

The hidden season: growing season is 50% longer below than above ground along an arctic elevation gradient

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Summary

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- There is compelling evidence from experiments and observations that climate warming prolongs the growing season in arctic regions. Until now, the start, peak, and end of the growing season, which are used to model influences of vegetation on biogeochemical cycles, were commonly quantified using above-ground phenological data. Yet, over 80% of the plant biomass in arctic regions can be below ground, and the timing of root growth affects biogeochemical processes by influencing plant water and nutrient uptake, soil carbon input and microbial activity.
- We measured timing of above- and below-ground production in three plant communities along an arctic elevation gradient over two growing seasons.
- Below-ground production peaked later in the season and was more temporally uniform than above-ground production. Most importantly, the growing season continued *c.* 50% longer below than above ground.
- Our results strongly suggest that traditional above-ground estimates of phenology in arctic regions, including remotely sensed information, are not as complete a representation of whole-plant production intensity or duration, as studies that include root phenology. We therefore argue for explicit consideration of root phenology in studies of carbon and nutrient cycling, in terrestrial biosphere models, and scenarios of how arctic ecosystems will respond to climate warming.

Introduction

Climate warming has led to a renewed interest in plant phenology (the timing of periodic life-history events, such as bud break), as vegetation is increasingly observed to become active earlier in spring (Wolkovich *et al.*, 2012; Richardson *et al.*, 2013) and – less frequently – to have a delayed senescence in autumn (Natali *et al.*, 2011). Evidence for this comes from local to landscape scales, with methods ranging from single shoot observations to remote sensing (Pau *et al.*, 2011; Wolkovich *et al.*, 2012). Changes in phenology and growing season length are expected to be most pronounced in regions with a strong seasonal climate (Pau *et al.*, 2011), such as the Arctic, where annual cycles are constrained by a short growing season, and where current and predicted warming rates are highest (ACIA, 2004). Accordingly, at northern high latitudes, vegetation phenology has been shown to be very responsive to warming (Barichivich *et al.*, 2013; Xu *et al.*, 2013) and most of the Arctic has on average gained > 3 days of growing season per decade since the 1980s (Xu *et al.*, 2013).

Critically, our knowledge about the length of the growing season and changes therein almost exclusively result from above-ground measures, which are used as sole indicators for whole-plant responses, even though over 80% of the plant biomass in arctic and alpine tundra can be located below ground (Mokany *et al.*, 2006; Iversen *et al.*, 2015). It is well known that fine roots are key elements in ecosystem function and biogeochemical cycles in terrestrial ecosystems, as plant roots move photosynthetically fixed carbon into the soil, take up water and nutrients, and stimulate soil microbial activity through the exudation of labile carbon from living roots and litter inputs of dead roots (Matamala *et al.*, 2003; Pendall *et al.*, 2004; Schmidt *et al.*, 2011). In high latitude systems which contain *c.* 50% of all global below-ground organic carbon (McGuire *et al.*, 2009), roots and their associated fungi drive long-term carbon sequestration (Clemmensen *et al.*, 2013). Most of these processes are directly linked to fine root production, and may consequently be affected by seasonal dynamics of root growth. As such, the timing of root production generally has important implications for fluxes of carbon, water and energy from the land surface to the

atmosphere (Keel *et al.*, 2012; Warren *et al.*, 2014). Similarly, the timing of root growth influences plant resource acquisition (Nord & Lynch, 2009), and microbial activity (Pendall *et al.*, 2004). A thorough understanding of vegetation–atmosphere carbon fluxes and large-scale biogeochemistry must therefore include the seasonal activity of nonphotosynthetic tissues such as roots (McCormack *et al.*, 2014; Smithwick *et al.*, 2014; Warren *et al.*, 2014), which will advance the accuracy of predictions from dynamic global vegetation models regarding the carbon cycle of the future (McCormack *et al.*, 2013; Fatichi *et al.*, 2014; Smithwick *et al.*, 2014).

However, data describing root phenology in natural communities are still scarce (Pregitzer *et al.*, 2000; McCormack *et al.*, 2014; Smithwick *et al.*, 2014), mainly due to methodological difficulties. Very few studies globally have directly compared phenology above and below ground, and most of those are from temperate forest ecosystems, where a roughly synchronized phenology between shoots and roots seems to be present (Pregitzer *et al.*, 2000; Abramoff & Finzi, 2015). Other studies, however, show that the timing of production can vary between roots and shoots (Palacio & Montserrat-Martí, 2007; Steinaker & Wilson, 2008; Steinaker *et al.*, 2010; Du & Fang, 2014; Abramoff & Finzi, 2015). Despite the large amounts of below-ground biomass and the importance of roots in linking above- and below-ground processes, very limited data exist about root phenology in arctic regions (but see Shaver & Billings, 1975, 1977; Sullivan & Welker, 2005), leaving root growth as one of the least understood parts of arctic ecosystem dynamics (Wookey *et al.*, 2009; Iversen *et al.*, 2015). Accordingly, in models commonly used to simulate ecosystem processes in arctic tundra, root phenology is either not represented (e.g. ArcVeg), assumed constant (e.g. MBL-GEM III), or – most commonly – assumed to be the same as leaves (e.g. DVM-DOS-TEM, LPJ-GUESS WhyMe, CLM4.5-BGC, Orchidee-WET) (Iversen *et al.*, 2015).

To better understand seasonal patterns of ecological and biogeochemical processes in arctic regions and how these may be affected by a changing climate, a thorough understanding of root phenology and its relationship to shoot phenology is needed. In addition, the influence of environmental factors, such as soil temperature and moisture, on root growth dynamics remains poorly understood and controversial (Tierney *et al.*, 2003; Joslin *et al.*, 2011) impeding our understanding of how climate change will impact fine root dynamics in arctic regions. Thus, we asked whether shoot phenology reflects or differs from fine root phenology, if the growing season is similar in length and timing above and below ground across arctic plant communities along an arctic elevation gradient, and which abiotic factors influenced seasonal patterns of root growth at our study site and whether those differed among plant communities. To address these questions, we performed *in-situ* measurements of phenology and compared the length of the growing season above and below ground during 2 yr in northernmost Sweden and additionally measured air and soil temperature as well as soil moisture. All measurements were done at three elevations with different temperature regimes and concomitantly shifting plant communities: sub-alpine birch forest

(500 m above sea level, asl), low alpine tundra (800 m asl) and high alpine tundra (1100 m asl).

Materials and Methods

Study area

We studied above- and below-ground phenology along an elevational gradient at Låkatjåkka (68°40'73"N, 18°37'97"E), in northernmost Sweden. The closest meteorological station is in Katterjåkk, c. 8 km west at 497 m asl, with average annual temperatures of -1.7°C (1961–1990) and an average annual precipitation of 843.7 mm (1961–1990) (Swedish Meteorological and Hydrological Institute, SMHI). The bedrock consists of feldspathic metasandstone, metagreywacke, quartzite, phyllite, metaconglomerate, schist and marble. Plots were located at three elevations, 500 (nine plots), 800 (10 plots) and 1100 m asl (10 plots), with plant communities changing along the elevational gradient from sub-alpine mountain birch forest (*Betula pubescens* ssp. *czerepanovii* Erh., with an understory of dwarf shrubs and grasses, e.g. *Empetrum nigrum* ssp. *hermaphroditum* (Hagerup) Böcher, *Vaccinium myrtillus* L., *Vaccinium uliginosum* L., *Vaccinium vitis-idaea* L., *Deschampsia flexuosa* (L.) Trin.), over low alpine tundra (e.g. *Bistorta vivipara* (L.) Gray, *Deschampsia flexuosa* (L.) Trin., *Carex bigelowii* Torr. Ex Schwein, *Empetrum nigrum* subsp. *hermaphroditum* (Hagerup) Böcher, *Salix herbacea* L., *Vaccinium myrtillus* L., *Vaccinium vitis-idaea* L.) to high alpine tundra vegetation (e.g. *Bistorta vivipara* (L.) Gray, *Carex bigelowii* Torr. Ex Schwein, *Festuca vivipara* (L.) Sm., *Salix herbacea* L., *Empetrum nigrum* subsp. *hermaphroditum* (Hagerup) Böcher). All of these are species that are common both in our larger study area and on a circumpolar level (CAVM Team, 2003). Taking Katterjåkk as a baseline (-1.7°C mean annual air temperature, 1961–1990, 500 m asl) and assuming a lapse rate of 0.6°C per 100 m increase in altitude, long-term mean annual air temperatures are expected to be c. -3.5°C at the 800 m site (low alpine tundra) and c. -5.3°C at the 1100 m site (high alpine tundra). Both our measured mean August temperatures (see the Results section), and the estimated mean annual temperatures (as well as the latitude of our study area) put the two higher elevations into the category of the low Arctic (Bliss & Matveyeva, 1992). Using an elevational gradient gave us a powerful space-for-time substitution to allow assessment of how ecosystems are likely to respond to climate warming over long time scales (Körner, 2007).

Phenology and growing season length above and below ground

We made biweekly observations of both root and shoot production from the end of June until the beginning of October in 2011 and during the complete snow-free period of 2012 (beginning of June to mid-October 2012). Root length was measured with minirhizotrons consisting of transparent tubes, made out of cellulose acetate butyrate, in the soil and a digital camera system, with which we took pictures of the soil interface, including roots, at the same spot at reoccurring times (Bartz Technology Corp.,

Carpinteria, CA, USA). This is a nondestructive method to observe temporal development of fine roots (Johnson *et al.*, 2001). Tube material has little effect on root production but can potentially influence root lifespan (Withington *et al.*, 2003), which is why it was held constant in this study. Two years before the beginning of measurements, one *c.* 1.5-m-long tube was installed horizontally in each plot. This was done at steps in the terrain, exposing the entrance portion while keeping the 1-m-long viewing section of the tube at a depth of *c.* 10 cm. This depth is where the majority of fine roots are situated (Jackson *et al.*, 1996; Iversen *et al.*, 2015), and we consistently avoided rocks and bedrock. Tape and a cap on the exposed part of the tube prevented light entry into the tube.

Root length was measured using the software ROOTFLY version 2.0.1 (Birchfield & Wells, Clemson University, Clemson, SC, USA). Root growth was calculated as the increase in root length (elongation of existing roots and the appearance of new roots) between two sampling times for each tube. In addition, for each sampling interval of 2 wk the percentage of growth compared with the total observed growth of the season within each tube was calculated to compare seasonal root production between plant communities and years.

Above-ground phenology was measured on the same dates as below-ground phenology by repeated digital photography. This has been shown to provide a valuable and reliable tool for deriving plant phenology in different vegetation types, including both start and end of the growing season, and photosynthesis (e.g. Keenan *et al.*, 2014; Toomey *et al.*, 2015). Each time, above each minirhizotron tube, downward-looking digital photographs (with a Nikon D60 camera; Nikon Corp., Tokyo, Japan, 3872 × 2592 pixels, 35 mm focal length) of a marked 40 × 40 cm² plot were taken, from the same position and with the same aperture. To eliminate reflections or shading, we used a white light tent (Lastolite, Leicestershire, UK) that diffused the light. For consistent white-balance and color measuring between plots and sampling dates we used a grey card. The percentage of green pixels in each subplot was calculated using Adobe Photoshop v.5 (Adobe Systems Inc., San Jose, CA, USA), and its increase within each sampling interval relative to the maximum percentage was used as above-ground production, whereas a loss of greenness was used as above-ground senescence. As bryophytes were abundant in the study area but do not contribute to root phenology, we manually excluded green pixels from bryophyte cover from the analysis.

During the first year of our study, we additionally marked shoots on five individuals of *Betula pubescens* subsp. *czerepanovii* Erh. and dwarf shrub species if present in the plots and monitored their elongation. We did not continue with those measurements but chose repeated digital photography as the more suitable method to measure growing season length above ground because sub-arctic and arctic vegetation is characterized by very slow shoot growth despite the rapid changes in leaf phenology, and only woody species were monitored for shoot elongation. Results from elongation measurement and repeated photography in the first year were positively correlated (Pearson's product-moment correlation $r=0.60$, $P<0.001$).

To quantify the temporal distribution of production, and compare it between roots and shoots and between the three elevations, we calculated an index D for each plot.

$$D = \frac{1}{(\sum(|P_t - P_m|))} \times 100 \quad \text{Eqn 1}$$

This index counts periods with production, thereby assigning more weight to those with high production (Steinaker & Wilson, 2008). For each plot, D was calculated as one divided by the sum of the absolute differences between the observed percent production value of each sampling interval (P_t) and the theoretical mean percent production of annual production for each sampling interval (P_m) if production was completely equally distributed (e.g. very few periods with high production would result in greater differences from a theoretical even distribution, and thus a smaller value for D). For convenience the result is multiplied by 100 (Steinaker & Wilson, 2008). As production is expressed as a percentage, the mean per cent production of annual production for each sampling interval P_m is a constant (100 divided by the number of sampling intervals of each plot). A higher D value thus indicates that production is more equally distributed (Eqn 1). The index was calculated for the growing season of 2012 during which we were sure to cover the entire season (we started and stopped measuring when plots were covered with snow). We also determined the end of the growing season below ground (the day of year at which 90% of the total yearly root growth was exceeded) and above ground (day of year at which 90% of the maximum above-ground vegetation cover was exceeded) in each plot. We chose to calculate 90% of each root growth and vegetation cover instead of 100% to exclude the possibility of very few, late-growing roots driving the observed pattern. Preliminary analyses suggest that the use of a greater percentage did not change the observed pattern.

In our study, we refer to 'growing season' as the part of the year during which plants grow or photosynthesize, including below-ground growth.

Abiotic parameters

Soil moisture and temperature were recorded as hourly means with two sensors each in six plots per elevation at 10 cm depth, that is, the depth corresponding to the root observations, from the end of June 2011 to mid-October 2012. Air temperature above the vegetation or forest understory was measured at 20 cm height in one plot per elevation (EC-5 sensors for air and soil temperature and ECT sensors for soil moisture, both Em50; Decagon Devices, Pullman, WA, USA). Mean, minimum and maximum daily values and values during each sampling period of 2 wk were calculated for both soil moisture and soil temperature.

Data analyses

To test for differences in distribution of production (D) between above and below ground and between elevations and their interactions, we used a linear mixed-effects model ANOVA (R

package 'nlme') with elevation and plant part (shoot or root) as fixed factors and plot as random factor. Similar analyses were used to examine if the end of the growing season depended on elevation or plant part. All data were graphically analysed for assumptions of normality and homogeneity of variance of the residuals with normal qq-plots and residual vs fitted plots of the model, respectively. The data were log- or square root-transformed if necessary. *Post-hoc* comparisons within factor combinations were done by Tukey's HSD test (R package 'multcomp').

Spearman's rank correlation coefficients were used for correlations between abiotic factors (air temperature, soil temperature and soil moisture) and root growth in the different sampling intervals. To further elucidate which factors influenced fine root growth and if there were differences between the plant communities, we used a variation partitioning to test how much of the variation in root growth at the different sites was explained by air and soil temperatures, and by the time of year which each sampling period encompasses ('time of year', e.g. early July). The latter served as an integrated proxy for photoperiod, which has previously been shown to influence root growth rates (Shaver & Billings, 1977), and time since initiation of growth after dormancy. Variation partitioning subdivided the explained variation of root growth into values for each of the explanatory variables and their combined effects (R package 'vegan'). Factors contributing significantly to the explanation of variance were identified before the analysis by using linear models for each predictor variable and the response, that is, root growth in mm. This left time of year (e.g. 'early July'), air and soil temperature to be included in the analysis, but not soil moisture or plot ID. Mean air and soil temperatures were chosen for the analyses, as neither minimum nor maximum temperature were consistently better

predictors. Explained variance < 0.5% was treated as zero (Legendre, 2008). All statistical analyses were performed using R 2.15.2 (R Core Team 2012, Vienna, Austria).

Results

Phenology and growing season length above and below ground

Above- and below-ground production patterns were not synchronous, in any plant community or either year (Fig. 1). Shoot production peaked early in the season and declined soon afterwards, but fine root production did not show coinciding peaks at any community (Fig. 1). Rather, below-ground production was more uniformly distributed over the growing season relative to above-ground production without a distinct peak. This was confirmed by the 'temporal distribution of production' (D) which reflected both the general length and the distribution of intensity of production. D was significantly greater below ground (mean $D_{\text{roots}} = 1.32$) than above ground (mean $D_{\text{shoots}} = 0.97$; $F_{1,2} = 24$, $P < 0.0001$), showing a longer and more evenly distributed production below ground. After the end of above-ground production, the level of greenness immediately declined instead of remaining constant and thus coincided with the onset of above-ground senescence (indicated by the arrows on Fig. 1). Below-ground production, on the other hand, was still ongoing and consequently continued while there was a substantial loss of greenness in the above-ground biomass.

Our data from the second year, when we started measurements while the majority of plots were still covered with snow, indicate that below-ground production started at least as early as above-

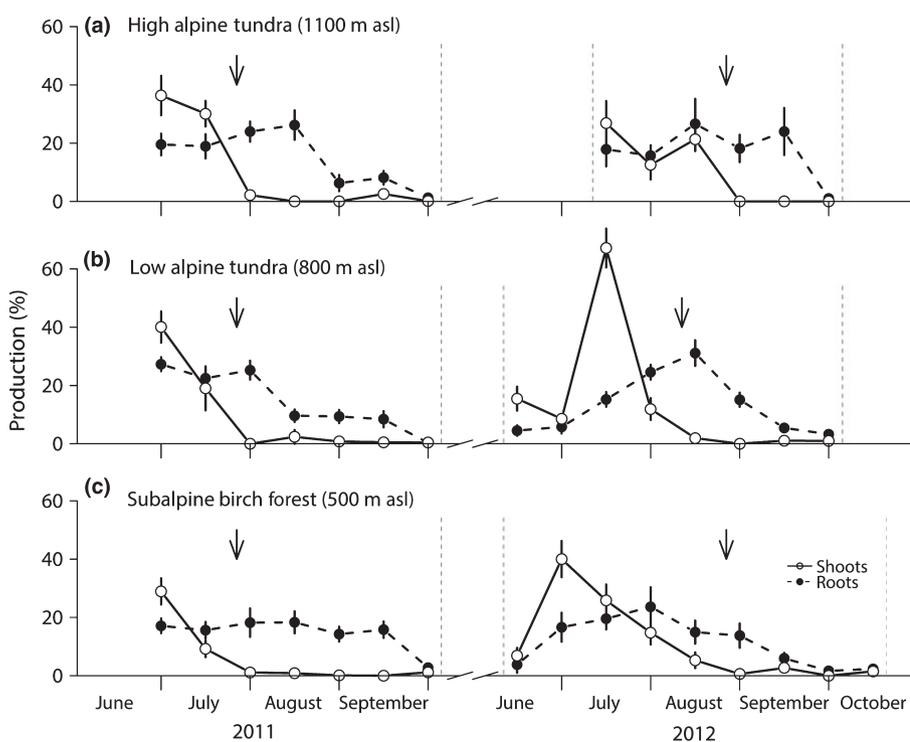


Fig. 1 Above- and below-ground production over the sampling period. Above-ground production is expressed as a percentage of the total green cover produced in each of the sampling intervals of 2 wk. Note that percentages do not add up to 100% in cases where production started before the onset of measurements. Below-ground production is expressed as the per cent production in each sampling interval of 2 wk in relation to the total observed production (i.e. total root growth). Dashed vertical lines indicate end or onset of accessibility to the elevations, that is, when the majority of plots at each elevation was covered in snow. Arrows indicate onset of above-ground senescence. Data is shown each for the (a) high ($n = 10$), (b) mid ($n = 10$) and (c) low elevation ($n = 9$) over two growing seasons. Error bars are \pm SE, above sea level.

ground production which was shortly after or directly at snowmelt. Yet, a striking difference between below- and above-ground production occurred towards the end of each growing season (defined as the day of year at which 90% of the total yearly root growth or 90% of the maximum above-ground vegetation cover was exceeded, see the Materials and Methods section), when fine root growth consistently continued after onset of leaf senescence at all elevations. Specifically, in 2011, below-ground production continued on average $40 \pm \text{SE } 5$, $54 \pm \text{SE } 4$, and $58 \pm \text{SE } 4$ days longer than above-ground production ($F_{1,2} = 399$, $P < 0.0001$) at high alpine tundra, low alpine tundra and sub-alpine birch forest, respectively, whereas in 2012 this was $30 \pm \text{SE } 4$, $40 \pm \text{SE } 3$, and $40 \pm \text{SE } 5$ days longer ($F_{1,2} = 218$, $P < 0.0001$; Fig. 2).

Abiotic parameters influencing fine root growth

During this study, mean air temperatures at 20 cm height in August measured at our sites were 10.3°C (sub-alpine birch forest), 6.5°C (low alpine tundra) and 5.9°C (high alpine tundra) in 2011 and 8.3°C , 5.5°C and 4.2°C in 2012, respectively. Air temperatures dropped below freezing point at the low and high alpine tundra sites repeatedly over the whole summer. Temperatures of -5°C or below can be seen as critically low for plants as they can induce tissue damage (Lindow *et al.*, 1982). Daily mean temperatures below this threshold occurred on all sites from October onwards. Soil temperatures at the depth of root observation, that is, 10 cm, on the other hand, reached such low temperatures only after November, or not at all in the case of the sub-alpine birch forest (Fig. 3). Average soil moisture in July and August was $0.226 \text{ m}^3 \text{ m}^{-3}$ volumetric water content (VWC) in the sub-alpine birch forest, $0.297 \text{ m}^3 \text{ m}^{-3}$ VWC in the low alpine tundra, and $0.335 \text{ m}^3 \text{ m}^{-3}$ VWC in the high alpine tundra.

Fine root growth increased with both increasing air and soil temperature (Spearman's $\rho = 0.54$, $P < 0.0001$ and 0.52 , $P < 0.0001$, respectively). By contrast, no correlation was found with soil moisture (Spearman's $\rho = -0.08$, $P = 0.2678$) suggesting that water availability was not a limiting factor in this study. Accordingly, air temperature, soil temperature and time of year

were identified as factors that significantly contributed to the explained variance in root growth. The subsequent variation partitioning then showed that air temperature, soil temperature and time of year combined explained a decreasing amount of variation in fine root growth with increasing altitude: 30% in sub-alpine birch forest, 22% in low alpine tundra (with an additional 8% explained by only air temperature and time of year), and 12% in high alpine tundra (Fig. 4). However, time of year as a single factor showed the opposite pattern and explained 0% of variation in the sub-alpine forest, 10% in low alpine tundra and 16% in high alpine tundra. This indicates that time of year becomes increasingly important with increasing altitude while the importance of temperature for timing of root production decreases.

Discussion

Phenology and growing season length above and below ground

Phenology was not synchronized above and below ground, in any plant community or either year, that is, there were no coinciding peaks in production. Above-ground phenology showed a distinct peak in the beginning of the season, which might have been even more pronounced with a tighter sampling interval, whereas below-ground phenology was more evenly distributed and the growing season lasted considerably longer below ground than above ground in the autumn. We thus revealed the occurrence of a 'hidden', below-ground growing season in which plants were still producing new roots weeks after above-ground production had ended and senescence had started. A loss of greenness with senescence corresponds to a reduction in photosynthetic activity (e.g. Keenan *et al.*, 2014; Toomey *et al.*, 2015). Accordingly, using shoot phenology as a measure for overall plant phenology severely underestimates the length of the growing season of an important part of annual production in our study systems.

Previous estimates of growing season length in the low Arctic are 84–100 days (Bokhorst *et al.*, 2008; Karlsen *et al.*, 2008), which corresponds to our own observations of above-ground

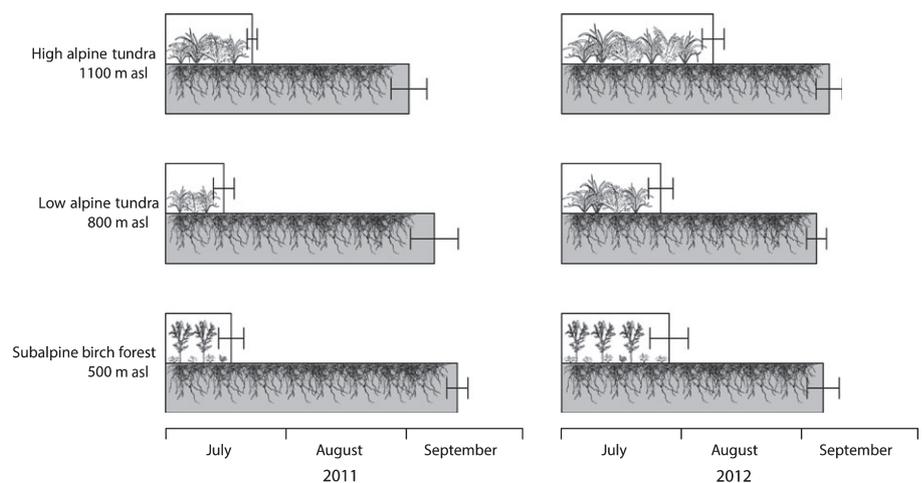


Fig. 2 Completion of the growing season above and below ground. White and grey bars show when 90% of the yearly above-ground cover and fine root growth were exceeded, respectively, after beginning of measurements, in high alpine tundra (at 1100 m above sea level (asl), $n = 10$), in low alpine tundra (at 800 m asl, $n = 10$) and in sub-alpine birch forest (at 500 m asl, $n = 9$). Error bars are $\pm \text{SE}$. Note that completion of 90% of the yearly above-ground cover coincided with onset of senescence, that is, loss of green cover.

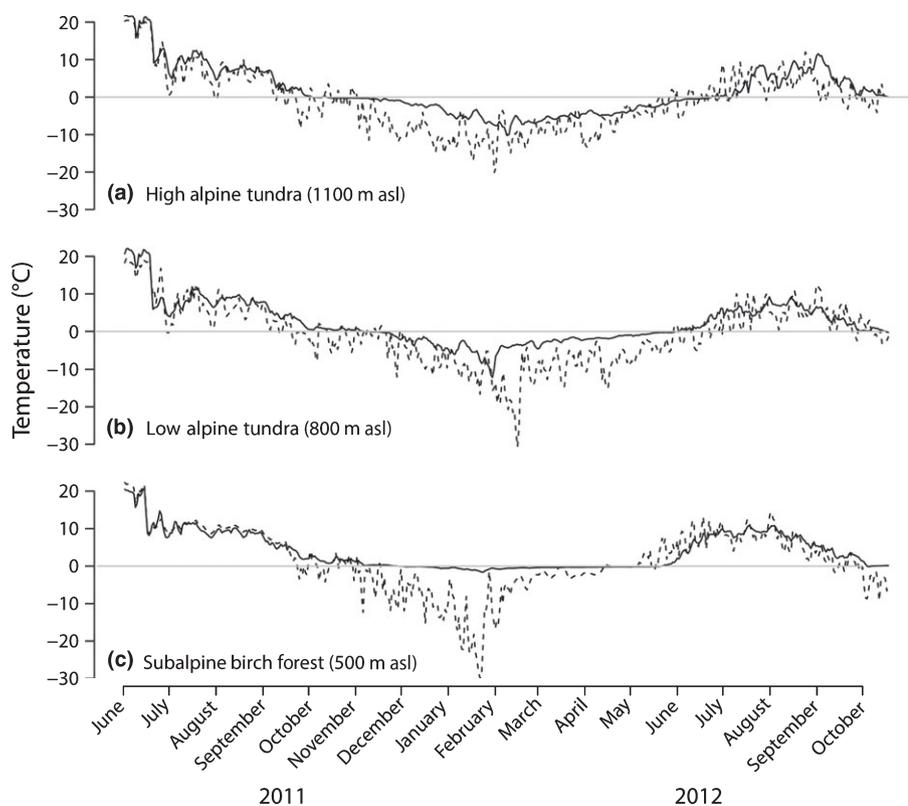


Fig. 3 Air and soil temperatures on the elevation gradient. Mean daily air temperatures above the vegetation or forest understory (dashed line, $n = 1$) and soil temperatures at 10 cm depth (solid line, $n = 6$) at the three elevations: (a) high alpine tundra (1100 m above sea level, asl), (b) low alpine tundra (800 m asl), (c) sub-alpine birch forest (500 m asl).

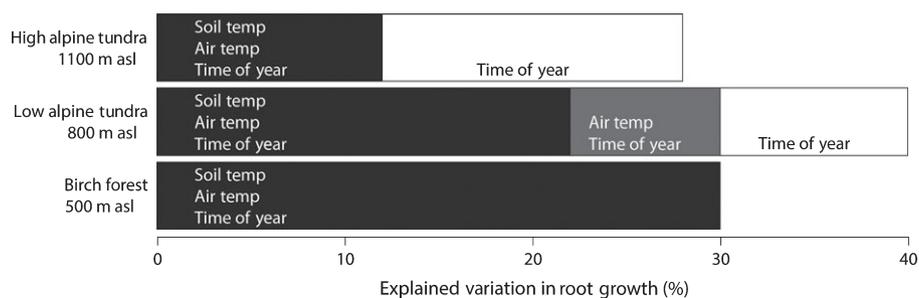


Fig. 4 Abiotic factors influencing fine root growth. Variation partitioning for factors explaining root growth during two subsequent growing seasons at high alpine tundra (1100 m above sea level, asl; $n = 10$; 56 individual observations), low alpine tundra (800 m asl; $n = 10$; 65 individual observations) and sub-alpine birch forest (500 m asl; $n = 9$; 83 individual observations) elevation between the corresponding explanatory variables soil temperature, air temperature and time of year (e.g. 'early July'). Bars show combined effects (joint labels) and variation explained by a single factor. Overall, models had an adjusted R^2 of 0.34 (1100 m asl), 0.45 (800 m asl) and 0.33 (500 m asl). For graphical representation, only explained variation of $> 5\%$ is shown. Only significant factors were included in the model, thus soil moisture is omitted.

growing season duration. However, when including the production of new roots, our results reveal that the growing season lasts *c.* 50% longer. Neglecting fine root phenology may thus obscure phenological responses of arctic vegetation to higher temperatures, especially in autumn. This could hamper predictions of the seasonal pattern of carbon exchange between the terrestrial ecosystem and the atmosphere, given the general importance of fine roots in carbon cycling (Matamala *et al.*, 2003). Indeed, it becomes increasingly evident that the 'shoulder seasons' are of special importance and may exert effects into the growing season, and should thus be a focal point in climate change research in the Arctic (Post *et al.*, 2009; Ernakovich *et al.*, 2014). An example is annual carbon budgets in the Arctic (McGuire *et al.*, 2009;

Ernakovich *et al.*, 2014) when warmer temperatures increase autumn soil respiration (of which roots are important contributors) more than photosynthesis and these ecosystems switch from carbon sinks to sources earlier in autumn (Högberg & Read, 2006; Piao *et al.*, 2008; Barichivich *et al.*, 2013; Richardson *et al.*, 2013).

The continuation of root growth in autumn implies the presence of a larger living root system, which may enable plants either to take up more nutrients during autumn or in the following spring in an ecosystem that is strongly nutrient limited. In spring, snowmelt provides a period of relatively high nutrient availability (Edwards *et al.*, 2006) during which arctic plants have been shown to take up nutrients (Edwards & Jefferies, 2010). Also the

autumn potentially provides a time of relatively high nutrient availability as decomposition is ongoing when soils are still warm, and thaw is at its maximum for sites underlain by permafrost (Schimel *et al.*, 2004; Weintraub & Schimel, 2005). In line with this, Olsrud & Christensen (2004) showed for a nearby tundra ecosystem that in mid-September most carbon was allocated to the finest roots, those parts of the root system that are most involved in nutrient uptake. Regarding carbon sources for the late root growth in our study, we assume that stored carbon reserves in the plants were allocated for fine root growth during autumn because at that time above-ground vegetation was already far into senescence. A similar mechanism has been observed in trees of other ecosystems, for example after defoliation (Vargas *et al.*, 2009; Gaudinski *et al.*, 2010).

Why do plants continue to grow roots well into autumn? Apart from using the relatively high nutrient availability in autumn, late root growth might be the result of more stable and higher temperatures in the soil compared with the air (Fig. 3). While shoots were facing the risk of freezing even at the end of summer, root systems were not as they are insulated by soil. Our observations did not include deep roots, but as deeper soil layers keep warm for longer than the shallower ones, the observed pattern could be even stronger in deeper layers. An analogous pattern has been proposed for the spring, when root systems have shown a time lag of initiation of growth compared with shoot growth (Steinaker & Wilson, 2008). We did not observe such a pattern of lagging root production, which may be a result of the high tolerance towards cool soil temperatures of arctic plant species (Shaver & Billings, 1975, 1977; Iversen *et al.*, 2015).

A recent review comparing peaks in production between shoots and roots across biomes showed that while roots and shoots are roughly in sync in temperate ecosystems, there can be a wide variation across and within biomes and shoots often precede roots in their production peaks (Abramoff & Finzi, 2015). Due to a paucity of data, arctic and sub-arctic ecosystems were not included in the review, but the biome that showed a pattern closest to what we observed was the boreal zone. There, root production peaked later than shoot production, and roots grew longer in autumn than shoots (Abramoff & Finzi, 2015). While this pattern relates to our own observations, the boreal below-ground growing season was only *c.* 16% longer, compared with 50% in our study system. The authors attributed the late season root growth mainly to a high presence of evergreen vegetation, as the deciduous species in the boreal zone showed a synchronous pattern similar to the temperate zone, whereas the evergreen species were driving the main pattern of the boreal biome (Abramoff & Finzi, 2015). In our case, however, it is very unlikely that the root growth late in the season can be attributed to evergreen species alone, as they made up < 10% of the vegetation cover in our plots. Thus, there may either be different causes behind late root growth in boreal and (low) arctic areas, or there is a more general pattern of relatively longer root growth related to the northward decline of both growing season length and mean air and soil temperatures irrespective of plant functional type.

Abiotic parameters influencing fine root growth

Rates of root growth are generally influenced by soil temperature, albeit depending on interactions with other resources and varying among species (Pregitzer *et al.*, 2000; Abramoff & Finzi, 2015). Thus, despite the global pattern of increasing root growth with increasing temperature, it remains unclear which factors are most important in driving patterns of root growth in a specific ecosystem or plant community.

Although soil temperature was overall positively correlated with root growth, we found that its relevance differed between plant community types and that temperature generally was most important in the sub-alpine birch forest. Time of year and thus photoperiod, on the other hand, displayed the opposite pattern with higher relevance higher up the gradient, in harsher climates. Similarly, it has been shown for above-ground phenology in trees that time of year is a better phenological cue than temperature in less predictable climates (Körner & Basler, 2010). As climate warming promotes the expansion of shrubs and trees in arctic regions, and a large proportion of the current tundra might be replaced with forest (40% by 2100) (ACIA, 2004), these findings have important implications. If root growth of relatively more productive systems, such as forests, responds more to temperature and those systems are thus more opportunistic, they might be able to profit more from warmer autumn temperatures than less productive tundra sites. For instance, this temperature sensitivity of forest species may enable them to better exploit patterns of future climate warming compared with tundra species. This in turn would likely enhance their performance via longer resource capture, and could lead to a positive feedback on shrub or forest encroachment into tundra ecosystems.

Conclusions

As root studies progressively emerge, it becomes clear that generalizations about root responses across ecosystems can be difficult (Norby & Jackson, 2000), as is the extrapolation of patterns from rather well studied systems, such as temperate forests, to arctic ecosystems. We showed clear differences in root and shoot phenology and growing season length that were more pronounced than what has previously been shown in almost any other biome. While a link between (remotely sensed) leaf area index and root traits has been demonstrated (Sloan *et al.*, 2013), we show here that neither generalizations from other ecosystems, nor projections of above-ground production to below-ground production, reflect seasonal dynamics of root growth in arctic plant communities. For instance, whereas above-ground changes in phenology due to climate warming mostly result in an earlier onset of the season and fewer responses at the end (Richardson *et al.*, 2013), roots might in addition to advanced initiation of growth (Sullivan & Welker, 2005) also respond strongly at the end of the growing season.

Our findings highlight the importance of explicitly considering root phenology in ecosystem processes and are crucial for all predictions that are only using remotely sensed data or other above-ground parameters as a measure for growing season length. While

further comparisons of above- and below-ground phenology are needed to justify generality for all arctic vegetation types, our study covered a broad gradient with plant species that are widely distributed both in the larger study area and on a circumpolar level. An explicit representation of root phenology is thus far missing from models commonly used to simulate ecosystem processes in arctic tundra even though fine roots are key elements of carbon, water and nutrient cycling, and terrestrial biosphere models are increasingly limited by incomplete descriptions of below-ground processes (McCormack *et al.*, 2013). Thus, our findings will help improving forecasts of carbon and nutrient fluxes with global climatic change if models no longer limit the duration of root production to the active above-ground growing season and explicitly consider the seasonality of root production, as well as empirical studies of root-mediated processes take the hidden below-ground growing season into account.

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Author contributions

S.D.W., G.B-W. and A.M. planned and designed the research. G.B-W. conducted fieldwork. G.B-W., A.M. and J.K. analysed the data. G.B-W. wrote the manuscript with contributions from all other authors.

References

- Abramoff RZ, Finzi AC. 2015. Are above- and below-ground phenology in sync? *New Phytologist* 205: 1054–1061.
- ACIA. 2004. *Impacts of a warming Arctic: Arctic climate impact assessment*. Cambridge, UK & New York, NY, USA: Cambridge University Press.
- Barichivich J, Briffa KR, Myneni RB, Osborn TJ, Melvin TM, Ciais P, Piao S, Tucker C. 2013. Large-scale variations in the vegetation growing season and annual cycle of atmospheric CO₂ at high northern latitudes from 1950 to 2011. *Global Change Biology* 19: 3167–3183.
- Bliss LC, Matveyeva NV. 1992. Circumpolar arctic vegetation. In: Chapin FS III, Jefferies RL, Reynolds JF, Shaver GR, Svoboda J, eds. *Arctic ecosystems in a changing climate. An ecophysiological perspective*. San Diego, CA, USA: Academic Press Inc., 59–90.
- Bokhorst S, Bjerke JW, Bowles FW, Melillo J, Callaghan TV, Phoenix GK. 2008. Impacts of extreme winter warming in the sub-Arctic: growing season responses of dwarf shrub heathland. *Global Change Biology* 14: 2603–2612.
- CAVM Team. 2003. *Circumpolar Arctic vegetation map. (1:7,500,000 scale), conservation of Arctic flora and fauna (CAFF) map no. 1*. Anchorage, AK, USA: US Fish and Wildlife Service.
- Clemmensen KE, Bahr A, Ovaskainen O, Dahlberg A, Ekblad A, Wallander H, Stenlid J, Finlay RD, Wardle DA, Lindahl BD. 2013. Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science* 339: 1615–1618.
- Du E, Fang J. 2014. Linking belowground and aboveground phenology in two boreal forests in Northeast China. *Oecologia* 176: 883–892.
- Edwards K, McCulloch J, Kershaw GP, Jefferies R. 2006. Soil microbial and nutrient dynamics in a wet Arctic sedge meadow in late winter and early spring. *Soil Biology and Biochemistry* 38: 2843–2851.
- Edwards KA, Jefferies RL. 2010. Nitrogen uptake by *Carex aquatilis* during the winter–spring transition in a low Arctic wet meadow. *Journal of Ecology* 98: 737–744.
- Ernakovich JG, Hopping KA, Berdanier AB, Simpson RT, Kachergis EJ, Steltzer H, Wallenstein MD. 2014. Predicted responses of arctic and alpine ecosystems to altered seasonality under climate change. *Global Change Biology* 20: 3256–3269.
- Fatichi S, Leuzinger S, Körner C. 2014. Moving beyond photosynthesis: from carbon source to sink-driven vegetation modeling. *New Phytologist* 201: 1086–1095.
- Gaudinski JB, Torn MS, Riley WJ, Dawson TE, Joslin JD, Majdi H. 2010. Measuring and modeling the spectrum of fine-root turnover times in three forests using isotopes, minirhizotrons, and the Radix model. *Global Biogeochemical Cycles* 24: 1–17.
- Högberg P, Read DJ. 2006. Towards a more plant physiological perspective on soil ecology. *TRENDS in Ecology and Evolution* 21: 548–554.
- Iversen CM, Sloan VL, Sullivan PF, Euskirchen ES, McGuire AD, Norby RJ, Walker AP, Warren JM, Wullschlegler SD. 2015. The unseen iceberg: plant roots in arctic tundra. *New Phytologist* 205: 34–58.
- Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* 108: 389–411.
- Johnson MG, Tingey DT, Phillips DL, Storm MJ. 2001. Advancing fine root research with minirhizotrons. *Environmental and Experimental Botany* 45: 263–289.
- Joslin JD, Wolfe MH, Hanson PJ. 2011. Factors controlling the timing of root elongation intensity in a mature upland oak stand. *Plant and Soil* 228: 201–212.
- Karlsen SR, Tolvanen A, Kubin E, Poikolainen J, Högda KA, Johansen B, Danks FS, Aspholm P, Wielgolaski FE, Makarova O. 2008. MODIS-NDVI-based mapping of the length of the growing season in northern Fennoscandia. *International Journal of Applied Earth Observation and Geoinformation* 10: 253–266.
- Keel SG, Campbell CD, Hogberg MN, Richter A, Wild B, Zhou X, Hurry V, Linder S, Nasholm T, Hogberg P. 2012. Allocation of carbon to fine root compounds and their residence times in a boreal forest depend on root size class and season. *New Phytologist* 194: 972–981.
- Keenan TF, Darby B, Felts E, Sonnentag O, Friedl MA, Hufkens K, O'Keefe J, Klosterman S, Munger JW, Toomey M *et al.* 2014. Tracking forest phenology and seasonal physiology using digital repeat photography: a critical assessment. *Ecological Applications* 24: 1478–1489.
- Körner C. 2007. The use of 'altitude' in ecological research. *TRENDS in Ecology and Evolution* 22: 569–574.
- Körner C, Basler D. 2010. Phenology under global warming. *Science* 327: 1461–1462.
- Legendre P. 2008. Studying beta diversity: ecological variation partitioning by multiple regression and canonical analysis. *Journal of Plant Ecology* 1: 3–8.
- Lindow SE, Arny DC, Upper CD. 1982. Bacterial ice nucleation: a factor in frost injury to plants. *Plant Physiology* 70: 1084–1089.
- Matamala R, Gonzalez-Meler MA, Jastrow JD, Norby RJ, Schlesinger WH. 2003. Impacts of fine root turnover on forest NPP and soil C sequestration potential. *Science* 302: 1385–1387.
- McCormack LM, Adams TS, Smithwick EAH, Eissenstat DM. 2014. Variability in root production, phenology, and turnover rate among 12 temperate tree species. *Ecology* 95: 2224–2235.
- McCormack LM, Eissenstat DM, Prasad AM, Smithwick EAH. 2013. Regional scale patterns of fine root lifespan and turnover under current and future climate. *Global Change Biology* 19: 1697–1708.
- McGuire AD, Anderson LG, Christensen TR, Dallimore S, Guo L, Hayes DJ, Heimann M, Lorenson TD, Macdonald RW, Roulet N. 2009. Sensitivity of the carbon cycle in the Arctic to climate change. *Ecological Monographs* 79: 523–555.

- Mokany K, Raison RJ, Prokushkin AS. 2006. Critical analysis of root: shoot ratios in terrestrial biomes. *Global Change Biology* 12: 84–96.
- Natali SM, Schuur EaG, Rubin RL. 2011. Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost. *Journal of Ecology* 100: 488–498.
- Norby RJ, Jackson RB. 2000. Root dynamics and global change: seeking an ecosystem perspective. *New Phytologist* 147: 3–12.
- Nord EA, Lynch JP. 2009. Plant phenology: a critical controller of soil resource acquisition. *Journal of Experimental Botany* 60: 1927–1937.
- Olsrud M, Christensen TR. 2004. Carbon cycling in subarctic tundra; seasonal variation in ecosystem partitioning based on *in situ* ¹⁴C pulse-labelling. *Soil Biology and Biochemistry* 36: 245–253.
- Palacio S, Montserrat-Martí G. 2007. Above and belowground phenology of four Mediterranean sub-shrubs. Preliminary results on root–shoot competition. *Journal of Arid Environments* 68: 522–533.
- Pau S, Wolkovich EM, Cook BI, Davies TJ, Kraft NJB, Bolmgren K, Betancourt JL, Cleland EE. 2011. Predicting phenology by integrating ecology, evolution and climate science. *Global Change Biology* 17: 3633–3643.
- Pendall E, Bridgman S, Hanson PJ, Hungate B, Kicklighter DW, Johnson DW, Law BE, Luo Y, Megegnal JP, Olsrud M *et al.* 2004. Below-ground process responses to elevated CO₂ and temperature: a discussion of observations, measurement methods, and models. *New Phytologist* 162: 311–322.
- Piao S, Ciais P, Friedlingstein P, Peylin P, Reichstein M, Lyssaert S, Margolis H, Fang J, Barr A, Chen A *et al.* 2008. Net carbon dioxide losses of northern ecosystems in response to autumn warming. *Nature* 451: 49–52.
- Post E, Forchhammer MC, Bret-Harte MS, Callaghan TV, Christensen TR, Elberling B, Fox AD, Gilg O, Hik DS, Høye TT *et al.* 2009. Ecological dynamics across the Arctic associated with recent climate change. *Science* 325: 1355–1358.
- Pregitzer KS, King JS, Burton AJ, Brown SE. 2000. Responses of tree fine roots to temperature. *New Phytologist* 147: 105–115.
- Richardson AD, Keenan TF, Migliavacca M, Ryu Y, Sonnentag O, Toomey M. 2013. Climate change, phenology, and phenological control of vegetation feedbacks to the climate system. *Agricultural and Forest Meteorology* 169: 156–173.
- Schimel JP, Bilbrough C, Welker JM. 2004. Increased snow depth affects microbial activity and nitrogen mineralization in two Arctic tundra communities. *Soil Biology and Biochemistry* 36: 217–227.
- Schmidt MW, Torn MS, Abiven S, Dittmar T, Guggenberger G, Janssens IA, Kleber M, Kogel-Knabner I, Lehmann J, Manning DA *et al.* 2011. Persistence of soil organic matter as an ecosystem property. *Nature* 478: 49–56.
- Shaver GR, Billings WD. 1975. Root production and root turnover in a wet tundra ecosystem, Barrow, Alaska. *Ecology* 56: 401–409.
- Shaver GR, Billings WD. 1977. Effects of daylength and temperature on root elongation in tundra graminoids. *Oecologia* 28: 57–65.
- Sloan VL, Fletcher BJ, Press MC, Williams M, Phoenix GK. 2013. Leaf and fine root carbon stocks and turnover are coupled across Arctic ecosystems. *Global Change Biology* 19: 3668–3676.
- Smithwick EAH, Lucash MS, McCormack ML, Sivandran G. 2014. Improving the representation of roots in terrestrial models. *Ecological Modelling* 291: 193–204.
- Steinaker DF, Wilson SD. 2008. Phenology of fine roots and leaves in forest and grassland. *Journal of Ecology* 96: 1222–1229.
- Steinaker DF, Wilson SD, Peltzer DA. 2010. Asynchronicity in root and shoot phenology in grasses and woody plants. *Global Change Biology* 16: 2241–2251.
- Sullivan PF, Welker JM. 2005. Warming chambers stimulate early season growth of an arctic sedge: results of a minirhizotron field study. *Oecologia* 142: 616–626.
- Tierney GL, Fahey TJ, Groffman PM, Hardy JP, Fitzhugh RD, Driscoll CT, Yavitt JB. 2003. Environmental control of fine root dynamics in a northern hardwood forest. *Global Change Biology* 9: 670–679.
- Toomey M, Ma Friedl, Frolking S, Hufkens K, Klosterman S, Sonnentag O, Baldocchi DD, Bernacchi CJ, Biraud SC, Richardson AD. 2015. Greenness indices from digital cameras predict the timing and seasonal dynamics of canopy-scale photosynthesis. *Ecological Applications* 25: 99–115.
- Vargas R, Trumbore SE, Allen MF. 2009. Evidence of old carbon used to grow new fine roots in a tropical forest. *New Phytologist* 182: 710–718.
- Warren JM, Hanson PJ, Iversen CM, Kumar J, Walker AP, Wullschlegel SD. 2014. Root structural and functional dynamics in terrestrial biosphere models – evaluation and recommendations. *New Phytologist* 205: 59–78.
- Weintraub MN, Schimel JP. 2005. The seasonal dynamics of amino acids and other nutrients in Alaskan Arctic tundra soils. *Biogeochemistry* 73: 359–380.
- Withington JM, Elkin AD, Bułaj B, Olesiński J, Tracy KN, Bouma TJ, Oleksyn J, Anderson LJ, Modrzyński J, Reich PB *et al.* 2003. The impact of material used for minirhizotron tubes for root research. *New Phytologist* 160: 533–544.
- Wolkovich EM, Cook BI, Allen JM, Crimmins TM, Betancourt JL, Travers SE, Pau S, Regetz J, Davies TJ, Kraft NJ *et al.* 2012. Warming experiments underpredict plant phenological responses to climate change. *Nature* 485: 494–497.
- Wookey PA, Aerts R, Bardgett RD, Baptist F, Bräthen KA, Cornelissen JHC, Gough L, Hartley IP, Hopkins DW, Lavorel S *et al.* 2009. Ecosystem feedbacks and cascade processes: understanding their role in the responses of Arctic and alpine ecosystems to environmental change. *Global Change Biology* 15: 1153–1172.
- Xu L, Myneni RB, Chapin FS III, Callaghan TV, Pinzon JE, Tucker CJ, Zhu Z, Bi J, Ciais P, Tømmervik H *et al.* 2013. Temperature and vegetation seasonality diminishment over northern lands. *Nature Climate Change* 3: 581–586.