INTRODUCTION

The productivity of plants in cold-limited ecosystems principally benefits from global warming causing the ‘Arctic greening’ in the tundra biome (Goetz et al., 2005) and the advancement of many alpine and polar treelines (Esper & Schweingruber, 2004; Harsch et al., 2009; MacDonald et al., 2008). Increased temperatures and improved nitrogen (N) availability as the result of accelerated organic matter decay resulting from a warmer climate trigger this response. The same combination of site factors limiting the productivity in...
boreal forests suggested a greening response to climate warming also in this forest biome (Jarvis & Linder, 2000; Kauppi & Posch, 1985; Myneni et al., 1997). However, remote-sensing studies point to a recent switch of parts of the boreal forests from temperature to drought limitation of productivity (Beck et al., 2011; Buermann et al., 2014). Tree-ring analyses indicate that at least parts of the boreal forests, which were already drought-limited when satellite data of vegetation greenness became widely available in the 1980s, might have switched to drought limitation earlier in the twentieth century with the beginning of climate warming (Babst et al., 2019; D’Arrigo et al., 2004).

Inferences of drought limitation in the published tree-ring and remote-sensing studies generally base on correlation analyses with climate data. This way, a multitude of case studies or biome-wide analyses have been produced suggesting that large parts of the global boreal forest are drought-limited (Lloyd & Bunn, 2007; Tei et al., 2017). Even though the influence of drought is undisputed, these correlation approaches, albeit numerous available, leave open whether N has remained a co-limiting factor for forest growth during the switch from temperature to drought limitation. Mostly, discussion on causalities is focused on physiological responses of the trees’ hydraulic system and its consequences for carbon assimilation, including hydraulic failure and stomatal closure reducing the net carbon gain and ultimately leading to carbon starvation (Anderegg et al., 2015; McDowell et al., 2008). These explanatory approaches imply a dominant role of water constraints in drought-exposed forests, which permits neglecting N as a potential key driver of the trees’ vitality and productivity. Yet, interactions between N and water supply on carbon assimilation in plants and, thus, productivity have been proposed repeatedly (Gessler et al., 2017; Mu & Chen, 2021). The bias towards climatic explanations of tree growth trends in boreal forests is obviously influenced by data availability: While climate data are available from global data sets and local weather stations, databases and supra-regional modelling approaches are not helpful to assess N availability for plants in a biome where the N budget is usually not dominated by atmospheric deposition (Galloway et al., 2008).

Forests at the southern edge of the boreal forest region in Inner Asia grow under highly continental climate with low and highly variable precipitation at the absolute drought limit for boreal forests (Dulamsuren et al., 2010, 2013). Thus, these forests can serve as model systems for conditions that might become more widespread in the boreal forest biome in a warming world. These drought-prone forests are part of the forest-steppe, where forests occur at moist places (preferentially on north-facing mountain slopes) and grasslands at dry sites. The grasslands are populated by pastoral nomads with their livestock grazing the forest edges and the interior of small forests (Lkhagvadorj et al., 2013a, b). We knew from previous studies that the N input from these free-roaming herds of livestock impacts the N content of tree bark and favours nitrophilic lichen species growing on it (Hauck et al., 2012; Hauck & Lkhagvadorj, 2013). Because of the extreme scarcity of arable farming, the lack of intense stationary animal farming, the low human population density with few traffic and industry in Mongolia, the atmospheric N deposition is generally low (Lv et al., 2019). Therefore, we were interested in the question whether the livestock, which was proven to influence the epiphytic lichen vegetation by local N inputs, might even impact the conifer stands of the forest-steppe on an ecosystem level. Therefore, we hypothesized that the livestock influences the N distribution in forests depending on their size and connectivity to grasslands, thereby shapes the forests’ productivity and interacts with the drought response of tree growth. Like in many studies (e.g. Babst et al., 2019; Lloyd & Bunn, 2007; Tei et al., 2017), we took tree-ring width as an indicator of growth and productivity. Although the radial stem increment reflects only one component of tree growth and forest productivity, it provides an informative basis on the variability of these parameters, because stemwood formation integrates a multitude of environmental influences (Zwiefel & Sterck, 2018) and because stemwood is the dominant component determining tree biomass and, thus, also changes in forest biomass (Dulamsuren et al., 2016). With our study relating dendrochronological results to parameters characterizing the forests’ N relations, we, therefore, wanted to give an answer to the question whether N limitation can generally be neglected in drought-limited boreal forests or if there are at least case examples suggesting that N limitation, which is well known from temperature-limited boreal forests (Jarvis & Linder, 2000), remains effective even under heavy drought limitation like in the Mongolian forest-steppe, which might reflect climatic conditions spreading in the boreal forest biome with progressive climate change (Buermann et al., 2014).

2 | MATERIALS AND METHODS

2.1 | Study area

Field work was carried out near Tosontsengel (Zavkhan province, 48°45’ N, 98°16’ E, 1700 m a.s.l.) in Mongolia’s forest-steppe region, ca. 630 km W of Ulan Bator and 550 km SW of Lake Baikal. Boreal forests in Mongolia (ca. 73,800 km²; Dulamsuren et al., 2016) are strongly dominated by Siberian larch (Larix sibirica Lede., covering 75–80% of the country’s total forest area. Therefore, we selected monospecific L. sibirica forests for our study. Principally, the vegetation in Mongolia’s mountainous forest-steppe consists of alternating patches of forests and grasslands of varying size. In this vegetation pattern, forests are basically limited to north-facing mountain slopes and moist valleys, whereas south-facing slopes and dry valleys are occupied by grasslands. The forest-steppe area is populated by mobile pastoralists, who keep mixed herds of sheep, goats, cattle, yak and horses on unfenced common pastures, where the livestock is not much herded. Although the livestock preferentially grazes on grassland, the animals also enter the forest along the edges and further into the interior in small forest stands. The dominant bedrock type in the study region is siliceous rock, including granite and metamorphic rock (e.g. schist). In addition, cover beds of aeolian sand, which can be several meters thick occur on lower slope positions.
Cambisols and Leptosols are the prevailing forest soils. The study area is located in the zone of discontinuous permafrost (Klinge et al., 2021).

2.2 | Climatic conditions in the study region

Meteorological data for the Tosontsengel region were obtained from the CRU TS 4.04 data set edited by the Climate Research Unit of the University of East Anglia, Norwich, and the Met Office in Exeter, UK. Temperature, precipitation and Standardized Precipitation Evapotranspiration Index (SPEI) data were downloaded for the period from 1901 to 2019 from https://climexp.knmi.nl selecting a resolution of 0.5° × 0.5° for the grid field of 48.5–49.0°N and 98.0–98.5°E. The climate in the study area is dominated by the Siberian High, which generates a highly continental dry and sunny climate for most of the year (September to April) and largely limits the inflow of moist air masses to the summer month when the Siberian High has collapsed. Cold winters (mean January temperature −31.2°C) and short summers (July temperature 12.8°C) result in a subzero mean annual temperature of −7.2°C (period 1901–2019). The area has been subjected to rapid climate warming at a rate of 0.48 K decade⁻¹ from 1980–2019, which is much higher than the global temperature increase over land from 1951 to 2012 of 0.12 K decade⁻¹ (IPCC, 2013). Regarding the period 1901 – 2019, it becomes evident that climate warming in the forest-steppe region of Tosontsengel has already exceeded the 2-degree threshold with a temperature increase of 2.5 K or 0.21 K decade⁻¹. Mean temperatures of the twenty-first century (2000–2019) have been distinctly higher with respect to mean annual temperature (−5.9°C) and summer temperatures (July: 14.4°C) compared with the long-term means, whereas winter temperatures have remained unchanged (January: −31.3°C). Mean annual precipitation amounted to 259 mm between 1935 and 2019 and has not changed significantly. Nevertheless, the strong increase in temperature has resulted in more frequent and more intense droughts, as shown by a significant decrease of the one-monthly SPEI since 1901 (Figure 1).

2.3 | Plot design

Our study design was developed to cover the variability of forest stand sizes and forest stand isolation found in the investigated forest-steppe landscape (Dulamsuren et al., 2019). We separated between stand size classes and between a forest-dominated and a grassland-dominated subregion of our study area abbreviated in the following as F and G, respectively. Stand size was varied between four different size classes with ascending size from class F1/G1 (<0.1 km²) via F2 (0.1–1.0 km²) and F3 (1.1–5.0 km²) to F4 (>5.0 km²). In the grassland-dominated subregion, only forests of the smallest stand size (G1) were investigated because larger forests were extremely rare. The realized stand sizes in these classes ranged from 0.07 to 24 km² as detected by remote-sensing analysis of satellite imagery: F1, 0.07 ± 0.02 km²; F2, 0.28 ± 0.09 km²; F3, 2.36 ± 0.48 km²; F4, 23.8 ± 5.4 km²; G1, 0.08 ± 0.01 km². The forest stands of classes F1 to F4 were selected in clusters, where every individual cluster included all four size classes. This way a potential effect of physiographic heterogeneity within the study area should be avoided. The clusters were evenly distributed over the forest-dominated subregion, whereas the individual forest stands of the different size classes were randomly selected from the cluster areas. The plots in the grassland-dominated subregion were randomly selected among the available forest stands of the smallest size class. Selection of clusters and plots was based on remote-sensing analysis of time series of forest distribution in the study region. Forest stands that recently had changed their size class were not selected as sample plots. Sample plots had a size of 20 m × 20 m and were selected in the interior of each forest stand and were all located on north-facing mountain slopes. Although selection was by random, moist depressions, which are not characteristic for most of the forest area, were avoided. In addition, recently burned and logged forest stands were excluded. The outermost 30 m of the forests were excluded from the plot search to avoid bias by direct edge effects. Six replicate plots were selected per forest classes yielding a total of 30 plots. Sampling was conducted during the summers of 2014 and 2015.

2.4 | Stable isotope and C/N analyses

Needle samples were collected from the sun crown of two dominant to subdominant L. sibirica trees per plot in August 2015, dried at 70°C and homogenized in a swing mill. Stable isotope analyses included the δ¹³C and δ¹⁵N ratios and were conducted in the Center for Stable Isotope Research and Analysis, University of Göttingen, Germany. Increasing (less negative) δ¹³C indicates increasing drought stress (Farquhar et al., 1982), whereas high δ¹⁵N
values reveal the opening of N cycle with increasing input of reactive N from outside the ecosystem (Zech et al., 2011). The instrumentation used for these analyses consisted of a Delta plus mass spectrometer, a Conflo III interface (both Finnigan MAT) and an NA 1110 C/N analyser (Carlo Erba Strumentazione). The element analyzer delivers also the total concentrations of C and N in addition to the isotope signatures.

N concentrations and C/N ratios of the soil were determined in 5 soil profiles per sample plot with one profile in each corner and one sampling point in the centre of the 20 m × 20 m plots (Dulamsuren, Klinge, et al., 2019). Sampling included the organic layer and the mineral soil at 0-1 m depth. Soil profiles were dug, and soil samples were taken in the centre of five depth intervals (0–20, 21–40, 41–60, 61–80 and 81–100 cm) with a steel cylinder of 240 cm³. The soil was dried at 70°C and sifted (2 mm mesh size) to remove stones and roots, which were weighted afterwards. Total carbon was determined with the C/N analyser (Vario EL III Elementar) in a subsample of the soil. In another subsample, the organic carbon was released by combustion at 600°C, and the remaining inorganic carbon was measured with the C/N analyser. Organic carbon was determined as the difference of total minus inorganic carbon content and used for calculating the C/N ratio. Another subsample of the soil was dried at 105°C until weight constancy to determine dry weight. N concentrations and C/N ratios for the mineral soil are mean values of the 5 depth segments, whereas the N pool density represents the sum of the stock size from 0 to 1 m depth.

2.5 | Epiphytic lichen recording

Epiphytic lichens were selected as indicators for local nitrogen loads. Lichen communities from L. sibirica forests in the Mongolian forest-steppe had been proven before to respond to reactive nitrogen availability from livestock (Hauck et al., 2012; Hauck & Lkhagavadorj, 2013). Four locally abundant epiphytic lichen species (i.e. Lecidella euphorea (Flörke) Hertel, Melanohalea exasperatula (Nyl.) O. Blanco et al., Physcia dubia (Hoffm.) Lettau, Xanthoria candelaria (L.) Th. Fr.) were selected, which had been identified as indicator species for forest sites that are exposed to moderate livestock densities (Hauck & Lkhagavadorj, 2013). This indicator species system by Hauck and Lkhagavadorj (2013) was based on a study with plot-based epiphytic lichen surveys (including data from 480 L. sibirica trees deriving from 24 plots of 20 m × 20 m in forests from the Mongolian forest-steppe located in the Mongolian Altai and the Khangai Mountains). These epiphytic lichen data were combined with the results of herder surveys, which were based on interviews and the collection of the position of herder camp data from 82 pastoralist households in the Mongolian Altai and 87 households in the Khangai Mountains. With this interdisciplinary approach, the distribution of epiphytic lichen species could be linked with the density of livestock in a fixed radius (1 km) around the sample plot and species characteristic for different livestock densities could be identified with an indicator species analysis after Dufrène and Legendre (1997). Because this indicator system was developed on a broad database from the Mongolian forest-steppe and as the study region in the Khangai was just 150 km apart from our study area, there is no doubt that this indicator system is applicable to our study sites. The influence on the lichen vegetation is through variations in the N supply from livestock excrements (Hauck et al., 2012; Hauck & Lkhagavadorj, 2013). The nitrogen is adsorbed directly from the atmosphere and not indirectly from the tree after root uptake from the soil (Hauck, 2010). Therefore, also effects from potential variations in the distribution of legumes living in symbiosis with N₂-fixing Rhizobium bacteria can be ruled out as a source for the variation in epiphytic lichen distribution. The cover of the selected indicator lichen species was estimated in percent on the lower 2 m of 20 L. sibirica tree trunks of a diameter at breast height (dbh) of ≥15 cm per sample plot. The sample trees were selected by choosing the first 20 tree individuals starting from the lower boundary line of the 20 m × 20 m plots (all located on mountain slopes). The cover of the four study species was summed up per tree for data analysis.

2.6 | Tree-ring data

Published data (Khansaritoreh et al., 2017) of first-order autocorrelation (AC) and mean sensitivity (MS) of radial stem increment and of missing-ring frequency (MRF) deriving from our sample plots were used for correlation analyses with foliar δ¹³C values. Usually, MS, AC and MRF are thought to be primarily controlled by climate (Hoffmann et al., 2018; Rigling et al., 2002). MS and AC describe different aspects of the inter-annual variance within a tree-ring series. The sensitivity quantifies the intensity of the high-frequency variance by calculating the difference in the tree-ring width of consecutive years divided by the mean tree-ring width of the 2 years. These pair-wise sensitivity values are calculated with a moving window for all consecutive years and averaged to MS for the entire tree-ring series. MS has been criticized by Bunn et al., (2013), because it is influenced by AC, but has remained the most widely used parameter for this kind of analyses. AC represents the results of linear Pearson correlations between two consecutive years and is also calculated with a moving window for the whole tree-ring series and subsequently averaged. This value provides information on the tree's ability to buffer stemwood formation from external influences. It is directly relevant to our study because this buffering capacity is primarily constituted by the tree's non-structural carbohydrate (NSC) reserves, which are, in turn, influenced by climate and N availability (von Arx et al., 2017; Li et al., 2018; Zweifel & Sterck, 2018). Both MS and AC were calculated from raw increment data, as standardization attenuates the signal; the formula for MS already includes a relativization in the denominator, when the result for the difference between the examined years is divided by the mean value for these years. MRF represents the
frequency of years where the environmental conditions were so unfavourable that no stemwood was formed and is given as percent value of years per tree-ring series, which is then averaged for all trees of a chronology.

The tree-ring data used for these analyses of MS, AC and MRF have been published in Khansaritoreh et al., (2017) along with a detailed methods description. The sampling design for wood cores was expanded beyond the 20 m × 20 m plots used for the other analyses in the present study to improve the representativeness of the tree-ring chronologies by adding data from a second 20 m × 20 m subplot per stand that was selected close to the first subplot. These data from the two subplots per stand were merged for the analysis. Wood cores from all trees of a 20 m × 20 m plot with a stem diameter ≥3 cm were sampled for tree-ring analysis with an increment borer of an inner diameter of 5 mm at 1.3 m height; wood cores were taken parallel to the contour lines. This way, ca. 1200 tree-ring series from 3 out of 6 of the replicate clusters containing one stand of each stand type were incorporated into the tree-ring chronologies and were also used for analysing the stands’ age structure. There were no significant differences in stand density (c. 1100–1880 trees ha−1), basal area (30–44 m2 ha−1), tree mean age (107–157 years) or maximum age (c. 270–340 years) between the stand types according to Duncan’s multiple range test (p ≤ 0.05; Khansaritoreh et al., 2017), even though this test is very sensitive to detect possible differences.

Tree-ring width was recorded with a Lintab 5 measuring system and Time Series Analysis and Presentation (TSAP)-Win software (Rinntech, Heidelberg, Germany). Cross-dating of the tree-ring series was done to check the quality of the tree-ring counts and to identify missing rings for the determination of MRF. A coefficient of agreement (‘Gleichläufigkeit’ [GL], Eckstein & Bauch, 1969) >65% and a (standard) t-value > 3 were required for integrating a tree-ring series into a mean curve; these criteria were met by ca. 90% of the samples, whereas the remaining samples were rejected for chronology building. GL and t measure the similarity between tree-ring series with respect to high-frequency (GL) and low-frequency (t) variance, respectively. In addition to a chronology for all trees of a stand or stand type, separate chronologies were established for individual age groups referring to the cambial age at 1.3 m above the ground: >160 years, 101–160 years, 61–100 years and ≤60 years. The representativeness of the chronologies for the studied stands was verified by calculating the expressed population signal (Wigley et al., 1984).

### 2.7 Statistical analysis

Statistical testing was done with SAS 9.4 software. Data were tested for normal distribution with the Shapiro–Wilk test. Pearson correlations were used for calculating the strength of linear correlations. Duncan’s multiple-range test was used for multiple comparisons between mean values. Standard errors (SE) are used as dispersion measure throughout the paper.

### 3 | RESULTS

#### 3.1 Stand size affects the forests’ N supply

Selecting forests of different stand sizes (F1 to F4; Figure 2) in the Mongolian forest-steppe, we found that the N supply increased with decreasing forest size. This became evident from narrowing C/N ratios with decreasing stand size in both the forests’ organic layer (r = 0.75, Figure 3) and the mineral soil (r = 0.40, p = 0.03). The increase of foliar N in the dominant tree species, *L. sibirica*, with decreasing stand size was only marginally significant (r = −0.29, p = 0.08).

#### 3.2 Livestock as the source of elevated N levels

Two independent proxies corroborate that the gradient in the forests’ N supply is driven by livestock: foliar δ15N signatures as well as nitrophilic lichens that were used as bioindicators of N deposition. Foliar δ15N decreased from +0.2‰ in the smallest forests (F1: <0.1 km2) to −3.8‰ in the largest forests (F4: >5.0 km2; Figure 4a); positive values are indicative of an open N cycle. The δ15N signatures in F1 forests, which were located like all F forests in a forest-dominated landscape section of the forest-steppe, were identical with those in forests of the same size in a grassland-dominated region (G1; Figure 4a). Yet, the foliar N content was low in the G1 forests (similar to that in F4 stands; Figure 3d), indicating the same source, but lower deposition rates for N in the G1 compared with the F1 forests.

Surveying the abundance of nitrophilic indicator species of epiphytic lichens for high livestock influence in the studied forests, we found that their abundance increased with decreasing forest size (Figure 4b) closely paralleling with the foliar δ15N of the larch trees (Figure 4a). In the G1 forests, epiphytic lichens were indicative of a low livestock pressure, which agrees with the low foliar N content despite an open N cycle (Figure 4c,d). In general, the cover of nitrophilic lichen species on the tree trunks was closely correlated with the larches’ foliar N content (Figure 4d).

#### 3.3 Interrelations between soil C/N, foliar N and stable isotope signatures

The substratum C/N ratio became narrower with increasing foliar δ15N, proving better N nutrition at sites with open N cycle due to fertilization by livestock. This relationship was closer in the intensely rooted organic layer (r = −0.72; Figure 5a) than for the mineral soil (r = −0.40, p = 0.01). Narrow C/N ratios in the organic layer (Figure 5b) and the mineral soil (Figure 5c) were associated with high foliar N content. Positive correlation of foliar N and δ15N (Figure 5d) confirms the beneficial effect of N deposition from livestock for the trees’ N supply.
3.4 | N supply interacts with the trees’ sensitivity to drought

The results of stable isotope analysis show that MS and AC were more closely related to N metabolism than to drought, which was the dominant climatic factor influencing tree growth in our study region. This remarkable finding was in line with the fact that the linear correlation of stand size was closer and the slope of the regression line steeper for foliar $\delta^{15}$N compared with the correlation with foliar $\delta^{13}$C (Figure 6a,b). MS increased with increasing foliar $\delta^{15}$N with correlation coefficients as high as $r = 0.99$ for mature trees with an age between 61 and 160 years (Figure 6c). Older trees showed a weaker, but still a close relationship ($r = 0.89$). The corresponding relationships with $\delta^{13}$C were not significant (Figure 6d).

With AC, linear correlations occurred both for $\delta^{15}$N and $\delta^{13}$C, but those for $\delta^{15}$N were closer than the relationships for $\delta^{13}$C at least for the age classes from 61–100 and 101–160 years (Figure 6e,f); for the >160-year-old trees, $r$ was −0.81 for $\delta^{15}$N and −0.83 for $\delta^{13}$C. Correlations with both $\delta^{15}$N and $\delta^{13}$C were negative. Furthermore, MRF increased with $\delta^{15}$N (Figure 6g), but was not significantly related to $\delta^{13}$C (Figure 6h). Multiple regression with $\delta^{15}$N and $\delta^{13}$C confirmed that adding $\delta^{13}$C to the model did not explain much more of the variance of MRF (multiple regression $[\delta^{15}$N, $\delta^{13}$C]: $R = 0.88$ vs. univariate regression $[\delta^{15}$N]: $r = 0.81$).

3.5 | N and soil organic carbon stocks

The soil organic carbon (SOC) stock density, which is critical in the role of boreal forests for climate change mitigation, increased with increasing total N stock density in the soil (Figure 7).

4 | DISCUSSION

4.1 | Relations between N supply, drought, tree growth and carbon stocks

Our results demonstrate that the productivity in drought-prone boreal forests is not solely controlled by water availability, but that N supply, which is well known to be co-limiting for temperature-limited boreal forests (Höglberg et al., 2017; Lupi et al., 2013), remains a crucial factor even at sites, which are regularly exposed to intense and prolonged drought spells. Even though conifer forests at the southernmost edge of the boreal forest in Inner Asia suffer from strong drought limitation of growth and regeneration and are subjected to...
a rapid increase in drought-induced mortality (Khansaritoreh et al., 2017; Liu et al., 2013), we found even tighter relations of tree growth with \(\delta^{15}N\) reflecting variations between the stands in the importance of external influences on the N cycle (Zech et al., 2011) than with \(\delta^{13}C\), which is an indicator of drought stress (Barber et al., 2000; Linares & Camarero, 2012; Walker et al., 2015). The low negative \(\delta^{15}N\) values in the large forests indicate a closed N cycle with most plant-available N deriving from stand-internal organic matter decomposition (Emmett et al., 1998; Zech et al., 2011). By contrast, the positive \(\delta^{15}N\) values in small stands are the result of an open N cycle with significant amounts of N transferred from outside into the ecosystem (Eshetu & Högberg, 2000; Swap et al., 2004). The \(\delta^{15}N\) is not affected by the animal stocking rate (Wittmer et al., 2011) in agreement with similar \(\delta^{15}N\), but divergent N concentrations in the F1 and G1 forests, as the latter were exposed to lower livestock densities. N availability was also a determinant of SOC stock density, which matches with earlier findings that SOC accumulation in forest soils increases with narrowing C/N ratio (Mellilo et al., 2011; Zhou et al., 2019).

The absence of other major sources for N (including atmospheric long-distance transport) in the remote Mongolian forest-steppe suggests that the grazing livestock is the external N source. Bioindication with epiphytic lichens confirms this view. By combining socioeconomic survey data from herder interviews with biodiversity data, earlier work showed that epiphytic lichens on the larch trees in the forests can serve as reliable indicators of average livestock density (Hauck & Lkhagvadorj, 2013). Elemental analysis of tree bark and the existing knowledge of the ecological preferences of the lichen species evidenced that variations in the local N deposition by the livestock was the causal link between livestock density and the occurrence of these indicator species (Hauck et al., 2012, 2014).
Correlation analyses of tree-ring parameters and stable isotope signatures show that N relations, rather than drought stress were crucial for the higher MS and MRF in small forests compared with large forest stands. Although usually high MS and MRF in drought-limited forests are interpreted as the primary result of sporadic periods with distinct water shortages (Liang et al., 2016; Novak et al., 2016; Rigling et al., 2002), the relationships to foliar $\delta^{13}C$, where high (less negative) values are the result of increased drought stress, reduced stomatal conductance and, thus, increased assimilation of $^{13}$CO$_2$ in the Calvin cycle (Farquhar et al., 1982), were all not significant (Figure 6d,h). Reduced AC with increased drought stress (i.e. increased $\delta^{13}C$) was to be expected, as the trees’ NSC reserves are exhausted in periods of low stomatal conductance, while the NSC reserves are the material prerequisite of constant growth (generating high AC) during alternating environmental conditions (von Arx et al., 2017). However, the correlation of AC with $\delta^{15}N$ was even
closer than with δ13C, pointing to a prominent role of N for replenishing the trees’ NSC pool. High AC is not an indicator of faster, but more constant growth, which is in line with high AC being associated with low δ15N, because the latter indicates a closed N cycle. The N supply from mineralization can be expected to be less variable than from the input by livestock, which might be highly variable due to random fluctuations in the local livestock density given the variable stocking rates in the Mongolian forest-steppe (Lkhagvadorj et al., 2013a, b; Takatsuji & Morinaga, 2020). The only marginally significant relationship of foliar N with forest size (in contrast to significant correlations between forest size and the C/N ratios in the organic layer and the mineral soil) portends that only parts of the surplus in available N in the small forests was allocated in the foliage to enhance the photosynthetic capacity, whereas another fraction was invested in growth (Aaltonen et al., 2017; Roth et al., 2021).

4.2 | Possible mechanisms for the impact of N supply on radial stem increment

The close association of high MS with high δ15N (and the latter with high foliar N content and narrow C/N ratios in the organic layer) suggests that the high growth variability boosting the MS value is even more triggered by pulses of N than by alternating dry and wet phases, because a dominant drought effect should have left an imprint by a close positive correlation between MS and δ13C, which was not found (Figure 6d). The significance of N for controlling MS suggests an important role of N-mediated variations in the NSC pool for growth variability, which is in line with a strong positive effect of N fertilization on wood NSC concentration observed in various tree species (Li et al., 2018). A critical role of the NSC reserves agrees with the observation that negative growth extremes in treering chronologies from these boreal forests are often responses to previous, but not current year’s droughts (De Grandpré et al., 2011; Dulamsuren et al., 2013; Khansaritoreh et al., 2017). Furthermore, this assumption matches with a fairly embolism-resistant xylem architecture of L. sibirica (Dulamsuren, Abilova, et al., 2019), which efficiently acclimates to inter-annual and site-dependent variations in moisture availability (Chenlemuge et al., 2015).

The most likely explanation for the link between N supply and NSC content (and growth) is the well-known capacity of N deficiency to reduce stomatal conductance (gₛ) by triggering stomatal closure (Ghashghaie & Saugier, 1989). Although it is unclear if this is the only pathway behind the influence of plant N on gₛ, Chapin et al., (1988) and Mu et al., (2018) could demonstrate that N deficiency stimulates the synthesis of abscisic acid (ABA), which is signalling the initiation of stomatal closure in the guard cells (Pantin et al., 2013). Radin and Ackerson (1981) demonstrated in cotton plants (Gossypium hirsutum) that N-deficient plants reduced gₛ earlier with the onset of experimentally induced drought conditions (at leaf water potentials far above the wilting point) than well-N-supplied individuals. Low gₛ results in low leaf-internal CO₂ concentrations (Cᵢ) and consequently the limitation of carboxylation by low Cᵢ (Broadley et al., 2001). Lowered CO₂ assimilation in the Calvin cycle depletes the plant’s NSC pool and the subsequent use of this reservoir for wood formation. If occurring over extended periods, it can ultimately even lead to death known as carbon starvation (Sevanto et al., 2014). It remains the question why gₛ is downregulated under N deficiency, even though the direct effect of gₛ is exerted on CO₂ uptake and transpiration, but not N metabolism. The most plausible answer to this question is the fact that slow growth in concert with low photosynthetic carbon gain is a key mechanism for preventing plants from nutrient imbalances and the development of nutrient deficiency symptoms; slow growth is, therefore, prevalent among plants from all low-resource environments (Chapin, 1991). This explanation is in line with an inhibitory effect of N deficiency on cell division and cell elongation at least in leaves (Broadley et al., 2001).

The depletion of the NSC pool is further triggered by increased protein degradation to free amino acids and finally soluble non-protein N (NPN) under N shortage (Fotelli et al., 2002; Gessler et al., 1998). This process, albeit improving the momentary plant-internal N availability, entails repair costs at the expense of the NSC reserves (Gessler et al., 2017; McDowell et al., 2008). The availability of N also affects assimilate production and growth by controlling the amount of proteins, which can be synthesized for photosynthesis (Reich et al., 1997); around 80% of the foliar N are reserved for photosynthesis (Evans & Seemann, 1989). However, the fortification of the light and dark reactions of photosynthesis by increased N supply is primarily relevant under high light conditions near light saturation to enhance the photosynthetic capacity (Aₘₐₓ), but not at lower photon flux density (Broadley et al., 2001). Therefore, though the influence of N on both gₛ and Aₘₐₓ might have become effective, it is likely that the control of gₛ was more relevant to influence growth variability of the L. sibirica stemwood. Moreover, an improved N supply could also enhance the trees’ capability for osmotic adjustment by boosting free amino acid production (Li et al., 2020) and intensify the defence against herbivores and pathogens (Simon et al., 2010). In addition to amino acids (especially proline: Hayat et al., 2012; Vance & Zaerr, 1990), nitrate ions also serve as osmolytes (Cárdenas-Navarro et al., 1999).

Higher MRF just in the better N-supplied forests seems to contradict a role of N for fostering tree growth. Yet, these forests are again also exposed to more variable N supply with open N cycles depending on random N deposition by livestock. High variability in the N supply could lead to imbalances in the biomass allocation to the foliage, the root system and water-conducting wood (Tarvainen & Näsholm, 2017), which could increase the tree’s vulnerability to drought and result in the complete failure of wood formation in individual years. The results of our analysis even seem to deny any direct drought influence on MRF, because the correlation between foliar δ13C and MRF was not significant. However, this result should be interpreted with care, as this correlation was based on only five data points for the five stand types. It is likely that a data set with more data points would have revealed a significant relationship. Nonetheless, it is clear from our analysis that the relationship of MRF with δ15N (Figure 6g) was closer than that with δ13C (Figure 6h). The
special setting in the Mongolian forest-steppe with variations in livestock pressure and thus N input on small spatial scales explains the dominant δ15N impact on MRF. In regions with more homogeneous N deposition (e.g. from air-borne, long-distance transport), it is plausible to assume a higher relative influence of climate on MRF when trees or stands of the same region are compared, but not necessarily between regions of different N deposition levels. While climate has always been seen as the key driver for MRF (Khishigjargal et al., 2014; Liang et al., 2016), any major contribution of variations in the N supply is unexpected and deserves further study. Khansaritoreh et al. (2017) took increases in MRF between the periods of 1900–1969 and 1970–2014 especially in the smallest forests (F1, G1) as a sign of increased aridity, whereas MRF remained constant in the largest forests (F4) over time. This interpretation is plausible given the decrease in SPEI during this period (Figure 1), but could have also been influenced by the strongly increased livestock numbers in the Mongolian forest-steppe since 1990 (Lkhagvadorj et al., 2013b).

Widespread increases in the productivity primarily of temperate, but also boreal forests, have been partly attributed to the increased atmospheric deposition of reactive N (Etzold et al., 2020; Schulte-Uebbing & de Vries, 2018; Thomas et al., 2009). These productivity increases are mostly the result of a combination of increased N deposition, management changes, climate warming and CO2 fertilization (Gedalof & Berg, 2010; Pretzsch et al., 2014). The N-related components are usually attributed to increases in Amax due to the augmentation of photosynthesis-related proteins and to increases in the leaf biomass (Fleischer et al., 2013). Most of these studies refer to temperate forests under much more favourable climatic conditions for tree growth and to higher deposition levels (e.g. up to a maximum of 40–60 kg N ha−1 a−1 in the study of Etzold et al., 2020) than in the Mongolian forest-steppe. Nitrogen deposition data are not available from our study area, but Lv et al., (2019) found 5.7 kg N ha−1 a−1 for steppe grassland in southwestern Mongolia. The total deposition in that area was dominated by the dry deposition of ammonia, followed by wet ammonium deposition. That study area was in close neighbourhood to arable land, which received a total deposition of 9.4 kg N ha−1 a−1. In our study area, the climate is too cold for arable farming, it is lowly populated, traffic is sparse and industry virtually lacking. Therefore, it is likely to assume an annual N deposition, which is even below 5.7 kg N ha−2 a−1. Here, the higher local N deposition from livestock in small forests was not high enough to cause higher annual stem increment compared with larger forests, as the mean annual stem increment was the same across forest types (Khansaritoreh et al., 2017), but it was apparently sufficient to compensate for the drier and warmer summer climate with decreasing forest size. The N-induced increases in the leaf area index (LAI) in temperate forests can increase the trees’ drought sensitivity by decreasing the ratio between LAI and the fine-root surface area (Gessler et al., 2017) and by its influence on the Huber value (i.e. the ratio between the sapwood cross-sectional area and the LAI; Carter & White, 2009). With respect to the tolerance of climate change-induced drought, the development of high LAI values is apparently a particular problem of shade-tolerant, late-successional tree species, which develop a large crown with extra-large LAI not only for photosynthesis but also for generating shade to exclude more light-demanding competitors (Leuschner, 2020). We do not have any LAI measurements available from our sample plots, but as larch is a strongly light-demanding tree and given the fact that we examine the effects of relatively low amounts of N deposition in our study, it is likely to assume that the temporarily and spatially varying N addition by livestock excrements exerts its main effect on gS, perhaps partly also on the amplification of photosynthesis-related proteins, but probably less likely on a significant increase in the LAI.

4.3 Regional and global implications for boreal forests

As even these strongly drought-exposed forest ecosystems in the Inner Asian forest-steppe revealed a pronounced influence of N availability on stemwood formation, it is safe to assume a general influence of N in boreal forests, regardless whether low temperatures or drought are the dominant climatic factors. The close relations of δ15N that were found with MS, AC and MRF suggest that a strong drought impact does not weaken the influence of N. On the contrary, since drought is inhibiting N mineralization (Beier et al., 2008), the magnitude of N limitation is likely to increase with increasing drought exposure (as with increasing cold in temperature-limited systems) (Kreuzwieser & Gessler, 2010). The much closer relationships with δ15N than δ13C in our study unveils that tree-ring and remote-sensing analyses, which attribute boreal forest productivity dominantly to drought (or temperature) (Babst et al., 2019; Barber et al., 2000; Beck et al., 2011; Dulamsuren et al., 2013), might sometimes miss an even stronger impact of N availability. A strong control by N could be the reason why correlation coefficients in climate-response analyses of annual stem increment are often relatively low despite frequent and strong drought exposure.

The Inner Asian forest-steppes are perfect model systems to demonstrate the influence of N on radial stem increment as an indicator of the productivity of drought-prone boreal forests, because in these specific environment livestock generates local gradients in N deposition. Since this deposition is highest in small forests, which are at the same time most strongly drought-exposed (Khansaritoreh et al., 2017), our data suggest that the present way of mobile pastoral livestock husbandry mitigates the forests’ vulnerability to drought in a rapidly changing climate (Tarvainen & Näsholm, 2017). This point is interesting, as livestock has so far only been discussed as a burden for the multiply stressed boreal forests in Inner Asia with respect to its detrimental impact on forest regeneration (Khishigjargal et al., 2013). Here, we show also beneficial effects for forest health and for maintaining or augmenting SOC stocks, which are critical for the boreal forests’ pivotal function in the global climate system. Severe drought limitation of forest productivity and forest health is preferentially found in the southern boreal zone (Liu et al., 2013; Peng et al., 2011), where (in contrast to most boreal forests) anthropogenic N deposition also has become relevant (Galloway et al., 2008).
Therefore, drought-nitrogen interactions can be expected to be an important global driver of forest productivity and vitality in the southern boreal zone.

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DATA AVAILABILITY STATEMENT
Data will be available on request from the authors.

CONFLICT OF INTERESTS
The authors declare no competing interests.

AUTHOR CONTRIBUTIONS
Both authors developed the concept, carried out field work, analysed data and wrote the paper.

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