify the surficial organic matter into humus forms (e.g., Zanella et al., 2011), in which case there are similarities between the two national systems, but also some differences as described in Table 1 (for further details see Appendix Tables A.1 and A.2). Here, we adopt a compromise between the two national systems (Table 1). It reduces the higher resolution of the N–poorer humus forms described in Sweden, but also the higher resolution of the intermediate and N–richer humus forms described in Germany.

Thus, we designated as mor the Swedish mor soils (i.e., mor type 1 and mor type 2, see Appendix Tables A.1 and A.2) as well as "typischer rohhumus" (typical raw humus) and "rohhumusartiger moder" (raw humus–like moder) in the German system, because they all had a C % of around 39% (Table 1 and 4, Appendix Table A.3). Soils designated moder soils had a C % of between 30 and 37 across the gradient, indicating a greater contribution of minerogenic particles than in mor. As regards mull–like moder soils, their C % varied between 14 and 22 in Sweden, which compared with 7% in Germany, a figure on par with that of the mull soils. We nevertheless decided to keep the German mull–like moder soils as such, because of their higher C/N ratio than the mull soils. However, as stated above, we used the 0–5 cm horizon for the German mull–like moder soils (cf. Fleck et al., 2019) because of the low

Table 1
The classes of humus forms described in the Swedish and German soil surveys and common classes (with translation in brackets) adopted for the comparisons made in this study. Detailed descriptions of the humus forms are given in the Appendix.

Swedish classification	German classification	Classification adopted here
Mår typ 1 (Mor type 1) Mår typ 2 (Mor type 2)	Rohhumus (raw humus) Rohhumusartiger moder (raw humus like moder)	**Mor**
Moder	Grawurzelfilzmoder (grass–root–blanket moder) Typischer moder (typical moder)	**Moder**
Mull–liknande moder (Mull–like moder)	Mullartiger moder (mull–like moder)	**Mull–like moder**
Mull	F–Mull Mull	**Mull**

contribution of organic matter (low % C), which was on par with that in mull soils.

We used the soil C/N ratio as metric describing the N supply (van Sundert et al., 2020), because it is possible to predict effects of organic matter C/N ratios on soil microbial physiology and hence on plant N supply (Myrold 1998; Robertson and Groffman, 2015). The general principle is that at low C/N ratios heterotrophic soil microorganisms are limited by C, and hence more likely to release N in forms available to plants, such as peptides, amino acids, ammonium and nitrate. In contrast, when the C/N ratio of the substrate is high, heterotrophic soil organisms retain N. Thus, ratios above 30 indicate a low plant N supply, while values below 20 indicate a high N supply (e.g., Fleck et al., 2019; Högberg et al., 2006, 2017; Myrold 1998, see also Fig. 1). Ratios below 25 of the topsoil are associated with a higher incidence of leaching of inorganic N from watersheds across Europe (e.g., Gundersen et al. 1998; Borken and Matzner, 2004; Rothwell et al., 2008) and N_2O emissions increase dramatically below 20 (Klemedtsson et al., 2005). Seen the other way around, plant root and microbial competition for N should increase progressively above a C/N ratio of 25 (Högberg et al., 2017).

Moreover, the C/N ratio is a robust indicator, not affected by the mixing of organic matter with mineral particles. It should be observed that the largest difference in C/N ratios between N-poor and N-rich forests occur in the litter and surficial soil layers (which we focus on), while their C/N ratios tend to converge deeper down in the soil profile (Callesen et al., 2007).

3. Results

3.1. Distribution of low and high soil N supply across the gradient.

We studied the frequencies of two–unit wide classes of soil C/N ratios by region along the gradient (Figs. 3–4). With the large number of observations for each region (between 1364 and 2087), we found close to normal distributions (Fig. 3). The percentage of soil C/N ratios > 25 declined successively from c. 91 in N. Norrland to 26 in Germany (Table 2). Hence, there are huge differences in C/N ratios between Germany and the three northern regions of Sweden, but much less of difference between Germany and southernmost Sweden (Götaland).

3.2. Distribution of different humus forms.

There are also large systematic changes in the contributions of different humus forms along the gradient (Fig. 5). In N. Norrland, with a forest area almost equal to that of Germany (9.7 and 10.3 Mha,

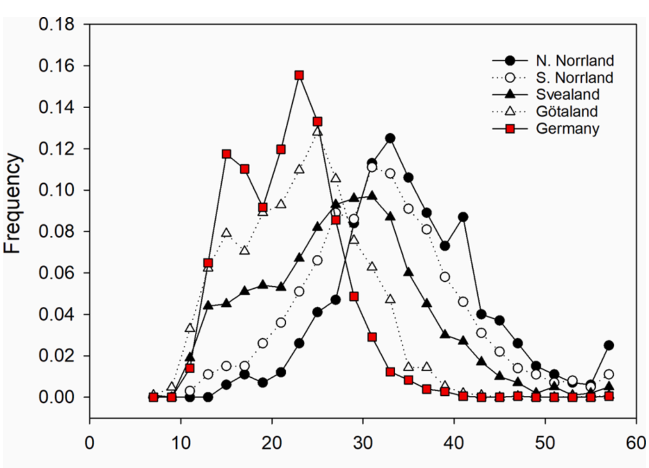

Fig. 3. Frequencies of soil C/N ratios (based on two–unit wide intervals) in forest soils in the four regions of Sweden and in Germany. Note that all samples with a C/N ratio above 56 are placed in the 56–58 class.

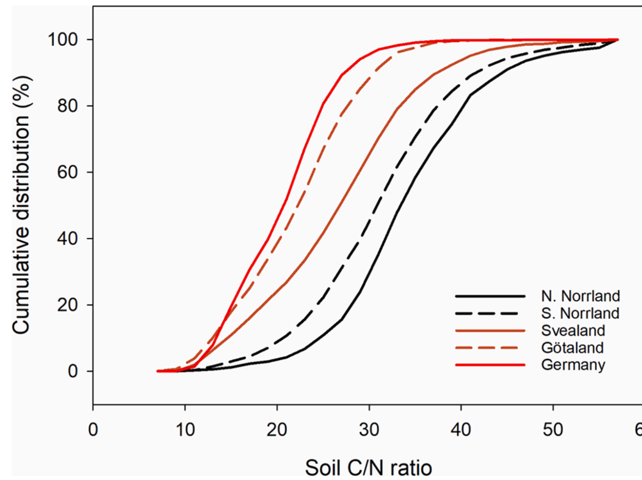

Fig. 4. Cumulative distribution of C/N ratios in forest soils among regions of Sweden and in Germany.

Table 2
Summary of data on forest area and soil C/N ratio by region in Sweden and in Germany. Mha = million hectares. Means ± 1.0 S.E.

Country or region	Area of forests (Mha)	No. of observations	C/N	Percent of soils with C/N > 25
N. Norrland	9.7	1364	35.3 ± 0.2	91.4
S. Norrland	6.9	1401	32.2 ± 0.2	81.4
Svealand	6.0	1740	27.7 ± 0.2	62.4
Götaland	5.4	2087	23.0 ± 0.1	39.4
Germany	10.3	1788	21.5 ± 0.1	26.3

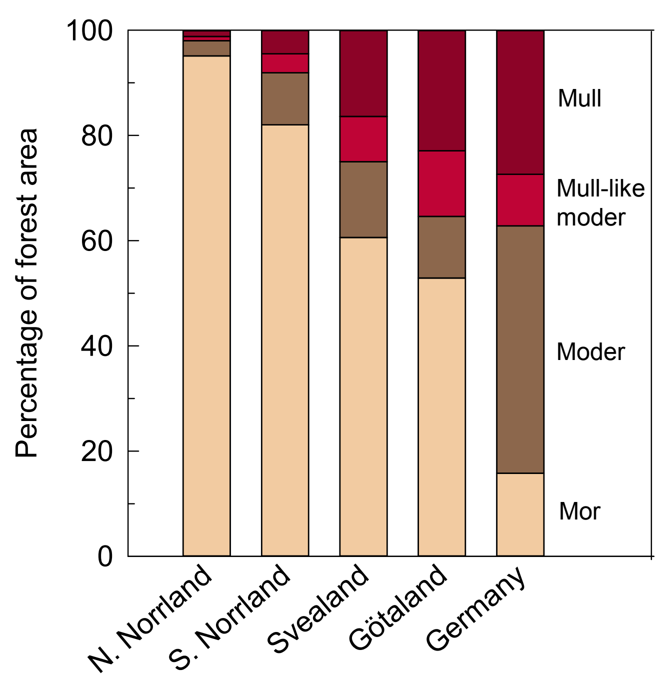

Fig. 5. Distribution of humus forms in forest soils along the gradient from northern Norrland, through southern Norrland, Svealand, Götaland to Germany. The humus forms are described in Table 1 and in the Appendix.

respectively), 95% of the soils have a mor–layer, which compares with only 16% in Germany. Even in southernmost Sweden, Götaland, mor soils make up 50% of the forest soils, i.e. these are three times more common than in Germany at large. The proportions of moder, mull–like moder and mull soils very clearly increase from north to south. In Germany, as much as 40% of the soils are mull soils, which compares with only 1% in N. Norrland (Fig. 5).

3.3. Similarities and differences between humus forms in the two countries.

The C/N ratios of the Swedish mor layers (mean 34) are clearly higher than those in mor in Germany (mean 26), but as regards the C/N ratios of the other humus forms, the differences between the countries or along the gradient are smaller (Table 3). In Sweden, the mean C/N ratio of mor as per region range from 36 in N. Norrland to 27 in Götaland in the south (Table 3). Actually, according to the Swedish subdivision of mor into mor type 1 and 2 (Table 1), the type 1, considered the N–poorest type, has a C/N ratio of 36.6 ± 0.3 (mean ± 1.0 S.E., n = 1052) and covers 77% of the area in N. Norrland. Mull soils are a particularly interesting example with the lowest C/N ratios in N. Norrland, 16, and in Germany, 17, while the C/N ratios are slightly higher in middle and southern Sweden (Table 3).

We examined the C % of the soils as an indicator of the mixing of the organic matter with mineral particles. There was a decline in C % from north to south (Table 4). The C % was, as expected, highest in mor (close to 40%), and declined in the expected order mor > moder > mull–like moder > mull (Table 4). A notable difference between countries is mull–like moder; the % C is 17 in Sweden as compared to 7 in Germany. In case of the other humus forms, differences in C % along the gradient were minor, indicating similarities among humus forms across the gradient. For example, the mull soils, which showed the lowest C/N ratios, also had the lowest % C among the humus forms.

Taken together, the above–mentioned data clearly show that there is a substantial decrease in C/N ratio of soils from north to south, while there is also on average a decrease in % C reflecting an increasing mixing of organic matter with mineral soil. The major change is, thus, a shift from a dominance of mor soils in the north to moder, mull–like moder and mull in the south (Fig. 5). The C/N ratios of the different humus forms do not change very much, with exception of the large decrease in the C/N ratio in the mor soils from 36 in northern Sweden to 26 in Germany (Table 3).

3.4. Relations between tree species and soil C/N ratios.

The soil C/N ratios in German were 27, 22, 19, 18 and 16 under *Pinus, Picea, Quercus, Fagus* and other broadleaved forests, respectively

Table 3
The C/N ratios of the different humus forms (cf. Table 1) region by region in Sweden, and weighted averages country by country. Weighting is based on the fractional contribution of each region or humus form to the respective aggregate. Means ± 1.0 S.E.

Country or region	Mor	Moder	Mull–like moder	Mull
N. Norrland	36.0 ± 0.2	27.3 ± 1.2	18.4 ± 1.7	15.6 ± 1.0
S. Norrland	33.8 ± 0.2	29.2 ± 0.6	21.2 ± 0.6	17.9 ± 0.6
Svealand	31.3 ± 0.2	28.4 ± 0.4	23.3 ± 0.4	20.1 ± 0.9
Götaland	26.8 ± 0.1	26.3 ± 0.5	22.8 ± 0.8	20.1 ± 0.7
Sweden	34.1*	27.8*	22.6*	17.4*
Germany	25.9**	24.8†	19.9 ± 0.6	16.5‡

* Weighted average for the four regions of Sweden.
** Weighted average for Typischer Rohhumus and Rohhumusartiger moder (cf. Table 1).
† Weighted average for Rohhumusartiger moder, Grazwurzelfilzmoder and Typischer moder.
‡ Weighted average for F–Mull and Typischer Mull.

Table 4
Percentage C (of dry soil) in different humus forms (cf. Table 1) region by region in Sweden, and weighted averages country by country. Weighting is based on the fractional contribution of each region or humus form to the respective aggregate. Means ± 1.0 S.E.

Country or region	Mor	Moder	Mull–like moder	Mull
N. Norrland	39.3 ± 0.2	32.1 ± 1.5	17.1 ± 2.5	8.9 ± 2.3
S. Norrland	38.0 ± 0.3	34.3 ± 1.2	21.5 ± 1.8	9.6 ± 1.2
Svealand	36.5 ± 0.3	32.0 ± 0.7	16.4 ± 1.4	8.3 ± 0.3
Götaland	34.6 ± 0.3	30.0 ± 0.6	13.8 ± 0.5	8.3 ± 0.3
Sweden	39.1*	32.1*	17.2*	8.8*
Germany	38.4**	35.4†	7 ± 0.3	6.9‡

* Weighted average for the four regions of Sweden.
** Weighted average for Typischer Rohhumus and Rohhumusartiger moder.
† Weighted average for Rohhumusartiger moder, Grazwurzelfilzmoder and Typischer moder.
‡ Weighted average for F–Mull and Typischer Mull.

(Fleck et al. 2019, Appendix Table A.4). Our data from Sweden are in the same direction with higher median C/N ratios under forests dominated by conifers (Fig. 6). The mean soil C/N ratios under forests with 0–20% and 80–100% broadleaves range between 36.7 and 28.1, 33.6 and 25.9, 29.3 and 15.9, and 24.7 and 16.0 in N. Norrland, S. Norrland, Svealand and Götaland, respectively. Hence, the average difference between these two classes is 9.6 ± 1.3. However, the variation within each class is large, especially within the 0–20% broadleaves class. Among such conifer–dominated forests there are those with very high C/N ratios, but also some with ratios as low as the lowest in forests dominated by broadleaves (Fig. 6).

4. Discussion

4.1. Differences in plant N supply.

Our study gives strong support for the hypothesis of a substantial difference in plant N supply between forests in northern and central Europe (Table 2, Figs. 2–3). Forest soils on minerogenic material in northern Sweden (i.e., N. Norrland) have a mean C/N ratio of 35.3 as compared to 21.5 in Germany. The general pattern across the gradient is apparent regardless of whether we compare percentages of different humus forms and their C/N ratios (Table 3), or if we just look at their frequencies or the cumulative distribution of C/N ratios (Figs. 3–4).

Interestingly, this does not mean that Sweden lacks forests with a high N supply. Even in N. Norrland, there are mull soils, albeit covering only 1.1% of the area (Fig. 5), with an average C/N ratio of 15.6, which is on par with the 16.5 of mull soils in Germany (Table 3). Note that proper mull soils in Germany, excluding the F–mull soils (Appendix Table A.2), have a C/N ratio of 14.5. Typically, low C/N ratio soils in N. and S. Norrland occur in local groundwater discharge areas (Högberg et al., 2017). Within distances of one hundred meters, there are often remarkably sharp transitions from very high C/N ratio (35–40) in the surrounding groundwater recharge areas to low C/N ratio (15–20) in the groundwater discharge areas (Giesler et al., 1998, 2002; Högberg et al. 2006, 2020). The proximity of high and low C/N soils show that both can occur under the same climatic conditions. In one discharge area, we found (Högberg et al., 2006) rates of gross N mineralization (based on ^{15}N pool dilution studies at ambient soil temperature), which were among the highest recorded (Booth et al., 2005). Furthermore, spruce trees may dominate groundwater discharge areas with very low soil C/N ratio (Fig. 6) in N. Norrland (Giesler et al., 2002), although broadleaved trees are often more common there than in the rest of the landscape. This suggests that edaphic soil conditions rather than effects of tree species cause the low C/N ratios at such sites. It is noteworthy in this context that the mean range in C/N ratios among humus forms are twice as wide in the north, from 15.6 to 36.0 in N. Norrland as compared to from 16.5 (for mull soils and F–mull combined) to 25.9 (for mor soils) in Germany

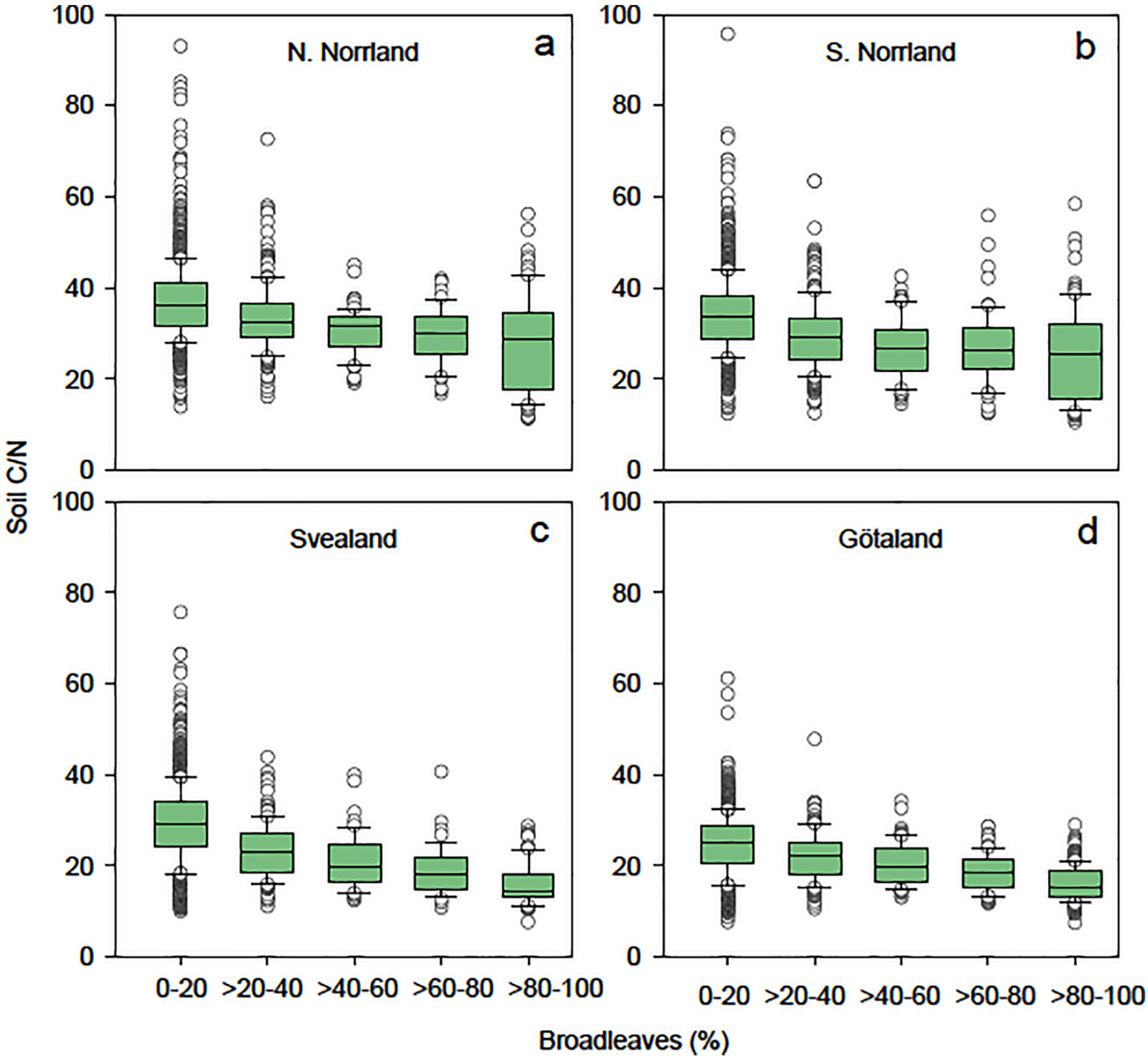

Fig. 6. Relation between soil C/N ratio and percentage of broadleaved trees in forests in regions of Sweden. The box plots show the median (horizontal lines), and the 25th and 75th percentiles (boxes), with error bars showing the 10th and 90th percentiles; outliers appear as circles.

(Table 3).

How stable are the soil C/N ratios? Experimental high long–term additions of N lowers the C/N ratio of naturally N–poor soils in Swedish boreal forest, but has not brought the ratio below 25. Twenty years of N additions at a rate of on average 108 kg ha^{-1} yr^{-1} lowered the soil C/N ratio in a pine forest from 40 to 28, while 40 years of N additions at on average 63 kg ha^{-1} yr^{-1} resulted in a ratio of 29 (Högberg et al., 2014). In another experiment with 20 years of N additions at 108 kg ha^{-1} yr^{-1}, the soil C/N ratio declined from 33 to 25 in a spruce forest (Blaško et al., 2013). The C/N ratios of 25–29 in these high N addition experiments in Sweden are still at the high end of German soils, where only mor and moder have comparable C/N ratios (Table 3). In Germany, recent decades of reduced N deposition may have contributed to an increase in C/N ratio of on average 1.6 between the NFSI 1 (the previous national forest soil inventory) and NFSI 2 (this study), corresponding to a change of 0.09 units year^{-1} (Fleck et al., 2019). We propose, nevertheless, that the gross differences in soil C/N ratios between Sweden and Germany are relatively stable.

4.2. Differences between humus forms.

The largest variation in C/N ratio among humus forms are found in the mor soils (Table 3). Their average ratios fall from 36 to 26 going from N. Norrland to Germany. This seems caused by increasing % N towards the south, since the % C is similar among regions (Table 4). In contrast, the C/N ratio of mull soils do not differ much along the gradient. Again, this means that there are very large differences in % N and hence the C/N ratio (Table 3) among the forests in N. Norrland, and that the variability among humus forms decreases when moving southwards. The decline in the percentage area of mor soils further contribute to the overall decline in soil C/N ratio when moving southwards (Figs. 4-5).

Mor is tightly interwoven by fungal mycelia. The root symbionts of trees, many of which are ectomycorrhizal fungi (ECMF), may constitute 30–40% of the total soil microbial biomass C under N–poor conditions (Högberg and Högberg, 2002; Högberg et al., 2010). Under higher N supply, trees allocate less C to their roots and ECM fungal symbionts (Högberg et al., 2010). This leads to a decrease in fungi, but an increase in the relative importance of bacteria (Högberg et al., 2007), loss of the tensile strength provided by fungal hyphae to the soil, and a shift to a mull–like structure created by soil animals, chiefly earthworms. These mix organic matter with mineral soil particles, which explains the low % C in mull soils. It is interesting that humus forms with a lower % C than mor increase southwards (Table 4 and Fig. 5), which may indicate an overall decline in the fungi/bacteria ratio in response to a higher N supply.

4.3. Effects of tree species, especially conifers vs. broad-leaves.

Tree species can affect the type of humus formed and its C/N ratio. This is unequivocally demonstrated in common garden experiments, in which different tree species have been planted on the same soil (Binkley and Giardina, 1998; Binkley and Fisher, 2020). When survey data (such as our data) are used to analyze effects of trees on soils, one may confound cause and effect. A difference may be there because certain species have been planted, or have established naturally on edaphically N–poor or N–rich soils specifically, rather than themselves being the cause of these conditions (e.g., Fleck et al., 2019; Binkley and Fisher, 2020).

The previous analysis by Fleck et al. (2019) of German forests (Appendix Table A.4) based on the soil survey data showed substantial differences between soil C/N ratios under different tree species. One should remember that this does not prove that these differences can be attributed to effects of trees on soils solely, although the overall pattern point in the same direction as results from common garden experiments (Vesterdal et al., 2008; Cools et al., 2014). Regarding the Swedish data, there is also a clear tendency that conifer–dominated forests with less broadleaved trees have higher soil C/N ratios (Fig. 6). Once again, this does not prove that the high soil C/N results from effects of the trees only, as few tree species other than conifers are able to establish forest stands on the N–poor soils, in particular. Moreover, the very low C/N ratios in some soils in forests dominated by conifers (Fig. 6), shows that conifers do not necessarily cause high soil C/N ratios. Common garden experiment are more suitable to demonstrate the effects of different tree species on soils, but do not cover a wide range of soil conditions as many have been established on relatively fertile former arable soils (Binkley and Fisher 2020). We propose that there is a need for common garden experiments in typical N–poor settings to clarify the interplay between tree species and edaphic conditions in the boreal zone. It should be mentioned that the percentage of broadleaves have increased in Swedish forests (Skogsdata, 2020) after the implementation of a new policy in 1993.

4.4. Implications for forest policy and forest management.

Forest policy and management can have very many objectives, which vary among regions because of socio–economic circumstances and natural conditions. For example, the role of the forests for the local community are different for N. Norrlańds ca. 0.5 million inhabitants with 9.7 Mha of forests than for Germanýs more than 80 million inhabitants with 10.3 Mha of forests. In Germany, around half the land area is used for agriculture or animal production, an area that could have been covered by forests under natural conditions. Probably, these land uses now occur on what was the most fertile forests soils. In Sweden, with harsher climate and poorer soils, agriculture and animal production occurs on only 8% of the land, most of it in southern Sweden. However, in northern Sweden, the Saami use forests for reindeer herding.

Such varying socio–economic conditions along with natural variations in climate and soils affect the options for forest policy and management. Here, we would like to return to and focus on the depiction in Fig. 1 of the relations among N supply and loss, tree growth and potential for tree below–ground competition for N. The figure is partly based on well–known relations between soil C/N and N loss. Let us first discuss the scenario to the left in the figure, i.e. a high plant N supply (low soil C/N ratio). Our study clearly shows that soils with a C/N ratio below 25 are common in Germany and Götaland, where they occupy 74 and 61% of the soils, respectively. In these forests, there is a greater potential for enhanced leaching of N and gaseous losses of N_2O after clear–felling, in particular when soil C/N ratios fall below 20 (Gundersen et al., 1998; Borken and Matzner, 2004; Klemedtsson et al., 2005; Rothwell et al., 2008). A study of forests in S. Sweden (mainly Götaland) found that the concentration of inorganic N in leachate correlated negatively with both soil C/N ratio and the ratio fungi/bacteria (Högberg et al., 2013). Median N losses from forests in Germany are estimated at 1.4 kg ha^{-1} yr^{-1} of N as emissions of N_2O and 2.6 kg ha^{-1} yr^{-1} of N as leaching of NO_3^-, i.e. altogether 4 kg ha^{-1} yr^{-1} of N (Fleck et al., 2019). Under such conditions, it is less likely that tree below–-ground competition for N leads to poor regeneration of tree seedlings (for which light may be more limiting). These considerations speak in favour of the use of selective felling systems, if shade–tolerant tree species can be used.

This situation contrast with the one in boreal forests with a high soil C/N ratio. In these, NO_3^- is a rare N species, but is produced locally in groundwater discharge areas with low C/N ratio (Högberg et al., 2006, 2017). Nitrification can also occur after clear–felling in less fertile soils, but the effect is transient as is the elevated leaching of inorganic N, which decreases as a rich flora of ground vegetation establishes in clear–fellings. Stream–water data show that leaching of inorganic N has been steadily decreasing the last three decades in boreal forests in northern Sweden, while these have been subject to rotational forestry involving clear–felling (Lucas et al., 2016). Leaching of inorganic N is as low as 0.01–0.3 kg ha^{-1} yr^{-1} of N in the closed forest, increases transiently and locally up to 0.5–10 kg ha^{-1} yr^{-1} of N during a few years after clear–felling. Nonetheless, the aggregated effect in larger rivers draining these landscapes is a mere 0.04– 0.3 kg ha^{-1} yr^{-1} of inorganic N (Sponseller et al., 2016). Emissions of N_2O from mineral soils are negligible, except for from local groundwater discharge areas with very low C/N ratios. Thus, the N cycle is in general “tight” in the boreal forests because the low supply of N does not exceed the N demand of trees and soil microbes. This limitation affects the regeneration of tree seedlings, which commonly is poor in closed forests (Aaltonen, 1919; Ruuska et al., 2008; Axelsson et al., 2014).

Can we be sure that this is due to competition for resources in the soil rather than competition for light? Trenching experiments inside forests eliminate the belowground competition by the surrounding trees for nutrients and water without changing the light conditions (Coomes and Grubb, 2000). Trenching promoted vigorous regeneration of pine seedlings (Romell and Malmström, 1945), while eliminating the production of sporocarps of ECMF (Romell, 1938, 1939). Similarly, in an experiment where all trees on 900 m^2 plots were girdled, which terminated their supply of photosynthate C to roots and mycorrhizal fungi (Högberg et al., 2001) there was a successful natural regeneration of pine seedlings. This started before the girdled trees started to lose their needles and the light conditions changed (Axelsson et al., 2014). Hence, in N–poor boreal forests, removal of the belowground competition from large trees and their ECMF mycelia promotes regeneration of tree seedlings.

Scientists making the first observations of this phenomenon a century ago did not have access to stable isotopes for studies of the function of mycorrhizal symbiosis under varying N supply. However, based on observations of the structure of the humus forms in the surficial soil horizon, and patterns of tree regeneration after fellings, they proposed that disturbance of the surficial organic mor–layer was essential for successful regeneration of tree seedlings in N–poor forests (Hesselman, 1926; Romell, 1934, 1935). They considered it necessary to “activate” (to increase the biological activity of) the mor–layer. Romell, although aware of the prevailing notion of mycorrhiza as a symbiosis beneficial for trees, even suggested that severing the C supply to the mycorrhizal fungi was positive for the regeneration by increasing rather than decreasing the N supply to tree seedlings (Romell, 1934, 1935).

Recent research based on ^{15}N tracer studies has revealed an unexpected and dynamic role of ECMF as major immobilizer of soil N in N–poor boreal forests (Näsholm et al., 2013; Hasselquist et al., 2016). The immobilization is the result of a high belowground C allocation by the trees in response to the low N supply, which leads to a large biomass of ECMF and vice versa under higher N supply (Högberg et al., 2010; Högberg et al., 2017). Under N–poor conditions, the ECMF keep much N for their own metabolic needs and fruiting, and transfer little N to their tree symbionts, but under higher N–supply, where N is in excess of fungal demand, more soil N is transferred to the tree canopy (Näsholm et al., 2013). Experimental shading of tree canopies reduced tree photosynthesis and belowground allocation of C to the ECMF, but increased transfer of labelled N from the ECMF to the tree canopy (Hasselquist et al., 2016). Such observations confirm RomelĺS idea about the role of ECMF as agent of N immobilization in N–poor forests. Hence, the above speaks in favour of using rotational silviculture with planting after clear–felling or natural regeneration under a few seed trees in the N–poor systems (high C/N ratio). The introduction of clear–felling has been followed by very substantial increases in forest growth in Sweden (and Norway and Finland). Model analysis suggests that improved management accounts for two–thirds of this increase, while the remaining one–third should relate to climate change (Henttonen et al., 2017), since N deposition is negligible in the north.

Based on the large variations in soil N supply found along the gradient we study, we propose to policy makers that they need to consider that one management system is not optimal for all conditions along the gradient. We advise forest managers to pay attention to where they are along this gradient and the local variations in their region. Equipment to measure soil C/N ratios in the field are not readily available, but the humus forms can be diagnosed directly in the field. The logically consistent results presented here suggest that practitioners could potentially be able to use diagnosis of humus forms to inform decisions about forest management after some training. In that case, we recommend to initially focus on more substantial rather than small differences in soil C/N ratios. With time and increasing experience, a more detailed local interpretation of variations in tree–soil interactions should be possible.

Finally, we call upon fellow scientists to challenge what we have proposed, but also to work more in general on an improved scientific underpinning of the large differences in function between N–rich and N–poor forests. We have already highlighted the paucity of common garden experiments testing the effects of tree species on N–cycling under low N supply. We also note that there is a lack of standardized experiments guiding forest management across large gradients of soil conditions, especially experiments focusing on effects of the presence of large trees for successful generation of tree seedlings. Such experiments should clarify if effects of management are due to alleviation of light or nutrient limitation.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.foreco.2020.118899.

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