OPINION PAPER

Shrub expansion in the Arctic may induce large-scale carbon losses due to changes in plant-soil interactions

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Abstract

Background Tall deciduous shrubs are increasing in range, size and cover across much of the Arctic, a process commonly assumed to increase carbon (C) storage. Major advances in remote sensing have increased our ability to monitor changes aboveground, improving quantification and understanding of arctic greening. However, the vast majority of C in the Arctic is stored in soils, where changes are more uncertain.

Scope We present pilot data to argue that shrub expansion will cause changes in rhizosphere processes, including the development of new mycorrhizal associations that have the potential to promote soil C losses that substantially exceed C gains in plant biomass. However, current observations are limited in their spatial extent, and mechanistic understanding is still developing.

Extending measurements across different regions and tundra types would greatly increase our ability to predict the biogeochemical consequences of arctic vegetation change, and we present a simple method that would allow such data to be collected.

Conclusions Shrub expansion in the Arctic could promote substantial soil C losses that are unlikely to be offset by increases in plant biomass. However, confidence in this prediction is limited by a lack of information on how soil C stocks vary between contrasting Arctic vegetation communities; this needs to be addressed urgently.

Keywords Shrub expansion · Arctic · Soil · Rhizosphere · Carbon cycle · Climate change

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Advances in understanding of above-ground vegetation change in the Arctic

The arctic tundra stores globally important amounts of carbon (C) and has the potential to strongly regulate feedbacks to climate change (Schuur et al. 2015). Many areas of the tundra are becoming more productive (Epstein et al. 2012), especially in the 'low Arctic' where tall, ectomycorrhizal (ECM) deciduous shrubs are increasing in stature and cover as a result of climate warming (Myers-Smith et al. 2011; Elmendorf et al. 2012a). Furthermore, the forest-tundra ecotone is slowly shifting northward, bringing ECM trees into the tundra (Rees et al. 2020). As tall shrubs and trees expand in range, they are predicted to overgrow large areas of: (1)

dwarf shrub communities which are comprised of short-stature evergreen and deciduous shrubs that mostly form ericoid mycorrhizal associations (ERM), and (2) sedge tundra which is dominated by non-mycorrhizal (NM) graminoid communities (Tape et al. 2006; Pearson et al. 2013; Mekonnen et al. 2018a). Predicted shifts in plant community composition over the coming century, particularly in the Low Arctic are in the order of hundreds of thousands of km^2 (Pearson et al. 2013), therefore the associated ecosystem changes and feedbacks could be at an equally large scale.

The aboveground response of plant communities to warming has been robustly constrained by decades of plot-level measurements (Elmendorf et al. 2012b). In parallel, satellites have documented ecosystem greening (Myneni et al. 1997; Reichle et al. 2018) and significant progress is being made in bridging the scale gaps between plot and satellites, while revealing further nuance with respect to the response of vegetation to extreme events (Myers-Smith et al. 2020). Through progressively more complex syntheses powered by a network of long-term tundra warming experiments (International Tundra Experiment (ITEX); Henry and Molau 1997), researchers have been successful in linking thousands of aboveground measurements of plant traits to environmental changes. This has developed an increasingly pan-Arctic understanding of vegetation dynamics in response to climate and other environmental drivers (Arft et al. 1999; Walker et al. 2006; Elmendorf et al. 2012a, b; Bjorkman et al. 2018).

Aboveground trait data have been key in raising hypotheses as to how plant community change will influence ecosystem processes and C storage (Myers-Smith et al. 2019). For example, leaf litter decomposition experiments suggest that the expansion of deciduous shrubs may promote a negative feedback to climate change due to increases in leaf litter production and the fact that their litter decomposes relatively slowly compared to forb, grass and sedge litter, and only slightly faster than litter from dwarf evergreen shrubs (Cornelissen et al. 2007). Aboveground plant traits are also well known to regulate wider ecosystem properties such as soil temperatures (Kropp et al. 2020), through interactions between canopy height and snow trapping in the winter (Sturm et al. 2005), or canopy leaf area and shading in the summer (Blok et al. 2010). Changes in canopy properties could therefore influence permafrost thaw and the exposure of permafrost C to degradation, depending on the relative strength of summer and winter

feedbacks. In their present state, models tend to predict an increase in soil C in high-latitude ecosystems as a result of increases in C inputs from greater plant productivity (Qian et al. 2010; Todd-Brown et al. 2013; Mekonnen et al. 2018b). However, the visible aboveground portion of tundra plant biomass is the tip of the C 'iceberg' (Iversen et al. 2015). Root biomass usually outweighs shoot biomass substantially and is closely linked with the large stores of soil C which are often concentrated towards the soil surface (Kuhry et al. 2013). It is therefore critical to consider rhizosphere processes when assessing whole ecosystem responses to shrub expansion.

The need for greater understanding of plant-soil interactions

The C-rich upper soil horizons in the active layer of tundra soils are under a range of different biologically-driven controls; plant life drives variation in small-scale soil processes that may have an important influence on soil C stocks. Variation in rooting traits such as turnover rate, morphology and mycorrhizal symbiosis (Iversen et al. 2015), root exudation and positive priming (Hartley et al. 2012; Keuper et al. 2020; Street et al. 2020) and associated microbial community structuring (Deslippe et al. 2011; Morgado et al. 2015), have the potential to exert a strong top-down control over patterns of soil C storage in arctic ecosystems. Despite this, soils in the Arctic are often contextualised and studied with broad-scale soil classifications and geomorphological controls in mind (Hugelius et al. 2013). These important syntheses emphasise the total size of the soil C pool and its potential to contribute to a large climate feedback as the Arctic warms, focusing on the potential for increases in soil heterotrophic activity as permafrost starts to thaw (Kuhry et al. 2013; Schuur et al. 2015). Tundra soils are, though, rarely studied in the context of the current plant community. When the two are measured in parallel it is often part of an experiment designed to test physico-chemical drivers of change, such as temperature (Rinnan et al. 2008; Clemmensen et al. 2012; Sistla et al. 2013; DeMarco et al. 2014), or nutrient availability (Mack et al. 2004), rather than plant community composition as a key biotic driver of soil organic matter dynamics. A major challenge is to understand the degree to which tundra plants control soil C stocks and how this interacts with climate drivers.

Without detailed studies that take into account both plant community composition and soil, we may miss some of the most immediate and dynamic controls over soil C storage. Equally, while aboveground-only studies are important in their own right, a much more comprehensive understanding of ecosystem dynamics under vegetation change requires similarly robust soil C measurements in parallel.

There is a small, but growing, body of work that considers C storage and process rates of plants and soils in the Arctic together. Comparisons between treeline forest and open ericaceous tundra heath (Sjögersten and Wookey 2009; Hartley et al. 2012), or moist acidic tundra (Wilmking et al. 2006), have found that forest soils store less C than adjacent tundra soils. More recently, researchers found that deciduous shrub-dominated plant communities also have the lowest soil C storage of measured treeless communities, despite having greater leaf area and productivity (Parker et al. 2015, 2020; Sørensen et al. 2018). In each case, these lower C stocks in the soils more than compensate for the greater plant biomass (Sloan et al. 2013). Here, we present two more datasets from the Low Arctic of Alaska (Fig. 1b) and Southwest Greenland (Fig. 1c), alongside published data from Sweden (Fig. 1a; Parker et al. 2015). These show that coverage of deciduous shrubs (*Betula nana* and *Salix glauca*) is not positively correlated with soil C stock across the three locations, and that shrub cover was in fact negatively related to soil C stocks in Sweden and Greenland. Furthermore, there was no observable relationship between standing litter stocks and shrub cover, which would be required as a key intermediary (Myers-Smith et al. 2019) if leaf litter inputs were driving soil C accumulation (Fig. 1b). Taken together, these data force us to acknowledge that we are overlooking key processes in terms of understanding how plant community composition and productivity control soil and ecosystem C storage.

Potential mechanisms explaining differences in soil C between vegetation communities

One of the most important mechanisms potentially explaining the differences in soil C storage between plant communities may be related to their dominant mycorrhizal association. ECM fungi are known to have the potential for varying degrees of extracellular hydrolytic and oxidative enzyme expression,

depending on the species (Lindahl and Tunlid 2015; Zak et al. 2019; Frey 2019). Restricting delivery of autotrophic C to ECM communities in a boreal forest has been shown to result in a large reduction of extracellular enzyme production, in particular, Mn-peroxidase (Sterkenburg et al. 2018). This enzyme is used by some ECM fungi (in particular *Cortinarius* spp. ;Bödeker et al. 2014) to decay complex organic matter molecules in order to mineralise N, especially in northern ecosystems with limited mineral N availability. Indeed, alleviation of N limitation by experimental fertilisation of boreal (Bödeker et al. 2014) and tundra (Dunleavy and Mack 2021) ecosystems results in reduction of oxidative enzyme production by mycorrhizal fungi. Given the majority of N in the tundra is bound in organic matter (Shaver et al. 1992), and this would need to be liberated to maintain enhanced tall shrub growth, N 'mining' in systems that have been colonised by tall ECM-shrubs has the potential to promote substantial soil C losses.

Furthermore, process-based studies indicate that C inputs from tall-stature shrubs and trees are unlikely to promote soil C sequestration following colonisation of arctic tundra. We now understand that much of the extra C fixed by high leaf area shrub communities (Street et al. 2007; Sloan et al. 2013) is rapidly allocated belowground, assimilated by microbial communities (Street et al. 2018), and then respired back to the atmosphere (Sørensen et al. 2018; Parker et al. 2020). As well as the activity of the ECMs themselves, the increase in new C inputs can promote the activity of saprotrophic microbes (Hicks et al. 2020) which can also stimulate the mineralisation of older soil C (Hartley et al. 2012; Keuper et al. 2020; Hicks et al. 2020; Street et al. 2020). Such positive priming responses, and associated increases in nutrient mineralisation, may further explain the low C stocks observed under tall-shrub canopies (Wilmking et al. 2006; Parker et al. 2015, 2020; Sørensen et al. 2018). Overall, following ECM colonisation, there appears to be limited potential for sequestration of new C inputs, but substantial potential for losses, depending on how autotrophic C is distributed and utilised in the rhizosphere.

ERM fungi are also well known to produce a broad range of extracellular enzymes and have a large capacity for direct organic N uptake (Smith and Read 2008), but our understanding of their ecology is still largely confined to laboratory studies (Read and Perez-Moreno 2003). However, it may be that they produce
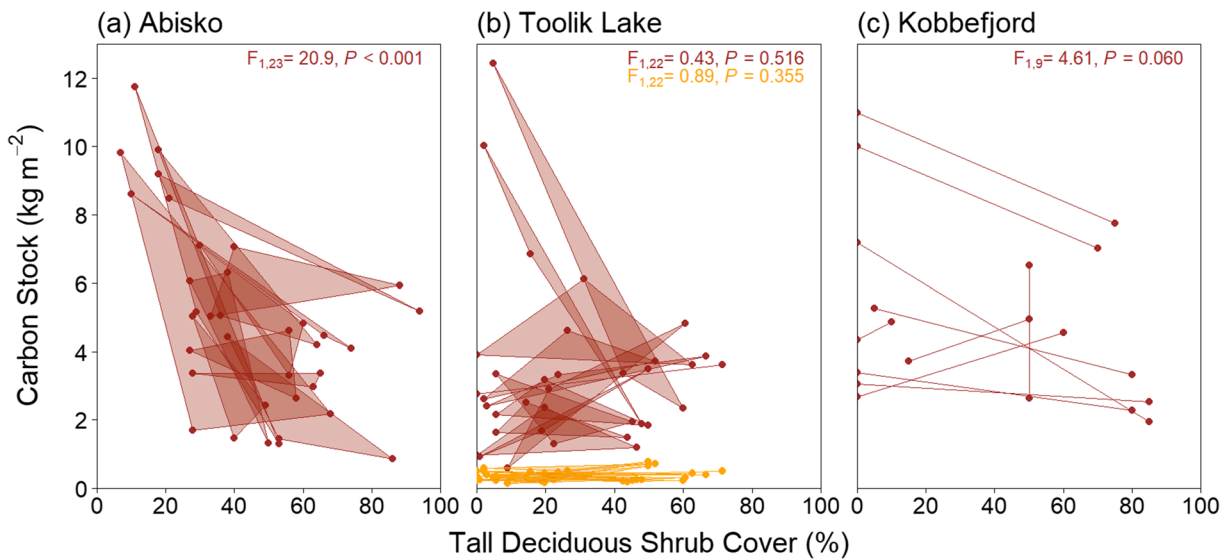
Fig. 1 Organic horizon soil carbon (red) and litter carbon (orange) in relation to varying tall deciduous shrub cover over multiple vegetation transitions at three tundra sites. Connecting lines and shade indicate geographically paired transects with 'low', 'medium' or 'high' shrub cover plots ('low' and 'high' only in (c)). For context, plots with 100 % tall deciduous shrub cover store approximately, 0.6 kg m^{-2} of biomass (not C) in tall shrub biomass (Chen et al. 2009). Statistics refer to results of linear mixed effects models testing the relationship between deciduous shrub cover and C stocks at each site. A description of methods can be found in Supplemental Information

extracellular enzymes at lower rates than some high-biomass, high-energy ECM fungi, or produce structures that are more resilient to decomposition after senescence (Clemmensen et al. 2015). Indeed, it was found in a boreal forest that, compared with ECM-dominated communities, areas that were dominated by ERM-associated plants showed greater C storage, potentially driven directly by lower turnover of C in ERM necromass (Clemmensen et al. 2015). The authors also suggested that differences in enzyme production and N acquisition strategies could further explain the differences in soil C storage between ERM and ECM communities.

To our knowledge there are no shrub or tree planting experiments in the tundra that have traced the effects on net ecosystem exchange of CO_2, or the dynamics of processes in the mycorrhizosphere. However, in an upland system where ECM trees were planted on ERM *Calluna vulgaris* moorland, significant soil C losses were observed at two of four sites, and increases in soil C storage were never observed, despite greater above-ground biomass (Friggens et al. 2020). Carbon stocks in ERM-dominated arctic heath communities may be similarly vulnerable following colonisation by ECM plants. Furthermore, soil C losses observed by Friggens et al. (2020) were greater under *Betula* (*B. pubescens* and *B. pendula*) species

than under *Pinus sylvestris*. Given that dwarf *Betula* spp. (*Betula nana* L. and *Betula glandulosa* Michx.) are one of the most important groups contributing to the expansion of deciduous shrubs in the Arctic (Myers-Smith et al. 2011), increases in the abundance of *Betula* spp. may be particularly important in promoting soil C losses.

In the data that we have presented, soil C stocks at Abisko and Kobbefjord were negatively related to shrub cover, but there was no detectable relationship at Toolik Lake (Fig. 1b). This raises an interesting contrast: ericaceous shrubs are less dominant at the Toolik Lake field site, which is moist acidic tundra comprised of a relatively even mix of sedges, mosses, deciduous shrubs and evergreen ericaceous shrubs (Chapin et al. 1995). In contrast, the low stature plots at Abisko and Kobbefjord are strongly dominated by ericaceous evergreen shrubs. The soil organic matter in ERM communities in Abisko are known to contain a high proportion of relatively easily decomposable O-alkyl compound classes (Sjögersten et al. 2003) which likely originated from a fungal necromass source (Clemmensen et al. 2013). Certain ECMs could be well adapted to breaking down fungal necromass which tends to turn over quickly, given an appropriate fungal community (Fernandez et al. 2015), therefore the soil C in ericaceous soils could

be particularly vulnerable to C loss following ECM shrub encroachment.

The relative importance of above- versus belowground changes

Deciduous shrub expansion and colonisation of lower stature tundra communities will result in an increase in aboveground biomass (Epstein et al. 2012), but the changes in belowground traits (as described above), including mycorrhizal status (Clemmensen et al. 2015), belowground biomass turnover rate (Sloan et al. 2013) and positive priming (Hartley et al. 2012; Street et al. 2020) may lead to an overall loss of C at the ecosystem level, at least when the community being colonised has a substantial component of ericaceous shrubs. Critically, the potential losses of soil C may be an order of magnitude greater than the potential gains in plant biomass. This is because, with much greater below-ground C stocks, even small pro-

portional losses in soil C can outweigh large proportional gains in aboveground biomass. Furthermore, there is an upper limit to the size that tall shrubs can grow before becoming limited by their own growth form at around 1 kg C m^2, based on remote sensing and ground-truthing of the most productive tall shrub tundra (Berner et al. 2018). Net ecosystem losses of C shortly after shrub colonisation does, however, assume that soil losses take place on a similar timescale to the gains in plant biomass. This may not be entirely the case, aboveground C gains and soil C losses will likely occur on different temporal scales, which studies addressing relatively recent shifts in vegetation distribution have to take account of. The recent evaluation of the consequences of tree planting on organic soils demonstrated that substantial C losses from soils can take place on decadal timescales (Friggens et al. 2020), similar to rates of tree biomass growth, but these dynamics could differ in the Arctic and Subarctic. We argue that, in the tundra, it is likely that variation in mycorrhizal traits and subsequent decom-
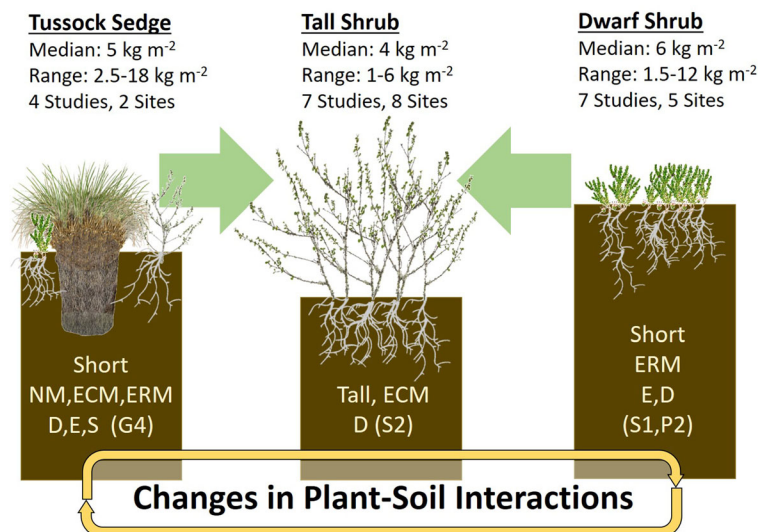

Fig. 2 Proposed consequences of soil C stocks following changes between three important tundra plant communities due to climate change. Relative size of brown boxes indicates best estimates of organic horizon C stocks (median of literature values, including the present study). Text in each box represents relative canopy height (tall or short), dominant mycorrhizal symbiosis (ectomycorrhizal, ECM; ericoid mycorrhizal, ERM; non-mycorrhizal, NM), (co)dominant plant functional type (deciduous shrub, D; evergreen shrub, E; sedge, S) and closest Circumpolar Arctic Vegetation Map (CAVM) classification (Walker et al. 2005). Green arrows indicate modelled vegetation transitions due to

climate change (Pearson et al. 2013). The number of studies (to our knowledge) that measure organic horizon C stocks in each plant community and the number of sites these studies cover are listed (see Table S1 for literature values and paper references). Potentially important changes in plant-soil interactions with changes in vegetation include a likely increase in root litter turnover rates, shifts in dominant mycorrhizal symbiosis and associated microbial community composition change, and increases in rhizosphere priming rates. *Tussock sedge diagram credit: N.R.Fuller, SayoStudio*

position in the rhizosphere will play a greater role in controlling patterns of soil C storage than variation in aboveground traits and leaf litter decomposition (Cornelissen et al. 2007). Furthermore, the evidence suggests that the large-scale expansion of tall deciduous ECM shrubs that is predicted over the coming century (Pearson et al. 2013) may promote a loss of soil C, especially when the tundra that is being colonised is currently ERM-dominated (Fig. 2).

Widespread soil sampling alongside vegetation sampling and analysis

To determine the consequences of changes in vegetation community distribution for C storage, we need to improve our ability to link aboveground plant traits with belowground plant traits and soil C storage. With ongoing monitoring of aboveground vegetation change, it may then become possible to improve predictions of the consequences for soil and ecosystem C stocks. We argue, however, that the scientific community is not yet in a position to do this.

There are timely and important initiatives taking place to increase measurements of, and synthesise knowledge on, belowground plant traits in the Arctic (Iversen et al. 2015). However, this still lags far behind the volume of data that is collected aboveground. Furthermore, even basic information on how much soil C is stored beneath different plant communities is very limited (Fig. 2, Table S1). Plant and soil responses to climate change are often studied independently, and there is a scarcity of studies that pair measurements of their stocks and processes at comparable scales. There is therefore the clear and pressing need for coordinated above- and belowground sampling, of the kind presented in Fig. 1, across the tundra biome. As we list in Fig. 2, there are only a handful of studies that explicitly measure soil C stocks in the organic horizon and these estimates only apply to a small number of sites. The Abisko and Toolik Lake sites (Fig. 1a and b) are two of the most studied sites in the Arctic for climate change research (Metcalfe et al. 2018), and increasing the diversity and geographical range of sites is essential to test the broader-scale applicability of above-belowground linkages. To this end, we present a simple protocol (Supplementary Information) for measuring plant cover, litter and organic horizon soil C stocks in parallel.

Conclusion

Major advances have been made in quantifying and understanding the changes in plant community composition that are taking place in the Arctic. However, we argue that predicting the consequences for biogeochemical feedbacks to climate change is currently constrained by the low number of combined studies of above- and belowground plant traits and soil C stocks. Such studies are urgently required to identify and quantify key relationships between plant communities and soil C. Critically, the data that we present here challenge the assumption that increasing plant productivity will promote greater ecosystem C storage and emphasise the need to make similar measurements across contrasting tundra ecosystems and plant communities. Such efforts offer the opportunity to move beyond plant- or soil-centric viewpoints, and to generate whole-ecosystem understanding of controls over C storage in arctic ecosystems.

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