



Københavns Universitet

Growing season leaf carbon:nitrogen dynamics in Arctic tundra vegetation from ground and Sentinel-2 observations reveal reallocation timing and upscaling potential

Westergaard-Nielsen, A.; Christiansen, C. T.; Elberling, B.

Published in:
Remote Sensing of Environment

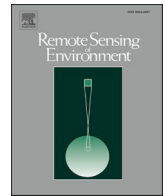
DOI:
[10.1016/j.rse.2021.112512](https://doi.org/10.1016/j.rse.2021.112512)

Publication date:
2021

Document version
Publisher's PDF, also known as Version of record

Document license:
[CC BY](#)

Citation for published version (APA):
Westergaard-Nielsen, A., Christiansen, C. T., & Elberling, B. (2021). Growing season leaf carbon:nitrogen dynamics in Arctic tundra vegetation from ground and Sentinel-2 observations reveal reallocation timing and upscaling potential. *Remote Sensing of Environment*, 262, Article 112512. <https://doi.org/10.1016/j.rse.2021.112512>



Growing season leaf carbon:nitrogen dynamics in Arctic tundra vegetation from ground and Sentinel-2 observations reveal reallocation timing and upscaling potential

A. Westergaard-Nielsen^{a,*}, C.T. Christiansen^{a,b}, B. Elberling^a

^a Center for Permafrost (Cenperm), Department of Geosciences and Natural Resource Management, University of Copenhagen, Denmark

^b Terrestrial Ecology Section, Department of Biology, University of Copenhagen, Denmark

ARTICLE INFO

Editor: Jing M. Chen

ABSTRACT

Plant nitrogen (N) use is an essential component of the N cycle in Arctic terrestrial ecosystems, and important processes include plant N uptake and reallocation during the growing season. While the availability of N to deciduous tundra plants in part relies on their internal reallocation of N from leaves to stems and roots during autumn senescence, the species-specific importance of reallocation timing and its community-wide implications on landscape- and regional-scales remains not well known. Here, we quantified leaf N contents and C:N ratios of four widespread shrub species in West Greenland from June through October and compared plot observations to landscape scale based on a new Sentinel-2-derived index. Our Sentinel-2 index captures overall N reallocation trends well across time and space at the plot level ($R^2 = 0.81$, $p < 0.001$). Using this novel approach is therefore relevant for upscaling of current and future changes in plant C:N dynamics. Using satellite data, we estimate the leaf N mass reallocated during senescence equaled about 0.8 g N m^{-2} from leaves to stems and roots. We conclude that (1) in-situ data from the entire growing season is critical to quantify timing and contrasting strategies of N allocation at species level, (2) key species such as *Salix glauca* are capable of halving their leaf N content during senescence, (3) Sentinel-2 (S-2) satellite data is a strong candidate for quantifying these plant functional dynamics in space and time. Our study has implications for research on competition among Arctic plants, litter decomposition and consequently carbon accumulation in tundra soils from a climate change perspective. Further, it captures plant functional dynamics during critical parts of the growing season, including autumn senescence which is generally more complex than capturing spring greenup. Lastly, our new index has important implications for remotely mapping temporal and spatial variation in substrate quality for both wild and domesticated herbivores, as it is a first step towards a tool to assess the tundra vegetation and fodder quality for cold region animal husbandry.

1. Introduction

Arctic tundra vegetation is undergoing substantial structural and functional change due to intensified climate warming in recent decades (Berner et al., 2020; Myers-Smith et al., 2020). Warming generally increases Arctic vegetation growth (Bjorkman et al., 2018a), thereby augmenting the relative importance of water and nutrient sources, primarily nitrogen (N) (Chapin et al., 2005; Shaver et al., 2006). In pristine Arctic tundra, plant available N is primarily a result of spatial reallocation, which occurs all the way from catchment scale (Skrzypek et al., 2015; Westergaard-Nielsen et al., 2020) to internal reallocation within

individual plants (Evans, 2001). Processes within deciduous plants include both N uptake and transfer to branches and emerging leaves during spring as well as reallocation to stems and roots during autumn senescence. The latter process serves to store N during winter (Chapman et al., 2006), but it is not yet well quantified at the plant species level. Increased knowledge of N availability and temporal patterns in N cycling and allocation strategies in dominant tundra plant species is therefore important for understanding growth feedbacks in Arctic ecosystems resulting from a warmer climate.

The ratio between carbon (C) and N (C:N) in plant leaves is a proven tool to assess and understand plant N dynamics and resource

* Corresponding author.

E-mail address: awn@ign.ku.dk (A. Westergaard-Nielsen).

<https://doi.org/10.1016/j.rse.2021.112512>

Received 26 February 2021; Received in revised form 5 May 2021; Accepted 12 May 2021

Available online 20 May 2021

0034-4257/© 2021 The Authors. Published by Elsevier Inc. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

optimization strategies (Mack et al., 2004; De Deyn et al., 2008; Semenchuk et al., 2015). However, there are a lack of studies focusing on species-specific leaf C:N dynamics with sufficient temporal resolution and extent to pinpoint important periods of changes. Equally important, we lack insight and tools to estimate the net effects of plant N-dynamics over larger tundra areas (Beamish et al., 2020; Myers-Smith et al., 2020), which is otherwise vital for our ability to project impacts of future ecosystem feedbacks to climate.

Warming-induced changes in tundra plant community composition can affect carbon-climate feedbacks in several ways. Observations and experimental open-top chamber (OTC) manipulations show that increased plant growth leads to greater above- and below-ground C storage (Elmendorf et al., 2012a; Elmendorf et al., 2012b; Sistla et al., 2013; Zamin et al., 2014). However, plants are not just responsible for C uptake, they also determine soil microbial decomposition rates, and thereby soil C storage, through species-specific differences in functional traits, such as leaf area and nutrient content (Bjorkman et al., 2018a). Moreover, differences in canopy height and leaf size, which again is linked to nutrient availability, affect ecosystem energy balance and soil thaw depth (Chapin et al., 2005; Blok et al., 2010). This has implications for microbial activity through enhanced regional warming or localized shading-induced cooling, respectively. As foliar plant litter is the most prominent input of C to the soil (Aber and Melillo, 2001), changes in the chemical composition of litter fall regulates nutrient cycling rates and soil organic matter storage (Christiansen et al., 2018a, 2018b; Parker et al., 2018). Low leaf C:N ratios, and high cellulose:lignin ratios, have long been known to catalyse decomposition (Melillo et al., 1989). Consequently, interactions and feedbacks between litter fall, soil N mineralization, and plant C dynamics in a climate change perspective have been increasingly studied at local Arctic sites for decades (e.g. van Heerwaarden et al., 2003; Jonasson et al., 2006; Semenchuk et al., 2015; Blok et al., 2016; Christiansen et al., 2018a, 2018b). Despite recent efforts in synthesising circumpolar-wide ecological responses to environmental change (Bjorkman et al., 2018a; Prev  y et al., 2019), it remains unclear how different tundra plant species will respond to ongoing warming in terms of build-up of plant biomass C and N. While single site studies are of great importance for improving our process understanding, it is challenging to upscale the findings from local sites to landscape- and regional scales for quantifications of the aggregated climate feedback effects. This is particularly important when considering recent evidence showing complex plant responses to climate warming at local scales (Myers-Smith et al., 2015; Phoenix and Bjerke, 2016; Myers-Smith et al., 2020). Here, one of the grand challenges is our ability to assess detailed nutrient contents and status of tundra canopies across space and time with regards to C:N ratios.

Remote sensing approaches facilitate effective monitoring of biome-wide tundra change. Vegetation indices from satellite remote sensing (such as NDVI) associated with plant cover have been used to quantify Arctic tundra aboveground biomass (Jia et al., 2006; Raynolds et al., 2012; Westergaard-Nielsen et al., 2015; R  s  nen et al., 2019), and for descriptive phenology during the Arctic growing season (Zeng et al., 2011; Karlsen et al., 2014; Park et al., 2016; Karami et al., 2017). Using satellite data, Park et al. (2016) reported an advancement in the onset of the Arctic growing season of 2.4 days per decade since 1982, oftentimes resulting from earlier snowmelt dates (Zeng et al., 2011; Westergaard-Nielsen et al., 2017; Pedersen et al., 2018). While optical satellite-based remote sensing can provide important data to indicate ecosystem changes and are scalable to global coverage, satellite imagery alone provides limited information on how climate warming continues to shape remote Arctic plant communities. Thus, challenges remain when using remote sensing tools to quantify plant biophysical or biochemical properties, such as plant height or leaf nutrient status (Beamish et al., 2020; Myers-Smith et al., 2020). In addition, satellite imagery alone does not shed light on functional phenology, e.g. what impact does climate change have on seasonal variations in canopy nutrient status and -reallocation, specific parameters causing plant stress, or absolute

photosynthesis rates. For that kind of functional detail, we need on-the-ground observations. This is an ongoing issue because in-situ validation datasets with high temporal and/or spatial sampling frequency remain rare for many Arctic regions, due to the challenging logistics associated with field campaigns in this part of the world. Nevertheless, recent plot-scale observations suggest diverging vegetation responses to climate change across the Arctic, e.g. with increased growth and primary productivity in some areas and decreased in others (Phoenix and Bjerke, 2016; Vowles and Bj  rk, 2019; Myers-Smith et al., 2020). These responses are highly difficult to capture with e.g. NDVI (Myers-Smith et al., 2020), emphasizing an important need for linking large-scale remote sensing methods to detailed vegetation dynamics on the ground.

Efforts have been made to link different spatial scales with focus on measuring vegetation qualities linked to their functioning, e.g. canopy N, C, and lignin. These efforts typically require either access to hyperspectral data (Martin and Aber, 1997; Smith et al., 2002; Martin et al., 2008; Hollinger et al., 2009; Knyazikhin et al., 2013) which constrains the spatiotemporal resolution and scalability, or include advanced modelling of the canopy radiative transfer system (Boegh et al., 2013; Jay et al., 2017) which rely on high-quality input datasets. However, literature reporting the performance of these methods to estimate dynamics of e.g. canopy N, C, or lignin in Arctic ecosystems is to our knowledge non-existent. This has led to an urgent need and requests for tools to better estimate functional plant changes from space (Myers-Smith et al., 2020), based on accessible satellite data with high spatiotemporal coverage, and validation with ground observations. In an Arctic context this lack of knowledge also stands in contrast to the relevance for herbivores such as reindeer (*Rangifer tarandus*) which rely on both plant quantity and feeding quality, and to the current trend of increased farming potential at high northern latitudes following climate warming. This pinpoints an urgent need to explore and optimize grazing and farming practices in the Arctic (King et al., 2018a, 2018b; Hannah et al., 2020).

Here, to the best of our knowledge (Beamish et al., 2020), we present the first growing season-long quantification of temporal fluctuations in Arctic tundra leaf C:N in combination with a remotely sensed scaling approach. We do this by pairing in-situ plant species-specific observations, obtained approximately weekly from June through October in Arctic Greenland, with imagery using a satellite-derived spectral index. This approach allows us to assess the empirical spatiotemporal relationship between in situ leaf C:N contents from four of the most common tundra shrub species and the integrated plant community-based spectral signal achievable from the 10–20 m spatial resolution S-2 satellites. In short, we (1) present and validate a novel methodology that is scalable from local plot to regional scales for dwarf shrub heath vegetation that is widespread across the circumpolar Arctic and (2) provide a unique quantification of plant species-specific dynamics of N, including estimates of when and how much of total above-ground leaf N mass is reallocated from leaves to stems and roots during autumn. This novel method advances our remote sensing capabilities to include assessments of temporal functional changes in tundra vegetation concerning leaf N content, timing of internal plant N-redistribution, and litter quality during senescence. Consequently, this study has implications for our understanding of climate-driven changes in Arctic tundra vegetation, regarding plant communities and C fixation as well as ecosystems with grazing, including future ambitions of human-introduced domestic grazers in the Arctic.

2. Methods

Our study was carried out from June through October 2016 in the   sterlien valley (69.25359   N, 53.51301   W), located on the southern part of Disko Island in West Greenland (Fig. 1). The in-situ study area covers approximately 0.1 km² on a gentle south-facing slope going from 60 m.a.s.l. to a few m.a.s.l. towards the Disko Bay shore. The   sterlien valley lies just east of the research station Arctic Station, and the area

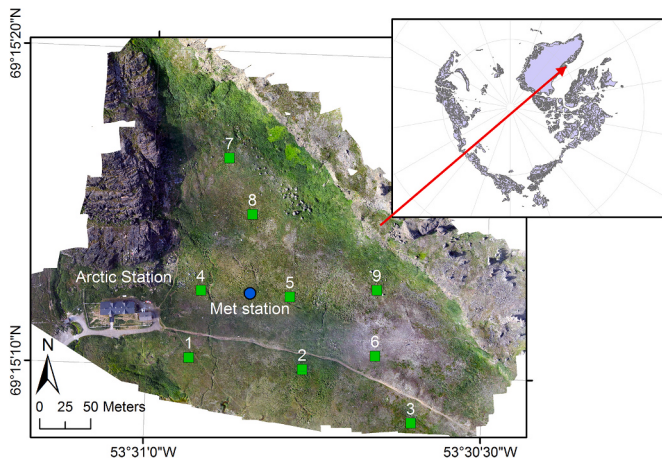


Fig. 1. UAV-based true color orthophoto of the study area in Østerlien valley, Disko Island, West Greenland. The green squares depict the nine sample plots. Meteorological data and continuous soil moisture data origins from measurements by the Meteorological station (Met station; blue circle). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

surrounding Østerlien has been studied systematically since 1996. Arctic Station's environmental monitoring programme became part of the Greenland Ecosystem Monitoring programme in 2018 (<https://g-e-m.dk/>).

2.1. Site climatology

The study area lies in a discontinuous permafrost zone (Obu et al., 2019) with mean annual summer (June–August) and winter (December–February) air temperatures of -3 ± 1.8 °C, 6.8 ± 1.3 °C, and -12.5 ± 3.9 °C, respectively (1991–2017 means $\pm$ SD; Zhang et al., 2019). From 1991 to 2017, the mean annual air temperature increased significantly by 1.6 °C per decade, mainly due to a pronounced winter warming of 3.2 °C per decade. A marked warming trend occurred in 1991–2005, while data for 2006–2017 show greater year-to-year variation with no significant trends in mean annual, summer, or winter air temperatures which is in line with general temperature trends in the region (Westergaard-Nielsen et al., 2018), see Zhang et al. (2019) for further details. Mean annual precipitation is estimated at ~ 400 mm (Hansen et al., 2006). The soil is well-drained and poorly developed from weathered basaltic bedrock parent material.

2.2. Site vegetation

Mesic dwarf shrub heath tundra dominates the Østerlien valley. The vegetation consists mainly of deciduous shrubs *Betula nana*, *Salix glauca*, and *Vaccinium uliginosum*, and the evergreen shrub *Empetrum nigrum*. Some graminoids, such as *Carex* sp. and *Poa* sp., and various mosses and lichens are present but to a much lesser extent than the dominant shrubs. This dwarf shrub dominated vegetation type belongs to the Circumpolar Arctic Vegetation Map (CAVM) subunits P1, P2, and S1, making the study area representative of up to 25% of the ice-free circumpolar low Arctic (CAVM subzones D and E according to Walker et al., 2005), including substantial parts of the ice-free Greenland (Karami et al., 2018).

2.3. Experimental setup and field sampling

In early June 2016, we established nine 1×1 m plots following a distributed sampling scheme with a minimum distance of 65 m between plots. We established each plot so that it provided representation of the vegetation in a surrounding area of 20×20 m to allow subsequent

comparison with S-2 satellite data. Based on spectral (red, green, blue) UAV data at 3 cm spatial resolution, we found the 20×20 m area around each plot to have a near gaussian distribution, and that the mean pixel value from the plots was within one standard deviation of all pixel values in the 20×20 m area. From this we concluded that selected plots represented as homogeneous an area as possible. The nine plots were dominated by different combinations of vascular plants *Betula nana*, *Salix glauca*, *Vaccinium uliginosum*, and *Empetrum nigrum*. We visited the plots 13 times during the 2016 growing season, with a median of eight days between visits from June 14th through October 15th. During each visit, we photographed the plots at nadir approximately 1.5 m above the surface (G1X camera, Sony, Tokyo, Japan). Each image covered an area of ~ 3 m². In addition, we randomly sampled 10 leaves of each of the four dominant plant species mentioned above. Leaves were collected at random from plant individuals growing within 1 m of each plot. Note that no leaves were collected inside plots. This approach allowed us to sample leaves continuously throughout the growing season, minimizing sampling stress on specific individuals, while obtaining unbiased photographs from within each plot.

We used photographs from 20th of July to estimate the percentage cover of each of the four dominant plant species by averaging a visual estimate of species cover from a 6×6 grid drawn across the photograph (supplemental fig. S1). Photographs from the remaining dates served for visual inspection of disturbances and phenology. The combined cover of the four shrub species was above 88% in all plots so we standardized cover of these four species to 100% cover, which also aided in compensating for leaf N in other, non-sampled, plant species. The remaining surface cover in the plots consisted of a combination exposed bedrock, mosses, lichens, and graminoids. The site coordinates were logged 5 times (GPSmap 62, Garmin Ltd., Kansas, USA), and the Euclidian averages were selected as the representative coordinates to decrease spatial uncertainty.

In addition to leaf sampling, site-level soil pore water was sampled 12 times at the Met Station (Fig. 1) during the study period for subsequent quantification of dissolved organic nitrogen (DON), NO_3^- and NH_4^+ . The soil nutrient sampling procedure and analysis followed Rasmussen et al. (2020).

2.4. Leaf carbon and nitrogen analyses

The sampled leaves were air-dried and stored at ambient conditions approximately one year before undergoing lab analyses at the Center for Permafrost (Copenhagen, Denmark). In this study, we consider the petiole as being a functional part of the stem (Pérez-Harguindeguy et al., 2013), and therefore to have no marked influence on the remotely sensed reflectance compared to the leaf blades. Consequently, we carefully removed petioles from the leaves in the lab. Subsequently, we homogenized (Retsch MM200 ball mill, Retsch GmbH, Haan, Germany) five leaves from each plant species at each of the 13 sampling dates, whereafter 3–4 mg subsamples were analyzed for C and N content in an elemental analyzer (Flash 2000, Thermo Scientific, Bremen, Germany) coupled in continuous flow mode to an isotope mass spectrometer (Thermo Delta V Advantage, Thermo Scientific, Bremen, Germany). We used pure gases of CO_2 and N_2 calibrated against certified materials of ^{15}N -(NH_4)₂SO₄ and ^{13}C -sucrose, as certified reference materials. Species-specific leaf C:N ratios and N content were subsequently derived as an average of all the analyzed leaves per species across the nine plots per sampling time. We report all leaf data as community-weighted means per plot, using the standardized percent cover of the four dominating plant species (Table 1), or we report data as species-specific means across all plots.

We used plant species-specific leaf mass per area (LMA) data, obtained from the Tundra Trait Team database (Bjorkman et al., 2018b) and calculated as specific leaf area (SLA)⁻¹, in order calculate canopy biomass N for each of our plots and sampling times. We used circumpolar-wide medians of LMA (using means instead of medians

Table 1

Standardized cover fraction distribution of the sampled shrub species in nine replicate plots in Østerlien valley, Disko Island, West Greenland. Prior to standardization, the total relative cover of the four shrub species was >88% for all plots.

Plot	1	2	3	4	5	6	7	8	9
<i>Salix glauca</i>	0.30	0.97	0.11	0.21	0.44	0.31	0.51	0.24	0.52
<i>Vaccinium uliginosum</i>	0.44	0	0.27	0.67	0.56	0.56	0.49	0.48	0.20
<i>Betula nana</i>	0.08	0.03	0.32	0.07	0	0.13	0	0.21	0.16
<i>Empetrum nigrum</i>	0.18	0	0.30	0.06	0	0	0	0.07	0.12

yielded similar LMA values per plant species).

We used database LMA data in combination with our own plot-scale leaf N content data and vegetation cover to calculate community-weighted peak-summer canopy N mass and autumn senescence N mass as follows:

$$\text{Canopy N} = \sum_{i-j} \text{Cover}_{\text{species } i-j} * \text{LMA}_{\text{species } i-j} * \text{N}_{\text{species } i-j} \quad (1)$$

Note that our estimation of Canopy N does not include N in above-ground stems. We did not estimate Canopy N for dates prior to July as leaves are still developing in June and our calculation used database LMA values that were collected primarily in July and August, i.e. when leaves are near to fully developed. Our estimation of Canopy N assumes that LMA remains constant during autumn senescence, which likely underestimates resorption efficiency and overestimates remaining N mass in near-senesced leaves (van Heerwaarden et al., 2003). Cover fractions of individual plant species varied between plots (Table 1), and by deriving a standardized weighing-factor for each species in each plot, we amplify the absolute importance of the present species in subsequent estimates of canopy N. The cover standardization builds on the assumption that the plots are fully covered by vegetation and that other plant species, which were not accounted for in our analyses (e.g., forbs or graminoids), have a similar N content to the shrubs investigated by us. While these relative cover estimates could add bias to our in-situ leaf C:N, the four sampled shrub species always covered >88% of the plots, and only Plot 9 had minor barren patches (approximately 3% of the area). Moreover, other plot-scale plant community cover analyses show that forbs and graminoids each cover ≤10% of the area in Østerlien (Christiansen, unpublished data), with forb and graminoid leaf %N being broadly similar to our three sampled deciduous shrub species (data from the Tundra Trait team database show that those species range between 1 and 4% N by leaf dry mass). We therefore argue that the alternative to standardizing the four measured species to a 100% cover (i.e. to assume no C or N in the plant species that are unaccounted for in our analyses but still constitute a minor part of the surface cover) is suboptimal and would lead to underestimation of canopy N. We acknowledge that our plant cover estimates based on top-down plot orthophotos likely underestimate total leaf abundance due to our limited ability to account for layered canopies (vertical variation and overlapping canopies/leaves). In Østerlien, all four sampled shrub species usually grow within multi-layered canopies, and our canopy N mass calculations do not account for N in sub-canopy leaves.

2.5. Satellite imagery

Satellite data were acquired from the sun-synchronous S-2A satellite, featuring the Multi Spectral Instrument with 13 spectral bands, and a spatial resolution between 10 and 60 m (Drusch et al., 2012). Due to converging satellite paths at higher northern latitudes, the satellite revisit time can be as low as 3 days in our study region. The image data were downloaded through the Copernicus Open Access Hub, and all imagery was radiometrically and atmospherically corrected using the Sen2Cor module with a maritime atmosphere setting (Louis et al., 2016). The satellite scenes in supporting table ST1 were found to match our criteria of maximum 50% cloud cover and proximity in time to the in-situ sampling dates (+/- 2.3 days on average). We then extracted

cloud-free satellite pixels, covering our field plots for subsequent comparisons. Band 6 (red-edge, 740 nm) and 11 (shortwave-infrared (SWIR), 1610 nm) were used to compute a normalized reflectance index (NRI) at 20 × 20 m spatial resolution:

$$\text{NRI}_{1610} = \frac{\rho_{740} - \rho_{1610}}{\rho_{740} + \rho_{1610}} \quad (2)$$

where ρ is bottom of atmosphere reflectance at 740 and 1610 nm, respectively. The index is based on a correlogram between the 13 satellite bands and in-situ C:N values, from which bands 6 and 11 (at 20 m spatial resolution) showed among the highest correlation coefficients (Pearson's rho). In addition, our approach is motivated by the nitrogen SWIR absorption features around 1510 and 1690 nm (Herrmann et al., 2010; Dechant et al., 2017), and the well-documented ability of the red-edge region to describe vegetation type and status (Horler et al., 1983; Gitelson et al., 2006; Meneghin et al., 2018). In addition, the red-edge is associated with chlorophyll, and thus indirectly with N content (Clevers and Gitelson, 2013). Although band 11 is not centered at either absorption wavelength, it overlaps with 1690 nm. Note that the SWIR bands, as well as the near-infrared bands are also affected by moisture levels on the Earth's surface. This feature is e.g. exploited using a Normalized Difference Wetness Index (NDWI) as proxy for soil moisture (Jørgensen et al., 2015) or plant canopy moisture (Gu et al., 2008). Other normalized difference indices combining SWIR and red-edge bands have been used to estimate vegetation water stress and canopy water content, e.g. Fensholt and Sandholt (2003) who used the MODIS band 2 and 6, or Zhang et al. (2018) who used S-2 band 8a and 11 to derive normalized difference infrared indices (NDII). Therefore, we computed NDWI based on S-2 band 12 and 8 (Gu et al., 2008), three NDII indices based on S-2 bands 8a and 11, bands 7 and 11, and bands 8 and 11 as well as the commonly used NDVI based on the standard band 4 and 8 (Erinjeri et al., 2018), to test the potential for isolation of unwanted noise from changes in moisture regime.

The S-2 satellites can suffer from inconsistent spatial accuracy at high northern latitudes due to inconsistencies in the elevation model used, which can vary with satellite orbit (Kääb et al., 2016). In our study area, we found shifts to be <10 m between orbits (satellite scenes were visually compared to a sub-meter accuracy orthophoto), possibly resulting from our study area being relatively flat, and consequently our in-situ plots were still located in the same pixels regardless of orbit. We were able to confirm this theory also by using the constant visible location of the nearby Arctic Station.

2.6. Data analyses

We used R v. 4.0.0 (RCore, 2016) to process data and calculate all canopy N estimates. Unless stated otherwise, we used least squares linear regression and *t*-tests for the correlation analyses (using Matlab 2018a, Mathworks, Natick USA).

When observing data points following an increasing or decreasing trend over time, we can estimate when in time a certain ratio of change in the data from their min to max has occurred. To quantify this timing in our satellite and in-situ datasets, we normalized the data to [0–1], interpolated linearly between data points, and extracted the dates when an increase or decrease (represented by the interpolation model) had reached 0.4, 0.5, and 0.6 of its change, respectively (using Matlab

2018a, Mathworks, Natick USA).

3. Results

3.1. Plot scale plant cover

We estimated cover fractions of the dominant shrub species based on camera photographs from each plot and its nearest surroundings as defined by the photograph's coverage. *S. glauca* was present in all plots, while *V. uliginosum* and *B. nana* were the second most frequent plant species (Table 1).

From visual inspection of weekly photographs, the relative canopy leaf area per species did not change noticeably from July to late September. Leaf coloring shifted from green to carotenoid-dominated between the 3rd and 10th of August for plot 2, 3, and 6, and between the 10th and 24th of August for the remaining plots.

3.2. Local growing season climate, soil water chemistry, and satellite NDVI

The rapid drop in soil moisture in early July reflects the shift from early-season saturated soils, due to snowmelt and subsequent lateral runoff, to a mesic soil moisture regime in summer (Fig. 2A). Plot-scale NDVI, derived from the S-2A data, followed an expected pattern with a rapid green up in June, following snowmelt, followed by a senescing phase starting in mid-August. Visual shifts in vegetation color, based on

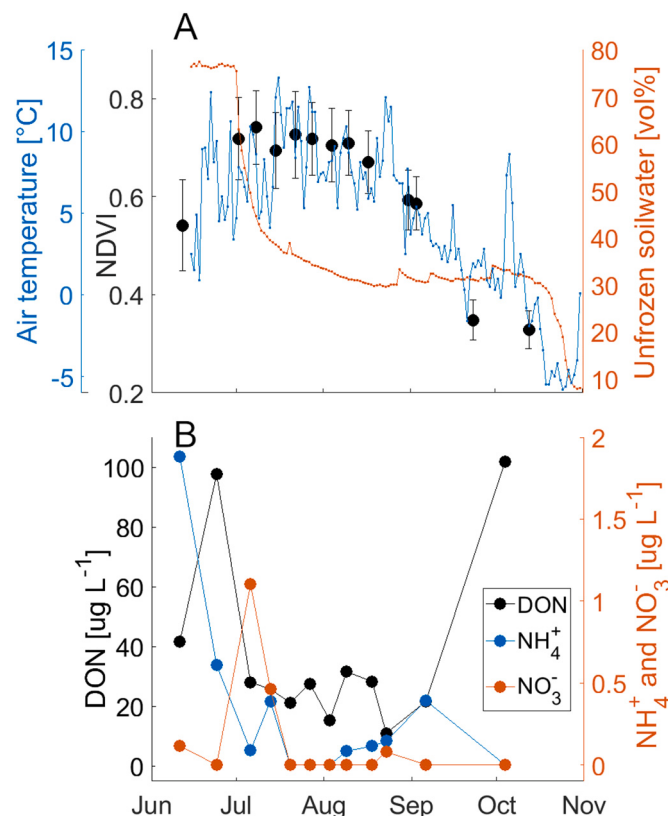


Fig. 2. (A) Air temperature at 2 m above terrain, soil moisture represented as unfrozen soilwater content at 10 cm depth, and mean plot-scale NDVI derived from S-2A data ($n = 9$ plots; ± 1 standard deviation). Microclimate data are from the Meteorological station in the middle of the Østerlien valley (see Fig. 1). Error bars show the NDVI standard deviation between plots. (B) Total mass of dissolved organic nitrogen (DON), nitrate (NO_3^-) and ammonium (NH_4^+), measured in soil pore water samples obtained in close proximity to the nine vegetation plots, based on soil water concentration integrated for the top 20 cm. See concentrations of the N-forms in the supplemental fig. S3.

plot photographs, appeared long before the first freezing temperatures around the 20th of September. Leaf color change followed the period of decreasing temperatures starting from late August (Fig. 2A and supplemental S2), which was also reflected as the period with significant increase in NRI_{1610} for all plots. This temperature drop coincides with 3 precipitation events on the 28th of August, 8th of September, and 30th September respectively, seen as local increases in soil moisture at 10 cm depth (Fig. 2A).

The summer of 2016 was largely an average summer in terms of soil moisture as well as air and soil temperatures according to Zhang et al. (2019), although spring snow cover was relatively low due to a warm early spring. This partly resulted in a drier summer than normal.

Soil water samples taken during the study period were analyzed for DON, NO_3^- and NH_4^+ . Throughout summer, the total mass of the organic N fraction were factors higher than inorganic N chemically bonded in NO_3^- and NH_4^+ in the soil water (Fig. 2B). However, all three components followed a similar seasonal pattern with relatively high availability in early spring, followed by a significant decline (below our detection limit for both solute concentrations and total mass of NO_3^- and NH_4^+) during peak growing season. DON, and to some extent NH_4^+ , increased markedly in late summer until freeze-in in early October, presumably due to leaching of litter fall. Solute concentrations are reported in supplemental fig. S3.

3.3. Seasonal dynamics in leaf C:N ratios

The analyzed leaf samples showed an expected difference in C:N through time between the deciduous and evergreen species. Specifically, *E. nigrum* had higher leaf C:N in the early and peak growing season than the three studied deciduous species, mainly due to lower N levels (Fig. 3A-C or supplemental fig. S4). In contrast, deciduous shrubs *B. nana*, *S. glauca*, and *V. uliginosum* showed a moderate increase in C:N starting already from the first sample on June 14th, and with a more distinct increase in the first half of August until the end of sampling on October 15th (Fig. 3A). For *B. nana*, we saw an unexpected decrease in C:N on the last sample date, however the difference falls within the standard error margin, and lab tests showed that the drop in C:N was caused by variation between the random leaves picked for analysis at this late phenological stage.

At the plot level, the shrub species cover varied according to Table 1. In general, the cover of *S. glauca* and *V. uliginosum* was most prominent across plots. The temporal change of leaf C:N at plot level is summarized in Fig. 3A. Looking at the N fraction only, *S. glauca* leaves contained about $\frac{2}{3}$ of the leaf N in August compared to July, and by early September, *S. glauca* leaves contained $\frac{1}{3}$ of peak summer %N. *B. nana* leaves reallocated leaf N slightly earlier than *S. glauca* as $\frac{2}{3}$ and $\frac{1}{3}$ of the highest measured leaf N remained in leaves by 12th of July and 22nd of August, respectively. For *V. uliginosum*, the corresponding dates were 29th of July and 5th of September, respectively. For the evergreen *E. nigrum*, leaf N dynamics followed a different pattern relative to the deciduous shrubs. *E. nigrum* leaf N content remained stable throughout summer, except for a slight decrease starting from late August (Fig. 3B).

3.4. Seasonal dynamics in canopy N mass

We calculated seasonal dynamics in canopy N mass for each shrub species (not shown) and for each plot based on in-situ leaf %N (Fig. 3B). The three deciduous shrub species showed a consequent decline in canopy N throughout the growing season, while canopy N for the evergreen *E. nigrum* was more stable over time, which is also reflected in measured leaf %N. When looking at community-weighted means at the plot-scale, plot canopy N varied between plots due to differences in species cover fraction. Plot 2 and 3 showed a distinct drop in mid- to late August, roughly halving their N. Plot 6 had an even earlier significant drop from early August, while the remaining plots displayed later drops, or a quite linear decline through the season (Fig. 4).

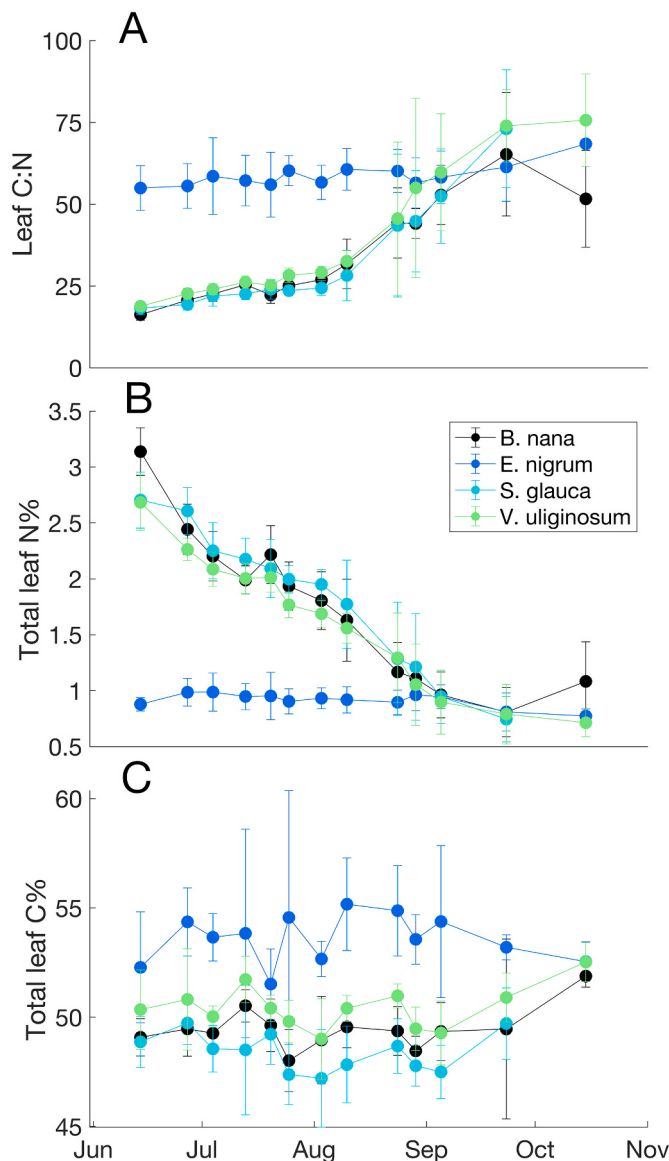


Fig. 3. (A) Seasonal leaf C:N dynamics for *B. nana*, *S. glauca*, *V. uliginosum*, and *E. nigrum*, sampled between June 14th and October 15th 2016 ($n = 9$ per plant species). (B) Total leaf N% at species level as an average measure across plots. Error bars show $\pm$ one standard deviation. (C) Total leaf C% at species level as an average measure across plots. Error bars show standard deviations.

3.5. Results from analyses of satellite indices

A regression analysis between satellite-indices from plot 5 (nearest to the soil moisture point measurement) showed that the near-surface soil moisture at 10 cm (Fig. 2A) and 30 cm depth was not correlated with NDWI as defined in section 2.6, nor with NRI_{1610} , NDVI, or the NDII. All tested satellite indices showed a weak correlation with soil moisture at 20 cm depth, and show thereby the potential importance of soil characteristics for the temporal variation in indices. However, we note that the correlation arise from data distributing as one period with stable satellite indices yet markedly decreasing soil moisture (July), and a subsequent period with marked change in satellite indices and stable soil moisture (August–September), suggesting a need for a dedicated experimental study setup to investigate the dynamics (supplemental fig. S5). Other soil environmental characteristics may be similarly important but are beyond the scope of this study.

We found that satellite-derived NDVI from the nine plots was significantly negatively correlated with the in-situ C:N ratios through

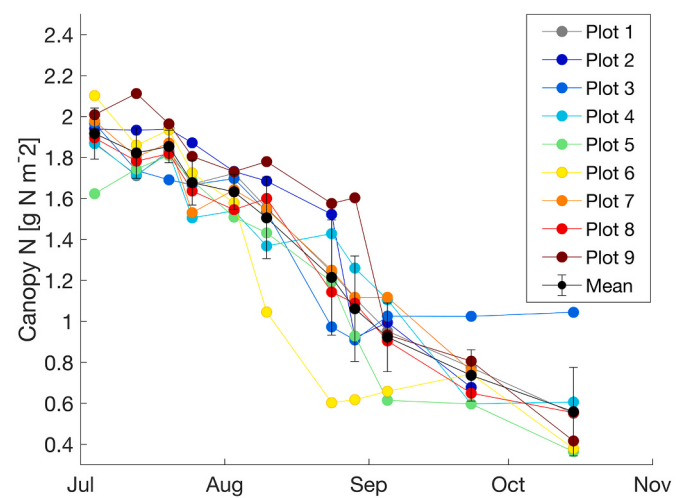


Fig. 4. Seasonal variation in community-weighted plot canopy N across the Østerlien valley, Disko Island, West Greenland, during the 2016 growing season.

the studied season, using one regression model per plot (Table 2). When evaluating the NRI_{1610} , again as one regression model per plot, we found a significantly better correlation (Fisher's Z transformation, $p = 0.037$) with in-situ C:N. A regression analysis comparing in-situ C:N and absolute values of NRI_{1610} (supplemental fig. S4) for all plots and sample times in one single model showed a significant correlation, however with visible uncertainty around the mean values of C:N and NRI_{1610} . This uncertainty greatly diminished when comparing C:N with a normalized NRI_{1610} dataset, yielding an 81% level of explanation (Fig. 5), and suggesting that the slope of linear fit lines varied between plots. Substituting NRI_{1610} with absolute NDVI showed a significant relationship, as did using a min-max normalized NDVI signal, so the explanatory level of the normalized NRI_{1610} was significantly better than NDVI (Fisher's Z transformation, $p = 0.04$). Two apparent outliers on Fig. 5B represent plot 3 and 6 showing a local earlier rise in C:N compared to the other plots (Fig. 5B). NRI_{1610} showed the highest degree of explanation of in-situ C:N compared to the three other computed NDIs, but the difference was not statistically significant (NDII results in supplemental table ST2).

When studying the temporal evolution of NRI_{1610} during the growing season we observed a small increase on average for the nine vegetation plots from the beginning of the sample period until mid-August, followed by a substantial increase from mid-August, and a leveling-off in mid-September. In absolute numbers, Plot 6 and 9 had a significantly

Table 2

Results of correlation analyses between in-situ C:N and satellite-derived indices (mse = mean square error).

Index	Slope	Intercept	R ²	p	mse
NRI_{1610} (average scores from independent analyses per plot)	0.0065	-0.1733	0.89	< 0.001	0.0012
NRI_{1610} (one regression model for all plots)	0.0059	-0.1527	0.53	< 0.001	0.0084
NRI_{1610} normalized (one regression model for all plots)	0.0190	-0.4422	0.81	< 0.001	0.0232
NDVI (average scores from independent analyses per plot)	-0.0081	0.9487	0.81	0.0011	0.0037
NDVI (one regression model for all plots)	-0.0070	0.9105	0.62	< 0.001	0.0086
NDVI normalized (one regression model for all plots)	-0.0165	1.3812	0.72	< 0.001	0.0301

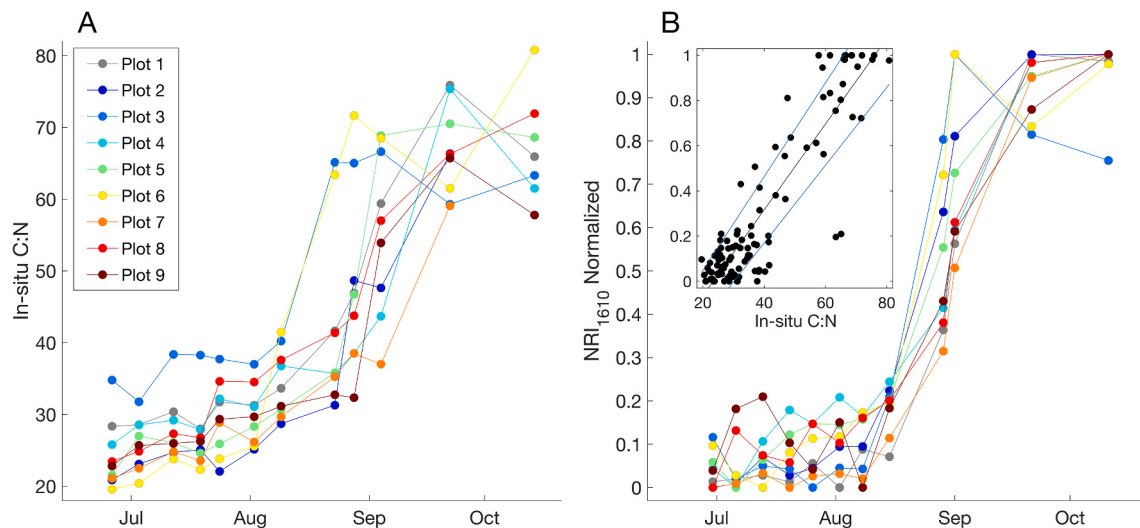


Fig. 5. (A) Seasonal leaf C:N dynamics in 2016 as plant community weighted averages across the nine plots ($n = 1$ per plot). (B) Min-max normalized NRI_{1610} through the growing season per plot. The inset is a scatterplot of in-situ C:N (x-axis) from all nine sites and the corresponding normalized NRI_{1610} (y-axis). The gray line depicts a linear least squares regression ($R^2 = 0.81$, $p < 0.001$, $\text{mse} = 0.023$, $y = 0.019x - 0.442$), the blue lines represent the 95% confidence bounds. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

higher initial NRI_{1610} values in the early season than the other plots, while also reaching the highest index values in late autumn (supplemental fig. S4A–C). A min-max normalization per vegetation plot allowed for a direct comparison of the range of shift over time between plots, showing lower variation between plots (Fig. 5B).

Since the general patterns between in-situ leaf C:N and NRI_{1610} were in good agreement, we extracted transitional dates from the temporal trends based on min-max normalized data of in-situ C:N, NRI_{1610} as well as NDVI. When using a 50% threshold, i.e., the date at which half of the seasonal change had occurred, we saw a statistically significant linear correlation where the timing of a 50% change in NRI_{1610} could explain 82% of the timing for 50% change in C:N. The correlation was significant at 40 and 60% seasonal change as well (Table 3), although with greater residuals (see supplemental fig. S6 for scatter plots). The NDII based on band 7 and 11 showed an equal R^2 to NRI_{1610} ($R^2 = 0.82$) but a marginally higher mean square error of 16.06 (see supplemental table ST3 for all NDII results). There were no significant relationships with C:N transition dates when using satellite-based min-max normalized NDVI.

Using the correlation between NRI_{1610} and leaf C:N (i.e., one regression model for all plots) we derived three maps, covering the studied heath area (Fig. 6).

4. Discussion

Plant uptake of available N and interspecific strategies for autumn N-reallocation are critical N-cycling pathways in terrestrial Arctic ecosystems. Differences in the amount and timing of internal N-reallocation will influence how distinct shrub species cope with current and future climatic changes, with implications for herbivore forage quality and availability as well as ecosystem C and nutrient cycling processes. Yet, methods to assess large-scale temporal and spatial dynamics in canopy N

contents are lacking (Beamish et al., 2020). Here, we demonstrate growing season and autumn variation in leaf C:N ratios at a relatively high level of temporal and spatial resolution, ensuring capturing of N reallocation patterns at the plant species level as well as integrated plant community effects for mixed dwarf shrub heath tundra. These findings are based on a development in remote sensing-based methods that allows us to take the first steps towards an upscaling of seasonal canopy C:N dynamics for large-scale assessments of functional plant phenology and leaf N dynamics in Arctic tundra.

4.1. Scaling leaf carbon to nitrogen patterns from plot to satellite imagery

By including S-2 satellite data, we target the knowledge gap between in-situ measurements of N-dynamics at the small-scale leaf process-level and estimates of impacts at larger landscape spatial scales. However, linking across spatial scales raises the question of representativeness. The sampled heath type is the second-most widespread vegetation class on Disko Island, covering $\sim 600 \text{ km}^2$ (Karami et al., 2018). On a pan-Arctic scale, this vegetation class corresponds to prostrate-shrub tundra (as defined by Walker et al., 2005), covering up to 25% of the ice-free land area across the Arctic (Walker et al., 2005). Being able to capture plant functional dynamics in this type of dwarf shrub heath from space would therefore be substantial for our understanding of climate feedbacks related to changes in vegetation composition (Lorant et al., 2014), spatial dynamics in carbon fixation and N-cycling in vegetation (Myers-Smith et al., 2020), and the perspective of increased extensive livestock grazing at high northern latitudes (King et al., 2018a, 2018b). Using a surface classification map by Karami et al. (2018) and our estimation of total canopy N, and assuming that autumn reallocation starts from August 10th (see Fig. 5A), we find a local reallocation of $\sim 0.8 \text{ g N m}^{-2}$ through the senescing phase before litter fall ($8.7 \text{ mg N m}^{-2} \text{ day}^{-1}$). This resorption corresponds to roughly 50% of peak growing season canopy N, similar to leaf N resorption efficiencies of deciduous tundra plant species (Chapin III et al., 1980; Chapin III and Moilanen, 1991). Scaling to dwarf shrub heath on the Disko Island, this corresponds to a biological mechanism likely transferring $\sim 480 \text{ t N}$ from leaves to stems and roots, and the remains to the soil surface to be recirculated through microbial breakdown of leaf litter.

The NRI_{1610} showed great potential for explaining the general temporal variation of C:N across plots, and it was statistically significantly better than NDVI. NDVI did not correlate with the derived C:N transition

Table 3
Results of transition date timing correlation analyses between satellite indices and in-situ leaf C:N (mse = mean square error).

Satellite index and % change	Slope	Intercept	R^2	p	mse
NRI_{1610} , 40%	1.3095	−74.787	0.49	0.0367	38.960
NRI_{1610} , 50%	2.0593	−254.895	0.82	< 0.001	15.897
NRI_{1610} , 60%	1.9891	−240.500	0.80	0.0012	17.644

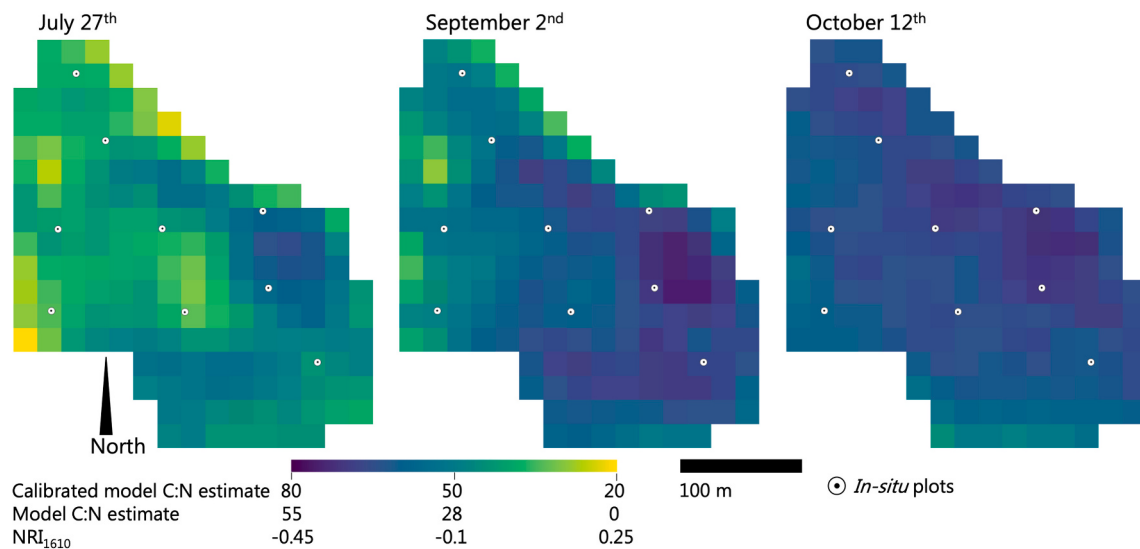


Fig. 6. NRI_{1610} and modeled C:N maps for three select dates, covering the heath in Østerlien valley. Model C:N estimate results from applying the linear regression model between NRI_{1610} and leaf C:N for all plots. The calibrated model C:N estimate was calibrated using measured in-situ C:N ranges.

dates at which a certain level of C:N change (presumably due to N reallocation) had occurred. In contrast, the NRI_{1610} functioned as a highly promising proxy for identification of these transition dates. Of the other three tested NDIs, NRI_{1610} performed only marginally better than when using band 7 and 11, showing that the use of a red-edge band is important to capture C:N dynamics, likely as a combined effect of vegetation type and the link between chlorophylls and N. Our findings therefore support the use of spectral indices other than NDVI. The use of SWIR wavelengths in NRI_{1610} questions to which extent the observed spectral changes result from changes in functional plant phenology or changes in surface moisture. Other studies have confirmed and utilized the SWIR sensitivity to estimate surface moisture at high northern latitudes (Bartsch et al., 2009; Jørgensen et al., 2015), however, most often as a proxy for conditions in the top surface 0–5 cm. (Sadeghi et al., 2017). In our case, there was no correlation between soil moisture at 10 cm and SWIR, nor did we observe a visual covariance over time (supplemental fig. S5), which could otherwise be used to disentangle the spectral signal into a moisture and plant-related component. By normalizing the NRI_{1610} signal, we are confident that we have mitigated any major potential biases between plots resulting from systematic differences in moisture regime.

Plant species vary in reflectance within the red-edge portion of reflected light, however, within-plant temporal dynamics such as changing leaf chlorophyll/carotenoid relationships also affect reflectance (Gitelson et al., 2006; Meneghin et al., 2018). Although the red-edge portion is barely visible to the human eye, the visible earlier shift in autumn coloring in plot 2, 3, and 6, relative to other plots, could be indicative of a relatively earlier N reallocation, even if there was visible variation in leaf color within plots. Fig. 5A shows an earlier marked increase in C:N for plot 3 and 6, suggesting a visible proxy for this phenomena. This is also evident on the NRI_{1610} signal for those plots (Figs. 5B) which shows a similar earlier index increase, although it does not fully mimic the range of C:N shift as seen from the two outliers in Fig. 5. We assign this to within-plot variation in leaf senescence stages, illustrating the challenge of representative leaf sampling during autumn senescence. Nevertheless, due to the close association between N and chloroplasts (Roberts et al., 2012), part of these mechanisms are arguably captured by the red-edge spectrum.

Finding and calibrating remotely sensed spatial proxies for the leaf N-dynamics is an important step towards bridging gaps between in-situ observations and ways to estimate the actual dynamics and implications over a larger spatio-temporal domain. The correlation between leaf C:N

changes and NRI_{1610} does not prove a direct link between N-content in leaves and their spectral properties. Indeed, the plants will transport and reallocate other important nutritional elements alongside N, e.g., phosphorus (P) and potassium (Chapin III et al., 1980), which could influence the observed spectral changes. However, what we show here for the first time is indeed a directly scalable satellite-based index which correlates with C:N reallocation mechanisms in a widespread tundra vegetation class where N is a critical limiting factor for growth (Weintraub and Schimel, 2005; Semenchuk et al., 2015; Pedersen et al., 2020), allowing for novel spatial assessments of plant reallocation strategies. Similarly, our approach describes the timing of a key functional phenological event in its autumn senescing phase, which is oftentimes more complex to capture using optical remote sensing than e.g. spring greenup (Zhang et al., 2018).

4.2. Temporal dynamics in species-specific leaf carbon and nitrogen content

As expected, we observed distinct growing season differences in leaf C:N dynamics between deciduous and evergreen shrub species. The deciduous shrubs all contained relatively high concentrations of leaf N at the first sampling time in mid-June, with leaf N declining throughout the growing season. This pattern indicates that the movement of N from seasonal storage in roots and stems and into new leaves during the first couple of weeks following snowmelt (i.e. at bud-break) had finished by our first sampling (Chapin III et al., 1980). During this time in June, soil soluble N availability peaks to a level likely controlled by climate, before rapidly declining to near-zero for the remainder of the growing season (Fig. 3C), indicating N limitation (Semenchuk et al., 2015; Rasmussen et al., 2020). Therefore, as leaves matured and increased in size during June and July (supplemental fig. S3), leaf C:N ratios gradually increased for all three deciduous shrubs due to competition with soil microbes for a decreasing amounts of soil N and a corresponding dilution of N with recent photosynthesized C compounds (Fig. 3A). Leaf C:N ratios began to increase at much greater pace in August, due to reallocation of N from leaves to stems and roots for winter storage, with the onset and rate of N reallocation being slightly offset between the deciduous species. *B. nana* lost half of its max leaf %N a week earlier (~25th of July) than *V. uliginosum* and two weeks before *S. glauca*, respectively. This is partly due to a higher initial leaf %N in *B. nana* than for *S. glauca* and *V. uliginosum*. The time when one-fifth of max *B. nana* leaf N remained was again a week earlier than *V. uliginosum* and two weeks before

S. glauca, respectively. Overall, this may suggest an earlier reallocation timing for *B. nana* and, to a lesser extent, *V. uliginosum* compared to *S. glauca*, although with some spatial variability between plots. Species exhibiting a slightly more opportunistic strategy N-use in late autumn are interesting in the light of increased relative climate warming in autumn, as has been served in Greenland (Westergaard-Nielsen et al., 2018) and in the Arctic in general (Walsh, 2014; Bintanja and Andry, 2017), although further research is needed to explore such plant-species/climate feedbacks. In contrast to deciduous shrubs, tundra evergreens typically have less biomass belowground and they tend to keep nutrients stored within their canopy (Chapin III et al., 1980), as exhibited here by relatively stable *E. nigrum* leaf N, and only subtle C:N change, throughout the measurement period.

Fig. 6 illustrate a first step towards spatiotemporal mapping of C:N, and cover a relatively homogenous area of tundra heath. Generally, the whole site exhibits an increase in C:N from peak season (July) to senescence (October), in line with individual satellite cells extracted from the nine plots. The highest spatial variation seems to occur during the early phase of senescence (September), in line with the between-plot variation observed in Fig. 5B. From a visual inspection it seems the 20 m spatial resolution could be sufficient to describe variation at a hectare-scale, however, there are indications of spatial autocorrelation, which we interpret as mainly resulting from autocorrelation in plant species composition. Using a single equation for all plots to model C:N does not capture the true variation. The calibrated model (linearly calibrated to in-situ C:N) yields much improved absolute results, underlining the critical importance of ground validation.

The patterns of N forms in the analyzed soil water samples showed similar dynamics to previously reported seasonal changes, with relatively higher availability in early spring, followed by a rapid decline likely resulting from increased microbial activity and plant photosynthesis (Roberts et al., 2009), and a near-zero plateau during the peak growing season. The rapid drop in soil water N during spring and summer indicate a critical N limitation (Semenchuk et al., 2015; Ras-mussen et al., 2020) underlining the relevance of using vegetation C:N dynamics as an indicator of N location in the general ecosystem. Lastly, we measured a brief increase in NH_4^+ and distinct increase in DON in the autumn. Such increases have previously been attributed to autumn freeze-thaw cycles damaging roots and thus limited plant N uptake (Christiansen et al., 2012). However, in our case it is more likely due to increased N input from litterfall (Semenchuk et al., 2015; Blok et al., 2018) which is further supported by the occurrence of rain events in September–October increasing the mobilization of ions from litter to soil.

4.3. Implications for natural and domesticated grazers

Seasonal changes in leaf nutrient concentrations have significant consequences for herbivore food preference. Arctic tundra ecosystems are nutrient-limited and plant species differ in tolerance levels and strategies to cope with nutrient availability. Even minor changes in soil nutrient pools may therefore alter competitive fitness of certain plant species. This can lead to plant species-specific winners and losers in a climate-change context, which may have major implications for both natural and domesticated grazers. For example, increased shrub growth may alter forage quantity and quality for caribou (*Rangifer tarandus*) (Zamin et al., 2017). In summer, Arctic ungulates selectively forage deciduous shrubs (Boertje, 1984; Manseau et al., 1996), such as *Betula* spp. and *Salix* spp., due to their common abundance and relatively high nutrient content compared to other shrubs (Mårell et al., 2006; Skarin et al., 2008). Changes in canopy N content are particularly important as greater leaf N provides greater nutritional value for herbivores. Consequently, warming-induced shrub dominance is likely to impact wild and domesticated *R. tarandus* populations through changes in forage quantity and quality (Zamin et al., 2017). Here, phenological changes are also very likely to affect herbivores in the Arctic.

Leaf nutrient contents are generally high when leaves emerge in spring, whereas nutrient contents decrease continuously until senescence in autumn, as seen here in this study and in others (Chapin III and Moilanen, 1991). For migrating herbivores, such as geese, early snow-melt leads to earlier onset of graminoid growth, and may result in decreased leaf N content when geese arrive (Doiron et al., 2015). As it is critically important for herbivores to maximize nutritional gain during the short Arctic growing season, trophic mismatches therefore pose a severe threat for herbivore population fitness during this decade (Couturier et al., 2009). This is also an issue for animal husbandry, mainly sheep in South and West Greenland, which relies on the quality of natural vegetation during summer when animals are grazing open lands. Here, optimal forage quality and the timing of moving animals indoors is a critical parameter, which can be optimized by improved knowledge of canopy nutrient content. This is particularly relevant when assessing year to year variations before investing in infrastructure such as sprinkler systems to allow for longer seasons, increased number of animals per area, or even mowing (King et al., 2018a, 2018b; Hannah et al., 2020). The methodology and results presented here show how such scaling for larger regions can be made based on on-going and free remote sensing products. We consider results presented here as the first step towards considerably improved quantifications of spatiotemporal variations in tundra canopy N content (or C:N ratios). Several critical knowledge gaps exist such as the performance in wetlands, and a decoupling with soil moisture regime, however it is a promising advancement for our efforts to manage both natural and domesticated herbivore populations now and in the future.

4.4. Implications for future sampling procedures, satellite-based studies and modelling of carbon dynamics

The marked changes in leaf C:N ratios reported here, at the plot community and individual plant species levels during the entire growing season, highlight that reported leaf C:N ratios should be related to a specific time of the growing season. Single snapshot measurements are not representative for the plants in question, not even relatively, as slightly divergent plant-specific reallocation strategies can occur. It also confirms the importance of picking leaves for litter degradation studies at the latest possible stage to avoid a bias towards too high litter N-levels, which in turn may result in overestimated breakdown rates and therefore underestimated C sequestration rates.

We propose that future studies should focus on experimental treatment plots with nutrient additions, e.g. N or P fertilizer addition studies, and possibly include greater spectral and spatial resolution image data in order to explore direct links between spectral properties and element cycling within tundra plants further. Such experimental plots need to be of sufficient size to accommodate the spectral resolution of available satellite imagery, and while this might be challenging there are certainly sites with plot sizes large enough to accommodate the needs. Moreover, it is arguably important to know the approximate cover fraction of species or similar diversity measures such as remote sensing-derived leaf area index estimations. It is also worth noting that our findings only relate to a specific vegetation class, and we see an urgent need for including contrasting climates, year to year variations, and different vegetation types to allow for calibrated scaling across even wider regions. Lastly, this study focuses on C:N ratios and future work should include and address the importance and scaling of other critical plant leaf characteristics, including protein content and lignin which is essential for plant quality as a forage source.

5. Conclusions

This study is an important first step towards bridging the gap between mechanisms of N-cycling at specific plant species and plot community levels in Arctic tundra with the integrated landscape results observed spectrally from space. The eligibility of the study is thereby as

a tool for quantifying spatiotemporal heterogeneity in dwarf shrub heath canopy C:N ratios. Similarly important, it demonstrates the importance of season-long sampling strategies for quantifying species-specific leaf N dynamics, both to improve our process-level understanding of tundra N-cycling and to guide future sampling strategies and modelling efforts linking leaf N contents to soil C sequestration rates. We recommend further controlled experiments to establish direct links between spectral properties compatible with easily accessible satellite data and element cycling, and we encourage further calibration efforts to extrapolate the usage of this new spectral methodology for other vegetation classes and moisture regimes.

Author contribution

Bo Elberling (BE), Casper Tai Christiansen (CTC), and Andreas Westergaard-Nielsen (AWN) designed the study and layout of field work. CTC conducted in-situ leaf sampling, plot photography, and canopy N modelling. AWN was responsible for analyzing leaf and satellite/UAV data as well as climate data. All authors contributed to writing the manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This work was supported by the Danish National Research Foundation (CENPERM DNR100), and University of Copenhagen (UCPH). We acknowledge the infrastructural support by Arctic Station (UCPH), and Greenland Ecosystem Monitoring (GEM) for climate and soil data. We are grateful for field assistance from Regjn Rønn and Alistair McConnell.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.rse.2021.112512>.

References

- Aber, J.D., Melillo, J.M., 2001. *Terrestrial Ecosystems*, Second edition. Brooks Cole, Pacific Grove, California, USA.
- Bartsch, A., Balzter, H., George, C., 2009. The influence of regional surface soil moisture anomalies on forest fires in Siberia observed from satellites. *Environ. Res. Lett.* 4 (4), 045021.
- Beamish, A., Reynolds, M.K., Epstein, H., Frost, G.V., Macander, M.J., Bergstedt, H., et al., 2020. Recent trends and remaining challenges for optical remote sensing of Arctic tundra vegetation: a review and outlook. *Remote Sens. Environ.* 246, 111872.
- Berner, J., Christensen, H.M., Sardeshmukh, P.D., 2020. Does ENSO regularity increase in a warming climate? *J. Clim.* 33 (4), 1247–1259.
- Bintanja, R., Andry, O., 2017. Towards a rain-dominated Arctic. *Nat. Clim. Chang.* 7 (4), 263–267.
- Bjorkman, A.D., Myers-Smith, I.H., Elmendorf, S.C., Normand, S., Rüger, N., Beck, P.S., et al., 2018a. Plant functional trait change across a warming tundra biome. *Nature* 562 (7725), 57–62.
- Bjorkman, A.D., Myers-Smith, I.H., Elmendorf, S.C., Normand, S., Thomas, H.J., Alatalo, J.M., et al., 2018b. Tundra trait team: a database of plant traits spanning the tundra biome. *Glob. Ecol. Biogeogr.* 27 (12), 1402–1411.
- Blok, D., Heijmans, M.M., SCHAEPMAN-STRUB, G., Kononov, A.V., Maximov, T.C., Berendse, F., 2010. Shrub expansion may reduce summer permafrost thaw in Siberian tundra. *Glob. Chang. Biol.* 16 (4), 1296–1305.
- Blok, D., Elberling, B., Michelsen, A., 2016. Initial stages of tundra shrub litter decomposition may be accelerated by deeper winter snow but slowed down by spring warming. *Ecosystems* 19 (1), 155–169.
- Blok, D., Faucherre, S., Banyasz, I., Rinnan, R., Michelsen, A., Elberling, B., 2018. Contrasting above- and belowground organic matter decomposition and carbon and nitrogen dynamics in response to warming in high Arctic tundra. *Glob. Chang. Biol.* 24 (6), 2660–2672.
- Boegh, E., Houborg, R., Bienkowski, J., Braban, C.F., Dalgaard, T., Dijk, N.V., Sutton, M. A., 2013. Remote sensing of LAI, chlorophyll and leaf nitrogen pools of crop- and grasslands in five European landscapes. *Biogeosciences* 10 (10), 6279–6307.
- Boertje, R.D., 1984. Seasonal diets of the Denali caribou herd, Alaska. *Arctic* 161–165.
- Chapin III, F.S., Moilanen, L., 1991. Nutritional controls over nitrogen and phosphorus resorption from Alaskan birch leaves. *Ecology* 72 (2), 709–715.
- Chapin III, F.S., Johnson, D.A., McKendrick, J.D., 1980. Seasonal movement of nutrients in plants of differing growth form in an Alaskan tundra ecosystem: implications for herbivory. *The Journal of Ecology* 189–209.
- Chapin, F.S., Sturm, M., Serreze, M.C., McFadden, J.P., Key, J.R., Lloyd, A.H., et al., 2005. Role of land-surface changes in Arctic summer warming. *Science* 310 (5748), 657–660.
- Chapman, S.K., Langley, J.A., Hart, S.C., Koch, G.W., 2006. Plants actively control nitrogen cycling: uncorking the microbial bottleneck. *New Phytol.* 169 (1), 27–34.
- Christiansen, C.T., Svendsen, S.H., Schmidt, N.M., Michelsen, A., 2012. High arctic heath soil respiration and biogeochemical dynamics during summer and autumn freeze-in-effects of long-term enhanced water and nutrient supply. *Glob. Chang. Biol.* 18 (10), 3224–3236.
- Christiansen, C.T., Lafrenière, M.J., Henry, G.H., Grogan, P., 2018a. Long-term deepened snow promotes tundra evergreen shrub growth and summertime ecosystem net CO₂ gain but reduces soil carbon and nutrient pools. *Glob. Chang. Biol.* 24 (8), 3508–3525.
- Christiansen, C.T., Mack, M.C., DeMarco, J., Grogan, P., 2018b. Decomposition of senesced leaf litter is faster in tall compared to low birch shrub tundra. *Ecosystems* 21 (8), 1564–1579.
- Clevers, J.G., Gitelson, A.A., 2013. Remote estimation of crop and grass chlorophyll and nitrogen content using red-edge bands on Sentinel-2 and -3. *Int. J. Appl. Earth Obs. Geoinf.* 23, 344–351.
- Couturier, S., Côté, S.D., Huot, J., Otto, R.D., 2009. Body-condition dynamics in a northern ungulate gaining fat in winter. *Can. J. Zool.* 87 (5), 367–378.
- De Deyn, G.B., Cornelissen, J.H., Bardgett, R.D., 2008. Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecol. Lett.* 11 (5), 516–531.
- Dechant, B., Cuntz, M., Vohland, M., Schulz, E., Doktor, D., 2017. Estimation of photosynthesis traits from leaf reflectance spectra: correlation to nitrogen content as the dominant mechanism. *Remote Sens. Environ.* 196, 279–292.
- Doiron, M., Gauthier, G., Lévesque, E., 2015. Trophic mismatch and its effects on the growth of young in an Arctic herbivore. *Glob. Chang. Biol.* 21 (12), 4364–4376.
- Drusch, M., Del Bello, U., Carlier, S., Colin, O., Fernandez, V., Gascon, F., et al., 2012. Sentinel-2: ESA's optical high-resolution mission for GMES operational services. *Remote Sens. Environ.* 120, 25–36.
- Elmendorf, S.C., Henry, G.H., Hollister, R.D., Björk, R.G., Björkman, A.D., Callaghan, T. V., et al., 2012a. Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecol. Lett.* 15 (2), 164–175.
- Elmendorf, S.C., Henry, G.H., Hollister, R.D., Björk, R.G., Boulanger-Lapointe, N., Cooper, E.J., et al., 2012b. Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nat. Clim. Chang.* 2 (6), 453–457.
- Erinjer, J.J., Singh, M., Kent, R., 2018. Mapping and assessment of vegetation types in the tropical rainforests of the Western Ghats using multispectral Sentinel-2 and SAR Sentinel-1 satellite imagery. *Remote Sens. Environ.* 216, 345–354.
- Evans, R.D., 2001. Physiological mechanisms influencing plant nitrogen isotope composition. *Trends Plant Sci.* 6 (3), 121–126.
- Fensholt, R., Sandholt, I., 2003. Derivation of a shortwave infrared water stress index from MODIS near- and shortwave infrared data in a semiarid environment. *Remote Sens. Environ.* 87 (1), 111–121.
- Gitelson, A.A., Keydan, G.P., Merzlyak, M.N., 2006. Three-band model for noninvasive estimation of chlorophyll, carotenoids, and anthocyanin contents in higher plant leaves. *Geophys. Res. Lett.* 33 (11).
- Gu, Y., Hunt, E., Wardlaw, B., Basara, J.B., Brown, J.F., Verdin, J.P., 2008. Evaluation of MODIS NDVI and NDWI for vegetation drought monitoring using Oklahoma Mesonet soil moisture data. *Geophys. Res. Lett.* 35 (22).
- Hannah, L., Roehrdanz, P.R., Fraser, E.D., Donatti, C.I., Saenz, L., et al., 2020. The environmental consequences of climate-driven agricultural frontiers. *PLoS One* 15 (2), e0228305.
- Hansen, B.U., Elberling, B., Humlum, O., Nielsen, N., 2006. Meteorological trends (1991–2004) at Arctic Station, central West Greenland (69°15'N) in a 130 years perspective. *Geogr. Tidsskrift-Danish J. Geogr.* 106, 45–55.
- Herrmann, I., Karnieli, A., Bonfil, D.J., Cohen, Y., Alchanatis, V., 2010. SWIR-based spectral indices for assessing nitrogen content in potato fields. *Int. J. Remote Sens.* 31 (19), 5127–5143.
- Hollinger, D.Y., Ollinger, S.V., Richardson, A.D., Meyers, T.P., Dail, D.B., Martin, M.E., et al., 2009. Albedo estimates for land surface models and support for a new paradigm based on foliage nitrogen concentration. *Glob. Chang. Biol.* 16, 696–710.
- Horler, D.N.H., DOCKRAY, M., Barber, J., 1983. The red edge of plant leaf reflectance. *Int. J. Remote Sens.* 4 (2), 273–288.
- Jay, S., Maupas, F., Bendoula, R., Gorretta, N., 2017. Retrieving LAI, chlorophyll and nitrogen contents in sugar beet crops from multi-angular optical remote sensing: comparison of vegetation indices and PROSAIL inversion for field phenotyping. *Field Crop Res.* 210, 33–46.
- Jia, G.J., Epstein, H.E., Walker, D.A., 2006. Spatial heterogeneity of tundra vegetation response to recent temperature changes. *Glob. Chang. Biol.* 12, 42–55.
- Jonasson, S., Castro, J., Michelsen, A., 2006. Interactions between plants, litter and microbes in cycling of nitrogen and phosphorus in the arctic. *Soil Biol. Biochem.* 38 (3), 526–532.
- Jørgensen, C.J., Johansen, K.M.L., Westergaard-Nielsen, A., Elberling, B., 2015. Net regional methane sink in high Arctic soils of Northeast Greenland. *Nat. Geosci.* 8 (1), 20–23.
- Kääb, A., Winsvold, S.H., Altena, B., Nuth, C., Nagler, T., Wuite, J., 2016. Glacier remote sensing using Sentinel-2. part I: Radiometric and geometric performance, and application to ice velocity. *Remote Sensing* 8 (7), 598.

- Karami, M., Hansen, B.U., Westergaard-Nielsen, A., Abermann, J., Lund, M., Schmidt, N. M., Elberling, B., 2017. Vegetation phenology gradients along the west and east coasts of Greenland from 2001 to 2015. *Ambio* 46 (1), 94–105.
- Karami, M., Westergaard-Nielsen, A., Normand, S., Treier, U.A., Elberling, B., Hansen, B. U., 2018. A phenology-based approach to the classification of Arctic tundra ecosystems in Greenland. *ISPRS J. Photogramm. Remote Sens.* 146, 518–529.
- Karlsen, S.R., Elvebakk, A., Høgda, K.A., Grydeland, T., 2014. Spatial and temporal variability in the onset of the growing season on Svalbard, Arctic Norway—measured by MODIS-NDVI satellite data. *Remote Sens.* 6 (9), 8088–8106.
- King, M., Altdorff, D., Li, P., Galagedara, L., Holden, J., Unc, A., 2018a. Northward shift of the agricultural climate zone under 21 st-century global climate change. *Sci. Rep.* 8 (1), 7904.
- King, E.G., Unks, R.R., German, L., 2018b. Constraints and capacities for novel livelihood adaptation: lessons from agricultural adoption in an African dryland pastoralist system. *Reg. Environ. Chang.* 18 (5), 1403–1410.
- Knyazikhin, Y., Schull, M.A., Bret-Harte, P., Mottus, M., Rautiainen, M., Yang, Y., et al., 2013. Hyperspectral remote sensing of foliar nitrogen content. *Proc. Natl. Acad. Sci.* 110 (3), E185–E192.
- Lorant, M.M., Berner, L.T., Goetz, S.J., Jin, Y., Randerson, J.T., 2014. Vegetation controls on northern high latitude snow-albedo feedback: observations and CMIP 5 model simulations. *Glob. Chang. Biol.* 20 (2), 594–606.
- Louis, J., Debaecker, V., Pflug, B., Main-Knorr, M., Bieniarz, J., Mueller-Wilm, U., et al., 2016. Sentinel-2 Sen2Cor: L2A processor for users. In: *Proceedings Living Planet Symposium 2016*. Spacebooks Online, pp. 1–8.
- Mack, M.C., Schuur, E.A., Bret-Harte, M.S., Shaver, G.R., Chapin, F.S., 2004. Ecosystem carbon storage in arctic tundra reduced by long-term nutrient fertilization. *Nature* 431 (7007), 440–443.
- Manseau, M., Huot, J., Crête, M., 1996. Effects of summer grazing by caribou on composition and productivity of vegetation: community and landscape level. *J. Ecol.* 503–513.
- Mårell, A., Hofgaard, A., Danell, K., 2006. Nutrient dynamics of reindeer forage species along snowmelt gradients at different ecological scales. *Basic and Applied Ecology* 7 (1), 13–30.
- Martin, M.E., Aber, J.D., 1997. High spectral resolution remote sensing of forest canopy lignin, nitrogen, and ecosystem processes. *Ecol. Appl.* 7 (2), 431–443.
- Martin, M.E., Plourde, L.C., Ollinger, S.V., Smith, M.L., McNeil, B., 2008. A generalizable method for remote sensing of canopy nitrogen across a wide range of forest ecosystems. *Remote Sens. Environ.* 12 (9), 3511–3519.
- Melillo, J.M., Aber, J.D., Linkins, A.E., Ricca, A., Fry, B., Nadelhoffer, K.J., 1989. Carbon and nitrogen dynamics along the decay continuum: plant litter to soil organic matter. *Plant Soil* 115 (2), 189–198.
- Meneghin, E., Volpato, A., Capellini, L., Bolzonello, L., Jurinovich, S., Mascoli, V., et al., 2018. Coherence in carotenoid-to-chlorophyll energy transfer. *Nat. Commun.* 9 (1), 1–9.
- Myers-Smith, I.H., Elmendorf, S.C., Beck, P.S., Wilmsking, M., Hallinger, M., Blok, D., et al., 2015. Climate sensitivity of shrub growth across the tundra biome. *Nat. Clim. Chang.* 5 (9), 887–891.
- Myers-Smith, I.H., Kerby, J.T., Phoenix, G.K., Bjerke, J.W., Epstein, H.E., Assmann, J.J., et al., 2020. Complexity revealed in the greening of the Arctic. *Nat. Clim. Chang.* 10 (2), 106–117.
- Obu, J., Westermann, S., Bartsch, A., Berdnikov, N., Christiansen, H.H., Dashtseren, A., et al., 2019. Northern hemisphere permafrost map based on TTOP modelling for 2000–2016 at 1 km² scale. *Earth Sci. Rev.* 193, 299–316.
- Park, T., Ganguly, S., Tømmervik, H., Euskirchen, E.S., Høgda, K.A., Karlsen, S.R., et al., 2016. Changes in growing season duration and productivity of northern vegetation inferred from long-term remote sensing data. *Environ. Res. Lett.* 11 (8), 084001.
- Parker, T.C., Sanderman, J., Holden, R.D., Blume-Werry, G., Sjögersten, S., Large, D., et al., 2018. Exploring drivers of litter decomposition in a greening Arctic: results from a transplant experiment across a treeline. *Ecology* 99 (10), 2284–2294.
- Pedersen, S.H., Liston, G.E., Tamstorf, M.P., Abermann, J., Lund, M., Schmidt, N.M., 2018. Quantifying snow controls on vegetation greenness. *Ecosphere* 9 (6), e02309.
- Pedersen, E.P., Elberling, B., Michelsen, A., 2020. Foraging deeply: depth-specific plant nitrogen uptake in response to climate-induced N-release and permafrost thaw in the high Arctic. *Glob. Chang. Biol.* 26 (11), 6523–6536.
- Pérez-Harguindeguy, N., Diaz, S., Gamier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., et al., 2013. New handbook for stand-ardised measurement of plant functional traits worldwide. *Aust. J. Bot.* 61, 167–234.
- Phoenix, G.K., Bjerke, J.W., 2016. Arctic browning: extreme events and trends reversing arctic greening. *Glob. Chang. Biol.* 22 (9), 2960–2962.
- Prevéy, J.S., Rixen, C., Rüger, N., Høye, T.T., Björkman, A.D., Myers-Smith, I.H., et al., 2019. Warming shortens flowering seasons of tundra plant communities. *Nature ecology & evolution* 3 (1), 45–52.
- Räsänen, A., Juutinen, S., Aurela, M., Virtanen, T., 2019. Predicting aboveground biomass in Arctic landscapes using very high spatial resolution satellite imagery and field sampling. *Int. J. Remote Sens.* 40 (3), 1175–1199.
- Rasmussen, L.H., Michelsen, A., Ladegaard-Pedersen, P., Nielsen, C.S., Elberling, B., 2020. Arctic soil water chemistry in dry and wet tundra subject to snow addition, summer warming and herbivory simulation. *Soil Biol. Biochem.* 141, 107676.
- Raynolds, M.K., Walker, D.A., Epstein, H.E., Pinzon, J.E., Tucker, C.J., 2012. A new estimate of tundra-biome phytomass from trans-Arctic field data and AVHRR NDVI. *Remote Sensing Letters* 3 (5), 403–411.
- RCore, T.E.A.M., 2016. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.
- Roberts, P., Newsham, K.K., Bardgett, R.D., Farrar, J.F., Jones, D.L., 2009. Vegetation cover regulates the quantity, quality and temporal dynamics of dissolved organic carbon and nitrogen in Antarctic soils. *Polar Biol.* 32 (7), 999–1008.
- Roberts, I.N., Caputo, C., Criado, M.V., Funk, C., 2012. Senescence-associated proteases in plants. *Physiol. Plant.* 145 (1), 130–139.
- Sadeghi, M., Babaeian, E., Tuller, M., Jones, S.B., 2017. The optical trapezoid model: a novel approach to remote sensing of soil moisture applied to Sentinel-2 and Landsat-8 observations. *Remote Sens. Environ.* 198, 52–68.
- Semenchuk, P.R., Elberling, B., Amtorp, C., Winkler, J., Rumpf, S., Michelsen, A., Cooper, E.J., 2015. Deeper snow alters soil nutrient availability and leaf nutrient status in high Arctic tundra. *Biogeochemistry* 124 (1–3), 81–94.
- Shaver, G.R., Giblin, A.E., Nadelhoffer, K.J., Thielert, K.K., Downs, M.R., Laundre, J.A., Rastetter, E.B., 2006. Carbon turnover in Alaskan tundra soils: effects of organic matter quality, temperature, moisture and fertilizer. *J. Ecol.* 94 (4), 740–753.
- Sistla, S.A., Moore, J.C., Simpson, R.T., Gough, L., Shaver, G.R., Schimel, J.P., 2013. Long-term warming restructures Arctic tundra without changing net soil carbon storage. *Nature* 497 (7451), 615–618.
- Skarin, A., Danell, Ö., Bergström, R., Moen, J., 2008. Summer habitat preferences of GPS-collared reindeer Rangifer tarandus tarandus. *Wildl. Biol.* 14 (1), 1–15.
- Skrzypek, G., Wojtuń, B., Richter, D., Jakubas, D., Wojczulanis-Jakubas, K., Samecka-Cymerman, A., 2015. Diversification of nitrogen sources in various tundra vegetation types in the high Arctic. *PLoS One* 10 (9), e0136536.
- Smith, M.L., Ollinger, S.V., Martin, M.E., Aber, J.D., Hallett, R.A., Goodale, C.L., 2002. Direct estimation of aboveground forest productivity through hyperspectral remote sensing of canopy nitrogen. *Ecol. Appl.* 12 (5), 1286–1302.
- van Heerwaarden, L.M., Toet, S., Aerts, R., 2003. Nitrogen and phosphorus resorption efficiency and proficiency in six sub-arctic bog species after 4 years of nitrogen fertilization. *J. Ecol.* 91 (6), 1060–1070.
- Vowles, T., Björk, R.G., 2019. Implications of evergreen shrub expansion in the Arctic. *J. Ecol.* 107 (2), 650–655.
- Walker, D.A., Raynolds, M.K., Daniëls, F.J., Einarsson, E., Elvebakk, A., Gould, W.A., et al., 2005. The circumpolar Arctic vegetation map. *J. Veg. Sci.* 16 (3), 267–282.
- Walsh, J.E., 2014. Intensified warming of the Arctic: causes and impacts on middle latitudes. *Glob. Planet. Chang.* 117, 52–63.
- Weintraub, M.N., Schimel, J.P., 2005. Nitrogen cycling and the spread of shrubs control changes in the carbon balance of arctic tundra ecosystems. *Bioscience* 55 (5), 408–415.
- Westergaard-Nielsen, A., Björnsson, A.B., Jepsen, M.R., Stendel, M., Hansen, B.U., Elberling, B., 2015. Greenlandic sheep farming controlled by vegetation response today and at the end of the 21st century. *Sci. Total Environ.* 512, 672–681.
- Westergaard-Nielsen, A., Lund, M., Pedersen, S.H., Schmidt, N.M., Klosterman, S., Abermann, J., Hansen, B.U., 2017. Transitions in high-Arctic vegetation growth patterns and ecosystem productivity tracked with automated cameras from 2000 to 2013. *Ambio* 46 (1), 39–52.
- Westergaard-Nielsen, A., Karami, M., Hansen, B.U., Westermann, S., Elberling, B., 2018. Contrasting temperature trends across the ice-free part of Greenland. *Sci. Rep.* 8 (1), 1586.
- Westergaard-Nielsen, A., Balstrøm, T., Treier, U.A., Normand, S., Elberling, B., 2020. Estimating meltwater retention and associated nitrate redistribution during snowmelt in an Arctic tundra landscape. *Environ. Res. Lett.* 15 (3), 034025.
- Zamin, T.J., Bret-Harte, M.S., Grogan, P., 2014. Evergreen shrubs dominate responses to experimental summer warming and fertilization in Canadian Mesic low arctic tundra. *J. Ecol.* 102 (3), 749–766.
- Zamin, T.J., Côté, S.D., Tremblay, J.P., Grogan, P., 2017. Experimental warming alters migratory caribou forage quality. *Ecol. Appl.* 27 (7), 2061–2073.
- Zeng, H., Jia, G., Epstein, H., 2011. Recent changes in phenology over the northern high latitudes detected from multi-satellite data. *Environ. Res. Lett.* 6 (4), 045508.
- Zhang, X., Jayavelu, S., Liu, L., Friedl, M.A., Henebry, G.M., Liu, Y., et al., 2018. Evaluation of land surface phenology from VIIRS data using time series of PhenoCam imagery. *Agric. For. Meteorol.* 256, 137–149.
- Zhang, W., Jansson, P.-E., Sigsgaard, C., McConnell, A., Jammet, M.M., Westergaard-Nielsen, A., Lund, M., Friborg, T., Michelsen, A., Elberling, B., 2019. Model-data fusion to assess year-round CO₂ fluxes for an arctic heath ecosystem in West Greenland (69 °N). *Agric. For. Meteorol.* 272–273, 176–186.