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LETTER

The carbon sink due to shrub growth on Arctic tundra: a case study in a carbon-poor soil in eastern Canada

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Abstract

The microbial respiration of ancient permafrost carbon represents a positive feedback to climate warming. However, warming-induced shrub expansion in circumpolar latitudes may partly offset these emissions, due to greater biomass and litter inputs than that of primary tundra vegetation. Quantifying this carbon sink is challenging as the simultaneous mineralization of ancient carbon renders the attribution of changes in soil carbon stocks uncertain. We measured the contribution of shrubs to the terrestrial carbon reservoir in a Low-Arctic region where ancient carbon stocks are among the lowest in the Arctic. The study site near the eastern shore of Hudson Bay is experiencing rapid *Betula glandulosa* Michx. expansion throughout lichen tundra. We find that the terrestrial carbon stocks (i.e. soil and vegetation) under a cover of low to medium-size shrubs is increased by 3.9 ± 1.3 kg m^{-2}, regardless of shrub cover age. Along water tracks, taller shrubs and the transition to moss understories provide an even greater increase in terrestrial carbon (6.5 ± 3.5 kg m^{-2}). Using published maps of vegetation change from 1994 to 2010, we estimate that the carbon sink associated to shrub expansion in our study area (5.228 km^2) has been 2.4 ± 0.8 Gg or 29 ± 9 g m^{-2} yr^{-1}. Extrapolating this result to the Arctic requires additional studies in representative environments.

1. Introduction

Arctic land masses represent one fifth of the emerged surface of the Earth and contain ca. 1300 Pg of frozen carbon in their permafrost (Hugelius *et al* 2014), a reservoir 1.5 times larger than the atmospheric one (ca. 830 Pg; (IPCC 2013). Currently, warming-induced permafrost thaw is releasing part of this ancient (i.e. perennially frozen) carbon into the atmosphere through microbial respiration. These CO_2 and CH_4 emissions have the potential to trigger a strong positive feedback to climate warming (Schuur *et al* 2008). However, these emissions may be partly offset by the simultaneous increase in primary productivity (i.e. plant growth) throughout the Arctic. The causes of shrub expansion have been detailed by (Myers-Smith *et al* 2011) and the main driver is climate warming and its consequences such as changes in snow cover and permafrost thaw. Permafrost thaw in particular favors nutrient recycling which contributes to shrub growth. Consequences of shrub expansion and growth include increases in both plant and soil carbon stocks through enhanced biomass production and subsequent soil organic matter (SOM) accumulation (Myers-Smith *et al* 2011).

Quantifying the balance between ancient carbon microbial respiration and increased primary productivity is difficult in many Arctic regions as long-term field experiments on the impacts of shrub growth on soil carbon often generated contradictory results. For example, in their two decade-long experiment in the Alaskan tundra, Sistla *et al* (2013) found that, although simulated Arctic summer warming increased shrub growth and litter inputs, it had no impact on total soil organic carbon (SOC) stocks, a result likely associated to the fact that surface (vegetation) inputs were compensated by ancient carbon mineralization. Nearby, Mack *et al* (2004), in their long-term (>20yr) fertilization experiment to simulate the positive effect of warmer temperatures on nutrient availability through an increase in soil microbial activity, observed a net loss of ca. 2 kg m^{-2} of carbon although ecosystem primary productivity doubled over the course of the experiment. The results of such studies may be difficult to extrapolate throughout the Arctic as ancient carbon mineralization rates vary both spatially and temporally. In contrast, Day *et al* (2008) observed a net total increases in soil and vegetation carbon stocks of about 300 g m^{-2} near Palmer Station (Antarctica) in a four-year warming experiment at a tundra site dominated by vascular plants. In their case, simulated warming did not alter SOC stocks at depths as soils were permafrost-free, had no ancient carbon and had only a thin (< 5 cm) organic layer overlaying glacial drift.

Surface inputs to the terrestrial carbon reservoir remain one of the largest sources of uncertainty in Earth system models (Todd-Brown *et al* 2014, Koven *et al* 2015, Crowther *et al* 2016, McGuire *et al* 2018). Some modeling studies (McGuire *et al* 2018) indicate that future increases in plant biomass could offset ancient carbon mineralization, while others reached an opposite conclusion (Abbott *et al* 2016). Field studies aiming to unambiguously quantify the contribution of plant biomass on the terrestrial carbon reservoir are thus needed.

In order to contribute to filling this knowledge gap, we conducted a study at a low Arctic tundra site near Umiujaq (Nunavik, 56.55° N, 76.55° W) where the impact of shrub growth on SOC accumulation could be quantified. The maps of (Hugelius *et al* 2014) suggest that SOC in the first meter of soil in this region is <5 kg m^{-2}, a result corroborated by our preliminary measurements in lichen tundra sites in the region (SOC < 2 kg m^{-2}). As dwarf birch (*Betula glandulosa* Michx.) has progressively been colonising the lichen tundra over the last decades, our study region appears suitable to quantify carbon stock changes in plant biomass and soils, with minimal noise associated to the mineralization of ancient carbon.

2. Materials and methods

2.1. Study area

Our study took place in Nunavik, a region currently experiencing one of the strongest greening trends in North America (Ju and Masek 2016). This greening trend is mainly driven by the expansion of dwarf birch (Ropars and Boudreau 2012, Tremblay *et al* 2012, Provencher-Nolet *et al* 2014). Based on dendrochronological data, Ropars *et al* (2015) argued that this greening trend likely occurred over the last two decades, a timeframe coinciding with the strong warming trend observed in Nunavik since the 1990s (Bhiry *et al* 2011).

Our study area is located four kilometers east of the village of Umiujaq, in the upper part of the Tasiapik Valley (figure 1(a); 56.56° N, 76.48° W). Located on the eastern shore of Hudson Bay, the upper valley is comprised of post-glacial fluvio-marine sandy sediments of the Tyrell Sea deposited during the last deglaciation (Lavoie *et al* 2012) and is characterized by discontinuous permafrost (Lemieux *et al* 2016). Soils are relatively young, poorly developed podzols and emerged from the sea *ca*. 7 000 to 6 000 years ago due to isostatic uplift (Lavoie *et al* 2012). As a result, SOC content in the upper valley is likely among the lowest in the Arctic (Hugelius *et al* (2014).

(Provencher-Nolet *et al* 2014) have mapped the vegetation cover changes in the Tasiapik Valley from 1994 to 2010, showing a transition from lichen to shrub tundra. During our 2017 field campaign, small shrubs (ca. 50 cm in height) were heterogeneously found throughout the lichen tundra in the upper valley (figure 1(b)). The tallest shrubs (ca. 1 m in height) were located within the main water tracks (figure 1(c)), consisting of channels where enhanced rates of water drainage allow greater primary productivity (Curasi *et al* 2016). These features often occur on hilly terrain and in valleys, particularly in permafrost regions where the frozen soil acts as a barrier for water drainage (Trochim *et al* 2016). Although little permafrost is found in the upper valley (Lemieux *et al* 2016), thaw ponds can be found lower down the valley, within 200 m of our sampling plots (figure 1(c)). These ponds could already be seen in the oldest aerial photograph of the valley dating back to 1957 (Natural Ressources Canada 1957) and were already surrounded by tall shrubs, suggesting that the establishment of these shrubs preceded the shrub expansion observed throughout Nunavik since the 1990s.

In September-October 2017, sixteen 1 m^2 plots were delimited in the upper Tasiapik Valley. The average elevation of our sampling plots is 132 ± 10 m, as determined by DGPS using a nearby geodesic point. Plots were placed on pure lichen mats ($n = 3$, hereafter referred to as lichen tundra), on small to medium shrubs (30 cm < height < 80 cm) with lichens ($n = 8$; hereafter referred to as medium shrub tundra) and on tall shrubs (*ca*. 1 m) with mosses, ($n = 5$; hereafter referred to as high shrub tundra). Some herbs and other shrub species (*Rhododendron groenlandicum* Oeder, *Vaccinium* sp.) were also present in low abundance. Those shrubs were in general not as tall as birches, about 50 cm high at the most for *R. groenlandicum* and less than 30 cm for *Vaccinium* sp. In wetter areas shrubs such as *Alnus viridis subsp. crispa* Turrill and *Salix planifolia* Pursh. were also observed but these were essentially absent from our plots. Lichens present were mostly *Cladonia spp.*, mostly *C.*

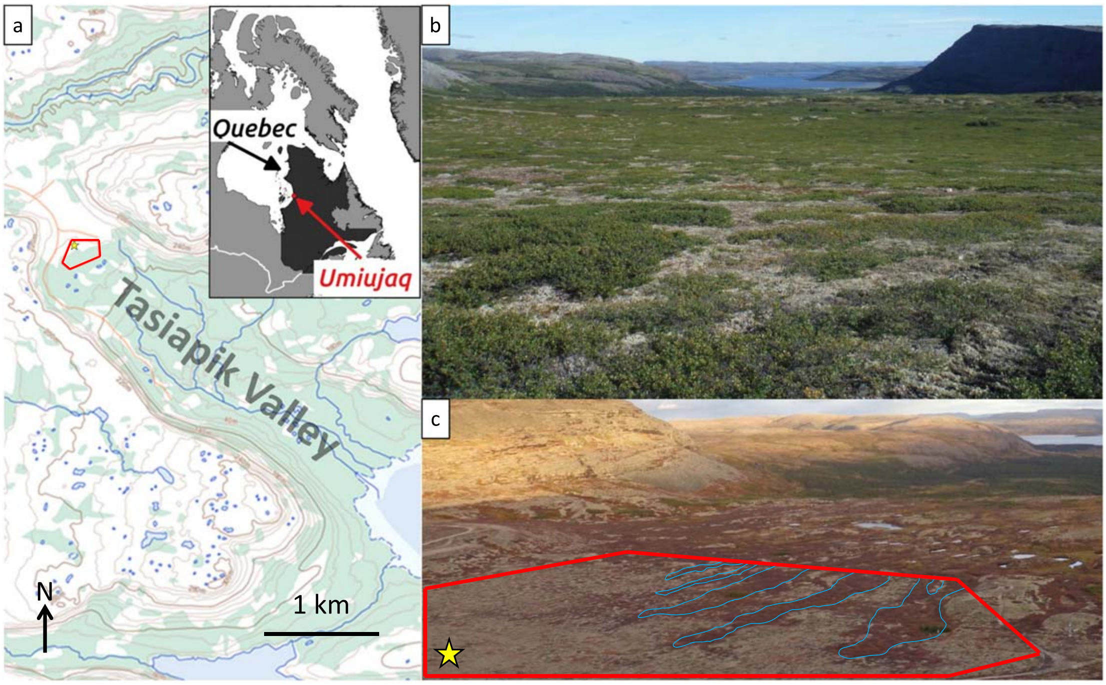

Figure 1. Location of the study area. (a) Map of the Tasiapik Valley region, modified from (NRCAN 2016). Contour lines are 20 m in elevation apart. Green areas are dominated by trees or shrubs. White areas are lichen tundra or rock. (b) Illustration of the recent expansion of dwarf birch throughout the lichen tundra of the upper Tasiapik Valley, Nunavik. The green vegetation is dwarf birch shrubs which have grown in recent decades while the yellow/beige vegetation is the original lichen vegetation. (c) Extent of the upper valley region studied (red), along with the main water tracks (blue). Thaw ponds can be seen further down in the valley, followed by forest-tundra with black spruce (*Picea mariana* Mill.) trees (Payette *et al* 2001). The yellow star shows the location from where photograph (b) was taken. Image (c) was taken in October 2017, when the dwarf birch had lost most of its foliar biomass. As a result, only the largest shrub canopies of the upper valley can be seen, revealing the main water tracks, outlined in blue.

stellaris Opiz and *C. rangiferina* L. with some *C. bellidiflora* and *C. coccifera*. Other lichen species included *Flavocetraria nivalis* L., *Alectoria ochroleuca* Hoffm., and *Stereocaulon paschale* L. Snow depth was recorded at each plot on April 9, 2018.

2.2. Soil carbon stocks

Soil pits were dug at each plot until reaching the C mineral horizon (figure 2). The upper 30 cm of the soil profile was sampled wth a 5 cm resolution (i.e. 0–5 cm, 5–10 cm…, 25–30 cm) with a spatula and placed in 50 ml centrifuge tubes. Dead mosses, decaying lichens and fine roots were included in the soil sampling. Soil density was measured using a 200 cm^3 cylinder (4.78 cm in diameter) using the same 5 cm depth intervals. Soil samples were frozen and brought back to the laboratory, where subsamples were weighed, dried at 70 °C for 72 h and weighed a second time in order to determine their gravimetric water content. The subsamples were sieved at 2 mm, ground in a ball mill grinder and analysed for their total carbon content using a Leco *TruMac CNS* (carbon, nitrogen, sulfur) *Macro Analyzer*, operating under oxygen flow at 1400 °C. Two additional subsamples per plot were used to measure the inorganic carbon content of soil horizons A and B. These samples were dried, ground and heated at 400°C for four hours before being placed in the CNS analyser. The organic carbon content of the soil was thus obtained by subtracting inorganic carbon from total carbon content. The uncertainty of the soil organic carbon stocks (kg m^{-2}) was estimated to be in the range of 11 to 13%, based on analytical error (about 5%) and on error in soil density measurement. Most of the error was caused by the density measurement, about 10%. This is due to errors in determining the size of the sampler (negligible), the sample weight (±0.2 g) and to difficulties in obtaining a perfect soil sample. This is actually the main cause of error, and could be due to the presence of roots or rocks, and sometimes difficulties in perfectly filling the sampler with soil.

2.3. Soil characterization

Using the same soil samples, granulometric analyses of soil horizons A and B were performed at each plot using the Horiba LA-950 Laser Particle Size Analyser. Prior to analysis, soil samples were dried at 400 °C, sieved at 2 mm and agitated in a deflocculating solution of 0.01 M sodium hexametaphosphate. For soil classification, the pyrophosphate-extractible Al and Fe contents of the B horizon were measured at two plots for each vegetation type (lichen, medium and high shrub tundra).

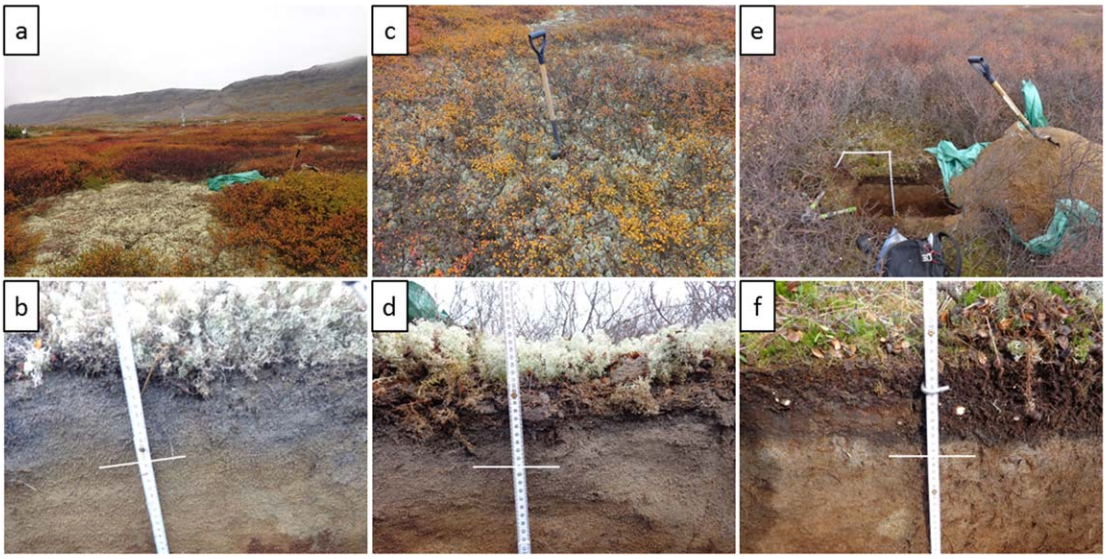

Figure 2. Three types of vegetation covers selected in the upper Tasiapik Valley. (a) Lichen tundra. The beige lichen patch is surrounded by dwarf birch with leaves in fall colors; (c) Medium shrub tundra with visible lichen understory; (e) High shrub tundra with visible green moss understory. On the second row, their respective soil profiles (b), (d), and (f) are shown in the same order. The horizontal lines on images b, d, and f are at the 10 cm depth.

2.4. Vegetation carbon stocks

Total biomass (dwarf birch, lichens and mosses) was determined at each plot, with the exception of graminoids, as their cover was too low. Above- and below-ground dwarf birch biomass was harvested within 1 m^2 plots (figure 2). Most of the root biomass was confined to the top 40 cm of soil, although finer roots could reach depths of 60 cm. The birch biomass was air-dried and weighed in Umiujaq. However, as dwarf birch samples were not fully dried, subsamples of small, medium and tall shrubs were brought back to Université Laval where they were thoroughly dried at 70°C for 72 h. Moisture correction factors, ranging from 30 to 50% (mass fraction) were then applied to the air-dried samples. To quantify lichen biomass, 20 $\times$ 20 cm sections of live lichen mats were hand-collected. Moss biomass was hand-collected over a 31.6 $\times$ 31.6 cm (0.1 m^2) area. Lichens and mosses were dried at 70°C for 72 h. Back in the laboratory, dried lichen, moss and birch samples were ground in liquid nitrogen and analysed for their carbon content using the CNS analyser. The error was estimated from the precision of the 1 m^2 sampling, the extrapolation of dry mass from the subsamples to the whole samples and from the analytical accuracy. The overall error (table S2 is available online at stacks.iop.org/ERC/1/091001/mmedia) was in the range 9 to 16%.

2.5. Tree-ring analysis

In September 2017, a minimum of three dwarf birch samples were taken at each plot to determine the age of the shrub cover. Although samples were taken at the junction between above- and below-ground biomass, the shapes of the junctions suggest they mostly originated from clonal growth rather than from seed germination. Therefore, the oldest shrub sampled at each plot would only provide a minimum age of the shrub cover. Analyses were performed in the dendrochronology laboratory of the Centre for northern studies (CEN) at Université Laval. The samples were boiled for a minimum of four hours, enabling thin sections of ca. 50 microns to be sliced using a microtome. The thin sections were then dyed in a safranin solution (1%) and glued on microscope slides using a 66% toluene solution (SHUR/Mount^{TM} Liquid mounting medium). Samples were then photographed using a binocular-mounted camera (Olympus sZ61 with a SC100 camera) and dated by visual ring counting.

3. Results

3.1. Soil characterization

Granulometric analyses (supporting information, figure S1) revealed that the upper valley consisted of sandy soils throughout the A and B horizons, with the exception of a loamy sand layer (ca. 89% sand, 11% silt, 0% clay) found within the first 5 to 10 cm of the A horizon at 10 of the 16 sites. A 10 cm thick surface layer of sandy loam (69.8% sand, 30.2% silt, 0% clay) was also found at one site. Soils were podzolic in appearance and were classified as brunisolic, according to the Canadian system of soil classification (Soil Classification Working

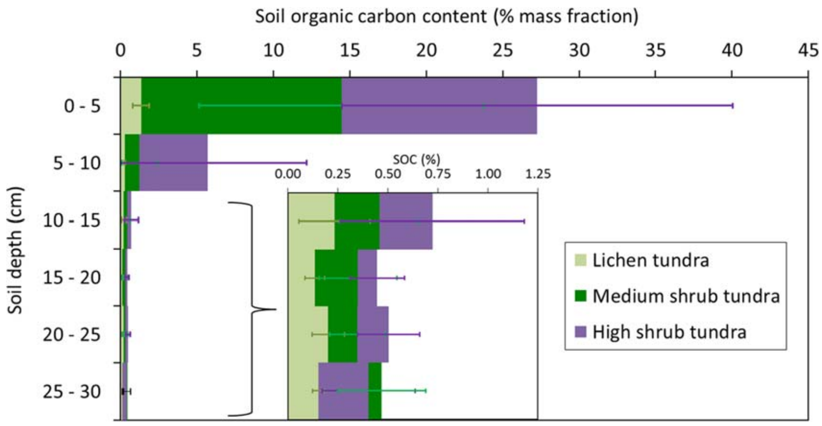

Figure 3. Average soil organic carbon content according to the type vegetation cover: Lichen tundra ($n = 3$), Medium shrub tundra ($n = 8$) and High shrub tundra ($n = 5$). Compared to the lichen tundra, both shrub tundra types have slightly greater SOC contents at depths (10–30 cm). The inserted graph shows a blown-up view of SOC content from a depth of 10 cm. Error bars represent standard deviations. The colored bars are overlain and all start at 0% carbon.

Group 1998). Such classification results from their low mass content of organic carbon (0.31 ± 0.18%), Fe (0.05 ± 0.04%) and Al (0.10 ± 0.09%) in the Bm horizon (Supporting information, table S1). Soils were acidic, with an average $CaCl_2$ pH of 4.10 ± 0.10 in the Bm horizon.

3.2. Snow depth

Snow depth in April 2018 was found to be relatively constant throughout the upper valley. Lichen tundra, medium shrub tundra and high shrub tundra had snow depths of 105 ± 30, 113 ± 8 and 115 ± 8 cm, respectively, resulting in a combined average of 110 ± 10 cm for all 16 plots. An automatic snow gauge and 2 time-lapse cameras revealed that snow depth in early April was within 15 cm of the peak depth reached on 14 May 2018. Detailed snow observations have been made in spring since 2012 (Domine *et al* 2015) and the snow depth recorded in spring 2018 was the highest observed.

3.3. Soil carbon content

Vegetation cover greatly influenced the visible amount of black organic matter in the uppermost 20 cm of the soil profiles (figure 2). Lichen tundra plots (figure 2(a)) only had a very thin layer of decomposing lichens within the first two centimeters of the sandy horizon (figure 2(b)). Their highest SOC content recorded between depths of 5 to 30 cm was on average 0.30% (mass fraction of dry soil; figure 3). Fallen leaves from nearby shrubs were often found in the lichen mats and likely contributed to the SOC content of these sites. Medium shrub tundra plots (figure 2(c)) contained a thicker layer of still distinguishable, decomposing organic matter in the uppermost 5 cm of the soil profiles (figure 2(d)). Compared to the lichen tundra, their SOC contents were slightly greater at depths, reaching 1.27% below 5 cm. The greatest SOC contents (figure 3) were however recorded at high shrub tundra plots (figure 2(e)), where soils had a thick organic horizon which almost reached 10 cm in depth and mainly consisted of decomposing mosses (figure 2(f)), so that between 5 and 10 cm the organic carbon content was 5.72%.

3.4. Total terrestrial carbon stocks

The total terrestrial carbon stocks (TTCS) of the upper Tasiapik Valley (figure 4) include the carbon stocked in the shrubs, in the understory vegetation and in the soil. Detailed data on terrestrial carbon stocks are given in the Supporting information, table S2. The lichen tundra contained the lowest TTCS (2.3 ± 0.4 kg m^{-2}), with SOC contributing only 1.4 ± 0.2 kg m^{-2} (figure 4). In comparison, total terrestrial carbon stocks in the medium shrub tundra averaged 6.2 ± 1.2 kg m^{-2} (figure 4) and most of this carbon was contained in the soil (4.3 ± 0.5 kg m^{-2}). Medium shrub carbon was 1.3 ± 0.3 kg m^{-2}, which compensated for the lower contribution of lichens at these plots. Lastly, the high shrub tundra held the greatest total terrestrial carbon stocks (8.8 ± 3.5 kg m^{-2}). Their SOC stocks of 6.2 ± 0.7 kg m^{-2} were also the greatest of the three vegetation covers, partly due to the thick layer of decomposing mosses found in the litter. Shrub biomass was also the greatest and contained on average 2.3 ± 0.7 kg m^{-2} of carbon. Green moss dry biomass varied greatly between plots and its carbon content ranged from 0.02 to 0.53 kg m^{-2}, adding on average 0.2 ± 0.2 kg m^{-2} of carbon to the terrestrial reservoir (figure 4).

SOC content was significantly associated with the carbon stock in the aboveground vegetation (shrubs, lichens, mosses), particularly when considering only lichen tundra and medium shrub plots ($F_{1,9} = 23.18$,

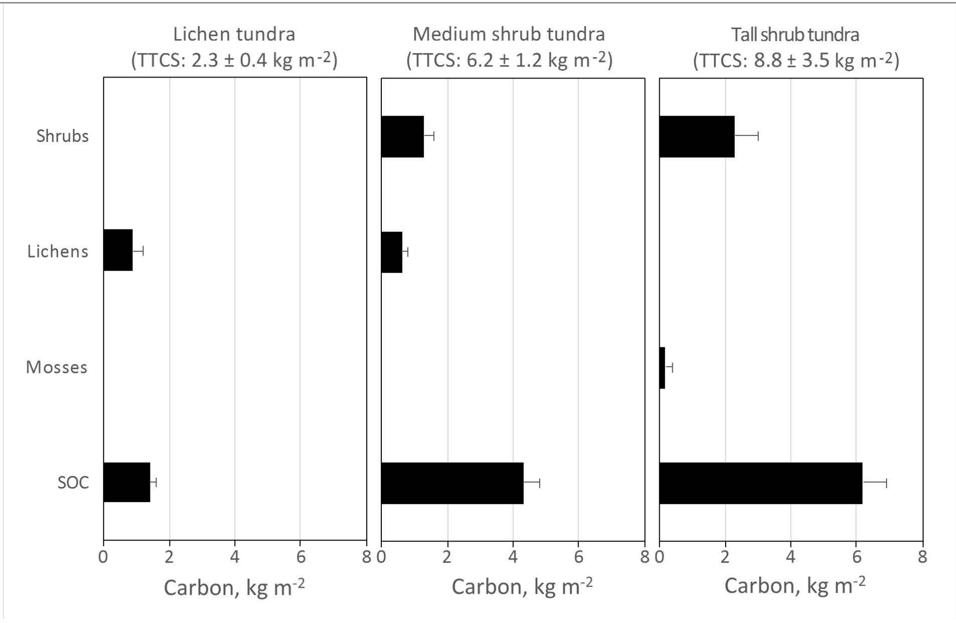

Figure 4. Distribution of total terrestrial carbon stocks (TTCS) in different compartments (soil, lichens, mosses and shrubs) of terrestrial ecosystems found in the upper valley. Plots are classified according to their vegetation cover.

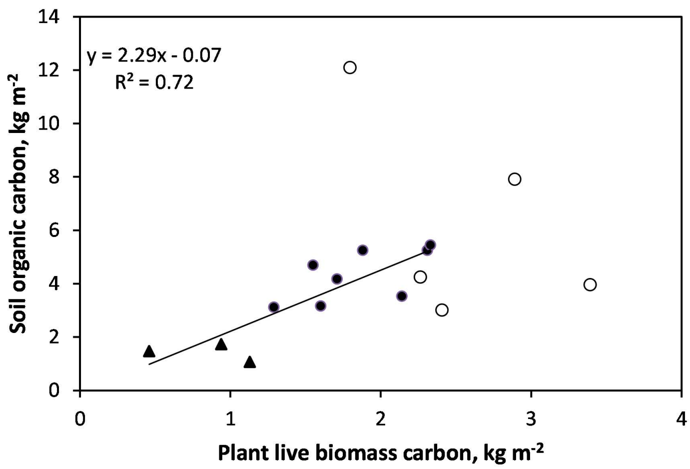

Figure 5. Relationship between soil organic carbon (SOC) content and plant live biomass carbon stock. Closed symbols represent plots sampled in the lichen tundra and in the medium shrub tundra vegetation type. Triangles are for lichen tundra and circles for medium shrub tundra. Open symbols represent plots sampled in the tall shrub tundra type. The regression line is based on data from the lichen tundra and medium shrub tundra plots. As the regression including also the tall shrub tundra was not significant, it is not shown here. Its equation is $y = 1.49 \times +1.58$, $R^2 = 0.17$.

$P = 0.001$; figure 5). As expected, the relationship was weaker ($F_{1,14} = 2.88$, $P > 0.05$) when tall shrub tundra plots were included.

3.5. Tree ring analysis

Dendrochronological data revealed that the minimal time elapsed since the establishment of the shrub covers ranged from 26 to 79 years (relative to sampling year 2017). Detailed data on shrub age are given in the Supporting information, table S3. A stem section micrograph used in age determination is shown in figure S2.

For medium shrubs, the data indicate no significant correlation between terrestrial carbon stocks and shrub age ($R^2 = 0.22$, $p = 0.24$; figure 6). Hence, the transition from lichen to medium shrub tundra resulted in a net gain of 3.9 ± 1.3 kg m^{-2} of carbon, independent of shrub age within the age range sampled. The slope of the correlation of figure 6 may actually suggest that carbon stocks slightly decreased as shrubs aged, but the trend is not significant. High shrub tundra plots are omitted from the regression because moss growth represents a different carbon sink than lichens. Due to insufficient data ($n = 5$), we did not conduct a separate regression for these plots.

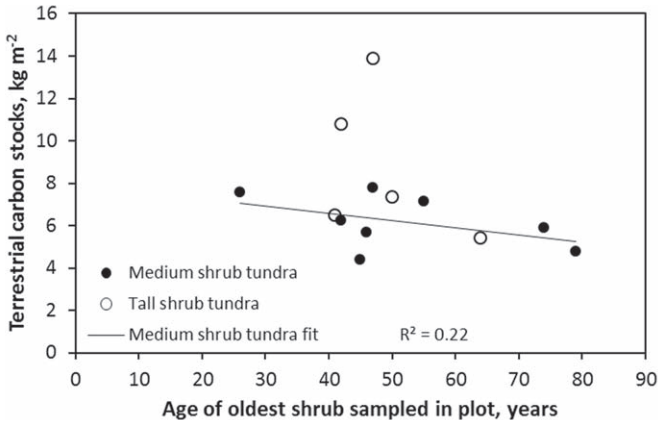

Figure 6. Plot of the terrestrial carbon stocks of the medium and tall shrub tundra plots (kg m^{-2}) as a function of the age of the oldest shrub sampled in the plot. The least square fit is just for the medium shrub tundra, and the correlation is not significant, $p = 0.24$. For comparison, the lichen tundra holds an average terrestrial carbon stock of 2.2 ± 0.4 kg m^{-2} (figure 4).

4. Discussion

4.1. The carbon stocks of tundra biomes

Our results indicate that the total terrestrial carbon stock in the upper Tasiapik Valley is a function of the complexity of the vegetation structure. Lichen tundra contained the lowest carbon reservoir (2.3 ± 0.4 kg m^{-2}), followed respectively by medium (6.2 ± 1.2 kg m^{-2}) and high shrub tundra (8.8 ± 3.5 kg m^{-2}). Thus, the observed transition from lichen tundra to medium shrub tundra in the upper valley has the potential to increase the terrestrial carbon stocks by 3.9 ± 1.3 kg m^{-2}.

Although comparative SOC data is limited in Eastern Canada, particularly in Nunavik, as shown by the absence of data in the soil carbon map of Hugelius *et al* (2014), our SOC data are generally at the lower end of data obtained in other parts of North America. For example, our SOC stocks in the high shrub tundra are roughly similar to the one of a mossy shrub tundra site near the northwestern Alaskan treeline (Wilmking *et al* 2006). There, the tundra consisted of an old floodplain with silt and sand deposits underlain by coarse material and permafrost at a depth of 40 cm. The surface organic horizon reached an average depth of 10.7 ± 7.1 cm and contained 6.21 ± 3.73 kg m^{-2} of carbon. The mineral horizon making up the remainder of the 30 cm of the soil profile contained an additional 3.2 kg m^{-2} of carbon. Radiocarbon dating revealed that at least part of this carbon was of modern origin. However, the shrub carbon sink could not be fully assessed as isotopically enriched carbon makes it difficult to evaluate the proportion of ancient carbon found in the mineral horizon (Levin *et al* 2010). In a similar study at Tulemalu Lake, in the continuous permafrost terrain of the Central Canadian Low Arctic, Hugelius *et al* (2010) compared the carbon stocks of various ecosystem types. The shrub tundra (mainly *Salix* spp. *and Betula* spp.) consisted of turbic cryosols made up of loamy glacial till and sandy glaciofluvial deposits with varying levels of peat. In the upper 30 cm of soil, SOC stocks were respectively 4.8 ± 3.5 kg m^{-2} for lichen tundra, 6.0 ± 3.0 kg m^{-2} for dry shrub tundra, 9.8 ± 5.2 kg m^{-2} for moist shrub tundra and 20.6 ± 4.1 kg m^{-2} for wet shrub tundra. Such differences between ecosystems appear to be driven by moisture, a result corroborating our findings in the Tasiapik valley. Deeper in the soil profile (from 30 to 100 cm), ancient carbon stocks, as revealed by radiocarbon dating, ranged from 7.0 ± 6.0 to 19.8 ± 10.9 kg m^{-2}. Again, the presence of both ancient and modern carbon (bomb carbon) in the superficial horizons clouds the shrub contribution to the SOC stocks.

Our study in the Tasiapik valley presents a much simpler situation. First, the generalized very low level of SOC in the mineral horizons (figure 3) allows us to associate the change in SOC content to plant community shifts, at least from lichen tundra to medium shrub tundra. Second, the transition from lichen tundra to medium shrub tundra has been well documented in the Tasiapik valley (Provencher-Nolet *et al* 2014), with most of the expansion believed to be recent, i.e. post 1990, as observed in other parts of Nunavik (Ropars *et al* 2015). The strong positive association between SOC content and above-ground plant carbon stock on well-drained sites suggest that SOC content is closely associated with the development of an erect shrub cover (figure 5). However, the lack of a significant relationship between SOC content and the age of the oldest stem in the plot (figure 6) was not expected. Such a result may indicate that a steady state between organic matter accumulation and degradation is reached in a short period, less than 30 years, perhaps even less than 20 (figure 6). That a steady state is reached for soil and terrestrial organic carbon is generally valid, and forms the basis of soil carbon modeling, see e.g. (Wang *et al* 2017) or (Nicoloso *et al* 2016). Regarding the time to reach steady state we are not aware of any relevant Arctic study but (Nicoloso *et al* 2016) modeled agricultural land in Kansas and found an equilibration time of about 30 years, in line with local measurements. While this mid-latitude study obviously took place under vastly different conditions, it may indicate that our observed equilibration time is not unreasonable.

Alternatively, it could also mean that stem clonal renewal is such that the age of the oldest stem found in a plot is not a suitable indicator of shrub age. Lastly, since we observed that some stems were more than 75 yr-old (figure 6 and table S3), i.e. they preceded shrub expansion by a few decades, it could be concluded that shrub age is not a valid indicator of shrub expansion at our study site. In any case, tree-ring dating here did not yield any conclusive results.

The relationship between SOC content and above-ground plant carbon stock was much weaker (and not significant) when tall tundra plots were added. Such a result is believed to be mainly associated with different edaphic conditions between lichen/medium shrub tundra sites, found mainly on well-drained sites, and tall shrub tundra sites found in water tracks. As a result, it appears highly unlikely that SOC content of medium shrub tundra site will be comparable to the one in tall shrub tundra sites sampled in this study due to significant edaphic differences. However, as the shrub cover will continue to grow vertically and get denser, mosses will eventually replace lichens underneath the shrub canopy (Schuur *et al* 2007, Paradis *et al* 2016). This process is likely to contribute to local increases in SOC content, although there might be an important variability between sites. In fact, green moss carbon stocks throughout tall shrub tundra varied greatly, from 0.021 to 0.528 kg m^{-2} (Table S2). The strength of this potential carbon sink thus cannot be determined without further study.

Preferential snow accumulation in shrub covers has been suggested as a having a positive impact on shrub growth, as the thermal insulation provided by the greater snow depth would prevent frost damage and increased nutrient availability via greater soil microbial activity (Sturm *et al* 2005). Here, we did not observe significant differences in snow depth between lichen tundra, medium shrub tundra and tall shrub tundra, even though (Paradis *et al* 2016) found a significant relationship between snow cover thickness and shrub height. Snow depth in spring 2018 was the greatest recorded since 2012 and it was greater than shrub height, as we saw no protruding branches. (Domine *et al* 2016) observed that shrubs increased snow depth only up to their own height, so that under the spring 2018 conditions, any impact of shrubs on snow accumulation could not be observed. Shrub effect on snow accumulation could nevertheless have taken place earlier in the season, as observed elsewhere (Paradis *et al* 2016, Barrere *et al* 2018).

4.2. The carbon sink in the tasiapik valley

Based on the results of (Provencher-Nolet *et al* 2014), shrub expansion from 1994 to 2010 led to a 12% (0.609 km^2) increase in shrub cover in the valley (5.228 km^2). As the majority of this expansion occurred by the growth of medium shrubs on the lichen tundra, it is possible to extrapolate our results to a valley-wide scale. Given a terrestrial carbon stock gain of 3.9 kg m^{-2} for the vegetation transition over 0.609 km^2, the areal increase of the medium shrub tundra within this 16yr-period induced a carbon sink of 2.4 $\pm$ 0.8 Gg of carbon throughout the entire valley, or an addition of 28 $\pm$ 9 gC m^{-2} yr^{-1} averaged over the valley area. As suggested by (Lemay *et al* 2018), shrub expansion in the valley is likely to continue in the future. Using land-cover change analysis and modeling, they projected that shrub cover should increase from *ca*. 60% in 2010 to *ca*. 70% in 2030, when it should essentially cease as shrubs would have colonized most of the available area. This future shrub expansion throughout the 5.228 km^2 valley would then add an additional 2.0 $\pm$ 0.7 Gg, resulting in a carbon sink of 4.4 $\pm$ 1.0 Gg from 1994 to 2030.

This case study is clearly insufficient to extrapolate to the circumpolar Arctic, but it does represent a useful case to help constrain future estimates of the permafrost carbon budget. (McGuire *et al* 2018) reported simulations of circumpolar permafrost carbon evolution until the year 2299 using 5 models. Under the RCP4.5 projection, simulated soil carbon stocks varied from gains of 70 Pg C to losses of 67 Pg C, while carbon gains in vegetation were also widely scattered, 69 $\pm$ 70 Pg C, showing that there are huge uncertainties in our understanding of the fate of permafrost carbon and in the contribution of vegetation changes to these stocks. To place our local results in perspective, the gain of 3.9 kg m^{-2} of carbon due to the lichen to shrub tundra transition observed here would translate into a 6.8 Pg C gain if extrapolated to the 1 733 000 km^2 of High-Arctic tundra (Walker *et al* 2005). Unfortunately, (Walker *et al* 2005) do not map lichen tundra separately so we cannot evaluate how the Arctic-wide transformation of lichen tundra into medium shrub tundra would affect the Arctic carbon stocks. Our last extrapolation then has limited value. In conclusion, (Turetsky *et al* 2019) evaluated research priorities to understand the contribution of permafrost emissions to future warming and stressed that 'we need to identify the extent to which plant growth will offset the carbon that is released by permafrost'. Many studies similar to that conducted here are therefore required for a reliable assessment of the evolution of the permafrost carbon budget.

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Social media abstract

Shrub expansion at a low Arctic site results in a carbon sink of about 4 kg per m^2.

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Supplementary material

Table S1: Chemical characterization of soil horizon Bm. Iron and aluminum pyrophosphate-extractable content (mass fraction) and soil pH measured in a 0.01 M $CaCl_2$ solution with a soil to water mass fraction of 1:2.

Vegetation	Site	% Al	% Fe	% C_{org}	pH $CaCl_2$
Lichen	L1	0.04	0.02	0.18	4.08
	L2	0.10	0.04	0.20	4.02
Birch + Lichen	BL2	0.04	0.01	0.28	4.06
	BL6	0.30	0.13	0.30	4.24
	BL7	0.11	0.06	0.65	4.09
Birch + moss	BM1	0.05	0.02	0.11	4.22
	BM2	0.08	0.04	0.45	3.98

Table S2. Detailed carbon data for the 16 plots studied in the upper Tasiapik Valley in September 2017.

Vegetation	Site	Lichen carbon stocks (kg m^{-2})	Birch carbon stocks (kg m^{-2})	Moss carbon stocks (kg m^{-2})	SOC stocks (kg m^{-2})	Surface carbon stocks (kg m^{-2})
Lichen	L1	1.13 ± 0.11	0	0	1.07 ± 0.13	2.20 ± 0.25
	L2	0.46 ± 0.05	0	0	1.47 ± 0.17	1.93 ± 0.22
	L3	0.94 ± 0.09	0	0	1.73 ± 0.20	2.67 ± 0.29
Birch + lichen	BL1	0.21 ± 0.02	1.08 ± 0.15	0	3.12 ± 0.36	4.41 ± 0.53
	BL2	0.52 ± 0.05	1.08 ± 0.13	0	3.16 ± 0.35	4.76 ± 0.54
	BL3	0.59 ± 0.06	1.55 ± 0.19	0	3.53 ± 0.39	5.67 ± 0.64
	BL4	0.18 ± 0.02	1.53 ± 0.19	0	4.18 ± 0.49	5.89 ± 0.69
	BL5	0.63 ± 0.06	0.92 ± 0.15	0	4.7 ± 0.52	6.25 ± 0.74
	BL6	0.82 ± 0.08	1.49 ± 0.24	0	5.25 ± 0.68	7.55 ± 1.00
	BL7	0.33 ± 0.03	1.55 ± 0.21	0	5.25 ± 0.59	7.12 ± 0.83
	BL8	0.73 ± 0.07	1.6 ± 0.23	0	5.45 ± 0.67	7.77 ± 0.97
Birch + moss	BM1	0	1.88 ± 0.20	0.528 ± 0.016	3.01 ± 0.32	5.13 ± 0.67
	BM2	0	3.27 ± 0.29	0.123 ± 0.004	3.96 ± 0.48	7.47 ± 0.92
	BM3	0	2.02 ± 0.25	0.244 ± 0.007	4.25 ± 0.46	6.51 ± 0.86
	BM4	0	2.87 ± 0.27	0.021 ± 0.001	7.91 ± 0.84	11.02 ± 1.26
	BM5	0	1.7 ± 0.17	0.096 ± 0.003	12.10 ± 1.35	14.04 ± 1.66

Table S3. Detailed dendrochronological data for the 16 plots studied in the upper Tasiapik Valley in September 2017.

Vegetation	Site	All measured birch ages	Max. birch age (yrs)	Age ratio (youngest /oldest)	Canopy height (cm)
Lichen	L1	-	-	-	0
	L2	-	-	-	0
	L3	-	-	-	0
Birch + lichen	BL1	21, 24, 35, 38 45	45	0.47	54 ± 5
	BL2	31, 34, 46, 54, 79	79	0.39	44 ± 5
	BL3	18, 25, 25, 27, 38, 46	46	0.39	46 ± 2
	BL4	38, 39, 42, 51, 74	74	0.51	76 ± 6
	BL5	20, 33, 42	42	0.48	31 ± 5
	BL6	21, 21, 23, 23, 26, 26	26	0.81	35 ± 5
	BL7	32, 51, 55	55	0.58	56 ± 4
	BL8	36, 39, 44, 47	47	0.77	46 ± 6
Birch + moss	BM1	39, 51, 64	64	0.61	62 ± 3
	BM2	26, 31, 31, 48, 48, 50	50	0.52	94 ± 12
	BM3	30, 33, 37, 41	41	0.73	104 ± 11
	BM4	23, 28, 30, 33, 42	42	0.55	102 ± 7
	BM5	21, 33, 36, 40, 40, 47	47	0.45	85 ± 11

Figure S1. A typical example of the granulometric distribution of the soils found in the upper Tasiapik Valley. (a) the surface of the A horizon from a depth of 0 to 5 cm; (b) the surface of the B horizon at a depth of 25 to 30 cm.

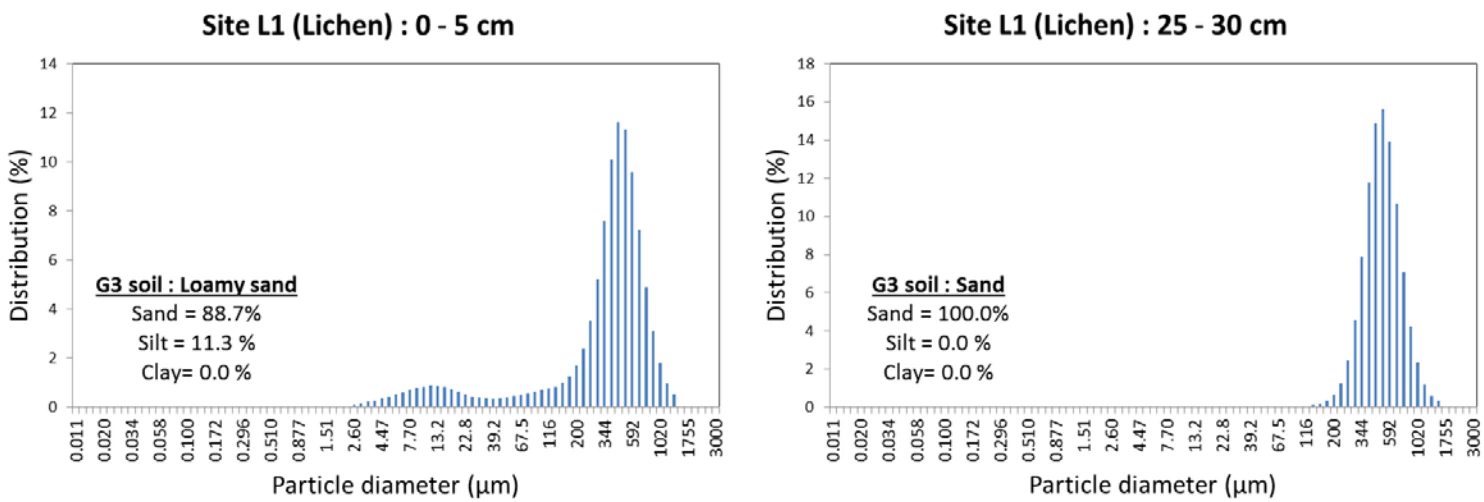

Figure S2. Micrograph of a thin section of birch stems dyed in safranin and used for age determination. Scale bar: 500 µm