Figure 1 Annual increment of stem volume in stands of young Norway spruce during a nutrient-optimization experiment, and relative effect of soil warming on the annual volume production at Flakaliden in northern Sweden. **a,** In the nutrient experiment, the treatments were: control (red circles), irrigation (blue triangles), solid fertilization (yellow circles) and combined irrigation and fertilization (green triangles); all started in 1987[9,10]. **b,** In the soil-warming experiment, volume growth values are given in per cent of that in 1994, before the start of the experiment. The low production in 1995 was the effect of massive cone production. Purple bars, non-heated control plots; blue bars, heated plots.

matter and mineralization of soil nutrients. A long-term soil-warming experiment (an increase of 5 °C at 10 cm depth, through the growing season[2]) at Flakaliden is revealing after five years that concentrations of foliar nutrients are increased and that there is a significant (more than 50%) increase in stem-wood growth of the trees on the heated plots (Fig. 1b). Thus, year-to-year variability in temperature could be influencing stem-wood growth through the availability of nutrients.

Although this experiment makes this point well, a note of caution is appropriate. After five years of warming, CO_2 efflux from the forest floor in warmed and non-warmed plots differs by less than 10%, which is not significant. The evidence from our experiment thus contradicts the idea that the projected rise in temperature is likely to lead to forests that are now carbon sinks becoming carbon sources in the foreseeable future. There is likely to be a limit to the amount of soil organic matter that is readily metabolizable in response to an increase in soil temperature, as well as an acclimation taking place in the temperature sensitivity of both autotrophic and heterotrophic respiration.

We conclude that the effects of temperature on the growth of trees in the boreal forest are mediated by the capture of CO_2 and nutrients much more strongly than by other physiological processes. Consequently, the variability from year to year in the net ecosystem and net primary production and in stem wood growth should be interpreted, in the first instance, in terms of the ability of the forest to capture carbon and nutrients.

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Vaganov and Hughes reply — The model we used, which is driven only by meteorological variables, reproduces the decadal timescale variations in relative tree-ring width indices that have been observed at three taiga sites in the Siberian subarctic separated by 85 degrees of longitude[1]. In our study, absolute differences in mean growth rate between sites, related to slowly varying site conditions such as nutrient status, are removed by converting to dimensionless indices with a mean of unity. The results from the fertilization experiment on young plantation spruce trees described by Jarvis and Linder are thus not in disagreement with our major findings.

Jarvis and Linder suggest that the effect of soil temperature on the timing of cambial initiation is indirect, rather than direct. We acknowledge that it is not possible to say whether the effects of temperature and moisture are direct or indirect using the methods we adopted, especially for wood increment, which results from a combination of different processes at the whole-tree and tissue levels. We would point out, however, that our simple model does a remarkable job of accounting for the changes observed over much of this century (see Fig. 4 of ref. 1), and that there is little room for improvement on this.

Their comments are relevant to the study of changes that the global carbon cycle might undergo in a changing climate, although we would counsel caution in assuming that any single mode of response will apply to the wide diversity of conditions found in the boreal forest. The problem is how to include the proposed indirect effects in quantitative models of the effect of climate variability on the variability of tree growth. In particular, what is the characteristic time of the response of wood formation to various environmental changes?

We know that, in the case of the meteorological variables used in the model we adopted, characteristic times generally range between a few days and one or two growth seasons. Thus, in some extremely cold years the same tree at the same average level of nutrients in the soil forms a tree ring an order of magnitude narrower than in warm years. Fertilization increases stem-volume growth and stand productivity[2]. This effect is revealed clearly, with a delay of some years, in non-permafrost soils. All the sites we investigated were on deep permafrost with a thin active layer.

Under these circumstances, then, can nutrient supply play a quantifiable role in the variation of interannual and inter-decadal growth rate in response to climate variability and change, even in the same site and in the same tree? In a warm year, the active layer will be deeper and warmer, leading to a higher rate of organic decomposition and additional turnover of nutrients for growth[3]. Whereas the direct effect of meteorological variables on wood formation is close to immediate, there is likely to be a significant delay in the operation of indirect effects related to nutrients, because the active layer is deepest and warmest in the later part of the season, namely in late July and August[4,5]. Thus, cumulative decomposition is greatest when wood formation is already almost complete, delaying effects at least until the next year. These delays will probably make it difficult to disentangle the direct and indirect effects of meteorological factors on tree radial increment. In the meantime, our model accounts for most of the observed inter-decadal variability in relative tree-ring growth.

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