In situ seasonal patterns of root auxin concentrations and meristem length in an arctic sedge

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Summary

- Seasonal dynamics of root growth play an important role in large-scale ecosystem processes; they are largely governed by growth regulatory compounds and influenced by environmental conditions. Yet, our knowledge about physiological drivers of root growth is mostly limited to laboratory-based studies on model plant species.
- We sampled root tips of *Eriophorum vaginatum* and analyzed their auxin concentrations and meristem lengths biweekly over a growing season *in situ* in a subarctic peatland, both in surface soil and at the permafrost thawfront.
- Auxin concentrations were almost five times higher in surface than in thawfront soils and increased over the season, especially at the thawfront. Surprisingly, meristem length showed an opposite pattern and was almost double in thawfront compared with surface soils. Meristem length increased from peak to late season in the surface soils but decreased at the thawfront.
- Our study of *in situ* seasonal dynamics in root physiological parameters illustrates the potential for physiological methods to be applied in ecological studies and emphasizes the importance of *in situ* measurements. The strong effect of root location and the unexpected opposite patterns of meristem length and auxin concentrations likely show that auxin actively governs root growth to ensure a high potential for nutrient uptake at the thawfront.

Introduction

Being mostly situated belowground, plant roots are hidden from view but important drivers for many ecosystem processes. For instance, roots take up water and nutrients and are the main conduit for carbon entering the soil via root turnover, exudation, and their fungal partners (Clemmensen *et al.*, 2013; Sokol & Bradford, 2019). Hence, seasonal dynamics of root growth play an important role in large-scale ecosystem processes, such as carbon and nitrogen cycling. However, current gaps in understanding of ecophysiological processes that govern root growth seasonality are limiting our ability to predict root growth behavior in response to environmental change.

Evidence is emerging that the seasonality of root growth often differs from aboveground growth patterns, especially in northern ecosystems (Abramoff & Finzi, 2015; Blume-Werry *et al.*, 2016; Sloan *et al.*, 2016; Liu *et al.*, 2021; Blume-Werry, 2022). Here, amounts and timing of root growth may be particularly important, as up to 80% of plant biomass and 30–90% of primary production is located belowground in arctic tundra (Iversen *et al.*, 2015; Ma *et al.*, 2021). Arctic soils are also important carbon stores, containing twice as much carbon as the atmosphere (Hugelius *et al.*, 2014; Schuur *et al.*, 2015), with roots and associated fungi as the main sources of soil carbon (Clemmensen *et al.*, 2013; Sokol & Bradford, 2019). At the same time, arctic tundra undergoes rapid changes with nearly four times higher warming rates than the global average (IPCC, 2021), resulting in increasing rates of permafrost thaw (Åkerman & Johansson, 2008; Fewster *et al.*, 2022; Smith *et al.*, 2022). In arctic soils, plants are restricted in their rooting to the upper part of the soil column that thaws out every summer, the so-called active layer. As temperatures increase and permafrost thaws, new opportunities are opening up for plants to interact with the newly thawed, cold soils depending on their seasonal and vertical rooting patterns (Keuper *et al.*, 2012, 2017; Blume-Werry *et al.*, 2019; Pickering Pedersen *et al.*, 2020). Arctic tundra soils are generally nutrient-poor and particularly limited in nitrogen availability; however, permafrost has about seven times higher nitrogen concentrations than the currently available rooting zone soil (Keuper *et al.*, 2012). Thus, thawing of permafrost opens up a new source of nutrients for plants, but this source only becomes available at the end of the season and deep in the soil, below the current active layer (Keuper *et al.*, 2012, 2017; Blume-Werry *et al.*, 2019). Field observations from the Arctic show that root growth can occur late in the season and, for some species, also in deep active layer soil close to the permafrost table (Blume-Werry *et al.*, 2016, 2019), which is much colder than surface soil during peak season. These strong changes in environmental conditions with depth and season provide an opportunity to investigate ecophysiological responses of plants to different temperatures and season *in situ*. Yet, a critical question remains unanswered: Can the knowledge gained from controlled laboratory experiments on root physiology be reliably applied to comprehend and elucidate the complex patterns of seasonal root growth observed in the ever-changing field conditions?

The development of the root system is largely governed by growth regulatory compounds, and one of the most important is auxin (indole-3-acetic acid, IAA). Most of our knowledge of the molecular players involved in auxin-related growth and developmental processes comes from research on the model plant species *Arabidopsis thaliana* (Roychoudhry & Kepinski, 2022). Still, data suggest that similar regulatory mechanisms exist in all higher plants (Brunoni *et al.*, 2019, 2020; Ramos Báez & Nemhauser, 2021). External signals also have a strong impact on plant development, and factors such as temperature, nutrient availability, and interaction with other plants and the soil microbiome influence not only root system architecture but also seasonal growth patterns (Roychoudhry & Kepinski, 2022). These external signals act through phytohormones, changing their metabolism, transport, and signaling within the tissues. The apex of all orders of roots contains root meristems, groups of cells that divide, differentiate, and elongate to form all cell types of the mature root system. Root meristem size is strictly regulated by the rate of cell division and differentiation, and it has been shown that low temperature, for example, inhibits root growth by reducing auxin accumulation in the root apex, leading to a reduction in meristem size and cell number (Zhu *et al.*, 2015).

It is important to integrate environmental conditions and within-plant signaling into our understanding of root growth throughout the growing season. Yet, our knowledge of the development of auxin concentrations and changes in meristem length mainly comes from studies with young *Arabidopsis thaliana* seedlings in nonsoil media. We are thus still far from understanding how roots respond to environmental cues under field conditions where they grow in a competitive environment, and how these responses are regulated within the plants. For example, while cold temperatures inhibit root elongation in *Arabidopsis thaliana* and its roots hardly grow at 4°C (Zhu *et al.*, 2015), roots of all arctic plant species regularly experience such cold temperatures. The roots of the sedges *Eriophorum vaginatum* and *Eriophorum angustifolium*, for example, have been shown to closely follow the thawfront, the transition zone from unfrozen to frozen soil, as it progressively deepens over the season and are hence growing in a comparatively cold environment (Shaver & Billings, 1975, 1977; Blume-Werry *et al.*, 2019). Most arctic soils are frozen solid over the winter and as temperatures increase during spring, soils gradually thaw out from the top. Temperatures in the surface soil therefore strongly increase during summer but deep soils stay cold throughout. Roots of plants growing in arctic permafrost soils thus experience a wide range of environmental conditions over the growing season and, if they root deeply, a strong gradient in soil temperature between the active layer close to the soil surface and the deepest thawed-out part, the thawfront, that at any given time has temperatures close to 0°C.

We used this depth-related gradient in soil temperature to sample root tips from both varying (surface soil) and stable cold soil temperatures (permafrost thawfront) over a growing season and aimed to advance our basic understanding of root ecophysiology under challenging environmental conditions in the field. For this, we selected *E. vaginatum* as our study species, a widespread and common circumpolar, monocot perennial sedge that forms an important component of vegetation across the Arctic (Iversen *et al.*, 2015; Chen *et al.*, 2020). It usually grows in tussocks (Wein, 1973; Cholewa & Griffith., 2004), though less pronounced at our study site than in a typical moist acidic tundra in Alaska (Molau, 2010). Aboveground, *E. vaginatum* is relatively small-growing, < 20 cm high (Ma *et al.*, 2022a), with low productivity of only four to six leaves per season (Cholewa & Griffith., 2004). Biomass production of *E. vaginatum* is generally higher below- than aboveground (75–90% of production is belowground; Chapin *et al.*, 1988) with relatively rapid elongation rates of roots (e.g. 1 cm d^{-1}, Forrest, 1971), and a root system that grows progressively downward as the soils thaw out over the summer leading to a full exploration of the thawed soil profile, down to soil depths of 60 cm or deeper (Blume-Werry *et al.*, 2019; Hewitt *et al.*, 2019; Ma *et al.*, 2022b). *Eriophorum vaginatum* roots are uniform, relatively thick compared with other arctic species (0.8 ± 0.01 mm, Chapin *et al.*, 1979), mostly unbranched and do not form mycorrhizas (Chen *et al.*, 2020), all of which made them very suitable for our ecophysiological study. In contrast to many other arctic plant species, the root system of *E. vaginatum* is classified as annual; thus, all roots are produced during the current season (Bliss, 1956; Chapin, 1974; Chapin *et al.*, 1979). Arctic tundra is generally nitrogen-limited, and usually more nitrogen is present in the surface soil (Pickering Pedersen *et al.*, 2020, 2022). Still, by growing deep roots *E. vaginatum* can avoid the intense competition for nutrients in the shallow surface soil, where most other plants concentrate their roots (Iversen *et al.*, 2015), and access subsurface water flowing at the thawfront at rates much higher than nutrient diffusion rates (Chapin *et al.*, 1988) and nutrients released from thawing permafrost (Blume-Werry *et al.*, 2019).

Eriophorum vaginatum is highly adapted to the harsh conditions prevailing in arctic tundra. It flowers very early in the spring directly after snowmelt and leaf growth starts while soils are still frozen, that is before access to soil nutrients and water (Defoliart *et al.*, 1988; Cholewa & Griffith., 2004). This results in an earlier start and peak of leaf production compared with root production (Chapin, 1974; Sullivan & Welker, 2005; Ma *et al.*, 2022a). Root growth of *E. vaginatum* is adapted to the varying conditions in moist and cold soils, such as are present in tundra, with a broad temperature range for growth and no specific low temperature optimum (Kummerow *et al.*, 1980). While the optimal root growth temperature is *c.* 20°C, 20% of maximum root biomass has been found to be formed at 5°C (Kummerow *et al.*, 1980), and it has even been described that more than 40% of an observed optimum production level was still reached at 0°C (Wein, 1973). Similarly, the related sedge *E. angustifolium* produced most root biomass at 5°C (Chapin, 1974) and showed the greatest root elongation rates at the bottom of the soil profile, where temperatures were lowest (Shaver & Billings, 1977).

Overwintering leaves of *E. vaginatum* are replaced by new ones, which continue to grow sequentially over the season, with new leaves getting nutrients translocated from old leaves (Defoliart *et al*., 1988; Cholewa & Griffith., 2004). *Eriophorum vaginatum* has a corm, a modified stem with leaf scars, which dies off at the bottom as the plant grows (Goodman & Perkins, 1968; Cholewa & Griffith., 2004; Siegenthaler *et al*., 2013, see also Supporting Information Fig. S1). All leaves and adventitious roots arise from the corm, and it enables *E. vaginatum* to efficiently store, transport, and relocate both assimilates and nutrients, resulting in an unusually high capacity for internal translocation and storage of nutrients (Cholewa & Griffith., 2004).

Specifically, in our study we asked the following research question:

(**1**) Can established methods of physiological root growth indicators, such as auxin levels and meristem length, be applied to the arctic sedge *E. vaginatum*, growing in natural plant communities in the field?

(**2**) Do auxin levels and meristem length in root tips of *E. vaginatum* differ between warmer surface soil and the colder permafrost thawfront in arctic tundra?

(**3**) How do *E. vaginatum* auxin levels and meristem length evolve over the growing season in surface and thawfront soils?

Materials and Methods

Study site and sampling design

Our study site was an ombrotrophic peatland underlain by permafrost in northernmost Sweden, close to Abisko ('Storflaket', 68°20048″N, 18°58016″E). The surrounding climate is subarctic with a mean annual air temperature of −0.1°C and a mean annual precipitation of 335 mm, 1981–2010 (data provided by the Abisko Scientific Research Station, Abisko, Sweden). Temperatures in this area are increasing rapidly; mean annual air temperatures increased by 2.58°C over the period from 1913 until 2006 (Callaghan *et al*., 2013). Due to these increasing temperatures, permafrost in northern Sweden is thawing and the active layer, the upper part of the soil column that thaws out every summer, has become deeper at rates ranging from 0.7 to 1.3 cm per year, a trend that has been accelerating (Åkerman & Johansson, 2008). At our study site, the active layer thickness is described as *c*. 60 cm deep (Johansson *et al*., 2013), which was also the case during the year of our study. However, as soils progressively thaw out over the season this maximum depth is only reached at the end of the growing season. Shortly afterward, soils freeze again as temperatures drop both from the soil surface down and from the thawfront up. The vegetation on the peatland is rather species-poor, and the vascular plant community consists of the graminoid *Eriophorum vaginatum* L. growing in matrix with dwarf shrubs, such as *Andromeda polifolia* L., *Betula nana* L., *Empetrum nigrum* ssp. *hermaphroditum* (Hagerup) Böcher, *Rubus chamaemorus* L., and *Vaccinium uliginosum* L. The peat is formed by *Sphagnum* mosses, dominated by the peatmoss *Sphagnum fuscum* (Schimp.) H. Klingg.

We sampled *E. vaginatum* root tips in six plots that each had a size of 10 × 20 m. Three of those plots were a bit drier and three a bit wetter, reflecting the range of moisture levels present at the study site. Plots were located *c*. 20–50 m from each other. We sampled root tips every 2 wk starting on 19 May and ending on 10 October 2016, which covered the majority of the snow-free season. The year in which we conducted our study was clearly very typical in terms of air temperatures (see Fig. S2). Roots of *E. vaginatum* are easily identified in soil samples as they are morphologically very different from the roots of all other species present at the site, with relatively large, white, and hardly branched roots compared with darker, brownish very fine and highly branched roots of all other species present at the site (Keuper *et al*., 2017; Blume-Werry *et al*., 2019; Hewitt *et al*., 2019). The relatively large root tips compared with those of all other present species were also easier to correctly sample and clean. Furthermore, *E. vaginatum* allowed us to sample only one class of roots, adventitious and not lateral roots, and it is the only species present in this site that so clearly follows the thawfront, allowing us to compare different temperature regimes without active experimental manipulation.

Abiotic parameters

Soil temperatures were recorded hourly (EC-5 sensors, Em50 loggers; Decagon Devices, Pullman, WA, USA) in three plots with detailed depth resolution as sensors were inserted at 0, 5, 15, 25, and 35 cm soil depth, and at 5 and 15 cm depth in two additional plots. Soil moisture was recorded similarly to soil temperature in three plots with high depth resolution (0, 5, 15, 25, and 35 cm), and in the two less detailed plots at 5 and 15 cm depth. Additionally, air temperature was recorded at one location.

Aboveground phenophases

While taking root samples in the field, we also visually assessed the aboveground phenophases of the *E. vaginatum* individuals present in the plot. We identified six different phenophases: 1 (male flowers, leaves beginning to be green on their base, and tillers starting to sprout), 2 (anthers on male flowers are senesced), 3 (first hairs on flower heads developed, not yet dispersing), 4 (Seed dispersal), 5 (all seeds dispersed), and 6 (leaf senescence has started and some leaves already senesced).

Root auxin analyses

Root samples for auxin analyses were taken in an area within each plot with high *E. vaginatum* density. We cut out a block of peat (monolith), *c*. 25 × 25 cm wide and all the way down to the thawfront, that is to the depth where we encountered frozen soil, with a breadknife and a shovel in one or two vertical sections.

Each peat monolith was divided into different depth classes, namely the 'thawfront soil', defined as the 10 cm above the frozen soil, and the 'surface soil', that is the uppermost 10 cm of the soil column. The actual depth of the thawfront sample and the distance between the surface soil sample and the thawfront soil sample thus varied with the season as soils thawed out more, reaching deepest in the end of September and beginning of October. Soil samples were transported into the laboratory, and for each depth class, we collected up to six root samples always consisting of five individual root tips each, depending on abundance of root tips. As *E. vaginatum* roots are usually unbranched (e.g. Chapin *et al.*, 1979), these were root tips from adventitious roots, not lateral roots. Each sample consisted of five root tips, each of them washed cleanly with milliQ water and cut to a length of 0.5 cm. Excess water was taken up with filter paper, and the root tips were put in an Eppendorf tube and immediately weighed and put into liquid nitrogen. Samples were stored frozen at −80°C until analysis. Excess peat and soil were put back into the field.

Extraction and purification of auxin were carried out as described previously by Novák *et al.* (2012) with minor modifications. Briefly, frozen root samples (10 mg fresh weight) were homogenized using a MixerMill (Retsch GmbH, Haan, Germany) and extracted in ice-cold 1 ml 50 mM sodium phosphate buffer (pH 7.0), containing 1% sodium diethyldithiocarbamate (antioxidant) and 5 pmol of $[^{13}C_6]$IAA internal standard. The pH was adjusted to 2.7 with 1 M hydrochloric acid, and the samples were purified by solid phase extraction on Isolute C8 (EC) columns (500 mg/3 ml; Biotage) prewashed with MeOH and 1% acetic acid in water. After sample application, the C8 columns were washed with 2 ml of 1% acetic acid in 10% methanol and then eluted with 2 ml of 1% acetic acid in 70% methanol. All eluates were evaporated at 37°C to dryness *in vacuo* and dissolved in 30 μl of mobile phase before mass analysis using a 1290 Infinity LC system and a 6490 Triple Quadrupole LC/MS system (Agilent Technologies, Santa Clara, CA, USA) operating in multiple reaction monitoring (MRM) mode. All auxin data were analyzed using MASSHUNTER software (v.B.05.02; Agilent Technologies), and IAA was quantified using the standard isotope dilution method.

Root anatomy

Root tips for root anatomy studies were taken from the same peat blocks and in the same manner as for root auxin analysis, described in the previous section, except that we only took one sample for each depth class and plot. For each sample, we collected three to five root tips, washed them clean with milliQ water, and cut the tips to a length of 2 cm. Root tips were fixed in fixative (50% methanol and 10% acetic acid) at 4°C. Samples stored for at least 12 h up to 1 yr were used. Samples were then dehydrated in a graded ethanol series, embedded in 6% solution of agarose at the temperature near the point of solification (*c.* 45°C) and left it solidify at room temperature into a 2-ml Eppendorf tube. The bottom of the Eppendorf tube was cut using a razor blade, and the agarose block containing the root sample was extracted from the mold and trimmed to generate a shape suitable for serial sectioning. Root longitudinal sections (40 μm thick) were obtained using a vibratome (VT1000S; Leica Biosystems, Nussloch, Germany), stained with toluidine blue for *c.* 0.5–1 min, mounted in 50% glycerol, and visualized under a Zeiss Axioplan light microscope (Carl Zeiss). Images were captured using the Axioplan digital camera and AXIOVISION v.4.5, see Fig. 1 for a representative example image of a *E. vaginatum* root tip with the transition zone indicated. For image compilation, Adobe PHOTOSHOP was used. Root meristem length was measured considering the distance between the quiescent center of the meristem and the noticeably elongated cortical cell in the outermost cortex cell layer that doubled in cell length compared with its distal neighbor as described in Kirschner *et al.* (2017) and carried out using IMAGEJ software (https://imagej.net/ij/).

Statistical analysis

We modelled the dependence of both response variables (auxin concentration and root meristem length) to the following predictor variables with linear mixed effect models: depth class (surface soil vs thawfront), sampling occasion (for auxin levels) or season (for meristem length, to be described later), and their interactions as predictor variables, and plots as random factors to account for spatial variability across the study site. For meristem length, we combined sampling from Weeks 20–26 into 'early', sampling from Weeks 27–31 into 'peak', and sampling from Weeks 36–41 into 'late' season, due to lacking observations and small replication rates, thereby improving the balance of the statistical tests and avoiding rank deficiencies. The response variables were non-normally distributed (visual inspection of the raw data), and we detected variance heterogeneity across individual predictor variables (Bartlett test < 0.05). We therefore applied log transformations to cure these deviations. We performed model selection with likelihood ratio tests and Akaike information criterion comparing the full models as described above with additive models (i.e. without interaction terms), and kept the full models including interactions in all cases. All statistics and visualization were performed with R including the packages LME4, LMERTEST, and GGPLOT2 (Bates *et al.*, 2015; Kuznetsova *et al.*, 2017; R Core Team, 2019).

Results

Abiotic conditions throughout the sampling period

Air temperatures at the study site during the study period showed a common seasonal pattern of highest values during July (Fig. S3). During much of the season, temperatures occasionally dropped below 0°C. At the beginning of our sampling period (19 May), soils in deeper soil layers (below 15 cm depth) were not thawed out yet, and toward the end of our sampling period (19 October), soils started freezing in the upper soil layers while they stayed warmer for a longer time in deeper layers (Fig. 2). Active layer thickness increased more or less linearly until Week 35, starting from *c.* 15 cm depth, after which the rate of thaw decreased and ceased, reaching over 60 cm depth at the end of the season (Fig. 3). Variation in soil temperatures did, as expected, vary with depth. Deeper soil layers showed less variation in temperature than shallower layers and the soil surface (Fig. 2). Thus, roots growing near the soil surface experienced a larger

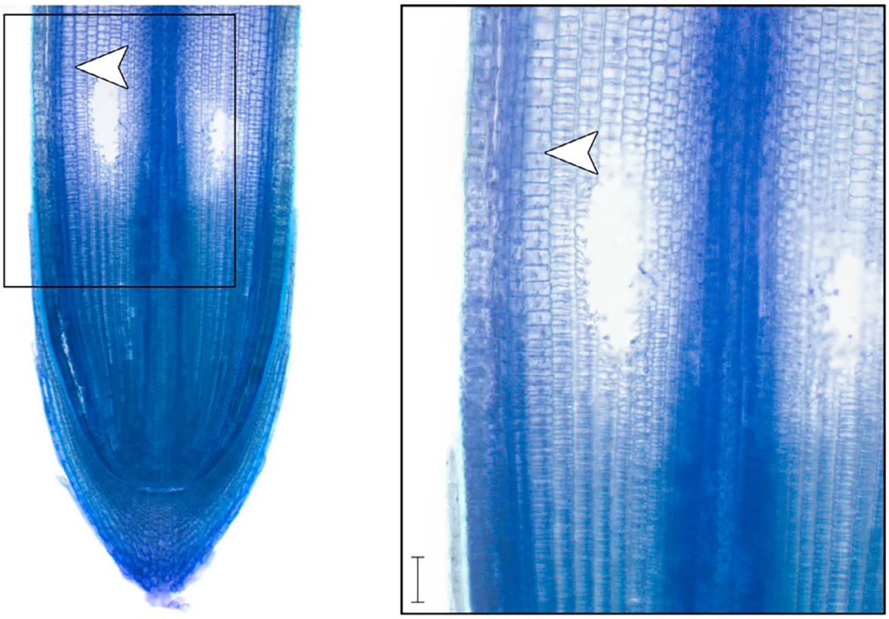

Fig. 1 Representative picture of a *Eriophorum vaginatum* root tip. Cell walls stained with toluidine blue. The arrowhead indicates the transition zone. The inset shows a magnified view of the transition zone. Bar, 50 µm.

variation in soil temperatures than roots at the thawfront. Soil moisture measurements were much more error-prone than temperature measurements but did show (1) differences between what we *a-priori* classified as 'drier' and 'wetter' plots, (2) the status change from frozen to unfrozen soil in deeper soil layers, and (3) higher variation in soil moisture in the upper soil layers (Fig. S4).

Measurement of auxin concentrations and meristem length on *E. vaginatum* growing *in situ*

Auxin concentrations in harvested root tips of *E. vaginatum* ranged from 4.3 to 732.4 pg mg^{-1} fresh weight, with an average of 90.1 ± 8.4 pg mg^{-1} (mean ± SE, Fig. 4). These values are similar in order of magnitude to what has been observed elsewhere in *Arabidopsis* (Hong *et al.*, 2014; Zhu *et al.*, 2015; Yuan & Huang, 2016) and *Picea abies* (Brunoni *et al.*, 2020), illustrating that indeed, *E. vaginatum* is a suitable species to assess auxin concentrations in root tips under natural conditions in the field. Similarly, we also deemed measurements of root meristem length of mature *E. vaginatum* individuals as suitable and informative. While meristem length in root tips (2652.2 ± 250.2 µm, mean ± SE, Fig. 5) was rather high compared with seedlings of *Arabidopsis thaliana* (Liu *et al.*, 2013; Yuan & Huang, 2016) or *Zea mays* L. (Tian *et al.*, 2008), it was in a similar order of magnitude as observed previously in *Triticum aestivum* L. (He *et al.*, 2014).

Changes in auxin concentrations and meristem length over the growing season in surface and thawfront soils

Across the whole season, auxin concentrations were almost five times higher in surface than in thawfront soils, with an average of 133.4 ± 12.8 pg mg^{-1} in surface soil and 26.9 ± 2.2 pg mg^{-1} at the thawfront (Fig. 4; Table 1). This difference is primarily driven by the tenfold increase in auxin concentrations over the season in surface roots (Table 1; Fig. 4), while auxin concentrations only doubled in the thawfront roots (significant interaction depth class × season).

Meristem length overall declined over the seasons and was, on average, almost double in thawfront (3111.7 ± 524.6 µm) compared with surface soils (2530.6 ± 284.5 µm, Fig. 5; Table 2). However, seasonal patterns of meristem length were different in surface and thawfront soils (significant interaction depth class × season). In surface soil, meristem length decreased from 4981.4 ± 375.6 µm in the early season to 1225.5 ± 97.5 µm in the peak season, to then increase again to 1930.3 ± 125.5 µm in the late season. In thawfront soil, meristem length decreased from 3974.1 ± 752.8 µm in the early season to 2033.7 ± 97.9 µm late in the season at the thawfront.

Aboveground phenophases

Aboveground development of *E. vaginatum* is relatively fast and starts directly after snowmelt (e.g. Ma *et al.*, 2022a), all studied individuals in all plots had already passed phenophase 1 (male flowers present, leaves beginning to be green on their base, and tillers starting to sprout) and were in phenophase 2 (anthers on male flowers senesced) at our first sampling date in the beginning of June. From mid-June until mid-July, all plants were in phenophase 3 (having the first hairs on flower heads developed but not yet dispersing). Seed dispersal (phenophase 4) was observed from the beginning of to mid-August, and all seeds were dispersed in the end of August and beginning of September (phenophase 5). Leaf senescence (phenophase 6) then started in mid-September (Fig. 4).

Discussion

Established root physiological techniques can be applied to adult plants sampled in the field

Most studies of root physiology focus on a few study species grown under controlled conditions, limiting our knowledge of

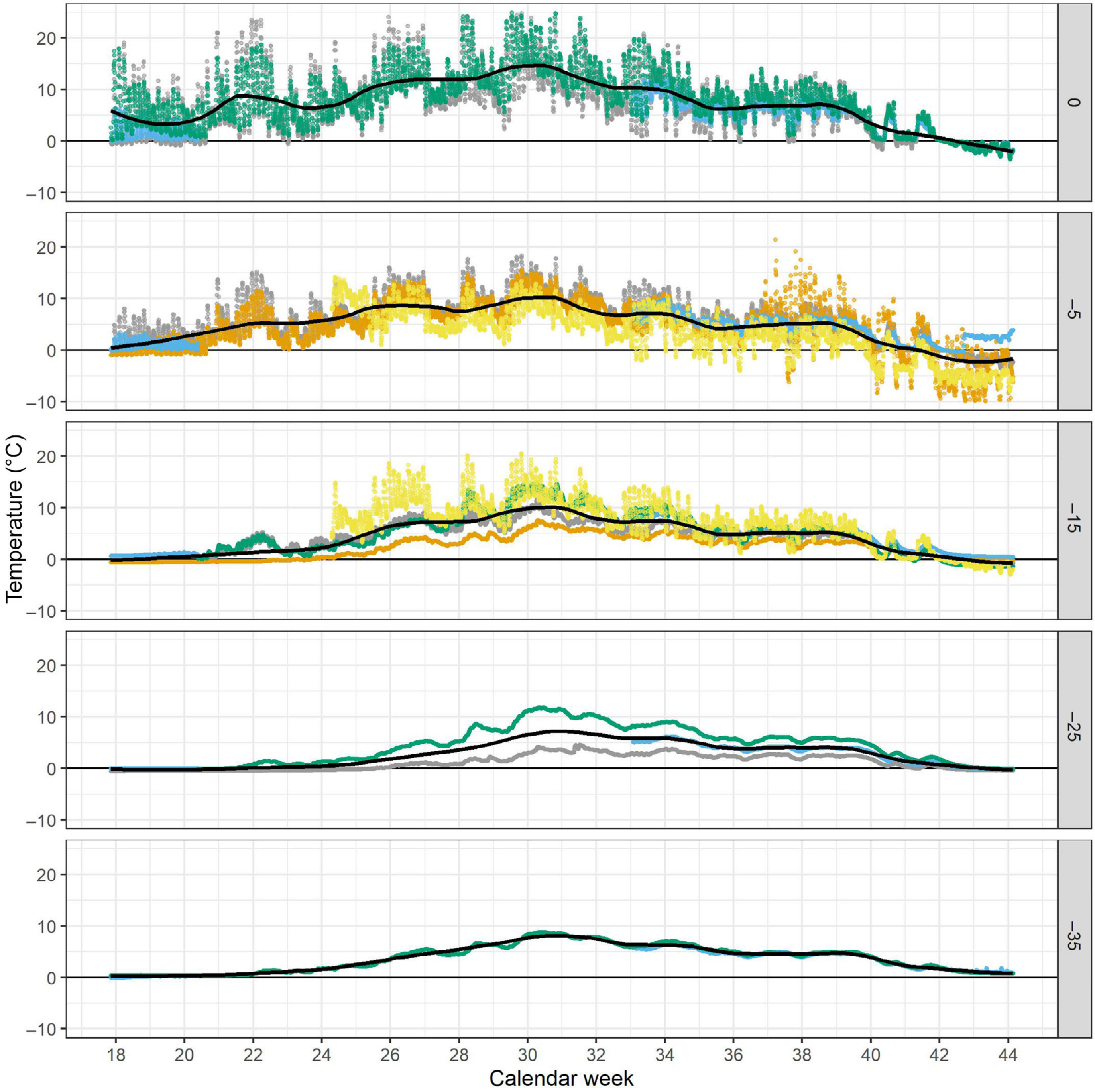

Fig. 2 Soil temperatures during our study period in different soil depths (0, −5, −15, −25, and −35 cm). Different colors represent measurements in different plots. The black line is a smooth line (loess, span = 0.2). Calendar Week 18 is 2–8 May, and Week 44 is 31 October to 6 November.

how broadly applicable observed patterns are to plants growing *in situ*. While it has been argued before that the inclusion of more species is needed in root physiology studies (Ramos Báez & Nemhauser, 2021), the next step, that is sampling in the field, can be messy and logistically challenging, especially in remote areas or when deeper soil layers are included. Yet, our study shows that established physiological methods can be applied to a new species growing *in situ* in natural plant communities with promising results. We detected differences in both root tip auxin concentrations and meristem length between soil depths and over the course of the growing season. Hence, we show that physiological methods can be applied in ecological studies, enabling us to address novel questions about the physiological mechanisms of (root) growth observed under field conditions.

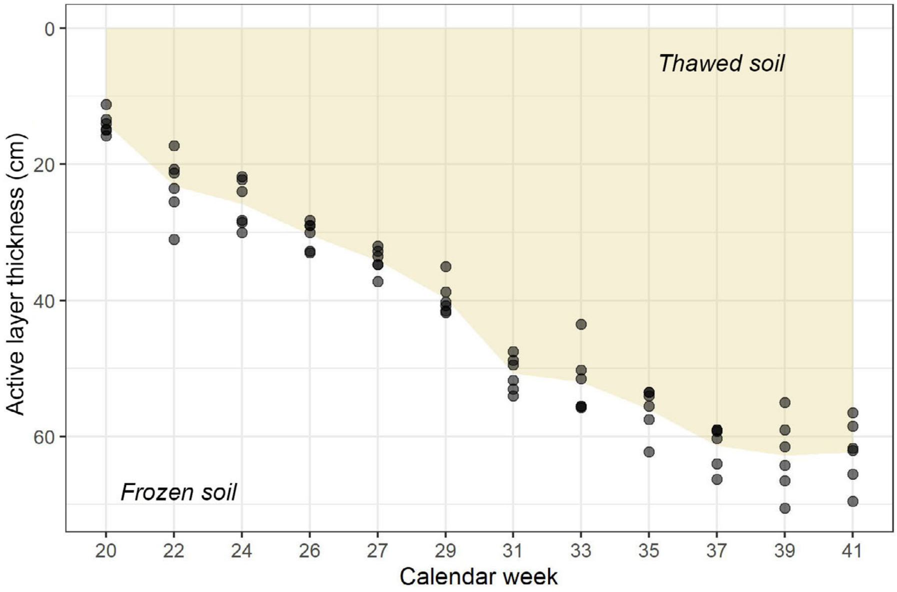

Fig. 3 Active layer thickness over time. Thawed soil is shaded in light brown. Each dot represents the measurement from one plot. Calendar Week 20 is 16–22 May, and Week 41 is 10–16 October.

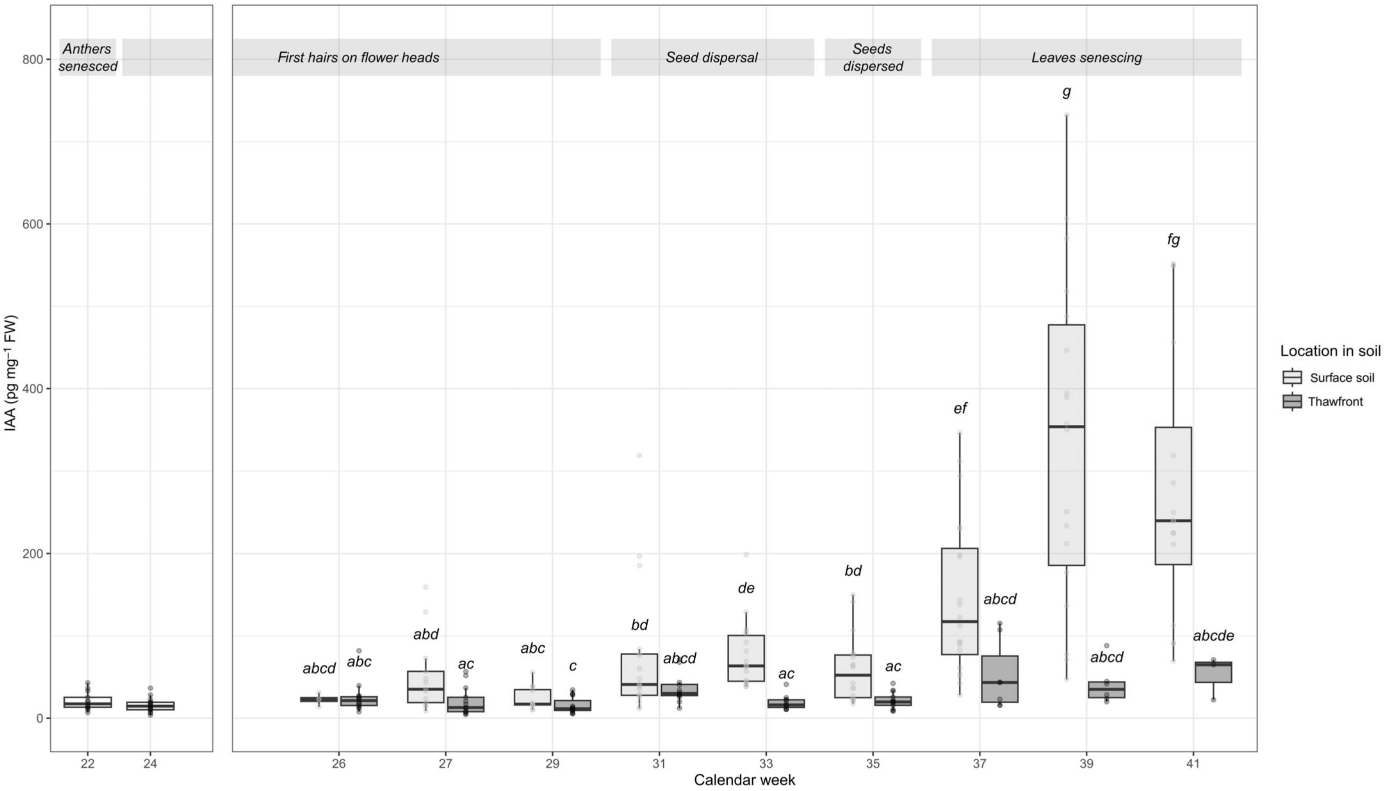

Fig. 4 Auxin concentrations in root tips of *Eriophorum vaginatum* over time and depth. Note that during Weeks 22 and 24 (left panel, white boxplots) surface and thawfront soils are identical; thus, those samplings are not included in the statistical analysis. Dots show individual observations, while boxplots are based on individual observations (lower and upper hinges correspond to the 25th and 75th percentiles, whisker extends from the hinge to the largest value no further than 1.5 times the interquartile range). Light grey signifies surface soil, and dark grey signifies thawfront soil. Letters show Bonferroni-corrected multiple comparison tests based on a linear mixed effects model, with groups (i.e. depth class and calendar week combinations), which do not share a letter being significantly different with $P < 0.05$. Calendar Week 22 is 30 May to 5 June, and Week 41 is 10–16 October.

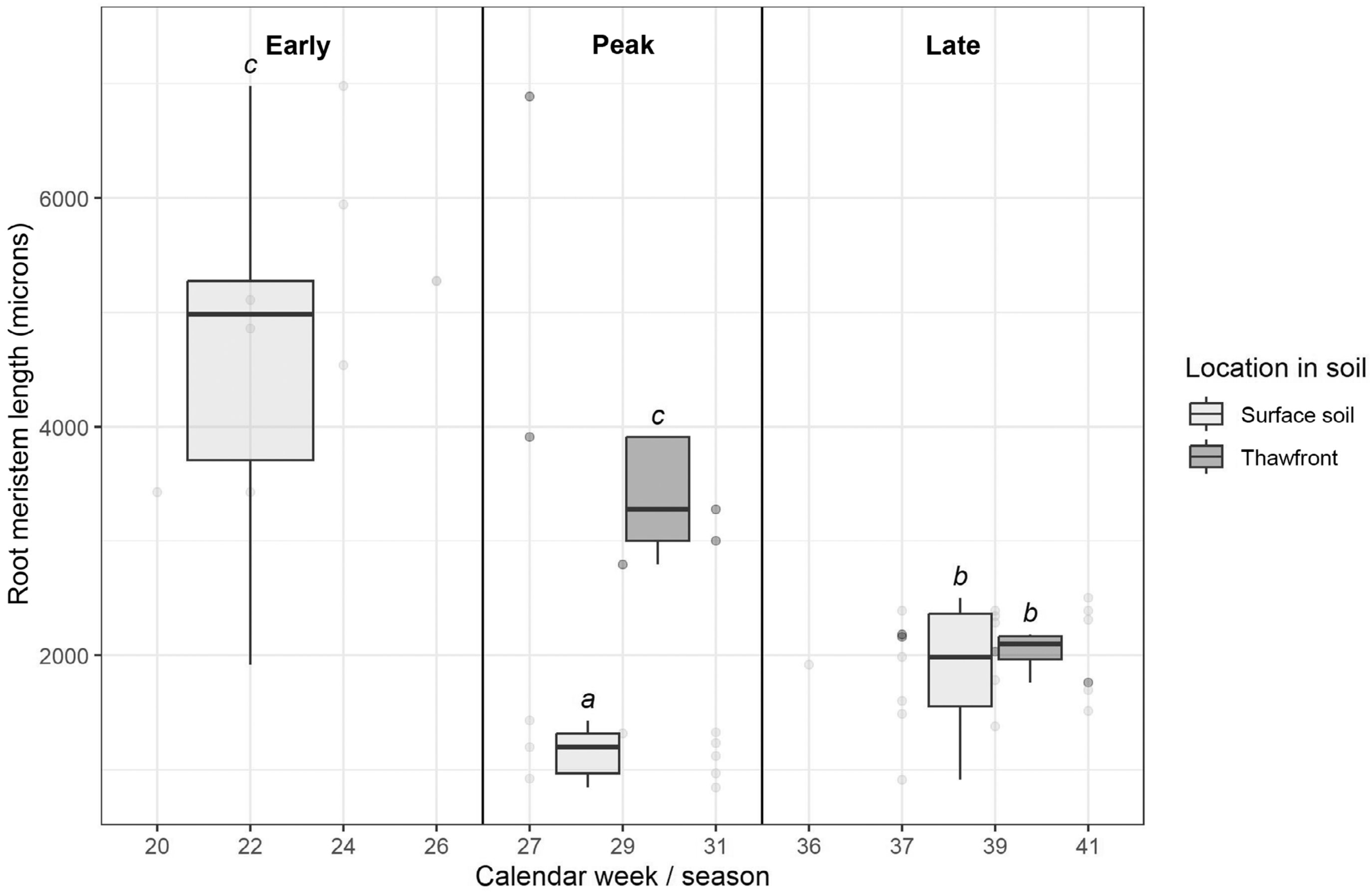

Fig. 5 Root meristem length in root tips of *Eriophorum vaginatum* over time and depth. Dots represent individual observations collected per calendar week, while boxplots are based on all observations within a season (i.e. a combination of calendar weeks; boxplots' lower and upper hinges correspond to the 25th and 75th percentiles; whisker extends from the hinge to the largest value no further than 1.5 times the interquartile range). Combining weeks into seasons was necessary for statistical analysis due to low replication rates, and seasons were defined based on initial data exploration. Please note that no data on root meristem length were collected during calendar Weeks 33 and 35, as well as from the thawfront during the early season. Letters show Bonferroni-corrected multiple comparison tests based on a linear mixed effects model, with groups (i.e. depth class and season combinations), which do not share a letter being statistically significantly different with $P < 0.05$. Calendar Week 20 is 16–22 May, and Week 41 is 10–16 October.

Table 1 *Eriophorum vaginatum* root tip auxin (IAA) concentrations in surface soil and at the thawfront over the sampling period based on linear mixed effect models.

Response	Sum.Sq	Mean.Sq	Numdf	Dendf	*F*.value	Pr.*F*.
Depth class	41.32	41.32	1	212.75	92.40	0.00
Sampling occasion	62.18	7.77	8	211.62	17.38	0.00
Depth class × sampling occasion	13.48	1.68	8	211.08	3.77	0.00

Table 2 *Eriophorum vaginatum* root tip meristem length in surface soil and at the thawfront in early and late season based on linear mixed effect models.

Response	Sum.Sq	Mean.Sq	Numdf	Dendf	*F*.value	Pr.*F*.
Depth class	2.18	2.18	1	35.67	39.22	0.00
Season	9.18	4.59	2	35.89	82.69	0.00
Depth class × season	1.91	1.91	1	37.03	34.40	0.00

Diverging patterns of auxin concentration and meristem length in surface and thawfront soils

In any soil profile, plant roots experience heterogeneous conditions for temperature, water, or nutrient content (Bengough *et al.*, 2006). However, few soils probably have such strong gradients in temperature as present in arctic tundra where surface soils warm during the summer but the thawfront is always close to 0°C. Roots of the same plant can thus experience very different temperatures, depending on where in the soil they are located. Cold stress generally limits root elongation (Karlova *et al.*, 2021), but our study species *E. vaginatum* has a high capacity for root growth even at very low soil temperatures (Wein, 1973; Kummerow *et al.*, 1980). Despite the adaptations of *E. vaginatum* to cold soils, we expected that auxin levels would be lower at the thawfront than in the much warmer surface soils, as this general pattern has been shown in previous studies on other species, mainly on *Arabidopsis thaliana* (e.g. Zhu *et al.*, 2015; Fei *et al.*, 2019; Karlova *et al.*, 2021; Tiwari *et al.*, 2023). Indeed, over the whole season, auxin concentrations were almost five times higher in surface than in thawfront soils. Interestingly, these differences in auxin concentrations in roots from the same population, potentially the same individuals, are much larger than those that have previously been observed on different individuals of *A. thaliana* growing under different temperatures (Zhu *et al.*, 2015).

In *A. thaliana*, low auxin accumulation usually correlates with a reduced root meristem size (Hong *et al.*, 2014; Zhu *et al.*, 2015). However, we found the opposite pattern: meristems were more than three times longer at the thawfront compared with surface soils during peak season, when auxin levels did not differ between thawfront and surface soils, and similarly long during late season when root tips at the surface had about five times higher auxin concentrations than those close to the thawfront. While this relationship between auxin concentration and root meristem length contrasts with findings from controlled laboratory studies on *A. thaliana*, higher meristem lengths close to the thawfront may be an ecological adjustment of our study species. A higher meristem length is usually associated with higher root elongation rates (Verslues & Longkumer, 2022), and indeed, roots in the thawfront soils are growing deep in the soil column and thus need to grow at a faster rate than their counterparts in surface soils to cover these long distances, especially at times when soils are thawing out fast. It thus seems likely that meristem length is a good indicator of root elongation rates, which also fits to the observation that meristem length at the thawfront decreases toward the end of the season, when soil thaw rates slow down. Meristem length has also been shown to increase with plant age in barley (Kirschner *et al.*, 2017), which may be another factor here, as deeper *E. vaginatum* roots likely are also older than more shallow ones. These previous data showing meristem increases with plant age were based on very young plants though, not established, perennial adult plants in field conditions. More field-based studies would thus be very valuable for improving our knowledge on the relationship between root age or root length and meristem length. Furthermore, other phytohormones, such as cytokinins, can regulate root growth and meristem length independent of auxin (Pernisova *et al.*, 2011; Schaller *et al.*, 2015) and may be at play here, even though auxin is generally considered to be very important, also in monocots (McSteen, 2010).

Auxin concentrations and meristem length both change over the course of the growing season but not in the same manner

To our knowledge, this is the first study on seasonal changes of auxin concentrations and meristem length, as laboratory physiological studies are inherently short-term and limited to seedlings or young individuals. Previous ecological studies showed that root growth of *E. vaginatum* at the same study site was highest in July and August, but continued until mid-September with growth in deeper soil layers lagging behind shallow layers (Blume-Werry *et al.*, 2019). Similar seasonal root growth patterns were found for different ecotypes of *E. vaginatum* in Alaska (Ma *et al.*, 2022a,b). We initially expected auxin levels to correlate positively with root growth rates and thus show a similar pattern with the highest levels during peak season in the middle of summer, and with thawfront roots lagging behind surface soil roots. Yet, we found continuous increases in auxin concentrations over the season in surface soils with the highest levels at the end of our measuring period. Root tips close to the thawfront, however, had relatively constant and lower auxin concentrations across the season. In the beginning of the season, surface and thawfront roots showed very similar levels of auxin concentrations, which is not surprising because at that time the surface and thawfront roots were still very close to each other and of similar age, and only slowly started to experience differences both in the environmental conditions and distance from the shoots and corm.

While we found generally higher auxin concentrations in roots of the warmer surface soils, auxin levels did not show the expected seasonal pattern of reaching the highest auxin concentrations in peak season when temperatures in the surface soils were highest. Thus, other factors than just temperature must be at play. Similarly, the aforementioned ecological studies have also suggested that root growth of *E. vaginatum* might not be much influenced by temperature (Blume-Werry *et al.*, 2019; Ma *et al.*, 2022b), which also fits its generally large capacity to grow roots at cold temperatures. The increase in auxin levels in surface soil roots at the end of the season coincided with aboveground senescence (Fig. 4). This increase could potentially be a seasonal within-plant allocation or redistribution of auxin steered from aboveground during which roots that are much closer to the corm, *that is* the surface soil roots, may experience stronger increases than those further away. This potential relocation of auxin to shallow roots at the end of the season could theoretically also be a basis for high growth early in the following season when surface soils thaw out much earlier than deeper soil layers. However, this seems rather unlikely, as *E. vaginatum* generally replaces its complete root system every year (Bliss, 1956; Chapin, 1974; Chapin *et al.*, 1979). Auxin accumulation normally stimulates growth in young, developing tissues in all higher plants (Matthes *et al.*, 2019), but the levels differ between plant species and is unknown for *E. vaginatum*. In roots, high auxin levels are also known to inhibit taproot elongation, although lateral root initiation is instead promoted by high auxin levels (Roychoudhry & Kepinski, 2022). It is possible that the auxin concentrations observed here reach growth-inhibiting levels in surface roots, especially toward the end of the season when chances of air and soil frost increase and plants may no longer allocate resources into ‘risky’ surface soil growth. Indeed, based on our data it is possible that auxin is actively involved in slowing down surface root growth while encouraging growth of thawfront root, as an adaptation to the specific conditions in arctic tundra with relatively high nutrient availability at the thawfront (Chapin *et al*., 1988). By making sure that resources are allocated to thawfront root growth for the longest time possible, *E. vaginatum* may experience a competitive advantage in arctic tundra through the regulation of root growth via auxin.

While auxin concentrations only showed seasonal patterns of increase in the surface and not in the thawfront soils, meristem length did change in both surface and thawfront soils but in opposite patterns. Meristem length decreased in thawfront and increased in surface soils from peak to late season, ending up at the same level. Meristem length started out high in the early season in the surface soil, which may indicate a high root growth rate in the beginning of the season despite low auxin concentrations, though it has previously been shown that root growth initiation of *E. vaginatum* lags behind leaf development (Ma *et al*., 2022a), which starts directly after snowmelt. During peak season, the patterns of meristem length diverged between surface and thawfront soils when meristem length was more than three times higher in thawfront than surface soils. As indicated previously, this may be related to the fact that roots at the thawfront have to cover a longer distance and thus need relatively high growth rates compared with surface soil roots. The thawfront roots of the peak season are of course also the ones that were in the surface soil during the early season, so maybe the same individual roots keep their meristem length relatively constant with a slow decline over the season. By contrast, more of the surface soil roots are newly formed over the season and thus may emerge later with shorter levels of meristem length as they do not need to grow over long distances. The similar meristem length in the late season in both surface and thawfront soils may indicate a general slowing down of root growth at the end of the (belowground) growing season, but knowledge of this is still lacking. To specifically elucidate the interplay of meristem length and auxin levels without any confounding factors, roots of *E. vaginatum* individuals could be treated with different levels of auxin in future laboratory studies. Furthermore, auxin levels and meristem length may be influenced by other environmental factors than temperature, for example concentration or source of nitrogen (e.g. Ötvös *et al*., 2021) although the main influence seems to be focused on lateral root formation and not adventitious root growth (e.g. Meier *et al*., 2020).

In conclusion, while exact reasons for the seasonal and spatial patterns in auxin concentration and meristem length remain unclear, it seems likely that auxin is actively involved in governing root growth to ensure high potential for nutrient uptake at the ever-moving thawfront. This ecological adjustment of growth could not have been seen without physiological methods and our study thus demonstrates the value of applying established physiological methods to more species which are growing in natural plant communities in the field. In the future, longer and more controlled studies, such as experimental manipulations in the field or common garden approaches, could further our understanding of how different environmental parameters, such as soil moisture, different soil types with varying density, nutrient concentrations over time and depth, or the presence of specific plant species in the community influence auxin concentrations and meristem length in *E. vaginatum.*

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Competing interests

None declared.

Author contributions

AM and KL conceived the idea. AM, GB-W, KL and PS designed the study. GB-W led the collection of the samples in the field, ON and FB led sample analysis in the laboratory. PS led the data analysis. GB-W wrote the manuscript with contributions from FB, KL, AM, JO and PS.

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Data availability

Data are available at figshare.com, doi: 10.6084/m9.figshare.25163669.v1.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information section at the end of the article.

Fig. S1 Two examples of *Eriophorum vaginatum*, sampled at our study site.

Fig. S2 Air temperatures measured at the Abisko Scientific Research Station from 2000 to 2016.

Fig. S3 Air temperature measured at our study site.

Fig. S4 Soil moisture during our study period in different soil depths.