

# Boreal forest biomass accumulation is not increased by two decades of soil warming

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**Increased soil organic matter decomposition with increasing temperature has been hypothesized to enhance soil nitrogen availability, consequently stimulating forest biomass production and offsetting decomposition-induced soil carbon losses<sup>1–5</sup>. This projection, however, is based on evidence gathered from short-term studies ( $\leq 10$  years)<sup>2,3,5</sup>. The key question for carbon sequestration is whether such responses are transient or persist over long forest rotation periods. Here we report on biomass production in a typical nitrogen-limited boreal *Picea abies* forest, exposed to 18 years of soil warming manipulation ( $+5^{\circ}\text{C}$ ) at a plot scale ( $100\text{m}^2$ ). We show that two decades of soil warming elicited only short-duration growth responses, thus not significantly increasing aboveground biomass accumulation. Furthermore, in combination with published work from this forest, our results suggest that increased decomposition is slight and ephemeral, and increased fine root production and turnover in deeper soil may be greater than increased decomposition, netting slightly more biomass, perhaps conserving the soil carbon stock. Thus, this long-term study does not support the notion that the projected increase in soil temperatures will cause either an increased carbon loss with decomposition or a compensatory growth increase from nitrogen mineralization.**

Increasing global temperatures due to anthropogenic greenhouse gas emissions can stimulate decomposition of soil organic matter, causing feedback positive feedbacks affecting future climate<sup>6–8</sup>. Boreal soils, containing the largest global organic carbon (C) pool<sup>9,10</sup>, are expected to release large quantities of C to the atmosphere in response to increased soil temperatures<sup>6,7</sup>. However, increasing decomposition would also promote nitrogen (N) mineralization, potentially leading to enhanced biomass production in the often N-limited boreal forests<sup>11,12</sup>. This could, therefore, partly or fully offset C losses from enhanced decomposition<sup>4,5</sup>. Indeed, experimental soil warming improved biomass productivity by up to 100% within the first decade in northern temperate hardwood<sup>5</sup> and boreal forests<sup>2,3</sup>, and such a compensating response has now been incorporated in Earth system models<sup>1,13</sup>.

For projections of forest C balance in a future climate, however, the key question is whether such strong increases in production persist over extended periods or are transient, as may be the case for decomposition and N mineralization, due to thermal acclimation of soil microbes to higher temperatures and depletion of labile soil organic matter<sup>14</sup>. If the effect on growth enhancement is in keeping with decomposition and the resulting N mineralization, be it ephemeral or persistent, the effect of warming on the C balance

may not be large. If, however, the warming effect on decomposition persists longer, or is greater than that on growth, C release from decomposition may overwhelm the capacity of the forest to sequester new C.

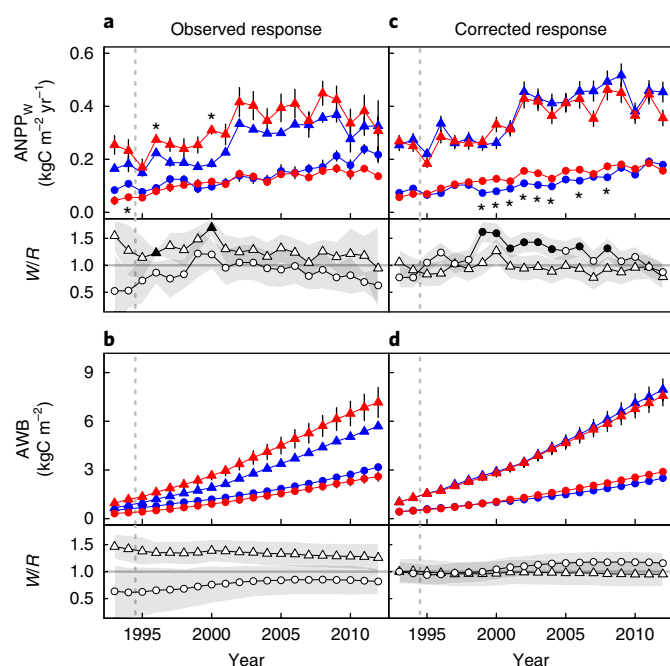
Our study, one of the few sufficiently long to allow assessment of the response of slow processes<sup>15</sup>, aimed at quantifying biomass production and N nutrition of trees exposed to soil warming for almost two decades in four  $100\text{m}^2$  sub-plots located in a nutrient-limited (unfertilized) plot and four in a nutrient-rich (fertilized) plot ( $1,000\text{m}^2$  each)<sup>16</sup>. As tree nutrition in the fertilized plots was kept at optimal levels<sup>17</sup>, a positive growth response to soil warming should reflect processes related to phenology, spring recovery of photosynthesis and length of growing season, rather than nutrition. The response of unfertilized plots should reflect the combined effects of warming on nutrient supply and the factors mentioned above.

As soil warming may lead to enhanced evaporation, all experimental plots were irrigated to eliminate an interaction with soil water availability. Aboveground net primary production of wood biomass ( $\text{ANPP}_w$ ) was estimated on the basis of a combination of annual measurements of tree dimensions and allometric functions based on a final harvest of sample trees (Supplementary Table 1). Tree N uptake and its source were examined on the basis of foliar N content<sup>17</sup> and natural stable isotope abundance ( $\delta^{15}\text{N}$ )<sup>18</sup>.

Before the commencement of warming,  $\text{ANPP}_w$  and standing biomass were different between soil warming and reference plots (Fig. 1a,b). Hence, to quantify the likely effect of soil warming on  $\text{ANPP}_w$ , we assessed the responses in two ways: observed  $\text{ANPP}_w$ ; and  $\text{ANPP}_w$  corrected for the pre-treatment differences using individual tree biomass from the larger nutrition experiment<sup>12</sup> ( $n=4$  plots of  $1,000\text{m}^2$  per treatment) as input to a size-relative production rate (for detailed methodology, see Methods).

In the fertilized plots, soil warming appeared to affect  $\text{ANPP}_w$  (significantly in only two years; Fig. 1a) but not the accumulation of aboveground wood biomass (AWB; minimum  $P=0.111$  in 2000; Fig. 1b). These responses were no longer detectable once the analyses accounted for pre-treatment differences in both variables (Fig. 1c,d). The observable effect of soil warming on  $\text{ANPP}_w$  in the unfertilized plot and the corresponding lack of growth response to soil warming in the fertilized plot suggests that the effect of soil warming on  $\text{ANPP}_w$  was mediated via soil nutrient availability (Fig. 1c); therefore, ecosystem responses obtained from the unfertilized plots probably reflect the effects of warming on nutrient availability, in particular N (refs. 2,11). In the unfertilized plot, the warming effect on  $\text{ANPP}_w$  corrected for initial differences,

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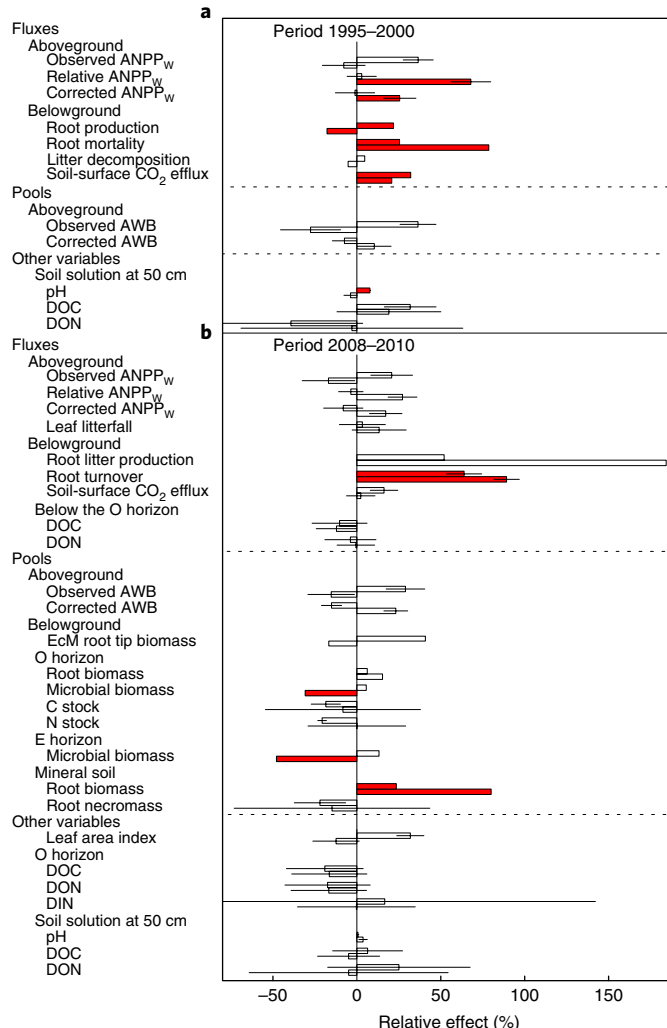


**Fig. 1 | ANPP<sub>w</sub> and AWB.** **a–d**, Observed ANPP<sub>w</sub> (**a**) and AWB (**b**) and corrected ANPP<sub>w</sub> (**c**) and AWB (**d**) for the pre-treatment differences, and their relative values in soil warming to the reference ( $W/R$ ) below each panel. Symbols indicate fertilized (triangle), unfertilized (circle), reference (non-heated; blue) and soil warming (red); the vertical dashed line indicates the initiation of soil warming treatment (April 1995); the error bars are standard errors ( $n = 2$  for observed and 4 for corrected). The asterisks indicate a difference between the reference and the soil warming plot (unpaired two-sample  $t$ -test,  $P < 0.05$ ); grey areas are 95% confidence intervals and filled symbols indicate a significant difference from 1 (one-sample  $t$ -test,  $P < 0.05$ ). Details of the correction for the pre-treatment differences are provided in the Supplementary Information.

persisted for a decade (Fig. 1c), yet was not sufficiently long or of sufficiently large magnitude to give rise to a greater AWB during the observed two decades (Fig. 1d;  $n = 4$ , minimum  $P = 0.160$  in 2009), reflecting a transient response. Therefore, either through conservative (observed) or liberal (corrected) scope of inference, our data do not support the expectation that enhancement of biomass production will offset soil C loss in response to warming soil in similar boreal forests.

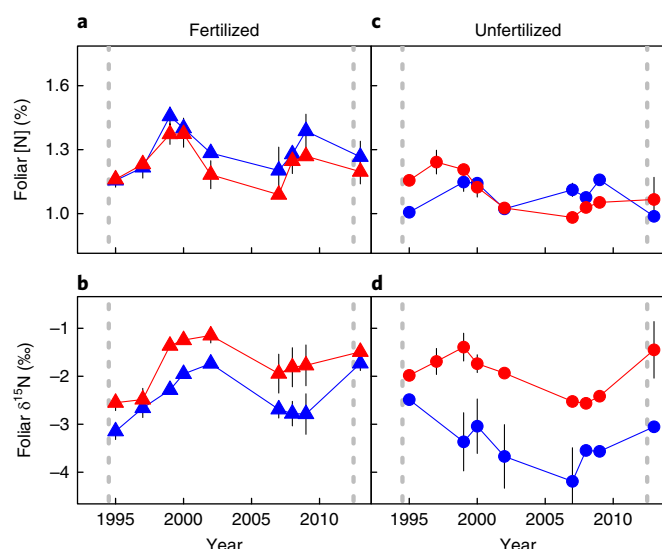
In the responses observed in the unfertilized plot early in the study (Fig. 1a), warming-induced extra ANPP<sub>w</sub> increased by  $44.6 \pm 19$  (s.e.) gC m<sup>-2</sup> yr<sup>-1</sup> averaged over the fourth and fifth years. In the fifth year, soil-surface CO<sub>2</sub> efflux was 110 gC m<sup>-2</sup> yr<sup>-1</sup> higher in the warmed plots<sup>19</sup> (Fig. 2a and Supplementary Table 2), consistent with the notion that increased decomposition supplied the necessary N to eliminate the pre-treatment difference in ANPP<sub>w</sub>.

The efficiency of N addition in producing ANPP<sub>w</sub> obtained from the Flakaliden nutrient optimization experiment, where this study was conducted, was 33.4 gC g<sup>-1</sup> N added as fertilizer<sup>12</sup>. According to this, and the observation that soil warming did not increase N exports through leaching (Fig. 2 and Supplementary Fig. 2), the increased production of  $\sim 45$  gC m<sup>-2</sup> yr<sup>-1</sup> in the warmed, unfertilized plots would require approximately 1.3 g m<sup>-2</sup> yr<sup>-1</sup> extra N. However, this is probably an overestimate because the efficiency of N utilization for growth is most likely lower where N is added as fertilizer than N released from mineralization. The N content of the humus layer (O horizon), litter input<sup>20</sup>, and litter decomposition rates<sup>19</sup> were unaffected by warming (Fig. 2), suggesting that the extra N needed



**Fig. 2 | Synthesis of responses to soil warming.** **a, b**, Relative soil warming effect on above- and belowground C and N fluxes, pools and other stand structural and soil chemical variables during the early period (1995–2000) (**a**) and following long-term warming (2008–2010) (**b**) in fertilized (upper bars) and unfertilized (lower bars) plots. The relative effect,  $(W - R)/R$ , where  $W$  is warming and  $R$  is reference conditions, was determined on the basis of the present study and on earlier published results from the experiment. Relative ANPP<sub>w</sub> is the normalized size-relative production rate (Supplementary Fig. 1). The red-coloured bars indicate a significant difference from 0 (two sample  $t$ -test,  $P < 0.05$ ); the error bars are standard errors; detailed information and sources are provided in Supplementary Table 2. DOC, dissolved organic carbon; DON, dissolved organic nitrogen; DIN, dissolved inorganic nitrogen; EcM, ectomycorrhizal.

was derived from the top 10 cm of mineral soil below the heating cables, where more than 80% of the fine roots were found<sup>21</sup>. Using the C and N stocks of the O horizon and top of the mineral soil, and the reported ratio of heterotrophic (decomposition) to total soil-surface CO<sub>2</sub> efflux from these layers ( $\sim 0.5$ )<sup>22</sup>, with no detection of N losses through leaching (Fig. 2), N release through mineralization could amount to  $\sim 2$  gN m<sup>-2</sup> yr<sup>-1</sup>, which is at the lower end of reported values of the first decade of soil warming experiments in northern forests<sup>4,5</sup> (1.2–6.1 gN m<sup>-2</sup> yr<sup>-1</sup>). This amount is enough to support the warming-induced production rise necessary to close the negative gap with the reference plot, and may be taken as support for the assumption that N mineralization may be involved in the initial response to warming. However, further analysis of



**Fig. 3 | Nitrogen in foliage.** **a–d**, Foliar N content and  $^{15}\text{N}$  natural abundance in fertilized (**a,b**) and unfertilized plots (**c,d**). Symbols: fertilized (triangle), unfertilized (circle), reference (non-heated; blue) and soil warming (red). The dashed lines indicate the initiation (April 1995) or termination of soil warming (September 2012). The error bars are standard errors ( $n=2$ ). Detailed statistical results are given in Supplementary Table 3.

published data from the earlier work on the same experiment (Fig. 2 and Supplementary Table 2, references therein) suggests that enhanced N mineralization, if induced, was ephemeral.

In the second decade of the treatment, fertilization increased tree N uptake ( $P < 0.001$ ; Fig. 3), leaf area index, needle litterfall and the C and N stocks of the O horizon<sup>20</sup> (Supplementary Table 2). Soil warming, on the other hand, had no significant effect on these values (Fig. 2b), hence not supporting the suggestion of increased N availability ( $P = 0.920$  for the warming effect on foliar N content; Fig. 3c). Moreover, an appreciably higher decomposition rate in the warming plots should, over time, have resulted in a smaller steady-state C pool in the O horizons of these plots, thus reducing N supply even if the decomposition rate remained higher.

In this N-limited forest, warming produced a short-term increase in soil  $\text{CO}_2$  efflux<sup>19</sup> and fine root mortality rate<sup>23</sup>, as observed in the second and third years of the treatments (Fig. 2a). After the first decade of warming treatment (Fig. 2b), however, warming-induced enhancement of soil-surface  $\text{CO}_2$  efflux diminished<sup>24</sup>, probably as an effect of an acclimation associated with the observed change in composition of the microbial community and reduction of microbial biomass<sup>24</sup>. This type of transient response was also observed in a northern temperate hardwood forest, exposed to a 26-year experimental soil warming<sup>15</sup>; a large enhancement of decomposition with commencement of soil warming disappeared within the first decade, remaining negligible for an additional decade, and returning in the third decade, but at lower enhancement. This suggests that increased decomposition and N mineralization, similar to growth responses observed after the commencement of warming experiments<sup>2,5</sup>, may not persist. However, in contrast to having little effect on wood biomass accumulation, warming may have resulted in a slight increase of C stock in the mineral soil by  $\sim 10 \text{ gC m}^{-2} \text{ yr}^{-1}$ , because warming (as opposed to fertilization) increased fine root biomass by  $72 \text{ gC m}^{-2}$  over 18 years despite doubling the turnover rate in that layer<sup>21,25</sup>, without increasing losses of C through decomposition<sup>22,24</sup> or through export of dissolved organic C (Fig. 2b). This is inconsistent with the observed similarity of fine root necromass between the treatments<sup>21</sup>; however, this similarity can be questioned

because fine root necromass is very difficult to separate from other soil organic matter components<sup>26</sup>.

Our data support the notion that a shift of tree N uptake from the top organic layer to deeper in the soil occurred as a response to soil warming. This is corroborated by a higher foliar  $\delta^{15}\text{N}$  (especially under native soil fertility,  $P = 0.002$ ; Fig. 3d) in warmed plots, a response that is consistent with root N uptake from the  $^{15}\text{N}$ -enriched, deeper soil horizons<sup>18</sup>. However, a higher foliar  $\delta^{15}\text{N}$  could also be mediated through ectomycorrhizal fungi<sup>18</sup>. Indeed, soil warming decreased ectomycorrhizal root tip biomass 17% under native soil fertility<sup>21</sup> (Fig. 2b), suggesting a reduced role in N uptake by the fungi. A reduction in the role of mycorrhizal fungi in N uptake is not consistent with higher N availability as reflected in foliar N concentration (Fig. 3). It is thus conceivable that, at the early stage of the experiment, warming-induced higher foliar  $\delta^{15}\text{N}$  under the unfertilized soil condition was due to stimulated N mineralization<sup>18</sup>, and following the depletion of the labile N pool of the shallow horizon (and perhaps decreased mycorrhizal role in N uptake), roots proliferated and acquired N deeper in the soil.

Soil warming studies, lasting  $\leq 10$  years, have reported a strong response of biomass productivity in northern temperate<sup>5</sup> and boreal forests<sup>2,3</sup>. In line with these reported responses, we also observed a more than twofold greater relative growth rate in the fifth and sixth years (Supplementary Fig. 1), yet during the entire treatment period, warming resulted in no greater accumulation either in AWB (Fig. 1b) or in total biomass including foliage, coarse- and fine-root biomass ( $P = 0.190$  in 2009). Even the liberal estimates showed negligible enhancement of  $\text{ANPP}_w$  (Fig. 1d), mostly reflecting normalizing and scaling operations. Assuming a second phase of decomposition increase over an additional decade<sup>15</sup> and employing our negligible response of biomass production would still have a marginal effect on biomass accumulation over a century-long rotation. Considering that the experimental protocol prevented soil drying and thus retardation of decomposition, the impact of a warmer climate on biomass accumulation may be even smaller. Thus, our analysis not only casts doubt on the potential of soil warming to increase both decomposition<sup>27</sup> and growth, but also highlights the need to tailor the length of experiments to an extended period in the life of a forest. In the very long boreal ecosystem succession (or management rotation), the duration of studies needed to understand whether a factor will permanently alter ecosystem function and structure, or will induce only a short-lived effect, must be much longer than a decade.

Nitrogen limitation curtails the response of forest biomass production to projected changes such as increased temperature and atmospheric  $\text{CO}_2$  concentration<sup>28,29</sup>. Consistent with these observations, Earth system models project an increased growth-related C pool sponsored by extra N released from warming-induced increase in soil organic matter decomposition as a compensatory mechanism for C loss from that same pool<sup>1,13</sup>. Our study does not support such a compensatory response, nor did earlier studies at our site detect a large increase in decomposition<sup>19,22,24</sup>. Indeed, warming could have increased the C stock of the mineral soil with increasing fine root biomass and turnover, without a similar increase in decomposition.

### Online content

Any methods, additional references, Nature Research reporting summaries, source data, statements of data availability and associated accession codes are available at <https://doi.org/10.1038/s41558-018-0373-9>.

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## Author contributions

S.L. established the experiment in 1994, and designed the present study together with H.L., T.N. and R.O. H.G. collected and analysed the water from the lysimeters. H.L. performed all of the final fieldwork. H.L. and R.O. processed the data, crafted the argument and wrote the paper with input from T.N., S.L., M.S. and T.L. All authors discussed the results and commented on the manuscript at all stages.

## Competing interests

The authors declare no competing interests.

## Additional information

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## Methods

**Setting.** The study was conducted within the Flakaliden long-term nutrient optimization experiment in northern Sweden (64°07'N, 19°27'E, 310 m a.s.l.). The main experiment was established in 1986 in a 25-year-old Norway spruce (*Picea abies* L. Karst.) forest to quantify the potential production by optimizing nutrient and water supply in replicated ( $n=4$ ) 2,500 m<sup>2</sup> plots surrounded by a 10-m-wide buffer zone. The net plots of 1,000 m<sup>2</sup> were used for sampling and measurements<sup>17</sup>. Stand density in 1986 was ~2,400 stems ha<sup>-1</sup>.

The soil is glacial till, a thin, podzolic, sandy soil, with an average depth of 120 cm, and the thickness of the humus layer varies between 2 and 6 cm. The soil is nutrient-poor, reflecting the short stature of even dominant trees, which reach 17–19 m in height at a reference age of 100 years<sup>30</sup>, corresponding to a mean annual increment of 3.0 m<sup>3</sup> ha<sup>-1</sup> yr<sup>-1</sup>. Soil water content is normally not limiting to tree growth<sup>12</sup>. Soil solution for chemical analyses was collected under the B horizon at a depth of 50 cm using 5–6 suction lysimeters per sub-plot. Detailed methods for sampling and chemical analyses can be found in ref.<sup>20</sup>.

The site belongs to the middle boreal sub-zone<sup>31</sup>, exposed to a harsh climate with long cool days in the summer and short cold days in the winter. The mean annual air temperature is 2.4°C and mean monthly temperature varies from –7.5°C in February to 14.6°C in July (means for 1990–2009). Mean annual rainfall is ~600 mm with approximately one-third falling as snow, usually covering the frozen ground from mid-October to early May. The length of the growing season (the period with a daily mean air temperature ≥ 5°C) averages ~150 days with a large inter-annual variation<sup>29</sup>.

In early summer 1994, four 100 m<sup>2</sup> sub-plots for the soil warming experiment were established within the buffer zones of an irrigated-fertilized plot and four within an irrigated-unfertilized plot<sup>16</sup>. Two sub-plots per treatment were subjected to soil warming and two were kept as a reference in each fertilization plot. In each of the soil warming plots, six 85-m-long, heating cables (DEVI Elektrovarme AB) were installed under the humus layer (~10 cm depth from soil surface) at 20 cm intervals; the reference plots were disturbed as if installing cables. The soil warming treatment was initiated in 1995 and operated during the growing season from the first week of April up to the end of November each year. At the beginning of April (about a month before expected soil thaw), soil temperature in the warming plots was increased by 1°C per week until the target temperature of 5°C above the reference plots was reached, and decreased by 1°C per week from early November or when soil temperature in the reference plots had reached 0°C<sup>31,16</sup>. All plots were irrigated to keep the soil water potential above –0.01 MPa throughout the growing season<sup>19</sup>.

**Destructive harvests.** Six trees covering the range of tree diameters at 1.3 m ( $D$ ) in each of the four treatments (three trees per sub-plot; eight sub-plots in total) were harvested in September 2013. Trees were cut ~0.1 m above the ground, and once on the ground tree height ( $H$ ) and length of live crown (LC) were measured (5 mm accuracy). The living crown was divided into five equal-length strata and two representative branches were collected from opposite crown quadrants in each of five strata<sup>32</sup>. Then, all remaining branches of each stratum were cut and weighed immediately in the field using a scale with 0.5 g accuracy. Height increments were measured for each of the recent 18 years, based on the length of branch internodes (10 mm accuracy). Stem discs were taken at the bottom and at 1.3 m, and every 1 m interval from the bottom. Each disc and stem section between discs were weighed in the field (2 g accuracy).

In the laboratory, shoots of each sample branch were separated into three age classes (current, one-year-old and greater than one-year-old), and the foliage was detached. Terminal shoots without foliage in sample branches were considered dead and discarded. A portion of fresh foliage (~5–50 g) from each age class in each stratum of each tree was scanned using a flatbed scanner (Epson 1600) and scans were analysed for projected foliage area using the ImageJ 1.50e software (Rasband, National Institutes of Health, USA). These samples were also dried and weighed (0.1 mg accuracy). The specific needle area (projected area) was calculated as the scanned foliage area of each sample divided by its dry weight. The remaining foliage for each age class and living twigs were oven-dried at 65°C to a constant weight and weighed separately.

The surfaces of stem discs at 1.3 m height and at the crown base were sanded and scanned using a flatbed scanner (Epson 1600), and tree-ring widths were measured on four perpendicular radii from the pith using WinDENDRO (Regent Instruments Inc.). Specific wood density was analysed from two strips (2 mm thick, 7 mm width) cut from the pith to the bark of each sample disc. The analyses were performed on samples in equilibrium with the conditioned atmosphere of the laboratory (23°C and relative humidity of 43%). The average density of each sample strip was determined with a standard gravimetric procedure using a density scanner (25 µm resolution). Due to shrinkage during the process, the specific wood density of each year was adjusted by a factor of 0.833, the ratio between the wood density of the discs and the basic wood density of the harvested logs.

**Non-destructive stand measurements.** The diameter at 1.3 m and height were measured on each tree in each of eight plots after the growing season (October–November) from 1993 to 2012, except during 2001–2005. The diameter was measured using an electronic caliper (Haglöf Inc.), and  $H$  was initially measured

using a measuring stick (10 cm accuracy) and after 1999 using a Vertex 4 Ultrasonic Hypsometer (Haglöf Inc.). To estimate  $D$  and  $H$  in 1992 to capture the initial increment in 1993, annual basal area increments (BAI) in 1993 from the harvested discs were used. The relative BAI (BAI/BA) was not related to tree size, but differed among years ( $P<0.001$ ) and between fertilization treatments ( $P<0.001$ ). Thus, we employed the mean relative BAI to the BA of each tree of the fertilized and unfertilized plots in 1993 to estimate each tree's  $D$  in 1992. Height in 1992 was estimated from double-logged  $D$ – $H$  relations in 1993–2000. The slope of the  $D$ – $H$  relations was not different among years ( $P=0.899$ ), but the slope describing unfertilized trees was higher than fertilized trees ( $P<0.001$ ); the intercept of the relations linearly increased with year ( $P<0.001$ ). Thus, we generated a double-logged  $D$ – $H$  relation for each of the fertilized and unfertilized plots in 1992, using one slope for each plot, and intercepts increasing with year separately for each plot. To gap-fill data for the period 2001–2005, the periodic increments of  $D$  and  $H$  between 2000 and 2006 for each tree were partitioned on the basis of the proportional increment of tree rings and height growth in each year measured from the harvested trees. The length of live crown (LC) each year was estimated from double-logged  $D$ – $LC$  relations for each plot derived from the 2013 harvested trees (Supplementary Table 1).

**Estimating aboveground standing biomass, annual production and leaf area index.** From the harvested trees, we developed allometric functions (Supplementary Table 1). The stem volume was calculated using Smailian's formula, and the dry mass of the stem and bark was estimated from the dry-to-fresh mass ratio obtained from the stem discs, multiplied by the total fresh mass of the stem and discs of each tree. A simple least-square linear regression was used to develop the functions after both response and predicted variables were log-transformed. The volume of stemwood and the biomass of stem bark were predicted using  $D^2H$ , and branch and foliage biomass were predicted using  $D$ . Each biomass component was estimated by applying these functions to continuous tree measurements in the field (and to those reconstructed for the missing period); biomass of stemwood was estimated by multiplying stem volume by wood density (dry mass/volume for sample trees; 0.386 g cm<sup>-3</sup> for unfertilized and 0.358 for fertilized trees); biomass of coarse roots was estimated using a function from the literature<sup>33</sup>. The annual increment in stem biomass was estimated by the difference in stem volume between years multiplied by the corresponding wood density, and the increment in branch biomass was estimated by the difference in biomass between years adding the annual branch turnover, determined on the basis of the rate of upward movement of the live crown and branch biomass per meter of the live crown in the lowest stratum<sup>32,34</sup>. ANPP<sub>w</sub> was estimated by summing biomass increments of stemwood and branches multiplied by a C content of 0.5 (ref.<sup>35</sup>). Leaf area index was estimated by combining foliage mass and specific needle area (projected area) of harvested trees, and scaling to the stand. The specific needle area was separately applied to foliage mass for each of three age classes in each of five strata of the live crown.

**Analyses of foliage N content and <sup>15</sup>N natural abundance.** The tree N uptake was examined using foliar N content and <sup>15</sup>N natural abundance<sup>18</sup> (expressed as δ<sup>15</sup>N). For these annual analyses, one-year-old shoots were harvested from whorl 7 (refs.<sup>17,36</sup>) of five trees per sub-plot, collected in September in each year except in 1996, 1998, 2001 and 2003–2006, and δ<sup>15</sup>N was not analysed in 1997 and 2012 due to insufficient samples. After sampling, all shoots were immediately immersed in liquid N and then stored at –18°C until drying at 85°C for 48 h; thereafter, needles were separated from the shoot axis and ground to powder (<0.12 mm) in a ball mill. For samples collected until 2009, N and <sup>15</sup>N of foliage were analysed using an automatic N analyser (Carbo Erba ANA 1500 Carbo Erba Strumentazione) and an isotope ratio mass spectrometer<sup>37</sup>, respectively; after 2009, N and <sup>15</sup>N of foliage were analysed using a Flash EA 2000 (Thermo Fisher Scientific).

Results from the isotope analysis are expressed relative to the international standard atmospheric N<sub>2</sub>, where  $R$  is the molar ratio <sup>15</sup>N/<sup>14</sup>N.

$$\delta^{15}\text{N} = \left( \frac{R_{\text{sample}}}{R_{\text{ref}}} - 1 \right) \times 1,000$$

**Data analysis, normalization and scaling.** Over an extended period of time, structure-related spatial variations, such as stand density and tree size<sup>38</sup>, and size distribution<sup>39</sup> also affect stand production (difference in biomass between measurement times), and the relative production rate<sup>40</sup> (production per biomass and time) and growth efficiency<sup>41</sup> (production per leaf area). However, accounting for initial conditions as a co-variate can often generate increasing bias towards the end of long-term treatment studies as initial tree size and production become progressively decoupled from later production behaviour, thus possibly masking or amplifying treatment effects. Therefore, we evaluated the response of biomass production in three ways: annual production (observed absolute response of ANPP<sub>w</sub>); relative production rate normalized by the pre-treatment relative production rate of each tree (relative response, hereafter normalized relative ANPP<sub>w</sub>); and corrected response, with production estimated on the basis of the

relative production rate scaled to the larger nutrition experiment<sup>1,2</sup> using biomass of individual trees ( $n = 4$  plots of 1,000 m<sup>2</sup> per treatment). As the larger experiment had a better representation than the warming sub-study (replications and treatment populations) and had similar initial stand conditions, the last analysis did not require normalizing by initial conditions.

We used a linear mixed model to analyse the normalized size-relative production rate, which accounts for the initial difference in relative production rate (equations (1) and (2)):

$$NPP_{ikl} = \alpha + \beta_1 \times AWB_{ikl} + \beta_2 \times W_i + \beta_3 \times AWB_{ikl} \times W_i + \beta_4 \times \varepsilon_{Rkl} + \varepsilon_{ikl} \quad (1)$$

where  $NPP_{ikl}$  and  $AWB_{ikl}$  are the  $ANPP_w$  and  $AWB$ , respectively, of the  $l$ th individual tree in the  $k$ th plot of treatment  $W_i$ . During the pre-treatment years (1993 and 1994), the intercepts ( $\beta_2$ ) for any treatment and year were not significantly different from zero (minimum  $P = 0.249$ ), and were forced through the origin. Thus, for the pre-treatment period, as a measure of relative difference in the relative production rate between treatments, we used the ratio of the model slopes (relative  $ANPP_w = \beta_1 + \beta_3$ ) of the soil warming treatment and its reference. Then,  $ANPP_w$  for all years was normalized for differences in the pre-treatment period, adjusting by the ratio (equation (2)):

$$NPP_{(cor)ikl} = NPP_{ikl} \times \frac{\beta_{1+3(sw)}}{\beta_{1+3(ref)}} \quad (2)$$

where  $NPP_{(cor)ikl}$  is the adjusted  $ANPP_w$  using the ratio of the slope between soil warming  $\beta_{1+3(sw)}$  and reference plots  $\beta_{1+3(ref)}$  in 1993–1994; using the adjusted  $ANPP_w$  in equation (2), the normalized size-relative production rate model was employed, separately for fertilized and unfertilized plots in each year. Residuals bias of the model was checked using predicted values for linearity of the model. The effect of soil warming was determined using the significance of the coefficient of the interaction ( $\beta_3$ ) at  $P < 0.05$ , after finding no significant intercept ( $\alpha$ ), except for fertilized plots in 2011 ( $P = 0.050$ ). The normalized relative  $ANPP_w$  are presented in Supplementary Fig. 1.

Using the  $AWB$  of individual trees from the main experiment ( $n = 4$ , 1,000 m<sup>2</sup>) as input to the relative production rate model (equation (1)), we corrected for pre-treatment differences. This model provided a good fit (normalized sum of squares between model and observation was 0.069), thus allowing scaling to the stand. Corrected variables between reference and soil warming plots were compared using a two-sample  $t$ -test. Statistical analyses were performed using R (v. 3.3.3): the

lme function in the nlme package was used to devise the relative production rate model (equation (1)).

## Data availability

The data that support the findings of this study are available from the corresponding authors upon request.

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