

Commentary

Why are Arctic shrubs becoming more nitrogen limited?

The Arctic tundra is becoming more productive, with further significant change expected over the coming decades. Biome-scale increases in Arctic plant productivity have, at least partly, been attributed to the expansion of tall woody shrubs (Mekonnen *et al.*, 2021a). Increasing productivity and shrub abundance will have profound consequences: from influencing surface energy balance and permafrost stabilization, to altered forage provision for herbivores, to determining the strength of global carbon (C) cycle–climate feedbacks from warming permafrost soils. Though there is solid evidence for increasing tundra productivity at the biome scale, the picture on the ground is more complicated. Plant growth has increased over time in some regions but not others, for reasons that are not fully understood – growth could be responding to a large number of interrelated factors as the Arctic warms. Some of these factors are unique to high-latitude environments; for example, the lengthening of the short snow-free growing season or enhanced nutrient release from thawing permafrost soils. Others are global, including rising atmospheric CO₂ concentrations or the direct effects of warming on tissue growth rates. In this issue of *New Phytologist*, Martin *et al.* (2022; pp. 670–686) presented dendro-ecological data that challenges our understanding of the links between Arctic environmental change and plant growth.

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Fertilization experiments in the mid–late 20th century demonstrated that tundra plant productivity and biomass accumulation are strongly nutrient limited, most frequently by nitrogen (N) (Shaver *et al.*, 1992). Mineral nutrient addition also tended to increase the abundance of deciduous shrubs in these experiments (Chapin *et al.*, 1995). It was understood that N supply to tundra plants came almost exclusively from the recycling of plant litter or soil organic matter (SOM), with minimal inputs from precipitation or N fixation. As a result, the prevailing view was that tundra plant responses to climate would be driven primarily by the indirect effects of temperature on

nutrient availability via enhanced mineralization (Shaver *et al.*, 1992). Gradual increases in nutrient availability in soils were expected to drive a long-term trend towards higher productivity, with positive feedbacks on nutrient turnover as deciduous shrubs replaced evergreen and nonvascular species with lower quality litter (Chapin *et al.*, 1995). These changes in tundra productivity and shrub abundance, which were anticipated > 30 years ago, appear to have been borne out. But the study by Martin *et al.* provides intriguing evidence that N limitation of shrub growth over that period may have increased, rather than decreased.

In a first for the Arctic, Martin *et al.* presented *Salix lanata* shrub-ring $\delta^{15}\text{N}$ data – supported by a novel model analysis – to explore the potential mechanisms linking shrub growth and N availability over multiple decades. Using data from 10 shrub individuals, they fit a suite of competing dynamic models, which relate ring width to shrub biomass via allometric equations, using wood $\delta^{15}\text{N}$ as a proxy for soil N availability. For all 10 individuals the most appropriate model included a linear relationship between N availability and biomass growth rate – consistent with growth limitation under low N conditions. Intriguingly though, the trend in wood $\delta^{15}\text{N}$ was negative for seven of the 10 shrubs, and the authors conclude that soil N availability for these individuals has decreased over time. This is the first time that declining plant $\delta^{15}\text{N}$ has been observed in the Arctic, but if widespread, this challenges the idea that the primary mechanism driving plant growth responses is the effect of temperature on soil N availability. These new results suggest any increase in soil N supply to these shrubs may have been exceeded by an increase in growth demand – stimulated perhaps by the direct effects of warming on tissues, increased access to other co-limiting nutrients, or in response to increasing atmospheric CO₂ (Bassirirad *et al.*, 2003; Craine *et al.*, 2018).

We do not yet know how increasing atmospheric CO₂ concentrations are impacting tundra ecosystems, and the link to vegetation change is unclear. Early manipulative experiments showed that – in contrast to the dramatic effects of nutrient addition on biomass and net primary production – leaf-level photosynthetic responses to elevated CO₂ (eCO₂) were generally short-lived (Tissue & Oechel, 1987). After 3 years, eCO₂ had no lasting impacts on *in situ* net ecosystem C balance in Alaskan tussock tundra (Oechel *et al.*, 1994). This type of response is in line with our understanding of nutrient-limited growth under eCO₂, although a faster response than in other systems. Therefore, CO₂ fertilization was not expected to have much future impact unless sink activity also increased with warming temperatures (Dormann & Woodin, 2002) (Fig. 1). In recent years the focus has remained on changes in temperature and nutrient availability as key factors driving shrub expansion (Myers-Smith *et al.*, 2015; Mekonnen *et al.*, 2021a). However, the long-term impacts of CO₂ on Arctic ecosystems have never been tested, and free-air CO₂ enrichment (FACE) experiments have not been possible owing to logistical

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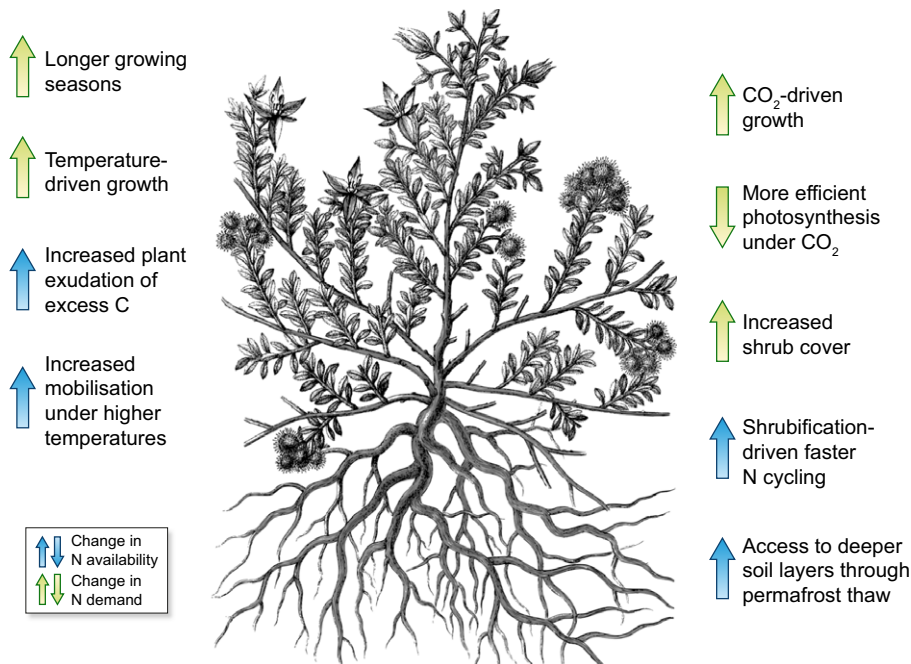


Fig. 1 Potential processes affecting changes in plant nitrogen (N) availability (blue arrows) and demand (green arrows) in Arctic ecosystems. Further observations and experiments are necessary to quantify each of these factors and the overall balance on changes in plant nutrient status.

challenges. Some clues do exist to suggest that eCO₂ may have longer term impacts on community structure; in one *in situ* study in Sweden in the 1990s plant height increased in the deciduous shrub *Vaccinium myrtillus*, but not in evergreen shrub species after 3 yr (Gwynn-Jones *et al.*, 1997). In a Swiss alpine treeline ecosystem, increased *V. myrtillus* growth was sustained for 9 yr under eCO₂, with little or no response in other ericaceous species (Dawes *et al.*, 2011). We do not know how long-term CO₂ fertilization influences the deciduous shrub species implicated in tundra shrub expansion (largely *Betula*, *Salix*, and *Alnus* species). Though it is difficult to determine direct causation from the Martin *et al.* study, it is possible the observed decrease in wood $\delta^{15}\text{N}$ is the footprint of increasing atmospheric CO₂ previously undetected in Arctic ecosystems.

The extent to which CO₂ fertilization is contributing to shrub expansion remains an open question. But even if cold, nutrient-poor Arctic conditions largely limit plant growth responses to eCO₂ (Fig. 1), stimulation of gross photosynthesis may still influence ecosystem function. FACE experiments in other ecosystems have shown that eCO₂ leads to a sustained increase in gross photosynthesis, even though growth responses are more uncertain (Walker *et al.*, 2021). In some cases, biomass production does not respond despite increases in gross primary production; old-growth, phosphorus-poor forest is one example (Jiang *et al.*, 2020). Belowground measurements are more sparse and difficult, but there is some evidence that plants invest the additional C from photosynthesis under eCO₂ into nutrient acquisition (Finzi *et al.*, 2007; Drake *et al.*, 2011); and under N limitation, this may be associated with soil C losses as a result of nutrient mining (Terrer *et al.*, 2021). Martin *et al.* found that including a plant–soil feedback mechanism better explained ring width and $\delta^{15}\text{N}$ for eight out of 10 shrub individuals. Together with the negative trends in $\delta^{15}\text{N}$ over time, this result would be consistent with an increase

in N mining by root-associated fungi in *S. lanata*. Recent *in situ* studies have shown that photosynthate stimulates C turnover in Arctic soils (Street *et al.*, 2020) linked to the activity of SOM degrading ectomycorrhizal (ECM) fungi (Clemmensen *et al.*, 2021). Increased belowground C allocation could therefore amplify C losses from Arctic soils, which are already vulnerable to warming and disturbance. Understanding the links between CO₂ fertilization, plant N demand, belowground C allocation, and fungal community composition will be important in predicting future Arctic C dynamics.

A key characteristic of Arctic vegetation is the high spatial heterogeneity in plant abundance and functional type. The dominant vegetation can vary from prostrate evergreen heath, to tussock sedges, to deciduous woody shrubs over distances of just a few metres. Plant biomass varies greatly between these communities, as does the dominant mycorrhizal association: from ericoid heath, to ECM deciduous shrubs, and arbuscular or nonmycorrhizal tussock sedges. Spatial variation in tundra plant communities is linked to topography and hydrology, which play an important role in determining soil nutrient availability. Saturated soils are common in tundra because permafrost impedes drainage, and nutrient turnover is inhibited where anoxia develops. However, where water is moving down slope or along water tracks, nutrient delivery to plant roots increases. Surface water flow is an important factor in determining plant abundance in Arctic landscapes (Rastetter *et al.*, 2004; Mekonnen *et al.*, 2021b). Interestingly, however, Martin *et al.* showed that though shrubs on hillslopes have significantly higher average stem $\delta^{15}\text{N}$ than lowland plants, the trend in $\delta^{15}\text{N}$ over time was still negative for two out of three hillslope individuals. So even in soils with apparently higher N availability, N limitation appears to have increased over time. Soil state factors, such as topography and parent material, as well as plant N acquisition strategy and mycorrhizal association, will



influence spatial patterns of plant N limitation. More work is needed to extend the Martin *et al.* study to understand how these spatial factors relate to variation in greening trends.

The future state of vegetation will play an important role in determining ecosystem function in the tundra biome, including potential feedbacks on climate via the carbon cycle and surface energy balance. However, there are still large gaps in our understanding of the limitations to Arctic plant growth; including the impact of soil nutrients, elevated CO₂, and the role of changing hydrology and belowground microbial communities. Martin *et al.* provide us with a crucial first insight into how tundra N dynamics have changed over the last decades.

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