



REVIEW PAPER

Root phenology in a changing climate

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Abstract

Plant phenology is one of the strongest indicators of ecological responses to climate change, and altered phenology can have pronounced effects on net primary production, species composition in local communities, greenhouse gas fluxes, and ecosystem processes. Although many studies have shown that aboveground plant phenology advances with warmer temperatures, demonstration of a comparable association for belowground phenology has been lacking because the factors that influence root phenology are poorly understood. Because roots can constitute a large fraction of plant biomass, and root phenology may not respond to warming in the same way as shoots, this represents an important knowledge gap in our understanding of how climate change will influence phenology and plant performance. We review studies of root phenology and provide suggestions to direct future research. Only 29% of examined studies approached root phenology quantitatively, strongly limiting interpretation of results across studies. Therefore, we suggest that researchers emphasize quantitative analyses in future phenological studies. We suggest that root initiation, peak growth, and root cessation may be under different controls. Root initiation and cessation may be more constrained by soil temperature and the timing of carbon availability, whereas the timing of peak root growth may represent trade-offs among competing plant sinks. Roots probably do not experience winter dormancy in the same way as shoots: 89% of the studies that examined winter phenology found evidence of growth during winter months. More research is needed to observe root phenology, and future studies should be careful to capture winter and early season phenology. This should be done quantitatively, with direct observations of root growth utilizing rhizotrons or minirhizotrons.

Key words: Belowground, endogenous, exogenous, phenology, root dynamics, root growth.

Introduction

One of the most sensitive indicators of a warming climate has been shifts in species phenology, which can have multiple repercussions on ecosystem processes and feedbacks on greenhouse

gases (Menzel *et al.*, 2006b; Cleland *et al.*, 2007; Rosenzweig *et al.*, 2008; Post, 2013; IPCC, 2014). The Intergovernmental Panel on Climate Change (IPCC) concluded that phenology

is the simplest way to track the ecological impacts of climate change (Solomon *et al.*, 2007), but explicit consideration of belowground phenological responses to climate change has been absent from all five IPCC assessment reports to date. Although air temperature may be the strongest control on aboveground plant phenology (Wielgolaski, 1999), very little is understood about the drivers of root phenology and how root phenology will respond to climate change.

Many studies examine drivers of root phenology by correlating all increases and decreases in yearly root production with a suite of biotic and abiotic factors. Root phenology may be controlled by different factors throughout the year, and this method may mask differences between the onset, peak, and cessation of root growth. Aboveground, leaf phenology is typically separated into discrete events, such as bud burst and leaf senescence, and these are quantitatively compared with abiotic and biotic factors. Flushes of root growth in summer may be controlled by factors other than the initiation of root growth in the spring. For this review, we conducted a literature search in Web of Science for studies that examined the phrase ‘root phenology’ or ‘roots’ with the terms ‘growth’, ‘dynamics’, and ‘production’. We also included several horticultural publications of which we were aware that did not come up in this search. We found 65 published papers that matched these criteria (see Table 2 for a list of studies). We focus on studies that used minirhizotrons or rhizotrons, as they allow researchers non-destructively to follow growth of the same roots throughout the year. While minirhizotron tubes and rhizotrons may impact total root production at the transparent wall–soil interface, particularly at shallow depths (Bragg *et al.*, 1983; Ephrath *et al.*, 1999), transparent wall techniques are probably the most accurate way to track the timing of root production (Majdi, 1996). Despite their benefits, only 58% of root phenology studies used rhizotron methods (Table 1). Only 29% (11 of 38 minirhizotron or rhizotron studies) of the studies reviewed here included quantitative evaluation of timing of root growth, such as the date that 10% of roots began growing or the date of first root growth (Table 1). Some studies examined the timing of root initiation, but this was usually done qualitatively.

We advocate for wider and more consistent use of quantitative approaches to characterize multiple aspects of root phenology, such that root initiation, peak root growth, and root cessation are explicitly defined. For

example, root initiation can be quantified as the date on which 50% of minirhizotron tubes or 50% of independent experimental units (when several minirhizotrons are used per experimental unit) contain the first root growth of the season. This perspective is widely established in studies of aboveground phenology, where the percentage of plants or plots in the emergent or flowering stages is a common metric (Zadoks, 1985; Post *et al.*, 2008; Parker *et al.*, 2011; Hoyer *et al.*, 2013). Furthermore, plants may rely on different cues for the initiation of root phenology in spring, and the timing of peak growth, and cessation of root growth in autumn, so consideration of these events separately is warranted.

Finally, we propose that root phenology may have different phenological controls compared with aboveground phenology, as mounting evidence suggests that onset and progression of root phenology do not simply track aboveground phenology (Abramoff and Finzi, 2015; Blume-Werry *et al.*, 2016). Furthermore, terrestrial biosphere models often include root growth as a fixed, synchronous fraction of leaf photosynthesis, but root growth is often asynchronous with leaf growth (Abramoff and Finzi, 2015). One important difference is that roots, unlike shoots, often do not experience winter dormancy (Fernandez and Caldwell, 1975). This may increase interannual variability in root phenology and decrease the likelihood that root and shoot phenology are synchronous. Below, we discuss ways in which environmental controls may differ among phenological events and between above- and belowground organs, evidence for a lack of winter dormancy, and the potential impacts of climate change on belowground phenology

Background

Aboveground plant phenology is a well-studied component of climate change, and temperature may be the most important environmental factor controlling the timing of spring phenology (Wielgolaski, 1999; Wolkovich *et al.*, 2012). For example, spring phenology has advanced by ~2.5 d per decade in Europe with recent warming (Menzel *et al.*, 2006a). However, the drivers of aboveground autumn phenology are less clear, but recent studies suggest that the timing of autumn leaf senescence is linked to the timing of spring budburst, with an earlier spring linked to earlier autumn leaf senescence (Keenan and Richardson,

Table 1. The number of studies that quantify the timing of events and found evidence of winter root growth

Only studies that used minirhizotron or rhizotron methods were examined for winter root growth measurements and quantification of root phenology.

	Percentage of papers	Number of papers
Minirhizotron or rhizotron methods	58	38 used rhizotron methods of 65 root phenology studies
Quantified timing of events	29	11 quantitative studies of 38 rhizotron studies
Measured winter growth	50	19 measured winter growth of 38 rhizotron studies
Evidence of winter root growth	89	17 observed winter growth of the 19 studies tracking roots in winter

Table 2. List of literature reviewed with citation, location, climate, vegetation type, species, whether the study used minirhizotron or rhizotron methods, whether the study was quantitative or qualitative, and whether the study found evidence of winter root growth

Reference	Location (climate ^a)	Vegetation	Species	Method ^b	Quantitative ^c	Winter data ^d	Winter growth ^e
Bevington and Castle (1985)	Florida, USA (temperate; hot summer)	Tree orchard, irrigated	<i>Citrus sinensis</i>	M	No	Yes	Yes
Blume-Werry <i>et al.</i> (2015)	Låktatjåkka, Sweden (cold; cold summer)	Forest, tundra	Subalpine mountain birch forest, low alpine tundra, high alpine tundra	M	No	No	–
Bonomelli <i>et al.</i> (2012)	Central Chile (temperate; dry warm summer)	Tree orchard, irrigated	<i>Prunus avium</i>	M	Yes	Yes	Yes
Broschat (1998)	Florida, USA (tropical; monsoon)	Tree	<i>Roystonea regia</i> , <i>Cocos nucifera</i> 'Malayan Dwarf', <i>Syagrus romanzoffiana</i> , <i>Phoenix roebelenii</i>	M	No	Yes	Yes
Burke and Raynal (1994)	New York, USA (cold; warm summer)	Tree	Northern hardwood forest dominated by <i>Acer saccharum</i> , <i>Fagus grandifolia</i> , <i>Betula alleghaniensis</i> , <i>Acer rubrum</i>	M	No	Yes	No
Comas <i>et al.</i> (2005)	New York, USA (cold; warm summer)	Vine, with and without irrigation	<i>Vitis labruscana</i> cv. Concord	M	No	No	–
Contador <i>et al.</i> (2015)	California, USA (temperate; dry, hot summer)	Tree orchard, irrigated	<i>Juglans regia</i> 'Chandler'	M	No	Yes	No
Curtis <i>et al.</i> (1994)	Michigan, USA (cold; warm summer)	Tree	<i>Populus grandidentata</i>	M	No	No	–
Edwards <i>et al.</i> (2004)	York, UK (temperate; warm summer)	Grass	Temperate grassland dominated by <i>Holcus lanatus</i>	M	No	Yes	Yes
Eissenstat <i>et al.</i> (2006)	New York, USA (cold; warm summer); California, USA (temperate; dry, warm summer)	Vine	<i>Vitis lambruscana</i> , <i>Vitis vinifera</i> , and <i>Malus domestica</i>	M	No	Yes	Yes
Flitter <i>et al.</i> (1999)	Cumbria, UK (temperate; warm summer)	Grass	Grassland dominated by <i>Festuca ovina</i> and <i>Agrostis capillaris</i>	M	No	No	–
Harris (1977)	Washington, USA (cold; dry hot summer)	Grass	Semi-arid rangeland, with <i>Agropyron spicatum</i> / <i>Poa sandbergii</i> , <i>Artemisia tridentata</i> / <i>Agropyron spicatum</i>	M	Yes	Yes	Yes
Harris <i>et al.</i> (1995)	New York, USA (cold; warm summer)	Tree	<i>Fraxinus pennsylvanica</i> , <i>Quercus coccinea</i> , <i>Corylus columa</i> , and <i>Syringa reticulata</i> 'Ivory Silk'	M	No	No	–
Head (1968)	Kent, UK (temperate; warm summer)	Tree	<i>Cydonia oblonga</i>	M	Yes	Yes	Yes
Hendrick and Pregitzer (1996)	Michigan, USA (cold; warm summer)	Forest	Northern hardwoods forests dominated by <i>Acer saccharum</i>	M	No	Yes	Yes
Hendrick and Pregitzer (1997)	Michigan, USA (cold; warm summer)	Forest	Northern hardwoods forests dominated by <i>Acer saccharum</i>	M	No	No	–
Ibacache <i>et al.</i> (1999)	La Serena, Chile (arid; cold desert)	Tree, irrigated	<i>Annona cherimola</i>	M	No	Yes	Yes
Janos <i>et al.</i> (2008)	Darwin, Australia (tropical savannah)	Savannah	<i>Eucalyptus tetrodonia</i> savanna	M	No	Yes	Yes
Joslin <i>et al.</i> (2001)	Tennessee, USA (temperate; hot summer)	Forest	<i>Quercus alba</i> – <i>Quercus prinus</i> forest	M	No	No	–
Marler and Willis (1996)	Florida, USA (tropical monsoon)	Tree, irrigated	<i>Litchi chinensis</i>	M	No	Yes	Yes

Table 2. Continued

Reference	Location (climate ^a)	Vegetation	Species	Method ^b	Quantitative ^c	Winter data ^d	Winter growth ^e
McCormack et al. (2010)	Alabama, USA (temperate; hot summer)	Tree, grass, forb; irrigated	<i>Pinus palustris</i> , <i>Quercus margaretta</i> , <i>Aristida stricta</i> , <i>Crotalaria rotundifolia</i> , <i>Asclepias tuberosa</i>	M	No	Yes	Yes
McCormack et al. (2014)	Pennsylvania, USA (cold; warm summer)	Tree	<i>Acer negundo</i> , <i>Acer rubrum</i> , <i>Acer saccharum</i> , <i>Carya glabra</i> , <i>Juglans nigra</i> , <i>Liriodendron tulipifera</i> , <i>Pinus strobus</i> , <i>Pinus virginiana</i> , <i>Populus tremuloides</i> , <i>Quercus alba</i> , <i>Quercus rubra</i> , <i>Sassafras albidum</i>	M	No	Yes	Yes
McCormack et al. (2015)	Pennsylvania, USA (cold; warm summer)	Tree	<i>Acer negundo</i> , <i>Acer rubrum</i> , <i>Acer saccharum</i> , <i>Carya glabra</i> , <i>Juglans nigra</i> , <i>Liriodendron tulipifera</i> , <i>Pinus strobus</i> , <i>Pinus virginiana</i> , <i>Populus tremuloides</i> , <i>Quercus alba</i> , <i>Quercus rubra</i> , <i>Sassafras albidum</i>	M	Yes	No	–
Mickelbart et al. (2012)	California, USA (arid; cold steppe)	Tree	<i>Persea americana</i>	M	No	Yes	Yes
Misson et al. (2006)	California, USA (arid; cold steppe)	Tree plantation	<i>Pinus ponderosa</i> -dominated plantation	M	Yes	No	–
Nomura and Kikuzawa (2003)	Sabah, East Malaysia (tropical rainforest)	Forest	Lower montane forest, upper montane forest, subalpine forest	M	No	No	–
Ploetz et al. (1992)	Florida, USA (tropical savannah)	Tree, irrigated	<i>Persea americana</i>	M	No	Yes	Yes
Pritchard et al. (2008)	North Carolina, USA (temperate; hot summer)	Tree	<i>Pinus taeda</i>	M	No	Yes	Yes
Psarras et al. (2000)	New York, USA (cold; warm summer)	Tree, irrigated	<i>Malus sylvestris</i> var. <i>domestica</i>	M	Yes	No	–
Quan et al. (2010)	Northeastern China (cold; dry winter; warm summer)	Forest, plantation	Mongolian oak forest, aspen–birch forest, hardwood forest, Korean pine plantation, Dahurian larch plantation	M	Yes	No	–
Reich et al. (1980)	Missouri, USA (temperate; hot summer)	Tree, irrigated	<i>Quercus alba</i> , <i>Q. marilandica</i> , <i>Q. velutina</i>	M	No	Yes	Yes
Repo et al. (2008)	Finland (cold; cold summer)	Tree, irrigated	<i>Pinus sylvestris</i>	M	No	No	–
Rytter (2001)	Uppsala, Sweden (cold; warm summer)	Shrub, irrigated	<i>Salix viminalis</i>	M	No	No	–
Steinaker and Wilson (2008)	Saskatchewan, Canada (cold; warm summer)	Forest, grassland	Native grassland and aspen forest (<i>Populus tremuloides</i>)	M	No	No	–
Steinaker et al. (2010)	Saskatchewan, Canada (cold; warm summer)	Tree, shrub, grass	<i>Festuca rubra</i> , <i>Koeleria gracilis</i> , <i>Poa compressa</i> , <i>Bouteloua gracilis</i> , <i>Schizachyrium scoparium</i> , <i>Rosa woodsii</i> , <i>Shepherdia canadensis</i> , <i>Symphoricarpos occidentalis</i> , <i>Prunus virginiana</i> , <i>Picea glauca</i>	M	Yes	No	–
Sword et al. (1996)	Louisiana, USA (temperate; hot summer)	Tree	<i>Pinus taeda</i>	M	No	No	–
Tierney et al. (2003)	New Hampshire, USA (cold; warm summer)	Forest	Dominated by <i>Fagus grandifolia</i> , <i>Acer saccharum</i> , and <i>Betula alleghaniensis</i>	M	No	No	–
Wan et al. (2004)	Tennessee, USA (temperate; hot summer)	Tree	<i>Acer rubrum</i> , <i>Acer saccharum</i>	M	No	No	–
Aerts et al. (1992)	Utrecht, The Netherlands (Temperate; warm summer)	Sedge	<i>Carex diandra</i> , <i>C. rostrata</i> , <i>C. lasiocarpa</i>	O	–	–	–

Table 2. Continued

Reference	Location (climate ^a)	Vegetation	Species	Method ^b	Quantitative ^c	Winter data ^d	Winter growth ^e
Barnes (2002)	Alabama, USA (temperate; hot summer)	Tree, irrigated	<i>Pinus taeda</i>	O	—	—	—
Bosac <i>et al.</i> (1995)	England, UK (temperate; warm summer)	Tree, irrigated	<i>Populus euramericana</i> 'Primo'	O	—	—	—
Burke <i>et al.</i> (1992)	New York, USA (cold; warm summer)	Tree, irrigated	<i>Acer saccharum</i>	O	—	—	—
Canham <i>et al.</i> (2012)	Western Australia, Australia (temperate; dry, hot summer)	Forest	<i>Banksia attenuata</i> , <i>Banksia ilicifolia</i>	O	—	—	—
Cardon <i>et al.</i> (2002)	Connecticut, USA (cold; hot summer)	Tree, with and without irrigation	<i>Quercus rubra</i>	O	—	—	—
Coll <i>et al.</i> (2012)	Aguero, Spain (cold; warm summer)	Forest	<i>Quercus ilex</i> , <i>Quercus faginea</i>	O	—	—	—
Côté <i>et al.</i> (1998)	Québec, Canada (cold; warm summer)	Forest	Forest dominated by <i>Acer saccharum</i>	O	—	—	—
Dornbush and Raich (2006)	Iowa, USA (cold; hot summer)	Grass	Cool-season meadow and warm-season meadow	O	—	—	—
Drew and Ledig (1981)	North Carolina, USA (temperate; hot summer)	Tree	<i>Pinus taeda</i>	O	—	—	—
Du and Fang (2014)	Great Khingan Mountains, China (cold; dry winter; warm summer)	Forest	<i>Betula platyphylla</i> – <i>Populus davidiana</i> forest; <i>Larix gmelinii</i> forest	O	—	—	—
Dušek and Kvet (2006)	South Bohemia, Czech Republic (cold; warm summer)	Shrub	<i>Salix caprea</i>	O	—	—	—
Haynes and Gower (1995)	Wisconsin, USA (cold; warm summer)	Tree plantation	<i>Pinus resinosa</i>	O	—	—	—
Hester <i>et al.</i> (2004)	Scotland, UK (temperate; warm summer)	Tree, irrigated	<i>Betula pendula</i> , <i>Pinus sylvestris</i> , <i>Sorbus aucuparia</i>	O	—	—	—
Kaakinen <i>et al.</i> (2004)	Northern Savonia, Finland (cold; cold summer)	Tree, irrigated	<i>Picea abies</i>	O	—	—	—
Kaur <i>et al.</i> (2012)	Nova Scotia, Canada (cold; warm summer)	Shrub	<i>Vaccinium angustifolium</i>	O	—	—	—
Kho <i>et al.</i> (2013)	Sarawak, Malaysia (tropical rainforest)	Forest	Lowland mixed dipterocarp forest	O	—	—	—
Konopka <i>et al.</i> (2005)	Brasschaat, Belgium (temperate; warm summer)	Forest	<i>Quercus robur</i> , <i>Pinus sylvestris</i>	O	—	—	—
Lahti <i>et al.</i> (2005)	North Karelia, Finland (cold; cold summer)	Tree, irrigated	<i>Picea abies</i>	O	—	—	—
Palacio and Montserrat-Marti (2007)	Jaca, Zaragoza, and Villamayor, Spain (cold; warm summer, Arid; cold steppe)	Shrub, forb	<i>Echinospartum horridum</i> , <i>Salvia lavandulifolia</i> , <i>Lepidium subulatum</i> , <i>Linum suffruticosum</i>	O	—	—	—
Papathodorou <i>et al.</i> (1998)	Greek Macedonia, Greece (temperate; hot summer)	Shrub	<i>Quercus coccifera</i>	O	—	—	—
Rojas-Jimenez <i>et al.</i> (2007)	Guanacaste, Costa Rica (tropical savannah)	Forest	<i>Enterolobium cyclocarpum</i>	O	—	—	—

Table 2. Continued

Reference	Location (climate ^a)	Vegetation	Species	Method ^b	Quantitative ^c	Winter data ^d	Winter growth ^e
Thompson and Puttonen (1991)	Helsinki, Finland (cold; warm summer)		<i>Pinus sylvestris</i> , <i>Picea abies</i>	O	-	-	-
Tingey et al. (1996)	California, USA (temperate; dry, hot summer)	Tree, irrigated	<i>Pinus ponderosa</i>	O	-	-	-
Vapaavuori et al. (1992)	Northern Savonia, Finland (cold; cold summer)	Tree, irrigated	<i>Pinus sylvestris</i> , <i>Picea abies</i>	O	-	-	-
Yamashita and Imamura (2007)	Fukuoka, Japan (temperate; hot summer)	Tree, irrigated	<i>Eustoma grandiflorum</i>	O	-	-	-
Zasada et al. (1994)	Oregon, USA (temperate; dry, warm summer)	Shrub, irrigated	<i>Rubus spectabilis</i>	O	-	-	-

^a Climate classifications based on reference of study location to standard climate classification scheme (Peel et al., 2007).
^b M, minirhizotron or rhizotron; O, other methods.
^c Yes, quantitative; No, qualitative.
^d Yes, measured winter root growth; No, no winter measurements.
^e Yes, evidence for winter root growth; No, no evidence of winter growth; -, not applicable (e.g. due to lack of measurements).

2015). Alternatively, warming may extend aboveground plant growth later into autumn (Marchand et al., 2004; Natali et al., 2012) or have limited effects on autumn phenology (Kummerow and Russell, 1980; Pudas et al., 2008). Recent experimental evidence indicates that CO₂ fertilization may further extend the length of the aboveground growing season in response to warming (Reyes-Fox et al., 2014).

Although the effects of warming on aboveground phenology are fairly well understood, the effects of warming on belowground phenology have received much less attention. In Fig. 1, we outline potential factors that may be important to root phenology. There is conflicting evidence regarding the relative influence of exogenous factors, such as soil temperature, and endogenous factors, such as photosynthate supply, on belowground phenology. In regions with a distinct winter season, root growth often increases as soil temperatures increase in the spring, and root growth over winter is limited (Comas et al., 2005; McCormack et al., 2014). Indeed, several studies have found a positive correlation between soil temperature and root production (Burke and Raynal, 1994; Steinaker and Wilson, 2008; Steinaker et al., 2010). Other studies, however, have failed to find a correlation with soil temperature, and suggest that endogenous factors, such as photosynthate availability, are more important to root phenology (Sword et al., 1996; Joslin et al., 2001; Tierney et al., 2003). The importance of photosynthetic activity was supported by links of photosynthetic photon flux density (PPFD) to root growth in temperate and upland grasslands in regions where cloudy days are common (Fitter et al., 1999; Edwards et al., 2004).

Endogenous and exogenous factors probably both play a role in root phenology (Fig. 1; Tierney et al., 2003; Steinaker and Wilson, 2008), and these roles may differ between species and environments as plants seek to balance their need to increase their competitiveness with maximizing carbon, water, and nutrient use efficiencies. Species-specific differences in phenological strategies are suggested by a common garden experiment in central Pennsylvania where root phenology differed widely between temperate tree species, with some species showing a conservative root phenology and others having high interannual variability in root phenology (McCormack et al., 2014, 2015). In the common garden, species from varied taxa were planted in the same field in replicated plots so they experienced the same environmental conditions. This suggests that different species may have different strategies to deal with interannual variability in resource supply and climatic constraints. For example, we expect that species for which root growth is more cued to shoot growth or to photoperiod would show less spring variability in root initiation than species that respond readily to increases in soil temperature. Moreover, we expect that controls on root growth will change over time, and below we outline the hypothesized influence of external and internal controls throughout the year.

Initiation of root growth

Because root growth may not begin below $\sim 5^{\circ}\text{C}$ in temperate environments (Alvarez-Uria and Koerner, 2007), soil temperature may be a direct control on root initiation. This is supported by the large suppression of winter root growth seen across many ecosystems in seasonal environments (Tierney *et al.*, 2003; Comas *et al.*, 2005). Once soil temperatures are favorable, carbon availability for root production may also constrain the timing of root initiation. The signal to produce new roots is then created by some unknown up-regulation of plant growth factors that increase the relative carbon sink strength of roots (Kozlowski, 1992).

Carbon for spring root growth may come from current photosynthate or stored carbohydrates. Carbohydrates, particularly starches, can accumulate in woody tissues in autumn, and these carbohydrates can fuel early spring root growth in the following year (Najar *et al.*, 2014). Stored carbohydrates may be particularly important in deciduous species that do not have photosynthetic tissues early in the season, as seen in arctic *Betula glandulosa* (Kummerow *et al.*, 1983). Early spring root growth may then be advantageous in regions where high nutrient availability occurs before air temperatures are favorable for leaf growth.

Early spring growth may also be important for resource pre-emption from competing species. Plants may outcompete neighbors by initiating root growth more quickly and gaining access to limiting resources (Harper, 1977; Harris, 1977). Eissenstat and Caldwell (1988), for example, found that an introduced cold-desert grass was able to compete more effectively with desert shrubs than native grasses by more quickly extracting water from the soil early in the growing season.

Drivers of peak root growth

Peak root growth comes at the expense of using carbon for aboveground growth, so peak root growth may represent a trade-off between competing plant sinks (Comas *et al.*, 2005). Because it is costly in terms of carbon, peak root growth may be timed to balance carbohydrate availability with periods of high nutrient and water availability. For example, species that

evolved in regions with mid-summer drought may be characterized by adaptations that reduce root growth in mid-summer and peak earlier in spring (Joslin *et al.*, 2001). Plants that are nutrient deficient may not be able to produce as many roots early in the season, but they may increase nutrient uptake by increasing peak root production in later spring and summer (Haynes and Gower, 1995). These increases in root growth to compensate for low nutrient stores may be controlled by plant growth regulators (Lopez-Bucio *et al.*, 2003). In competition, plants may also advance the timing of peak root growth in order pre-emptively to access resources and limit the fitness of neighbors (Eissenstat and Caldwell, 1988; Dybzinski *et al.*, 2011).

Because soils are probably above limiting temperatures by the time peak production occurs, we hypothesize that soil temperature plays a smaller role in determining peak root growth than in root initiation. We also expect that stored carbohydrates play a smaller role in the timing of peak root growth if leaves (and photosynthate production) are already present and current photosynthate is available. In species such as evergreens that potentially photosynthesize year-round, albeit at low rates during winter, or in species with high carbohydrate stores, peak root growth may not be tightly coupled to peak leaf growth, and root growth may continue fairly consistently throughout the growing season. In other species, root production may be limited by current photosynthate, and root production may have a large peak after leaf production begins. Furthermore, these contrasting patterns can co-occur within the same ecosystem. For example, Lyr and Hoffman (1967) found that root production peaked in early summer for some species, whereas other species in the same environment grew their roots more uniformly throughout the growing season (Fig. 2). Links between PPFD and root production support the importance of photosynthesis to root phenology and potentially to peak root growth. For example, Edwards *et al.* (2004) found in British grasslands where cloudy days are common that variation in PPFD was the best predictor of root growth.

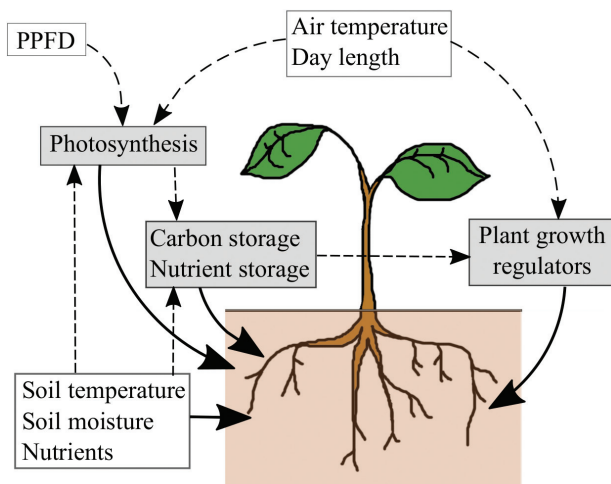


Fig. 1. Potential controls over root phenology. Solid lines indicate direct controls and dashed lines indicate indirect controls on root phenology. Gray boxes represent endogenous controls; and white boxes represent exogenous controls. PPFD is photosynthetically active flux density.

Cessation of root growth: implications for a lack of winter dormancy

Very little is currently understood about drivers of autumn root phenology. Similar to aboveground production, root growth may slow as temperature (in the soil) and carbohydrate availability decrease. Unlike aboveground production, photoperiod probably does not exert strong control on

autumn root phenology. If photoperiod were a strong control, then root growth would cease at some point in autumn and not begin again until spring. Although root growth may be limited below certain temperatures, we suggest that roots are not normally dormant during winter, and growth can occur year-round if conditions become favorable. Of 19 studies that measured winter root growth, 89% detected evidence of winter growth (Table 1). For example, Fernandez and Caldwell (1975) recorded root growth even in near-freezing soils during winter in cold-desert plants, Bauerle et al. (2008) recorded winter root growth in *Vitis* spp. in a Mediterranean climate, and Onipchenko et al. (2009) found snow roots growing into snow packs in an alpine environment. Additionally, snow removal studies lead to soil freezing and cause increased fine root mortality (Tierney et al., 2001), which suggests that these roots were not dormant. Photoperiod may be a stronger cue in some species with root systems that senesce over winter. For example, Shaver and Billings (1977) found

that some arctic graminoid species use photoperiod as a cue for seasonal root cessation. This may be a way in which they resorb carbohydrates and nutrients in these strongly nutrient-limited systems before the soils freeze and the roots senesce. However, in other arctic shrubs and grasses, there was no evidence that root growth necessarily slows as photoperiod decreases (Fig. 3). Photoperiod may be an important control to some species but not others.

Potential impacts of climate change

Given the uncertainty concerning controls on root phenology, it is unclear how climate change will impact the timing of root growth. Altered root phenology could have strong impacts on plant resource acquisition (Nord and Lynch, 2009). A large portion of global carbon is stored in roots (Robinson, 2007), with up to five times higher biomass belowground than aboveground in shrublands, tidal marshes, grasslands, and tundra (Mokany

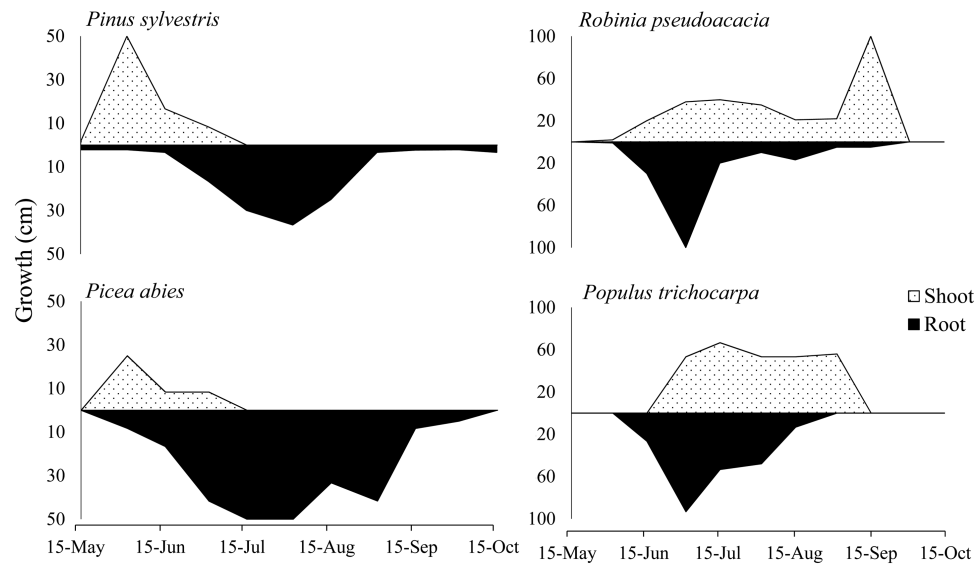


Fig. 2. Seasonal shoot and root growth in two deciduous species and two evergreen species in the Eberswalde root laboratory in Germany. Shoot growth is indicated by the dotted area and root growth by the solid area. Reprinted from International Review of Forestry Research 2, Lyr H, Hoffmann G. Growth rates and growth periodicity of tree roots, 181–206. Copyright 1967, with permission from Elsevier.

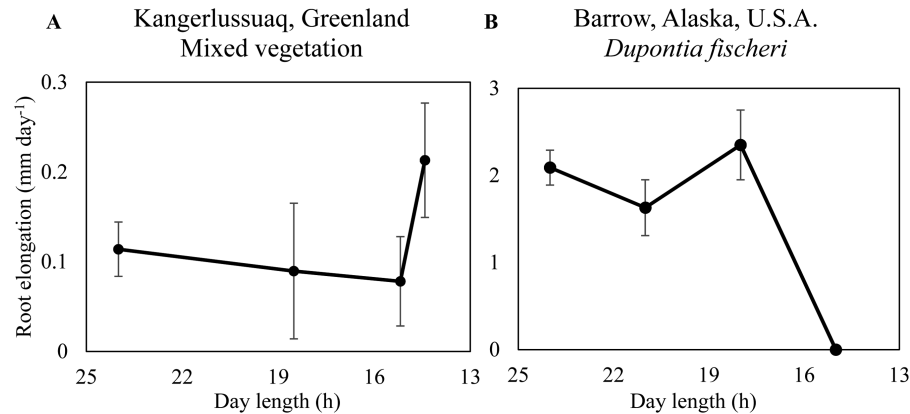


Fig. 3. Root elongation at different photoperiods. (A) Average root elongation (mm d⁻¹) at decreasing day lengths from July to September in mixed vegetation plots in Kangerlussuaq, Greenland. Error bars indicate the SEM (n=24 at all day lengths). (B) Average root elongation (mm d⁻¹) of *Dupontia fischeri* at decreasing day lengths in Barrow, AK, USA. The photoperiod was experimentally controlled in phytotrons. Error bars indicate the SEM (n=120 at 24 h, n=24 at 21 h, and n=6 at 18 h). Panel B of figure adapted from Oecologia, Effects of daylength and temperature on root elongation in tundra-graminoids, 28, 1977, 57–65. Shaver GR and Billings WD. © by Springer-Verlag 1977. With permission of Springer

et al., 2006). Aboveground phenology may be a particularly poor indicator of overall ecosystem productivity in regions with more belowground than aboveground biomass (Blume-Werry *et al.*, 2016). Many studies track aboveground phenology either directly or by remote sensing (e.g. Sitch *et al.*, 2007), but these do not account for changes in root phenology. This increases the uncertainty of predicting carbon fluxes in terrestrial ecosystems with a large fraction of the biomass belowground.

Despite the importance of root production in determining whole-plant responses to climate change, very few studies have directly examined the influence of warming and elevated carbon dioxide concentrations ($[CO_2]$) on root phenology. In the Arctic, experimental warming caused earlier root growth (Sullivan and Welker, 2005) and increased root production (Sullivan *et al.*, 2008). In a scrub-oak ecosystem, elevated $[CO_2]$ increased fine-root production in spring and autumn, which may be due to increased carbon availability for root production during periods critical to resource acquisition (Brown *et al.*, 2009). Experimental evidence is lacking from other ecosystems, however, and more studies are needed that clearly assess the impacts of warmer air temperatures and elevated $[CO_2]$ on the timing and amount of root production.

We hypothesize that altered precipitation regimes may shift the timing of peak root growth, particularly given evidence that water stress often causes root production to shift to more favorable times of year (Joslin *et al.*, 2000). Because root production can be suppressed during periods of drought (Joslin *et al.*, 2001), we expect peak root production to shift to the wettest times of year in regions with reduced annual precipitation. In regions with increased precipitation, peak root growth may no longer be water limited and may shift to periods when other factors, such as PPFD, are most available.

The upper soil layer may be more influenced by warming, given that air temperature affects the temperatures of shallow soil more than deep soils. Therefore, ecosystems with high

root biomass near the surface, such as in the Arctic, may be particularly affected by global warming. Elevated $[CO_2]$ has been found to increase deep root production in forested ecosystems (Iversen, 2010), and this may extend phenology of deep roots. We speculate that if elevated $[CO_2]$ cause more carbon to be shuttled to deep roots, deep roots may have advanced root initiation and delayed root cessation, as long as temperatures are not limiting. The influence of depth on phenology is examined in more detail below.

The importance of depth

Root phenology differs by depth in certain ecosystems and may be under different controls (Canham *et al.*, 2012), so we expect that warming, elevated $[CO_2]$, and altered precipitation regimes will affect shallow and deep roots differently. Phenology may be shifted later in the season at deeper depths, where soil is slower to warm in the spring and may retain moisture from winter soil recharge. In shrub species in Utah, initiation of root growth began later with increasing soil depth, which may be related to the concurrent seasonal increase in soil temperature at each depth (Fig. 4). For example, in mid-April, soil temperatures at 40 cm were 5 °C and root production from 30 cm to 40 cm was 1.1 mm d⁻¹ cm⁻¹, and by late May soil temperatures at the same depth were 14 °C and root production was 3.5 mm d⁻¹ cm⁻¹. Deep root growth may also allow the plant to access deep water stores during the driest period of the year (Fernandez and Caldwell, 1975). Similarly, shallow roots in phreatophytic *Banksia* spp. grow in a pulse, synchronously with aboveground tissues, but deeper roots grow constantly throughout the year, as they have access to a constant deep water source (Canham *et al.*, 2012). Deep root growth may also be timed to use deep water storage during times of water stress, reducing the impact of seasonal droughts (Hendrick and Pregitzer, 1996).

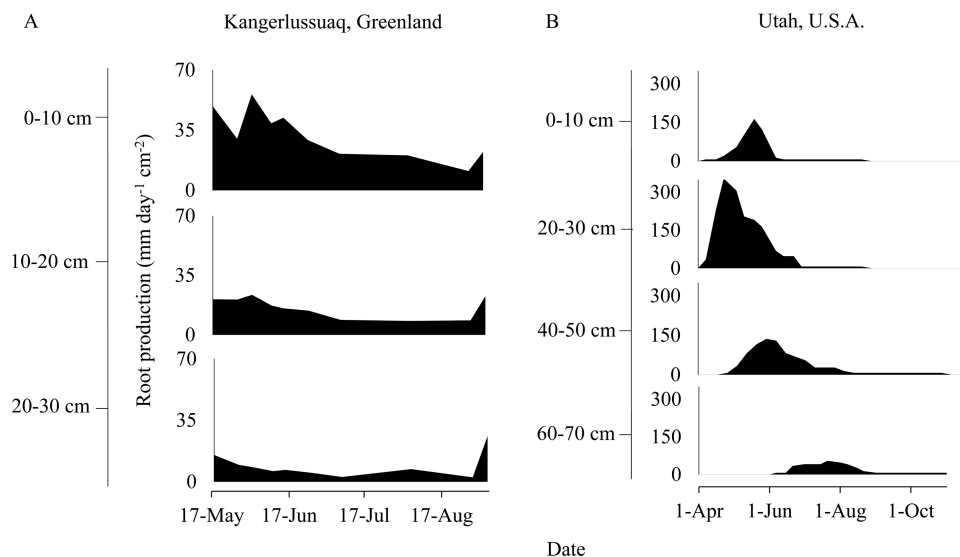


Fig. 4. Seasonal root production at three 10 cm depth intervals. (A) Average daily root production (mm d⁻¹ standardized to a 50 cm² observation window) in mixed vegetation plots in the Arctic near Kangerlussuaq, Greenland. The timing of root production was not significantly different between soil depths, but soil temperature was significantly different between soil depths. (B) Average daily root production (mm d⁻¹ in a 50 cm² observation window) in *Artemisia tridentata* in Curlew Valley, UT, USA. Panel B of figure adapted from *Journal of Ecology*, Phenology and dynamics of root growth of three cool semi-desert shrubs under field conditions, 63, 1975, 703–714, Fernandez OA, Caldwell MM. © British Ecological Society. With permission of Wiley.

The phenology of shallow roots may be more strongly influenced by environmental factors, such as soil moisture and temperature, than deeper roots (Hendrick and Pregitzer, 1997). For example, in loblolly pine (*Pinus taeda* L.) in the southeastern USA, a mid-summer drought reduced new root growth in shallow soil layers, but root initiation continued in deeper soils (Sword *et al.*, 1996). However, root phenology may not always differ by soil depth (Fig. 4). Despite strong seasonal changes in soil temperature with depth, root phenology in southwestern Greenland was not significantly different across soil depths, even if most roots were produced close to the soil surface (RD and DMA, unpublished data).

Future directions and conclusions

Future studies can more accurately tease apart the controls on phenology if they focus on the explicit timing of events. Use of minirhizotrons or rhizotrons is probably the most accurate way to do this, because destructive methods, such as soil coring, do not follow the same roots through time and will often miss the precise occurrence of new root growth. Because it is unlikely that roots are truly dormant in winter and because roots do not necessarily track aboveground growth, root measurements should begin very early in the season or persist through winter months when feasible. Some previous studies may have missed the onset of root growth if measurements were taken too late in the season or were not taken often enough throughout the year. For example, one study found that root growth preceded leaf growth (McCormack *et al.*, 2015), but another study with less temporally resolved observations using the same plants found root production to peak after major leaf expansion (McCormack *et al.*, 2014). Future studies that continue observations throughout the winter or begin root measurements prior to leaf emergence, that do not assume root phenology tracks aboveground phenology, and that quantitatively evaluate phenology will enjoy greater success at teasing apart the controls on root phenology. Given that root and shoot growth may respond differently to climate change, this is essential in determining the future impacts of warming on whole-plant carbon use. Because root and shoot phenology often are not synchronous and may not be influenced by warming in the same way, root phenology research is critical to understanding shifts in whole-plant growth with climate change.

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