

Plant–soil interactions in a deglaciated landscape: Root exudation reflects environmental severity.

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Research Article

Keywords: Svalbard, climate change, root exudates, polar willow, biogenic elements

Posted Date: February 21st, 2024

DOI: <https://doi.org/10.21203/rs.3.rs-3701528/v1>

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Abstract

The growth of shrubs in the Arctic is a key factor affecting environmental and vegetation changes framed by the currently accelerated dynamics of global warming. One of the phenomena involved in the shrubification of the Arctic is root exudation, which plays a part in nutrient acquisition by plants and thus the growth of both individual plants and whole communities. It is not known, however, to what extent root exudation differs across different environments in the Arctic tundra, how important its role is in covering the nutrient demands of plants and what significance this might have for soil properties and vegetation succession. To shed light on the topic, we studied the content of biogenic elements in soils of different maturity following deglaciation, the age structure of the climax species *Salix polaris*, exudation by its roots, and the concentrations of different nutrients in its roots and leaves in the forefield of the Nordenskiöld glacier in the Svalbard archipelago. Our results reveal that polar willow shrubs have a greater relative propensity towards exudation, and thus larger potential for investing into growth, under more severe environmental conditions, which may be attributable to the stage of their root system development or the level of competition they face. This finding should be taken into consideration when interpreting current vegetation development and plant succession in the Arctic. Nevertheless, to what extent this relationship stays stable in the context of ongoing climate change remains a question to be explored.

Introduction

The climate in the High Arctic has been warming rapidly in recent years and much more significant changes are being projected (Chapin et al. 2005; IPCC 2022). Over the past four decades (1980–2020), the seasonal minimum sea ice area in the Arctic has been decreasing by 93,000 km² per year, representing a 12.6% decrease per decade (NASA 2023). The effects of the changing climate are also reflected in air and permafrost temperature variations, in the depth of seasonal defrosting, and in altered plant phenology. Because shrubs are particularly sensitive to such changes, they are frequently employed in studies of how the Arctic environment responds to climate warming (Myers-Smith et al. 2015).

The ongoing changes in the prevalence of shrubs in the High Arctic will inevitably influence many ecosystem processes, which can either delay or exacerbate the effects of warming in tundra ecosystems, alter nutrient availability and the global net carbon balance, and, last but not least, affect the albedo and associated energy fluxes (Wookey et al. 2009; Tape et al. 2006; Myers-Smith et al. 2015). Models projecting future climate change scenarios need to consider individual climate-induced changes in the structure and functioning of tundra plant communities, both above and below ground, because these changes will result in complex feedback loops leading to substantial releases of CO₂ and CH₄ into the atmosphere (Euskirchen et al. 2007). It is therefore crucial to better understand how the most common Arctic shrubs behave during early stages of soil development. The aim is to more accurately estimate the dynamics of shrubification in the Arctic tundra. One key factor limiting plant growth in the Arctic is the soil content of biogenic elements (Stimmler et al. 2023), precipitation (Weijers 2022; Buras et al. 2017) and temperature (Weijers et al. 2017; Lehejček et al. 2017). At the same time, soil temperature directly influences the activity of soil microorganisms and the accessibility of mineral nutrients necessary for plant nutrition (Schmidt et al. 2002). In Arctic soils, where many elements are available in forms hard to access by shrubs, root exudates play a significant role. Exudation is a strategy of plants for releasing mineral nutrients to get rid of toxic elements (Neumann and Romheld 2007). Plant root exudates contain simple low-molecular-weight non-aromatic carboxylic acids, including amino acids, that, together with carbohydrates, phytosiderophores, phenolics and enzymes, improve the acquisition of mineral nutrients required for plant growth (Inderjit and Weston 2003; Dakora and Phillips 2002; Mimmo et al. 2014).

Plant root excretions are known to be a key factor controlling the immediate soil environment. Through root exudation, plants can influence the composition and volume of the soil microbiota or change the chemical and physical characteristics of the soil from which they grow (Post et al. 2009). The degree and quality of root exudation is nevertheless also affected by many other factors such as the plant species concerned, the age of the root, light intensity, nutrient accessibility, the type of soil, soil oxygen content, soil moisture, pH, temperature, soil organisms and other stress factors (Marschner 1995).

Exudation of low-molecular-mass organic acids (LMMOAs) plays a role in nutrient acquisition (especially of P, Fe, Mn and Zn) by plants growing in nutrient-poor soils; for example, they can chelate Fe and Mn out from their oxides and thus make them available for plant uptake (Marschner 1995; Dakora and Phillips 2002). Similarly, organic acids form Ca, Al and Fe complexes in the soil and thereby release P for uptake by plants (Dakora and Phillips 2002). Conversely, however, nutrients present in the soil also enhance the exudation of LMMOAs, particularly with in relation to the supply of N, P and K (Grayston et al. 1997). The release of LMMOAs by plant roots attracts microorganisms into the rhizosphere, where they play a great role by making nutrients available for plant uptake through their diverse metabolic processes (Marschner 1995).

Based on the assumption that plant exudation is a key factor affecting the content of biogenic elements in the soil, we hypothesize that it varies considerably depending on the maturity of the soil and the age of shrubs (stage of primary succession) in the High Arctic. To explore this hypothesis, we set out to study plant exudation within the first generation of vascular plant colonization to see if it is driven by nutrient availability in the context of a less developed root system and how differs from that in climax tundra vegetation, where competition stimulates exudation in already developed root systems. The aim of this study is therefore to explore the environmental relationship between the content of selected biogenic elements and that of small organic acids in polar willow roots as a function of soil and plant age.

Materials and methods

Study sites

We collected data for this study in the High Arctic tundra at localities in the bay of Adolfbukta located at the head of the Billefjorden fjord in the central part of the Svalbard archipelago. The Nordenskiöldbreen glacier (78.67°N, 16.78°E) is the only tidewater glacier in the Billefjorden catchment. It has been retreating since the culmination of the Little Ice Age at the end of the 19th century (Allaart et al. 2018). The climate is the main factor affecting mass loss of the glacier and its retreat rates. After the Little Ice Age, the mean annual temperature has risen by about 4°C; as a result, the Nordenskiöldbreen glacier has been in retreat (at a mean average linear retreat rate 35 m • year⁻¹; Rachlewicz et al. 2007). The annual precipitation sum in the area is typically < 200 mm and the annual air temperature is about - 6.5°C (Strzelecki 2017). The northern forefield of the Nordenskiöldbreen glacier is characterized by metamorphic rocks, mainly mica schist, calc-pelitic schists and marble (Dallmann et al. 2004).

We divided the area into four zones (Fig. 1) according to the time for which they have been exposed after the glacier retreated, using GIS data based on aerial photographs provided by the Norsk Polar Institute (1936, 1961, 1990 and 2007): the first zone (26–54 years after deglaciation), the second zone (55–107 years after deglaciation), and the third zone (~ 10,000 years after deglaciation) (Luláková et al. 2023). An extra “zero” zone was established in the recently deglaciated area (< 26 years after deglaciation) as a control zone (devoid of vascular plants) for soil analysis only. We evaluated the plant species composition in each zone using vegetation relevés and 2-m × 2-m plots of homogeneous vegetation, in which we estimated the cover of each species as a percentage of the plot area, the cover of stones and the cover of the biological soil crust (mostly dominated by lichens).

Study species and sampling design

The polar willow (*Salix polaris*, family *Salicaceae*) is a long-lived, deciduous, dioecious, prostrate tundra dwarf shrub with a circumpolar Arctic distribution (Boulanger-Lapointe et al. 2014).

We sampled *S. polaris* shrubs within the three zones of succession delimited above so as to cover different age cohorts. To avoid the sampling of clones, we sampled individuals growing at least 5 m apart. We collected a total of sixteen individuals: four from each vegetated zone plus four extra shrubs in zone 2 to better capture the age population structure. Each time, we extracted the complete individual, including its roots, from the soil and stored it for subsequent dendrochronological analysis.

We took samples of the mineral soil (5 cm high) either from the bare surface devoid of plants or after removing the soil crust where present. At each site, we pooled three independent soil samples from four subsamples spaced one metre apart (42 mixed samples in total, Fig. 1).

We determined the age of *S. polaris* individuals by a standard dendrochronological procedure from high-quality thin cross-sections (e.g. Schweingruber 1996). We employed the serial sectioning method (Kolischuk 1990) to detect missing or wedging rings, which are a common phenomenon in climate-limited environments (Owczarek and Opała 2016). This entailed taking tree-ring measurements of cross-sections cut at different heights and cross-dating the obtained series at the intra-individual level (Lehejček et al. 2023). The first cross-section was always cut at the root collar and was followed by cross-sections evenly spaced across the shrub body so that the distances between the cross-sections were approximately 3 cm.

Slices no thicker than 20 µm were extracted from all cross-sections using a sledge microtome. The slices were stained using a 1 : 1 solution of Safranin and Astra blue and embedded in Canada balsam (Schweingruber et al. 2013). The entire area of each slice (i.e. the whole cross-section) was photographed at 100× magnification and the images were used to measure annual rings along multiple axes and to detect partially missing annual rings and other growth defects (Bär et al. 2006). Measurements were obtained from the images

using NIS-Elements software for two radii per cross-section. The first measurement was always performed for the longest radius whereas the second measurement, aimed to reveal partially missing rings, was made at an angle of at least 90° to the first radius (Bär et al. 2006). To assess plant age, cross-dating was done mostly visually using PAST5 software (Knibbe 2014), first at the cross-sectional level by comparing ring radius measurements and, secondly, at the level of the whole individual by comparing mean cross-sectional series (Schweingruber et al. 1990). In total, we were able to use a series of all sixteen individuals. The presented ages should be understood as conservative minimum ages because the number of samples, combined with the harsh climate conditions, does not allow for precise age determination.

Chemical analyses

Samples of willow leaves and roots were rinsed with distilled water and subsequently rid of excess water by drying at 25°C. They were then homogenized by manual crushing using clear glass mortar and pestle sets.

The determination of mineral nutrients was carried out after the acid digestion of samples, following the method previously described by Vaněk et al. (2010). Initially, 0.5 g (+ 0.005 g) of the sample was kept overnight at laboratory temperature in a closed, but not sealed, Teflon vessel (Savillex, USA) containing 10 mL of 65% HNO₃ (p.a., Lach-Ner, CZ). The Teflon vessel was then sealed and the mixture was heated to 120°C on a hot plate for two hours. The digested solution was then quantitatively transferred into a 50-mL volumetric flask, which was then filled to its nominal volume with deionized water (conductivity < 0.055 µS·cm⁻¹). The solution was diluted (10×) and filtered through 0.45-µm Nylon disk filters (Cronus, UK) prior to analysis by means of inductively coupled plasma optical emission spectrometry, commonly known as ICP–OES.

An ICP–OES spectrometer (DUO iCap 7000, Thermo Scientific, USA), operating at 1.15 kW with the respective nebulizer and auxiliary gas flow rates of 0.5 and 1 L • min⁻¹, was used for to determine the concentrations of the target elements, which were detected at the following spectral lines of the following wavelengths: Ca (317.933 nm), Fe (238.204 nm), K (766.490 nm), Mg (279.079 nm), P (177.495 nm), S (180.731 nm) and Zn (202.548 nm). The quality of digestion and analysis was controlled using blanks and standard reference materials (NIST SRM 1575a Pine Needles and NCS DC 73351 Tea).

Hot deionized water extraction was performed according to Vondráčková et al. (2015). The extract was subsequently filtered through a nylon membrane filter (0.45 µm), and ion chromatography (IC) and ICP–OES were used for the determination of anions and elements.

The ion chromatography method using the ICS 1600 and ICS 6000 systems (Dionex, USA) was used to determine the basic inorganic anions and small organic acids in the extract (citrate, oxalate, malate, lactate, acetate, formate, butyrate, valerate, tartrate and isocitrate). The analysis was performed on an AS11-HC analytical and guard column with a KOH mobile phase and a gradient of 1–35.2 mM for 1–65 min (Hubová et al. 2018). The chromatograms were processed using Chromeleon 6.80 (Dionex, USA). The detection limit was calculated for each anion, presuming a 3 : 1 signal-to-noise ratio (Shabir 2003).

Soil samples were homogenized, sieved (through a sieve with a mesh size of 2 mm) and quickly air-dried in a thin layer. The total content of Ca, K, Fe and P was determined by X-ray fluorescence (Delta Premium XPD 6000, OLYMPUS INNOV-X, USA) under standard laboratory conditions (Tejnecký et al. 2015). Exchangeable Ca²⁺, Mg²⁺, K⁺, Na⁺, Al³⁺, Fe³⁺ and Mn²⁺ were extracted in 0.1 mol • L⁻¹ BaCl₂ (2.5 : 30, w/v) according to UNECE (2006). Effective cation exchange capacity (CEC) was calculated as a sum of exchangeable cations and potentiometrically determined H⁺. Labile elements (Ca, K, Mg, Fe) and also PO₄³⁻ were extracted using deionised water (1 : 10, w/v). The concentration of the extracted elements was determined employing ICP–OES (Duo iCAP 7000, Thermo Scientific, USA) and PO₄³⁻ was determined by IC (ICS 1600 Dionex, USA, see above). The pH of the water extracts (active pH) was measured potentiometrically (with an inoLab pH Level 1 device from WTW, Germany).

Statistical analyses

The values obtained from the individual measurements were evaluated by ANOVA. Differences passing the significance test at the 95% confidence level ($p < 0.05$) were considered statistically significant. If a determined value was lower than the detection limit of the analytical method used (IC or ICP–OES), it was replaced by one-half of the detection limit. For a visual assessment of normality, the Shapiro–Wilk test was employed. The analyses were performed with STATISTICA 12 (StatSoft, USA).

Results

Dendrochronological analyses and vegetation characteristics

The most common vascular plant in Adolfbukta bay is *Dryas octopetala*, followed by *Saxifraga oppositifolia*, *Carex rupestris* and *Salix polaris* (Appendix Table 1). The first zone is dominated by *Saxifraga oppositifolia* whereas *Dryas octopetala* dominates in the second and third zone. *Carex rupestris* is also common in the third zone. *Salix polaris* increases its abundance towards the older zones, confirming its increasing role in ecosystem succession. In the last zone, significantly older individuals were recorded (23–38 years) as compared with the younger zones, which are occupied by first-generation shrubs (7–23 years), see Appendix Table 2.

Table 1

Average values of basic soil properties in the Nordenskiöldbreen glacier forefield (CEC – cation exchange capacity in meq • kg⁻¹; ex – exchangeable elements, H₂O – water-extractable elements and PO₄³⁻ in mg • kg⁻¹; small letters indicate significant differences between groups, ns – not significant).

Zone (years)	n	pH H ₂ O	CEC	Caex	Mgex	Kex	CaH ₂ O	MgH ₂ O	KH ₂ O	PO ₄ ³⁻ H ₂ O
			(meq • kg ⁻¹)	(mg • kg ⁻¹)						
0 (< 25)	9	8.75 b	68 b	1151 b	79.3 b	104	398 b	54.4 b	40.8 b	0.14 a
1 (25–54)	7	8.99 bc	46.7 ab	774 ab	39.8 a	96.5	80.6 a	7.86 a	9.77 a	0.11 a
2 (55–107)	18	8.98 c	35.8 a	546 a	39.9 a	99.8	77.5 a	10.99 a	22.6 ab	0.29 a
3 (~ 10,000)	6	8.27 a	160 c	2826 c	184 c	75.8	174 a	34.69 b	37.2 b	0.65 b
	p	< 0.001	< 0.001	< 0.001	< 0.001	ns	< 0.001	< 0.001	0.054	0.012

Table 2

The average total amount of selected biogenic elements in the roots of the Arctic willow roots and leaves (mg • kg⁻¹, n = 6); (r) – roots, (l) – leaves; Small letters indicate significant differences between groups; ns – not significant.

Zone (age)	Ca(r)	Ca(l)	K(r)	K(l)	P(r)	P(l)	Fe(r)	Fe(l)	Mg(r)	Mg(l)	S(r)	S(l)	Zn(r)	Zn(l)
0 (< 25)	5,491	14,802 b	4,348 b	12,066	1,286 a	2,473 a	548	409	1,734	4,053 b	372	3,160 b	307	693
1 (25–54)	7,040	13,285 b	3,644 ab	11,784	1,806 b	5,164 b	293	165	2,013	3,797 b	480	2,469 ab	254	499
2 (55–107)	8,539	9,182 a	3,173 a	8,763	818 a	1,976 a	444	493	1,644	2,730 a	453	1,914 a	238	1021
3 (~ 10,000)	ns	0.018	0.024	ns	0.004	0.0003	ns	ns	ns	0.006	ns	0.050	ns	ns

Quantitative characteristics of soil of different ages

All the soils sampled were alkaline (the pH ranged from 8.27 in the third zone to 9 in the first and second zone; Table 1). However, large differences in cation exchange capacity (12.0–207 meq•kg⁻¹) were found. This was related to the high content of Ca, which dominated the exchangeable bases. Exceptionally high values of Ca, as well as Mg, were found in the third zone. Other elevated values of exchangeable Ca were found in samples from zone 0 (average: 1,151 mg • kg⁻¹). The contents of these two exchangeable elements were closely correlated, as indicated by the Spearman's correlation coefficient (Ca and Mg correlation coefficient r = 0.915, p < 0.001). As a result, the correlations between CEC and Ca and Mg were very close (Ca vs CEC r = 0.997, p < 0.001; Mg vs CEC r = 0.931, p < 0.001). For all soil elements, we found a distinctive pattern of higher values in zone 0, a drop in zones 1 and 2, and a rise in the last zone 3.

Allocation of elements in polar willow samples

The concentrations of microelements in various parts *S. polaris* varied. The highest concentrations of the elements under study (Ca, K, S, Mg and P) were found mainly in the leaves, except for Fe, which was to a large extent allocated to the roots (Table 2). We revealed changes in the content of biogenic elements in plants with increasing soil age. The concentrations of Ca(l), K(r) and Mg(l) in the polar willow decrease with soil age. The amount of P(r), P(l) and S(l) varies with the age of the soil, too. The largest amount of P(r), P(l) and S(l) was found in the second zone. There are no or statistically insignificant trends for any of the other nutrients contained in the willow roots and leaves.

Exudation by polar willow roots

The derivatives of small organic acids contained in the roots of the polar willow were mainly malate, citrate, oxalate, formate, lactate and acetate (Table 3). The content of butyrate, valerate, tartrate and isocitrate was below the detection limit. There were significant differences in the contents of small organic acids and P between the three zones of glacial retreat. Roots in the early growth stage exuded more malate whereas the average content of malate in the first zone was twice as high as in the other zones. By contrast, the average content of formate was twice as high in the third zone as in the younger zones. The content of hot-water-extractable P in roots was, statistically significantly, the highest in the second zone in compared with the third zone. There were no statistically significant differences in the content of lactate, acetate, oxalate and citrate in the willow roots.

Table 3

Average amount (mean and standard deviation) of hot water-extractable small organic acids and hot water-extractable total P in the roots of polar willow roots (mg • kg⁻¹, *n* = 6; small letters indicate significant differences between the groups; ns – not significant)

Zone (age)	Lactate	Acetate	Formate	Malate	Oxalate	Citrate	P
1 (25–54)	108 ± 25.5	294 ± 79.0	334 ± 169 a	5,410 ± 1,318 b	251 ± 48.6	4,748 ± 2,440	546 ± 365ab
2 (55–107)	153 ± 72.6	303 ± 59.6	335 ± 153 ab	2,605 ± 917 a	207 ± 16.4	2,490 ± 1,170	981 ± 499 b
3 (~ 10,000)	104 ± 22.4	289 ± 78.1	599 ± 235 b	2,796 ± 806 a	225 ± 33.4	2,982 ± 1,704	308 ± 107 a
<i>p</i>	ns	ns	0.079	0.002	ns	ns	0.031

There were, however, negative correlations between the average concentration of citrate and malate in the roots of the polar willow and the average total content of P in the different zones: $R_{0.05} = -0.342$, *n* = 18 and $R_{0.05} = -0.368$, *n* = 18, respectively (Fig. 2). There was a general trend of decreasing malate and citrate values with increasing P values and *vice versa*.

Discussion

Primary succession and soil properties

The age structure of local populations of *Salix polaris* varies markedly in the forefield of the Nordenskiöldbreen glacier. The initial successional zone 0 is completely devoid of vascular plants whereas zones 1 and 2 already host the first generation of dwarf shrubs, which prompt changes in their soil environment soon after their establishment. The most mature willow population is found in the oldest, successionally most advanced zone 3, deglaciaded ca 10 ka BP (Klysz et al. 1988). Lastly, the shrub population in zone 3 (30 years old on average) represents the climax community, which is supported by data from nearby sites in the bay of Petuniabukta, where the age of *S. polaris* individuals rarely exceeds fifty years (Buchwal et al. 2013).

Every soil is a result of diverse soil-forming processes, and deglaciation usually provides a relatively low-complexity environment in which pedogenesis is yet to be initiated (Bernasconi et al. 2011). Our findings, in the context of the alkaline soil pH, indicate that the high content of exchangeable Ca²⁺ and Mg²⁺ comes from the carbonate parent material in this region. Calcium is usually the dominant basic cation in soil cation exchange reactions and typically accounts for more than 70% of base saturation (own data, not shown). In addition, the availability of P, which is commonly considered limiting (see Göransson et al. 2016), varies with the time since deglaciation. However, its absolute concentrations at the study site might not limit plant growth, because we have measured its high absolute allocation in plant tissues. Besides, Ca and Mg, when solubilized by LMMOAs, nutrients are available in high supply and may accumulate close to roots (Neumann and Romheld 2007). The higher values for all elements in zone 0 likely represent initial ecosystem reserves that immediately got partly depleted as plant succession progressed (including through root development) and under the influence of local climatic conditions (precipitation, snow melt; Breen and Lévasque 2008; Le Moullec et al. 2020). The elevated content of soil nutrients bound to organic matter in the most mature zone 3 indicates that a successional equilibrium in soil conditions is reached in this zone (Wietrzyk et al. 2018).

The content of biogenic elements in polar willow roots and leaves depends on the age of the soil and the role of root exudation in nutrient uptake.

Our data demonstrate that the content of biogenic elements in the roots and leaves of the polar willow varies depending on the age of the soil. We suggest that Ca, Mg and K, which are abundant after deglaciation, are consumed in the initial stages of plant succession and that their relative role decreases with subsequent soil development. This, however, does not apply to P, which is available in greater abundance in zone 2. On the other hand, low absolute concentrations do not necessarily indicate P scarcity (Street et al. 2018). One of the mechanisms of the mobilization of phosphorus in the form of Fe, Al and Ca phosphates is the release of organic acid anions (Neumann and Römheld 2007). Further secretion of various organic acids by plant roots acidifies the rhizosphere, supports the dissolution of inorganic P and improves P availability by making it easier to transport P inside the root system (Hinsinger 2001). Based on the studies of Gerke et.al. (2000), Neumann and Römheld (2007), and Giles et.al. (2014), it can be stated that the citric, malic acid and oxalic acid, which are all polycarboxylic acids, cause higher P mobilization than other organic acids. Plants that are able to excrete large amounts of organic acids to satisfy their P demand do so directly into their root zone, where it is most effective (Neumann and Romheld 1999). Based on the results of our present study, we propose that *S. polaris* exudes organic acids from its roots in order to solubilize P and satisfy its demand for the element. In the polar willow, the intensity of exudation and the amount of small organic acids decrease as the concentration of P in the roots increases, which is documented by the statistically significant negative correlations between the concentrations of phosphorus and those of malate and citrate in our data. Also in line with this trend are our observations for the fully vegetated zone 3, where the concentration of phosphorus decreased again even though the amount of secreted acids increased. We assume that competition plays an important role in this reverse trend, as zone 3 is a fully vegetated tundra environment. This corresponds to the findings of Lévesque and Svoboda (1999), who described a trend of lower P availability in sites with comparably higher plant cover in the Canadian Arctic. Moreover, our results from a nearby site in the glacier forefield (Hájek, unpublished results) indicate that the polar willow there has only a weak ability to obtain P (evidenced by a 0.5‰ content of P in its leaves) and therefore exhibits a high N : P ratio compared to willows of the same species in other fully vegetated environments. This contrasts with our findings for other species competing for habitat space in the same environment, such as *Saxifraga oppositifolia*, in which P and N concentrations (and thus the N : P ratio) remain stable across different environments.

We therefore suggest that the observed variability in exudation rates is not driven solely by nutrient unavailability in the forefield of the glacier. Instead, we propose that it provides insight into the complex processes by which plants invest the resources they have in order to secure less available nutrients at a stage when their root system is still underdeveloped (zone 1 with the youngest shrubs) and when they face strong competition (zone 3, fully vegetated tundra). Based on the above, temperature is probably the key factor limiting plant growth, but to what extent this relationship is stable in the context of the currently observed climate change and whether it is likely to result in an expansion of shrubs remains unanswered.

Conclusion

The potential root exudation rate of the High Arctic dwarf shrub *S. polaris* (polar willow) is linked to the availability of nutrients, competition and the age of the soil since glacier retreat. Our detailed study of the specificity and content of LMMOA in the soil is indicative of the biological activity and development taking place within initial soils, plant root exudation and nutrient availability, confirming the role of these excreted compounds in nutrient uptake by the polar willow in the Nordenskiöldbreen forefield. The observed variation in the content of nutrients, especially phosphorus, in polar willow roots growing in initial soils can likely be explained by the fact that, in the early stages of growth, they need a considerable amount of P; however, their root system is not yet fully developed (because the shrubs are younger), so the plants do not need to invest as much in root exudation. Similarly, on the other side of the successional scale, in the fully vegetated tundra, where there is greater competition from other plants, a higher intensity of exudation is needed to cover the nutrient needs of polar willow individuals. Both environments thus put strong pressure on the willow shrubs, which respond by increasing their root exudation. By contrast, in zone 2, polar willows and other plants have a better-established root system and yet there is little competition, so plants do not have to invest much in root exudation. Our study brings insight into the allocation of scarce plant resources over the course of succession and thus provides a ground for the understanding and modelling of vegetation change. Future studies should nevertheless better explain the role of increasing Arctic temperatures in observed vegetation changes and their impact on nutrient availability.

Declarations

Author contribution: JL and VT conceived the idea for this study and designed it. JL, PK, VT, PL, TH collected the samples. AH, PK, KN, OD, VT processed and analysed the samples. JL, AH, VT analysed the data. VT performed the statistical analysis. JL wrote the draft of the manuscript. VT have contributed to the respective chapters of this article. All authors have reviewed, amended and approved the final version of the manuscript.

Funding: This study was partially funded by Czech University of Life Sciences Prague Internal project No. SV23-2-21130.

Conflict of Interest: The author JL is a Deputy Minister of the Environment of the Czech Republic, all the results and interpretations were prepared before he accepted the position. The authors declare that they have no conflict of interest.

Ethical approval: This article does not report of the results of any studies involving animal or human subjects.

Availability of data and material: The datasets generated or utilized in the current study are available from the corresponding author upon reasonable request.

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Figures

Fig. 1

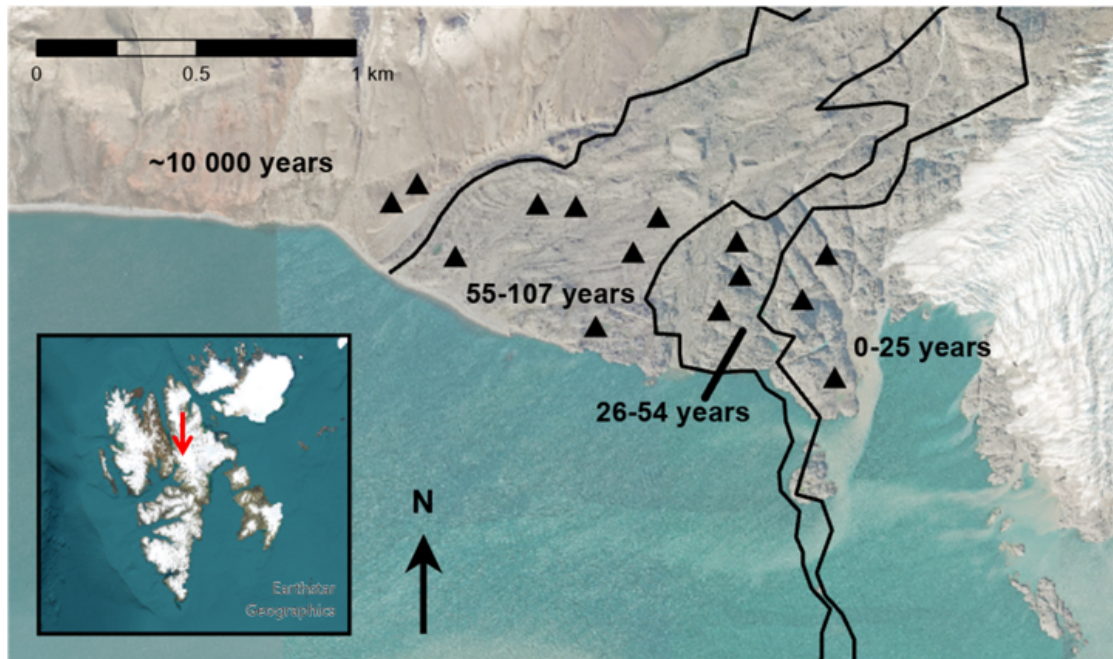


Figure 1

Sampling sites (black triangles) in the Northern forefield of the Nordenskiöldbreen glacier with marked zones of deglaciation (black lines) based on satellite imagery provided by the Norsk Polar Institute (2015); the background map comes from World Imagery provided by ArcGIS Pro (ESRI, version 2.8.0 2021), Source: Esri, Maxar, Earthstar Geographics and the GIS User Community.

Fig. 2

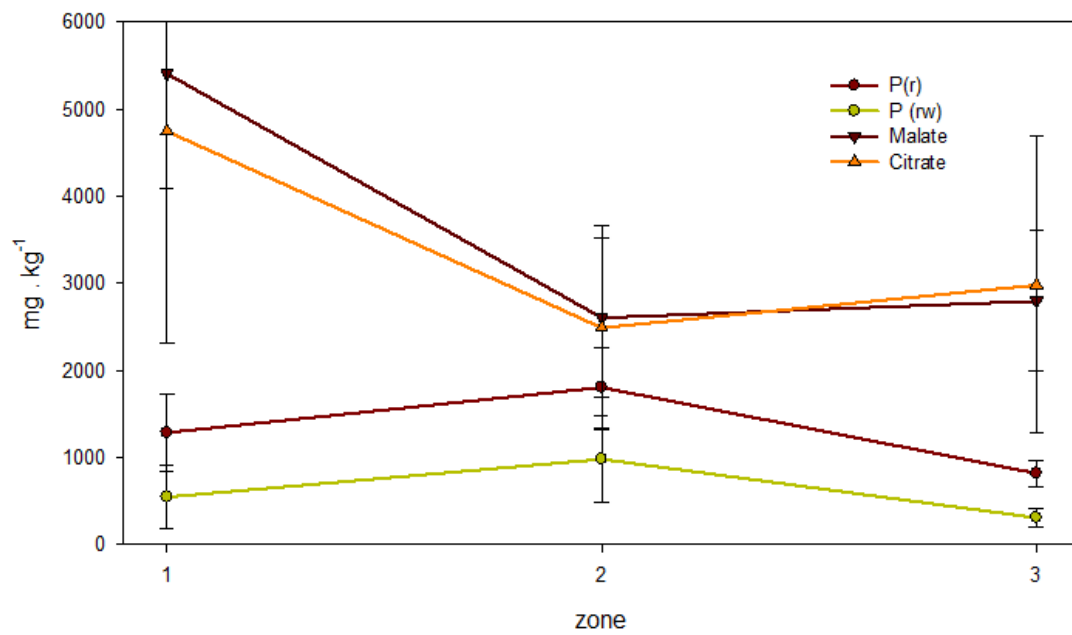


Figure 2

Opposite trends in malate and citrate content and in the concentration of phosphorous in the roots of Arctic willow in the Nordenskiöldbreen glacier forefield (means, $n=6$; P(r) – total content of P in roots, P(rw) – total content of hot water-extractable P)