Contrasting synchrony in root and leaf phenology across multiple sub-Arctic plant communities

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Summary

1. Roots account for > 50% of net primary production in many ecosystems and are widely accepted as playing a fundamental role in ecosystem carbon and nutrient cycling. Despite this, the timing and controls of root production and the relationships between root and leaf phenology are still poorly understood in many plant communities, making it challenging to elucidate broad scale patterns and to predict ecosystem responses to a changing climate. Here, we investigate and compare the extent of synchrony of community-level fine root and leaf production in 10 widespread sub-Arctic plant communities, including deciduous forest, evergreen shrub, deciduous shrub and sedge-dominated communities.

2. We show that across contrasting plant communities, timing of leaf production does not vary substantially, but there are considerable differences in timing of root production between woody plant- and sedge-dominated vegetation. In sedge communities, root production occurs early in the growing season, soon after the peak of leaf production, whereas in woody plant communities, leaf and root production are highly asynchronous, with the majority of root production occurring late in the growing season.

3. Seasonal dynamics of root growth were not consistently correlated with soil temperature, suggesting that differences in timing of production relate to inherent differences between plant functional types. This raises important questions as to the drivers of root production, the functional reasons underlying these contrasting plant strategies, as well as the consequences for microbial communities and nutrient cycling of such contrasting timing of carbon inputs to soil.

4. *Synthesis.* We demonstrate that major differences exist in the synchrony of temporal dynamics of leaf and root production between woody plant and sedge-dominated sub-Arctic vegetation. The substantially greater asynchrony in root and leaf production in woody plants compared with sedges suggests that vegetation change associated with climate warming will result in significant shifts in timing of carbon fluxes to soil, and highlights the need for separate leaf and root components in ecosystem carbon and nutrient cycle models.

Key-words: asynchrony, carbon allocation, leaf phenology, plant–soil (below-ground) interactions, root phenology, seasonal dynamics, sub-Arctic

Introduction

Root production frequently accounts for > 50% of net primary production. Thus there is growing recognition that to improve overall understanding of ecosystem carbon and nutrient cycling, more focus is needed on understanding the timing and control of root growth, and the relationships between root growth and leaf growth (Jackson, Mooney & Schulze 1997; Pregitzer *et al.* 2000; McCormack *et al.* 2014). Synchronous measurements of root and leaf growth are essential for understanding the seasonal dynamics of carbon allocation within plants, and therefore whole plant responses to their environment and plant competition (Farrar & Jones 2000; Steinaker, Wilson & Peltzer 2010; Poorter *et al.* 2012). Root growth dynamics, which are less well characterized than shoot dynamics for most ecosystems, determine the capacity of plants to take up ephemeral soil nutrient and water resources, and thus are also a key element of understanding and predicting ecosystem functional responses to a changing climate (Sullivan *et al.* 2008).

At the broad scale, root and shoot growth are generally asynchronous, with peak root growth occurring before peak shoot growth in the sub-tropical biome, but lagging behind in Mediterranean, temperate and boreal biomes (Abramoff &

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Finzi 2015). Simultaneous measurements of root and shoot phenology remain scarce, however, and few studies have been undertaken north of the boreal forest (Iversen *et al.* 2015). Northern high-latitude ecosystems contain globally significant stores of soil carbon and are already experiencing climate warming, with average temperatures predicted to increase by more than 6 °C by 2100 (Tarnocai *et al.* 2009; Bekryaev, Polyakov & Alexeev 2010; Sanderson, Hemming & Betts 2011). Critically, these regions have below:above-ground biomass ratios of > 6:1, amongst the highest worldwide, so understanding root dynamics is especially important (Jackson, Mooney & Schulze 1997; Mokany, Raison & Prokushkin 2006; Iversen *et al.* 2015). Although there has been an increasing focus on below-ground research in recent years (e.g. Sullivan & Welker 2005; Deslippe & Simard 2011), understanding of root growth dynamics in high-latitude systems remains limited in comparison with extensive knowledge of shoot growth (e.g. Shaver & Kummerow 1992). Further, many current models predicting the effects of global change on Arctic and sub-Arctic ecosystem carbon and nutrient cycling use leaf growth dynamics as a proxy for root growth dynamics, and thus empirical data are urgently required from this region to inform modelling and provide data for model parameterizations (Abramoff & Finzi 2015; Iversen *et al.* 2015).

The Arctic and sub-Arctic regions comprise highly spatially heterogeneous vegetation, with plant communities dominated by contrasting plant functional types changing over scales of tens of metres (Wookey *et al.* 2009; Fletcher *et al.* 2012). Across biomes, no significant differences in asynchrony between root and leaf growth were observed between herbaceous, shrub and tree growth forms (Abramoff & Finzi 2015), but at finer scales, substantial variation in the coupling of root and leaf phenology has been observed between plant communities and between species experiencing similar environmental conditions (Steinaker & Wilson 2008; Steinaker, Wilson & Peltzer 2010; McCormack *et al.* 2014). Further, investigation of such differences in synchrony of root and leaf growth for the plant communities of the Arctic and sub-Arctic is essential to predict the impacts of vegetation change such as the widespread increase in shrub abundance (Sturm, Racine & Tape 2001; Myers-Smith *et al.* 2011) on ecosystem carbon and nutrient cycling.

Based on observations of boreal systems, Steinaker & Wilson (2008) hypothesized that contrasting vegetation types may occur along a continuum from complete synchrony between leaf and root production to complete temporal separation. A closer coupling is predicted in short stature vegetation with a large below-ground component, such as grass and sedge-dominated communities, than in taller vegetation with a large above-ground component. In shorter vegetation, leaf production may be delayed relative to leaf production in tall vegetation, as low soil temperatures limit translocation of nutrients and carbohydrates from below-ground stores in tussock crowns or rhizomes (e.g. Chapin, Johnson & McKendrick 1980), and thus leaf and root production occur synchronously later in the growing season. In contrast, in

trees and shrubs, reserves located in above-ground woody tissue (Sprugel 2002) can enable rapid leaf production response to rising air temperatures and the onset of leaf production before root production. This hypothesis held true in a field and common garden study (Steinaker & Wilson 2008; Steinaker, Wilson & Peltzer 2010), but as some Arctic and sub-Arctic sedge species have early leaf growth and maximal root extension at low temperatures (Bliss 1956; Shaver & Billings 1975, 1977), northern high-latitude ecosystems present an ideal opportunity to test its broader applicability to predict plant functional type differences at local scales.

Additionally, understanding the drivers of root production across multiple ecosystems is essential for understanding overall plant strategies (Kikuzawa *et al.* 1996; Jackson *et al.* 2001). Environmental factors such as soil temperature and soil moisture explain dynamics of root production well in some forest species (for example, Teskey & Hinckley 1981; Burke & Raynal 1994), but not in others (Hendrick & Pregitzer 1996; Joslin, Wolfe & Hanson 2001), whereas availability of recent photosynthate from above-ground is also important (Fitter *et al.* 1999; Farrar & Jones 2000). In Arctic sedge species, root production and temperature were either negatively or not correlated (Shaver & Billings 1977), but similar investigations of woody plant species are lacking.

In this study, we use simultaneous measurements of root and leaf production, air temperature and soil temperature from 10 plant communities in two sub-Arctic regions to investigate the synchrony of root and leaf production in sedge- and woody plant-dominated vegetation, and to determine relationships between production dynamics and soil temperature.

We hypothesized that (i) root and leaf growth are more synchronous in sedge-dominated communities than in woody plant-dominated communities, (ii) fine root production is strongly correlated with soil temperature in woody plant communities, but not in sedge-dominated communities and (iii) despite contrasts in synchrony between vegetation types, common patterns observed within functional types will allow estimates of below-ground dynamics from above-ground observations to be made at the functional type level.

Materials and methods

FIELD SITES AND VEGETATION COMMUNITIES

The study was conducted at two sites in the Scandinavian sub-Arctic region. The first site was located in the Petsikko area, 20 km south of the Kevo Sub-Arctic Research Institute (69°45′N, 27°01′E), Finland ('Kevo'). The annual average temperature here is −2 °C, average July temperature is 13 °C and annual precipitation is 263–597 mm (Kevo Research Station weather data; http://www.kevo.utu.fi/turkimus/saa). The site covered an area of approximately 1 km^2 and comprised a transition through multiple plant communities (detailed below) from wetland to mountain birch forest. Soils ranged from permanently waterlogged to well-drained beneath the forest.

The second site was situated approximately 3 km south of the Abisko Scientific Research Station (68°35′N, 18°82′E) in Sweden ('Abisko'). Annual average temperature at the Abisko Scientific Research Station is −1 °C, average July temperature is 11 °C, and

annual precipitation 225–475 mm (ANS weather data; http://polar.se/en/abisko-naturvetenskapliga-station/vaderdata/). This site covered approximately 4 km² and was located on a slight north-facing slope, encompassing the landscape-scale transition from mountain birch forest at an altitude of ~530 m to shrub tundra at ~720 m. Soils were shallow (generally < 0.4 m) and well-drained throughout. Both sites lacked permafrost, though ice-wedges were present within hummocks on the margins of the wetland at Kevo.

Five vegetation communities were selected at each site, representing the most common vegetation communities present in the sub-Arctic landscape and encompassing a range of plant functional types (Table S1 in Supporting Information). At Kevo, these communities consisted of: (i) deciduous forest dominated by mountain birch (*Betula pubescens* Ehrh.) with evergreen shrubs directly beneath the trees (referred to as "Kevo Forest – *B. pubescens*"); (ii) sparse heath vegetation on relatively flat ground close to the birch forest margin, dominated by dwarf evergreen shrubs ('Kevo Forest margin – *Vaccinium vitis-idaea/Empetrum nigrum* heath'); (iii) dense shrub vegetation dominated by the evergreens *Ledum palustre* L. and *E. nigrum* L. on the upper parts of hummocks around the margins of the wetland ('Kevo Wetland margin – mixed shrubs'); (iv) abundant *Eriophorum angustifolium* Honck. (sedge) in permanent pools ('Kevo Wetland – *E. angustifolium* lawns') and (v) *Carex rostrata* Stokes (sedge) dominated lawns on the fringes of open water ('Kevo Wetland – *C. rostrata* lawns').

At Abisko, the five communities comprised: (i) deciduous forest dominated by mountain birch with a largely evergreen dwarf shrub understorey ('Abisko Forest – *B. pubescens*'); (ii) heath vegetation dominated by the deciduous shrub *Betula nana* L. over an evergreen understorey of *E. nigrum* and *V. vitis-idaea* L., adjacent to the mountain birch forest and approximately 10–15 m from the nearest trees ('Abisko Forest margin – mixed shrubs'); (iii) exposed heath with almost continuous cover of the evergreen dwarf shrub *E. nigrum* at 720 m a.s.l. ('Abisko Exposed ridge – *E. nigrum* heath'); (iv) shrub vegetation dominated by taller *B. nana* with a understorey of ericaceous shrubs ('Abisko Moderately sheltered plateau – tall *B. nana*') and (v) tall (c. 1 m) deciduous shrub vegetation dominated by a mixture of *Salix* L. species and with a ground layer of forbs and grasses ('Abisko Snowbed – tall *Salix*').

SEASONAL DYNAMICS OF LEAF PRODUCTION

The seasonal dynamics of production were measured in eight replicate 1 m × 1 m plots established in separate patches in each of the 10 vegetation communities (80 plots in total).

Above-ground measurements were made at the species-level for the dominant species in each community (Table S1). In shrub species, six shoots per plot were tagged with numbered cable ties at the start of the field season (late May: 2008 in Kevo and 2009 in Abisko). In dwarf birch (*B. nana*), which has long/short shoot dimorphism (Bret-Harte, Shaver & Chapin 2002), twelve shoots, six long and six short were tagged per plot. In the two mountain birch forest communities, branches were also tagged on 50 separate trees surrounding the study plots, including both long and short shoots as for *B. nana*, and in sedges, six tillers were tagged. Bud burst in shrub and tree species was recorded on all tagged shoots at weekly intervals using a qualitative scale (1 = first signs of bud swelling, 2 = bud cracked and 3 = first leaf fully expanded; Phoenix *et al.* 2001). Following bud burst, extension of all tagged shoots was measured using digital callipers, measuring from the shoot tip back to the bud scar. In sedges, the length of the green portion of all individual leaves was recorded

(*sensu* Sullivan & Welker 2005). Measurements were taken at approximately weekly intervals until no further extension was recorded (late July–early August).

To determine the relationships between recorded shoot length (shrubs and trees) or leaf length (sedges), and leaf area, 30 shoots or tillers of each species were harvested from each plot type (close to the plots but not within them) at six occasions during the growing season. On harvested shoots, leaf area was measured using a flatbed scanner (G3010, Hewlett Packard) and digital image analysis software (SigmaScan Pro 5) in Kevo, and using a leaf area meter (Delta-T digital image analysis system, Delta T, Burkwell, UK) in Abisko. The two methods were cross-calibrated using 30 samples of each species. These relationships were used to convert bud-burst and shoot extension measurements to species level seasonal leaf area dynamics.

Species-level measurements were combined to the plot level by weighting according to aerial per cent coverage estimates of species abundance at peak season (early August). Estimates were made by placing a 0.75 × 0.75 m quadrat over the minirhizotron (described below) and recording cover of all species to the nearest 5%. Evergreen species values were adjusted to reflect proportions of current year's leaves determined from the concurrent shoot harvest, in which current and previous years shoot increments were processed separately. For low abundance species on which no growth measurements were made, the seasonal growth dynamics of species of the same functional type were assigned. This had little influence on the plot level values due to the small weighting of these species by leaf area.

Plot-level values were converted to percentage leaf area production in each measurement interval. This measure enables direct comparison between dynamics of leaf area and root length production, and between communities differing widely in total leaf area (Steinaker & Wilson 2008). Values were then divided by number of days in the interval to standardize for differences in interval length.

SEASONAL DYNAMICS OF FINE ROOT PRODUCTION

Seasonal dynamics of fine root production were determined using the minirhizotron technique (Johnson *et al.* 2001). Minirhizotrons consisted of 0.3–0.7 m lengths of 70 mm diameter clear acrylic tubing with a plastic cap sealed over the lower end. These were installed at 45° into the soil surface directly adjacent to the plots in which leaf production measurements were made. The minirhizotrons were not installed within the plots because of the potential for disturbance to the tubes during above-ground measurements and *vice versa*. Sections of tube protruding above-ground were wrapped in a layer of black tape to exclude light and a layer of white tape to reduce absorption of heat. A white plastic cap was placed over the end to exclude precipitation and removable lengths of foam were inserted to insulate the minirhizotrons (these were only removed when root scans were being taken). At Abisko, minirhizotrons were installed in autumn 2006 and at Kevo in spring 2007. Root images at the Abisko sites were taken two growing seasons after installation and at the Kevo sites one growing season after installation. It is considered that the difference in bedding-in time may have influenced total production values (only relative production is considered here), but measurements at lower temporal resolution in 2008 in Abisko and 2009 at Kevo suggest that seasonal dynamics were captured well. All minirhizotron tubes were colonized by substantial numbers of roots at the start of measurements.

A full scan of each minirhizotron tube (between two and eight images per tube, image size 19.55 cm × 21.57 cm, resolution 300

dpi) was taken at approximately 10-day intervals throughout the growing season using a CID-600 root scanner (CID Bioscience, Camas, WA, USA). At Kevo, there were a total of 11 scanning dates during the period 3 June–3 September 2008 and at Abisko, 14 scanning dates 25 May–18 September 2009.

A complete image for each date was compiled in ADOBE PHOTOSHOP CS2 (Adobe Systems Inc., San Jose, CA, USA), and then registered in MAPINFO PROFESSIONAL v. 8.0 (Pitney Bowes Business Insight, New York, NY, USA). All visible roots were digitized manually, with the corresponding image from the preceding scan date displayed on an adjacent monitor for comparison. Root length was computed, the digitized image stored and then overlaid onto the following image for new root growth to be added. The first scans from the growing season were checked against scans from the end of the preceding growing season to verify that the initial image was taken prior to the start of current season root growth. Verification of the procedure was carried out by repeating the analysis for a subset of images and variation in fine root length production was found to be low (< 2% of total length recorded). The length values were then converted to percentages of annual total root length per interval and divided by the number of days in each interval.

AIR AND SOIL TEMPERATURE

Air temperature at 2 m height was recorded at half-hourly intervals using HMP45 sensors (Vaisala, Helsinki, Finland) located on a total of four eddy covariance towers in close proximity to the measured plots.

Soil temperature at 5 cm depth was logged at 30-min intervals using one data logger per community (TinyTag and TinyTag Plus, Gemini Data Loggers (UK) Ltd, Chichester, UK) in all communities except the two wetland communities at Kevo, where the instability of the ground surface and changing water levels meant it was not possible to place available logging equipment directly in the study communities. Soil temperature at the soil surface and 5, 10, 15 and 20 cm depth was also measured close to midday on each root scanning date in every plot using a Testo temperature probe (Testo Ltd, Alton, UK), and confirmed that wetland soil temperatures were similar to those of adjacent hummock and forest plots.

STATISTICAL ANALYSES

The temporal differences between leaf and root production was estimated as the difference between the highest peaks in production rate. To test for differences in duration of root and leaf production within the different vegetation communities, the number of days in which 90% of production occurred (from 5 to 95% of total production) was estimated for each plot (DL$_{90}$ = duration of 90% of leaf production and DR$_{90}$ = duration of 90% of fine root production). This measure was chosen in preference to total time period in which production was greater than zero to better reflect the main period of leaf or root growth (Steinaker & Wilson 2008; Steinaker, Wilson & Peltzer 2010). Durations of production amongst communities were compared using one-way ANOVA, and durations of root and leaf production within communities were compared using paired t-tests. Soil temperatures between communities were compared using repeated measures ANOVA. Air temperature and soil temperature data were averaged over each production measurement interval and compared with leaf and root production rates using Pearson's product moment correlations. All statistical analyses were carried out using R (R 2.8.1, R Development Core Team, Vienna, Austria).

Results

SEASONAL DYNAMICS OF LEAF AND FINE ROOT PRODUCTION

Leaf area production in all eight woody plant communities occurred early in the growing season, with rates rising sharply to maxima in late June–early July, before declining steeply and ceasing in mid-August (Fig. 1a–c, f–j). In four communities at Abisko, a small peak in rates of leaf area production also occurred at the start in the growing season in late May (Fig. 1g–j). At the species level, leaf area production occurred as a single peak, except for *B. nana*, which showed an early season peak as short-shoot leaves expanded rapidly. Short-shoot leaf expansion did not result in a separate peak in *B. pubescens*, due to more gradual leaf expansion into the main production period. Overall, leaf area production began and peaked approximately 2 weeks earlier in the deciduous shrub species (*Salix* spp., *B. nana, V. uliginosum*) than in the evergreens species, but there was also within-group variation, with *E. nigrum* commencing new growth earlier than *L. palustre* and *V. vitis-idaea* (data not shown).

In the two sedge-dominated communities, rises in leaf production rates occurred at a similar time to woody plant communities, but remained high for a longer period (mid- to late-July; Fig. 1d–e). The two sedge species studied showed similar leaf area production dynamics, with a broader peak commencing in early June, and gradual decline of leaf area production. Leaf senescence was not formally quantified, but was observed at both sites from mid-August, with little green leaf area in all species besides evergreen shrubs remaining by the second week of September.

In all woody plant communities, fine root and leaf area production were strongly asynchronous. At Kevo, fine root production in shrub and forest communities increased sharply in mid-July, as rates of leaf production declined, and continued to rise to a peak in late August, near to the end of the sub-Arctic growing season (Fig. 1a–c). Overall, the duration of leaf area production was approximately 8 weeks, similar to that of fine root production (Table 1: comparison including all three communities, DR$_{90}$ = 50 days, DL$_{90}$ = 47 days, paired t-test, $P = 0.47$), but the peak rates were separated by approximately 7 weeks, almost half of the total 2008 growing season. In similar woody plant communities at Abisko, fine root production rates increased slowly during the period of leaf area production and were again highest between mid-July and mid-August (Fig. 1f–j). Root production in woody plant communities declined throughout late August and early September but had not ceased entirely during the final scanning interval (10–18 September), such that the duration of root production significantly exceeded the duration of leaf production (Table 1: comparison including all five communities DR$_{90}$ = 69 days > DL$_{90}$ = 50 days, $P < 0.001$).

In contrast to woody plant communities, in sedge-dominated vegetation root and leaf production were closely coupled early in the growing season. Fine root production in the *E. angustifolium* lawn community increased sharply only 1 week later
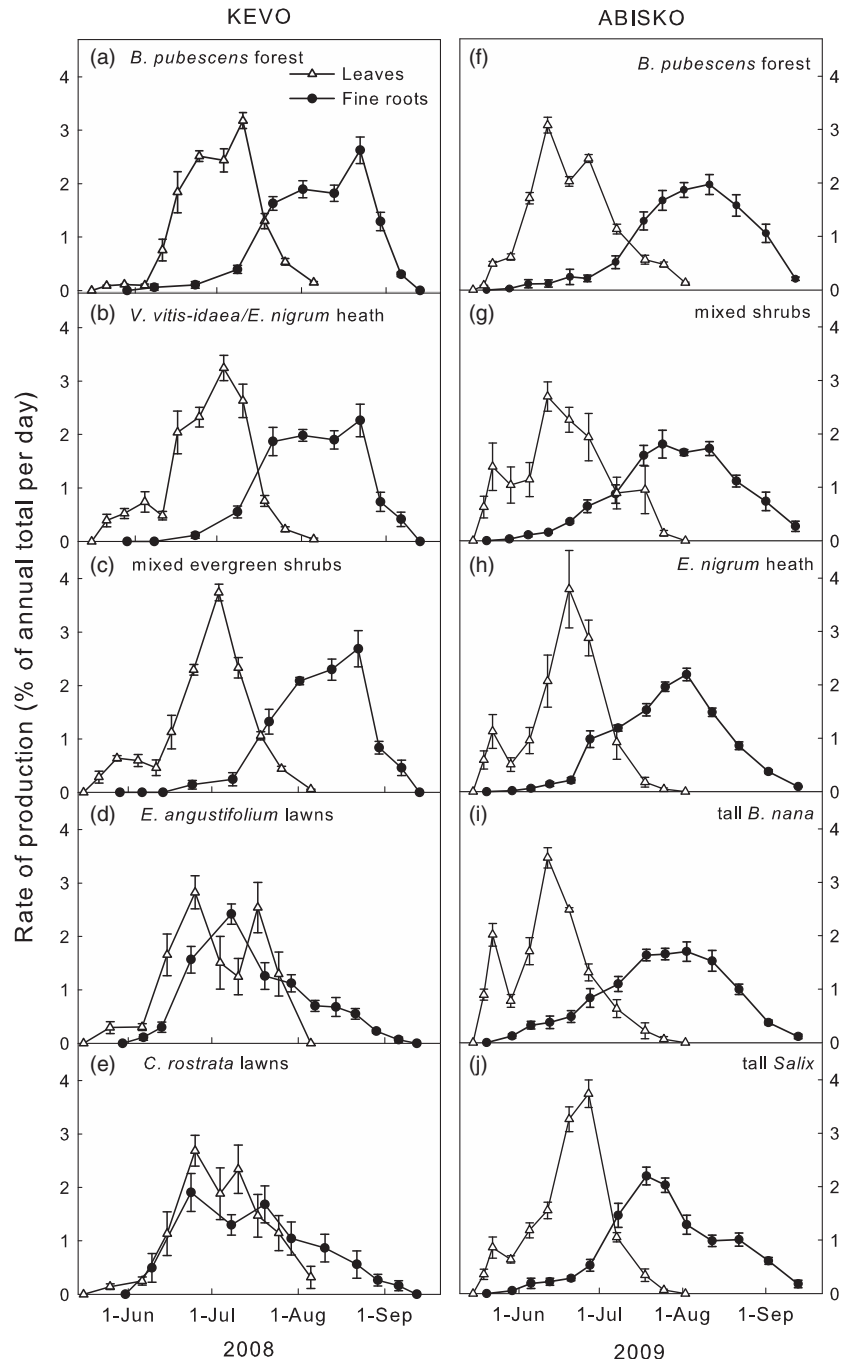
Fig. 1. Mean (±1 SE) rates of leaf and fine root production in ten sub-Arctic plant communities ($n = 8$) in Kevo, Finland, and Abisko, Sweden.

than the increase in leaf area production (Fig. 1d), whereas in the *C. rostrata* lawn community, the rise in root and leaf production rates occurred simultaneously. In both communities, rates of root production peaked in early July, remained high for between 2 and 3 weeks and then declined steadily until early September (Fig. 1d–e). In both sedge communities, the majority of root production prior to late August consisted of extension of existing roots, while in late August and early September new roots were initiated at the top of the soil profile. This late season root production resulted in the duration of fine root production exceeding the duration of leaf area production, though this was only statistically significant at the 10% level ($DR_{90} = 69$ days > $DL_{90} = 50$ $P < 0.1$; Table 1).

PRODUCTION DYNAMICS AND TEMPERATURE

Leaf area production and growing season air and soil temperatures were significantly correlated only in the two wetland communities at Kevo (Table 2). In woody plant communities, leaf area production was initially concurrent with rising soil temperatures in Kevo, but declined despite continued warm temperatures (Fig. 2a,c), whereas in Abisko, leaf area production rates peaked and then declined as soil temperature continued to rise (Fig. 2b).

In woody plant communities, correlations between both soil and air temperature and fine root production varied between sites. Soil temperatures at Kevo in 2008 peaked early in the growing season, when root production rates remained low

Table 1. Mean (n = 8) duration (days) of 90% of total leaf (DL) and fine root (DR) production in ten arctic plant communities during 2008 (Kevo, Finland) and 2009 (Abisko, Sweden). Differences between duration of leaf and root production were determined by paired t-test for each community

Site	Habitat	Plant community	DL$_{(90)}$ Days ($\pm$SE)	DR$_{(90)}$ Days ($\pm$SE)	Comparison DL$_{(90)}$ DR$_{(90)}$
Kevo	Forest	*Betula pubescens*	41 (1)	52 (4)	*
	Forest margin	*Vaccinium vitis-idaea/Empetrum nigrum* heath	49 (2)	52 (2)	ns
	Wetland margin	Mixed evergreen shrubs	52 (1)	49 (3)	ns
	Wetland	*Eriophorum angustifolium* lawns	50 (5)	61 (4)	(*)
	Wetland	*Carex rostrata* lawns	49 (5)	63 (5)	(*)
Abisko	Forest	*B. pubescens*	53 (1)	63 (5)	(*)
	Forest margin	Mixed shrubs	51 (2)	70 (2)	***
	Exposed ridge	*E. nigrum* heath	45 (3)	64 (3)	**
	Moderately sheltered plateau	Tall *Betula nana*	49 (2)	74 (1)	**
	Snowbed	Tall *Salix*	50 (1)	72 (1)	**

ns, not significant.
(*)$P < 0.1$, *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

Table 2. Correlations (Pearson's product-moment) between mean (n = 8) plant leaf and root production, and air and soil temperatures in ten arctic plant communities during the growing season (defined as production of relevant component > 0). Air and soil temperatures are averages of half-hourly temperature logs during the production interval. Leaf and root production data were log-transformed prior to analysis

Site	Habitat	Plant community	Air temperature Leaves	Air temperature Roots	Soil temperature Leaves	Soil temperature Roots
Kevo	Forest	*Betula pubescens*	+0.64*	+0.30 (ns)	+0.51 (ns)	+0.24 (ns)
	Forest margin	*Vaccinium vitis-idaea/Empetrum nigrum* heath	+0.31 (ns)	+0.10 (ns)	+0.04 (ns)	+0.23 (ns)
	Wetland margin	Mixed evergreen shrubs	+0.47 (ns)	−0.05 (ns)	+0.29 (ns)	+0.32 (ns)
	Wetland	*Eriophorum angustifolium* lawns	+0.78*	+0.85***	+0.67*	+0.81***
	Wetland	*Carex rostrata* lawns	+0.83*	+0.83**	+0.75*	+0.83**
Abisko	Forest	*B. pubescens*	−0.12 (ns)	+0.97***	+0.17 (ns)	+0.81***
	Forest margin	Mixed shrubs	−0.50 (ns)	+0.86***	−0.44 (ns)	+0.91***
	Exposed ridge	*E. nigrum* heath	−0.46 (ns)	+0.80**	−0.42 (ns)	+0.93***
	Moderately sheltered plateau	Tall *Betula nana*	−0.69 (ns)	+0.91***	−0.54 (ns)	+0.96***
	Snowbed	Tall *Salix*	−0.43 (ns)	+0.93***	−0.08 (ns)	+0.96***

ns, not significant.
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$.

(Fig. 2a), but at Abisko in 2009, soil temperature rose gradually and root production rates were significantly correlated with soil temperature in all five communities (Table 2; Fig. 2b). In sedge communities, the rise in soil temperature coincided with maximum rates of root production, leading to strong correlations (Fig. 2c; Table 2).

Discussion

Here, we present the findings of the first study to investigate synchrony of root and leaf production across a diverse range of sub-Arctic plant communities. Our results showed a fundamental difference between woody plant communities and sedge-dominated communities in seasonal root dynamics, but smaller differences in seasonal leaf dynamics. Consequently, the degree of synchrony of leaf and root production varied according to the dominant plant functional type, with root and leaf production more closely coupled in sedge communities, suggesting interspecific differences in dynamic allocation strategies used by plants in response to the sub-Arctic environment.

SEASONAL DYNAMICS OF LEAF AND ROOT PRODUCTION

In this study, maximal rates of leaf area production occurred in all plant communities during June and July, consistent with observations in similar sub-Arctic vegetation (e.g. Campioli *et al.* 2009). The presence of the deciduous shrub *B. nana*, which elsewhere has been observed to dominate tussock tundra plant communities following simulated climate warming (van Wijk *et al.* 2004), resulted in a bi-modal pattern of leaf area production at the community level, whereas the majority of woody species showed a single sharp production peak. Sedge leaf growth in both studied species occurred in a broader peak, consistent with the sequential leaf growth pattern of Arctic sedges (Jonasson & Chapin 1985). Overall, the minor differences in timing of leaf production which occurred between woody plant communities were accounted for by both interspecific differences in leaf dynamics and by differences in micro-climate which influenced the timing of budburst and leaf out of all species (Murray & Miller 1982; Kummerow *et al.* 1983). Such interspecific differences in
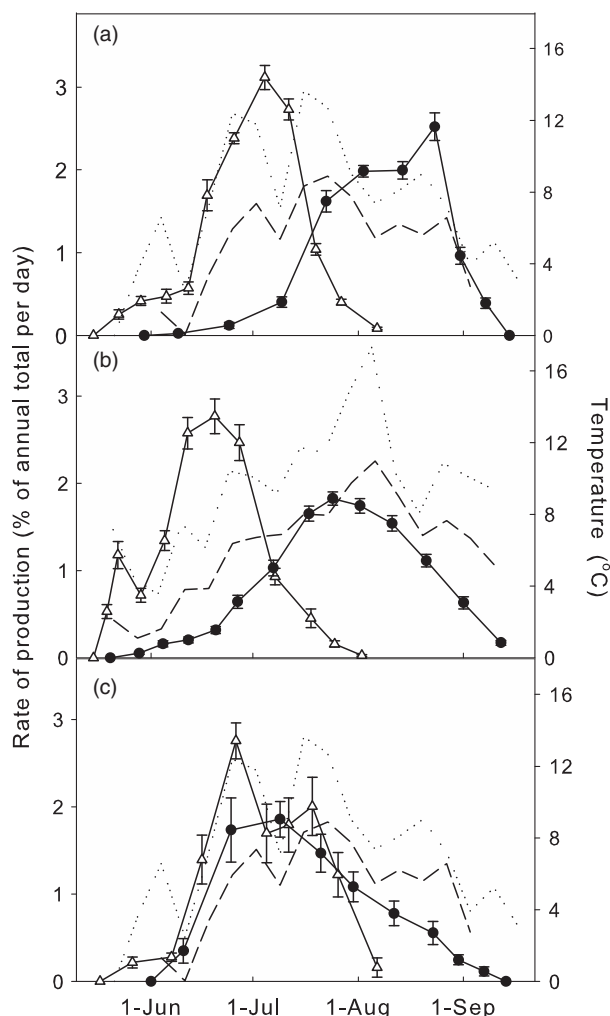
Fig. 2. Mean rates of leaf production (open triangles), fine root production (filled circles) and air temperature (dotted line), soil temperature (dashed line) in (a) woody plant communities at Kevo in 2008 ($n = 24$) (b) woody plant communities at Abisko in 2009 ($n = 40$) and (c) sedge-dominated communities ($n = 16$) at Kevo in 2008.

above-ground production dynamics are similar to the spread of patterns observed below-ground (e.g. Lyr & Hoffman 1967; McCormack *et al.* 2014), suggesting similar above- and below-ground variability in strategies for acquisition of temporally variable resources.

In sedge communities, root production was highest early in the growing season, during the period of high leaf production, and continued through above-ground production declines into leaf senescence, consistent with previous studies of arctic graminoid species and communities (Shaver & Billings 1975, 1977; Kummerow & Russell 1980; Sullivan & Welker 2005). The early growth of roots before leaves are fully expanded in these sedge communities requires carbon to be translocated from stored reserves in rhizomes to new root growth, as in the Arctic sedge *E. vaginatum* (Chapin, Johnson & McKendrick 1980). Further, late season root growth when carbon uptake is low requires either re-translocation of carbon from senescing leaves, or when leaves have fully senesced, utilization of stored carbon reserves. Since soil temperatures remain

high, this late season allocation may allow for efficient replenishment of nutrient (nitrogen and phosphorus) reserves depleted during the growing season (Chapin, Johnson & McKendrick 1980; Chapin & Shaver 1989). The observed late-season sedge root growth in both *E. angustifolium* and *C. rostrata* was a combination of new root initiation close to the soil surface and extension of existing roots deep in the soil profile. The allocation to new roots late-season (which then over-winter) may also facilitate early season nutrient uptake and early root elongation at the thaw front where nutrient availability in recently thawed soil may be high (Weintraub & Schimel 2005; Edwards & Jefferies 2013).

In woody plant communities, we observed limited root growth early in the growing season, although root tips from previous years (which extended later in the season) were observable, suggesting that this was not a temporal effect of slow tube colonization by new roots. This is in contrast with the study of Kummerow *et al.* (1983), which demonstrated new root growth occurring more than 10 days before bud-burst in the evergreen arctic shrubs *L. palustre* and *C. calyculata*. Such differences may result from differences between direct growth observations using minirhizotrons and the more subjective classification of live/dead root tips. Substantial inter-annual variations, as demonstrated in some temperate tree species (McCormack *et al.* 2014), may also occur in sub-Arctic woody plant species and communities. Nonetheless, the consistency of our observations across communities and locations suggests considerable confidence in our findings.

In sedge tundra communities, root production occurred substantially earlier than in adjacent woody plant communities with similar soil temperature regimes. One possible explanation for this functional type difference is that differences in root longevity may be important in determining intra-annual timing of root production. Although root longevity of arctic plant species is not widely known, arctic sedges such as *E. angustifolium* and *E. vaginatum* have annual or near-annual root systems (Shaver & Billings 1977; Sullivan & Welker 2005), whereas shrubs such as *B. nana* have a longer-lived network of fine roots (Sullivan *et al.* 2007). If root systems of sedges are short-lived, growth early in the season may be essential to maximize return on investment and provide nutrients to sustain leaf growth, whereas in woody plants, existing root systems would supply this demand and resources could be allocated to maximize above-ground growth. The lack of a spring flush of root production in arctic woody plants (Kummerow *et al.* 1983; Burke & Raynal 1994; Steinaker, Wilson & Peltzer 2010) suggests either that low soil temperatures early in the growing season limit root production in these ecosystems, or that the early expansion of leaves is of greater overall advantage.

The differences in seasonal dynamics of root production between sedges and woody plants may also be linked to the differing mycorrhizal status of the two functional groups. The sedges found in the communities studied here are predominantly non-mycorrhizal (Iversen *et al.* 2015), whereas in the woody plants, ecto- or ericoid mycorrhizal fungi are an important component of plant nutrient uptake (Clemmensen

et al. 2006). The strategy of root growth early in the season may be essential for non-mycorrhizal sedges to obtain sufficient nutrients to support continued growth (though this does assume minimal uptake from over-wintering roots). In woody plants with ericoid or ecto-mycorrhizas, seasonal patterns of mycorrhizal fungal activity may differ from those of roots and, consequently, seasonal nutrient uptake could be less closely coupled with root growth. The phenology of mycorrhizal fungal growth and activity has yet to be elucidated in sub-Arctic ecosystems, and further investigations may provide additional insights into the seasonal patterns observed in these communities.

Overall, our findings support the hypothesis that leaf and root production are more synchronous in low-stature graminoid vegetation than in taller woody plants. Since the environmental conditions of photoperiod and soil temperature did not differ amongst the studied communities, this indicates fundamental differences in physiology and allocation strategy between the two functional groups. In sub-Arctic ecosystems, however, greater synchrony was achieved in sedge-dominated communities through earlier onset of root production, rather than the delay in leaf production shown in other non-Arctic systems and species (Steinaker & Wilson 2008; Steinaker, Wilson & Peltzer 2010). In other systems, low soil temperatures were thought to delay leaf growth in low-stature graminoid vegetation through limiting translocation of carbohydrate and nutrient reserves from below-ground storage. This constraint may not apply to Arctic sedges, either because early growth can be fuelled from nutrient storage in over-wintering leaf portions (Chapin, Johnson & McKendrick 1980), or because key processes can take place at temperatures close to zero (e.g. Shaver & Billings 1975). Declines in PAR soon after snowmelt likely makes early leaf expansion important to maximize light capture throughout the growing season. In sub-Arctic and Arctic ecosystems, nutrient availability is strongly limiting and ephemeral (Lipson, Schmidt & Monson 1999; Weintraub & Schimel 2005; Buckeridge *et al.* 2010), and differing root growth strategies may reflect variations both in seasonal nutrient dynamics and total nutrient availability between microhabitats (e.g. Chapin *et al.* 1988; Chu & Grogan 2010). In sedges, which generally grow in sparse, open canopies, nutrient availability may be the most limiting factor throughout the growing season, resulting in continuous allocation to roots. In contrast, woody plants growing in more dense canopies may be light limited, resulting in early allocation to shoot growth (Poorter *et al.* 2012).

The contrasting degrees of synchrony in leaf and root production shown here demonstrate the importance of understanding temporal dynamics in multiple communities and growth forms at the landscape scale (Steinaker & Wilson 2008). Woody plants comprise approximately 75% of the global dataset on synchrony of root and leaf phenology (Abramoff & Finzi 2015); our findings suggest that an increased focus on other plant functional types, especially graminoids, is needed to understand consequences of vegetation change resulting from a changing climate. In all 10 sub-Arctic plant communities, seasonal dynamics of root and leaf production

were not wholly synchronous, and included root production fuelled by translocation of stored carbon. This suggests that in ecosystem carbon and nutrient cycle models of high-latitude ecosystems: (i) allocation of carbon to roots and leaves should be a variable parameter at the sub-annual scale; (ii) that root production should be possible in the absence of current photosynthesis and (iii) root seasonal growth and related soil processes should be specific to plant functional type.

RELATIONSHIP BETWEEN SOIL TEMPERATURE AND ROOT PRODUCTION

Correlations between root production and soil temperature in woody plant communities varied according to site, from no significant correlation in the three woody plant communities at Kevo (2008), to strong correlations in all five woody plant communities at Abisko (2009). In the Kevo woody plant communities, poor correlations were observed because root growth did not take place early in the growing season, despite soil temperatures comparable with periods when substantial root growth occurred. The strong positive correlations between root growth and soil temperature in Abisko may merely reflect the strong seasonality of the ecosystem: soil temperature rises may be co-incident with increasing root growth because there is a limited period of plant activity, during which photosynthates are available for new root growth, rather than because soil temperature is a key driver of root production. Previous analyses of patterns of root extension in arctic sedge species in relation to soil temperature have demonstrated that in *E. angustifolium*, extension is negatively correlated with soil temperature (Shaver & Billings 1975, 1977), and that root extension rates in two other sedges are largely independent of soil temperature providing soils are not frozen (Shaver & Billings 1977). Our findings confirm that the lack of correlation is more broadly applicable to woody plants, and that the strategy of root production late in the growing season is not a result of limiting soil temperatures early in the year. Rather, the allocation to root growth late in the growing season may reflect above-ground requirements for stored and recently fixed carbon early in the season for shoot growth, the size and locations of plant carbon and nutrient stores, and the potential for nutrient uptake and water uptake from existing long-lived roots (Chapin *et al.* 1975; Farrar & Jones 2000).

IMPLICATIONS OF DIFFERENCES IN ROOT–LEAF SYNCHRONY BETWEEN SEDGES AND WOODY PLANTS

In many regions of the Arctic, woody shrubs are expanding and encroaching in sedge-dominated tundra ecosystems (Sturm, Racine & Tape 2001; Myers-Smith *et al.* 2011), with this change expected to continue with further climatic warming (van Wijk *et al.* 2004). Although at the ecosystem scale, below-ground processes depend on both allocation to existing roots and to new root production, our findings suggest that a significant consequence of these changes will be a decoupling of new root and shoot growth arising from any increase in

woody vegetation abundance. New root growth is an important determinant of the flux and composition of carbon to the soil via root exudation, and timing of production should be considered alongside the static root traits which influence below-ground ecosystem processes (Bardgett, Mommer & De Vries 2014). Our findings suggest that woody plants create a more concentrated late season below-ground carbon flux than graminoids, such that the majority of new root growth in woody plants takes place when sub-Arctic soils are warmer and drier. Such interactions of roots with environmental controls may determine the nature and extent of plant influence on soil stability and soil carbon storage, seasonal dynamics of microbial community size and composition, and organic matter decomposition (Drake *et al.* 2011; Averill, Turner & Finzi 2014; Bardgett, Mommer & De Vries 2014). Root growth dynamics strongly influence dynamics of overall root system size, and thus the seasonal dynamics of soil respiration. Root carbon inputs are also an important driver of methane production in wetter Arctic and sub-Arctic soils, such that the broad differences in the timing of carbon inputs observed here may influence the timing and magnitude of emissions from these systems (Riley *et al.* 2011).

Overall, this work has shown fundamental differences in the synchrony of leaf and root production between sedge and woody plant-dominated sub-Arctic vegetation. This highlights the need for separate leaf and root production dynamics in ecosystem carbon and nutrient cycle models, with parameters specific to plant functional type. The differing synchrony between sedge and woody plant leaf and root production has important implications for understanding the functional impacts of vegetation change at northern high latitudes, and we suggest that future research should explicitly consider the linkages between seasonal plant growth dynamics and ecosystem processes.

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Data accessibility

Root phenology, leaf phenology and soil temperature data to be made available at the Environmental Information Data Centre (http://eidc.ceh.ac.uk) by December 2015.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Seasonality of solar radiation.

Table S1. Plant community composition.