Research review

Are above- and below-ground phenology in sync?

Author for correspondence:
Adrien C. Finzi
Tel: +1 617 353 2453
Email: afinzi@bu.edu

Rose Z. Abramoff and Adrien C. Finzi

Department of Biology, Boston University, 5 Cummington Mall, Boston, MA 02215, USA

Summary

Globally, root production accounts for 33–67% of terrestrial net primary productivity and influences decomposition via root production and turnover, carbon (C) allocation to mycorrhizal fungi and root exudation. As recognized above ground, the timing of phenological events affects terrestrial C balance, yet there is no parallel understanding for below-ground phenology. In this paper we examine the phenology of root production and its relationship to temperature, soil moisture, and above-ground phenology. Synthesizing 87 observations of whole-plant phenology from 40 studies, we found that, on average, root growth occurs 25 ± 8 d after shoot growth but that the offset between the peak in root and shoot growth varies > 200 d across biomes (boreal, temperate, Mediterranean, and subtropical). Root and shoot growth are positively correlated with median monthly temperature and mean monthly precipitation in boreal, temperate, and subtropical biomes. However, a temperature hysteresis in these biomes leads to the hypothesis that internal controls over C allocation to roots are an equally, if not more, important driver of phenology. The specific mechanisms are as yet unclear but they are likely mediated by some combination of photoassimilate supply, hormonal signaling, and growth form.

Introduction

It is widely acknowledged that roots play a fundamental role in terrestrial C cycling, consuming up to 70% of net primary production (Grier *et al.*, 1981; Jackson *et al.*, 1997), yet there is little understanding of the factors controlling patterns of root growth (Pregitzer *et al.*, 2000). Fine root production can occur in a single flush but often occurs in multiple flushes throughout the growing season (Reich *et al.*, 1980; Bevington & Castle, 1985; Harris *et al.*, 1995; Steinaker *et al.*, 2010). Soil temperature, moisture and nutrient availability affect the growth of roots (Fukuzawa *et al.*, 2013; Noguchi *et al.*, 2013), but there is often no temporal correlation between these abiotic factors and root growth apart from obvious growing-to-nongrowing season transitions (Hendrick & Pregitzer, 1996; Joslin *et al.*, 2001; Supporting Information, Table S1). In these cases, internal signaling such as photoassimilate transport may control root growth (Sloan & Jacobs, 2008), such that roots cannot grow when shoots are consuming the majority of photoassimilate. Supporting this, several studies have observed patterns of alternating root and shoot growth (Drew & Ledig, 1980; Reich *et al.*, 1980; Cardon *et al.*, 2002; Mickelbart *et al.*, 2012).

Most conceptual and terrestrial biosphere models allocate C below ground as a fixed fraction of net C uptake, which by definition makes root phenology synchronous with above-ground growth (Table 1). The purpose of this review is to show that current data support asynchrony between above- and below-ground growth. We acknowledge that the available data are few and that inference regarding broad-scale patterns is subject to change as more data become available. We hope, however, that bringing currently available data to light in this regard will generate the collection of new data, and refine current understanding of below-ground phenology and its relevance at the ecosystem scale.

A compilation of available data

It is commonly assumed that root growth peaks early in the growing season and is therefore synchronous with above-ground growth (Medvigy *et al.*, 2009). While this can be true (Misson *et al.*, 2006; Scagel *et al.*, 2007), there are many exceptions (Lahti *et al.*, 2005;

Table 1 Parameters for phenology and carbon allocation in terrestrial biosphere models

Model	Above-ground phenology	Below-ground phenology	C allocation	Citations
TRIFFID	Temperature	n/a	Allometric relationships (root = leaf, stem ∝ leaf) and partitioning into 'spreading' and 'growth' based on LAI	Cox (2001)
Hyland	n/a	n/a	Fixed coefficients	Friend *et al.* (1997), Friend & White (2000) and Levy *et al.* (2004)
PnET-BGC	GDD	Monthly turnover rate	Linear function of foliar production	Kram *et al.* (1999)
ORCHIDEE	GDD Soil moisture	Some root growth at leaf onset, stress can cause root death	Allocation fractions for leaves, stems, roots determined based on water, light and N avaiibility	Krinner *et al.* (2005)
3PG	PAR number of frost days	Stress affects root growth	Allometric relationships	Landsberg & Waring (1997)
IBIS	TemperatureProductivity threshold	n/a	Fixed fraction of C uptake allocated to leaves, stems, roots	Mcguire *et al.* (2001)
TEM	Evapotranspiration	n/a	Not explicit	Mcguire *et al.* (2001)
ED2	Logistic functions derived from MODIS data	n/a	PFT-dependent allocation relationships, root : leaf varies with water or N limitation	Medvigy *et al.* (2009)
CLM 4.0	GDD Soil moisture Day length	n/a	Fixed ratios of fine root : leaf and coarse root : stem	Oleson *et al.* (2010) and Thornton & Zimmerman (2007)
LPJ-GUESS	GDD Soil moisture	Stress affects root growth	Allometric relationships, PFT-dependent root : leaf biomass varies with water and N availability	Sitch *et al.* (2003) and Smith *et al.* (2013)
TREGRO	GDD NSC status	GDD NSC status	Allocated based on priority leaf > branch > stem > coarse roots > fine roots	Weinstein *et al.* (1991)
BIOME-BGC	Temperature Photoperiod Climate-specific GDD	n/a	PFT-dependent allometric ratios such as root : leaf and stem : leaf	White *et al.* (1997)
Sheffield- DGVM	Temperature and soil moisture	n/a	LAI optimized to maximize C uptake, wood and roots receive a constant PFT-dependent fraction of remaining C	Woodward *et al.* (1995) and Woodward & Lomas (2004)

n/a, not applicable; GDD, growing degree-days; LAI, leaf area index; PFT, plant functional type; NSC, nonstructural carbohydrate.

Willaume & Pagès, 2006; Palacio & Montserrat-Marti, 2007). Some studies report root growth lagging shoot growth by several weeks, an observation attributed to air temperature warming faster than soil temperature in the spring (Steinaker & Wilson, 2008). Others report root growth preceding shoot growth by several weeks to months (Ploetz *et al.*, 1992; Broschat, 1998). In a common garden study in Pennsylvania, some species, such as *Acer negundo* and *Pinus strobus*, had large interannual variability in root phenology while others, such as *Liriodendron tulipfera*, did not (McCormack *et al.*, 2014), suggesting that some trees may be environmentally cued while others are inflexible in their timing (i.e. phenological programming *sensu* Hendrick & Pregitzer, 1996; Joslin *et al.*, 2001).

To address broad-scale patterns in phenology, we conducted a literature survey to quantify the offset between the maximum in root and shoot growth in woody and herbaceous perennial plants. Web of Science was searched using the following keywords: belowground phenology, root phenology, root allocation, and root growth in combination with shoot phenology, aboveground, stem growth, leaf out, budburst or greenness. We considered only studies

that simultaneously measured both root and shoot production. Of the 13 934 results from the keyword search, only 40 studies had suitable data. There were a total of 87 datasets containing shoot and root growth for 63 species (see 'Paper selection', 'Gross and net root production', 'Monthly root and shoot growth', and 'Temperature and precipitation data' in Notes S1 for a more detailed description of the data used in this survey). The data are compiled in Tables S2 and S3. Each observation was classified into one of four biomes (boreal, temperate, Mediterranean, and subtropical) based on Whittaker's biome classification system (1970). In order to visualize findings from the literature, we quantified the difference between peak shoot and root growth using the following equation:

$$\text{Offset (days)} = \text{DOY}_{\text{maximum root}} - \text{DOY}_{\text{maximum shoot}}, \qquad \text{Eqn 1}$$

where DOY is the day of year of maximum root or shoot growth as indicated. In plants with multiple root and shoot flushes, maximum root or shoot growth rate was used to calculate offset. Positive offset values therefore indicate peak shoot growth preceding the peak in root growth, whereas negative values would indicate root growth

preceding the peak in shoot growth. Differences in root and shoot data collection methods marginally affect offset ($F_{6,80} = 2.17$, $P = 0.055$), so they were included in stepwise model selection (see 'Offset' in Notes S1). Soil coring methods tended to detect later root growth relative to shoot growth.

Primary data findings

There was wide variation in the timing of maximum shoot growth relative to root growth (Fig. 1). In the majority of cases, maximum shoot production occurred before root production (offset > 0 in 54 out of 87 observations) and the mean offset for all studies (25 ± 8 d) was greater than zero (one-sample t-test; $t = 3.15$, df = 86, $P < 0.01$), indicating that root and shoot growth are not synchronous on a broad geographic scale. There was no difference in offset between tree, shrub and herbaceous growth forms.

As the data are largely from extratropical, northern hemisphere localities, there is a significant correlation between growth and temperature (Table 2; Fig. S1). At the biome scale, subtropical plants were significantly different from all other biomes, with the peak in root growth occurring 45 ± 19 d ($n = 11$) earlier than shoot growth, whereas offset in boreal, Mediterranean, and temperate biomes occurred 48 ± 8 ($n = 20$), 36 ± 19 ($n = 11$), and 28 ± 12 d ($n = 45$) after shoot production, respectively (Fig. 2a). The generally late root relative to shoot growth in boreal biomes might, however, be confounded with tree growth form. Conifer ($n = 14$) root growth peaked 44 ± 12 d later than deciduous tree species ($n = 20$, Fig. 2b).
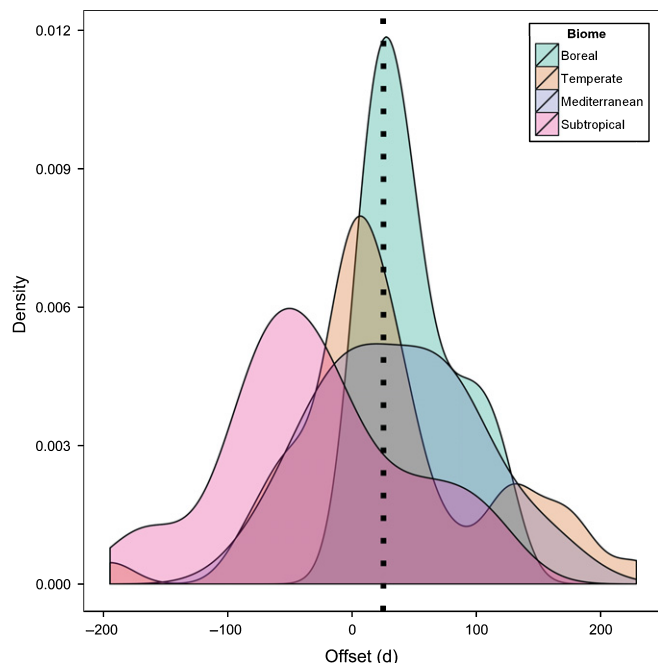
Similar to temperature, there is a positive linear correlation between growth and mean monthly precipitation (MMP) in boreal and subtropical biomes (Table 2). In these biomes, median monthly temperature (MMT) and MMP are highly correlated ($\rho = 0.89$ and $\rho = 0.85$ for boreal and subtropical climate variables, respectively), so it is difficult to separate the precipitation from the temperature effect. By contrast, precipitation predicts growth poorly in temperate and Mediterranean biomes (Table 2). In the temperate data set, precipitation did not have large seasonal variation (Fig. 3b). In the Mediterranean data set, shoot growth occurs in a large spring pulse following winter rain, whereas root growth appears to proceed at a steadily rising rate over the year (Fig. 3c).

To visualize the phenology of root relative to shoot growth, we plotted the proportion of peak root growth as a function of peak shoot growth and generated a hysteresis plot for each biome. Deviations from the 1 : 1 line indicate dominance of root relative to shoot growth (or vice versa) across the year (Fig. 3e–h). In boreal ecosystems, root growth remains low throughout spring shoot expansion with the largest proportion of root growth observed in the summer through autumn (Fig. 3e). In temperate ecosystems, however, root growth is entirely proportional to shoot growth, with all data plotting closely to the 1 : 1 line (Fig. 3f). The Mediterranean observations are unlike the others. There is no clear hysteresis between root and shoot growth (Fig. 3g). The subtropical biome is similar to the temperate biome in that root growth mirrors shoot growth not deviating from the 1 : 1 line (Fig. 3h).

Some implications of the data

The available data suggest that root and shoot growth is largely asynchronous. At broad spatial scales, temperature and precipitation influence this asynchrony, for example, the positive offset between peak shoot and root growth with decreasing annual temperatures (data not shown). As suggested by Steinaker &

Fig. 1 Kernel density curve of the offset (in d) between the maximum in root and shoot production (offset = $DOY_{maximum\ root} - DOY_{maximum\ shoot}$, where DOY refers to day of year from 1 to 365) in 63 tree, shrub, and herbaceous species from 40 studies (Supporting Information, Table S2), grouped by biome. The black vertical dotted line is the grand mean of all offset values.

Table 2 Regression statistics for the proportion of maximum monthly root or shoot growth as a function of median monthly temperature (MMT) or mean monthly precipitation (MMP)

Biome	Organ	MMT	R^2_{adj}	MMP	R^2_{adj}
All biomes	Root	0.02***	0.48	0.01*	0.09
	Shoot	0.01**	0.21	0.01**	0.17
Boreal	Root	0.02***	0.79	0.01***	0.83
	Shoot	0.02*	0.47	0.01**	0.67
Temperate	Root	0.02***	0.80	0.01**	0.01
	Shoot	0.02***	0.75	0.011^{NS}	0.01
Mediterranean	Root	0.01^{NS}	0.01	0.01^{NS}	0.18
	Shoot	0.01^{NS}	0.00	0.01^{NS}	0.01
Subtropical	Root	0.05**	0.61	0.01*	0.37
	Shoot	0.04*	0.38	0.01*	0.31

The slope estimates (β) for MMT are in units of growth °C^{-1} and MMP growth mm^{-1} precipitation. Significant variables and overall model significance are indicated by the following: NS, not significant; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.
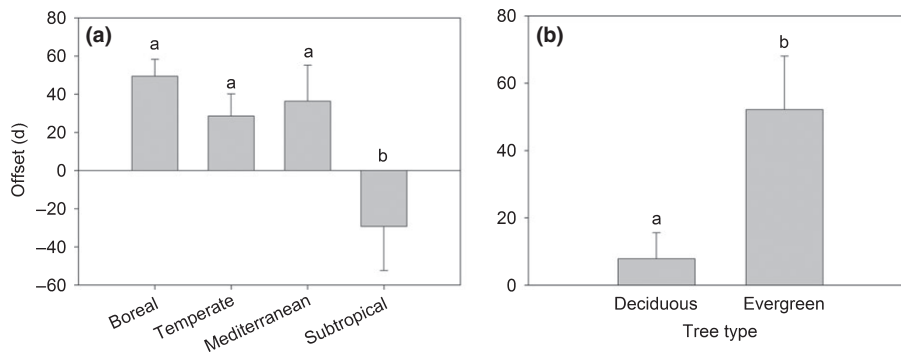
Fig. 2 (a) Offset (in d) between maximum shoot and root production for 87 observations averaged across four biomes: boreal, temperate, Mediterranean, and subtropical (Table S2). Letters indicate a statistically significant difference in means ($\alpha = 0.05$) calculated using Tukey's honestly significant difference (HSD) after one-way ANOVA (offset ~ biome + root collection method; biome, $F_{3,80} = 5.0$, $P = 0.0032$; root collection method, $F_{3,80} = 2.67$, $P = 0.053$; model, $F_{6,80} = 3.83$, $P = 0.0021$). (b) Deciduous ($n = 20$) trees had a significantly smaller offset than did evergreen ($n = 14$) trees (ANOVA, $F_{1,32} = 7.52$, $P = 0.009$).
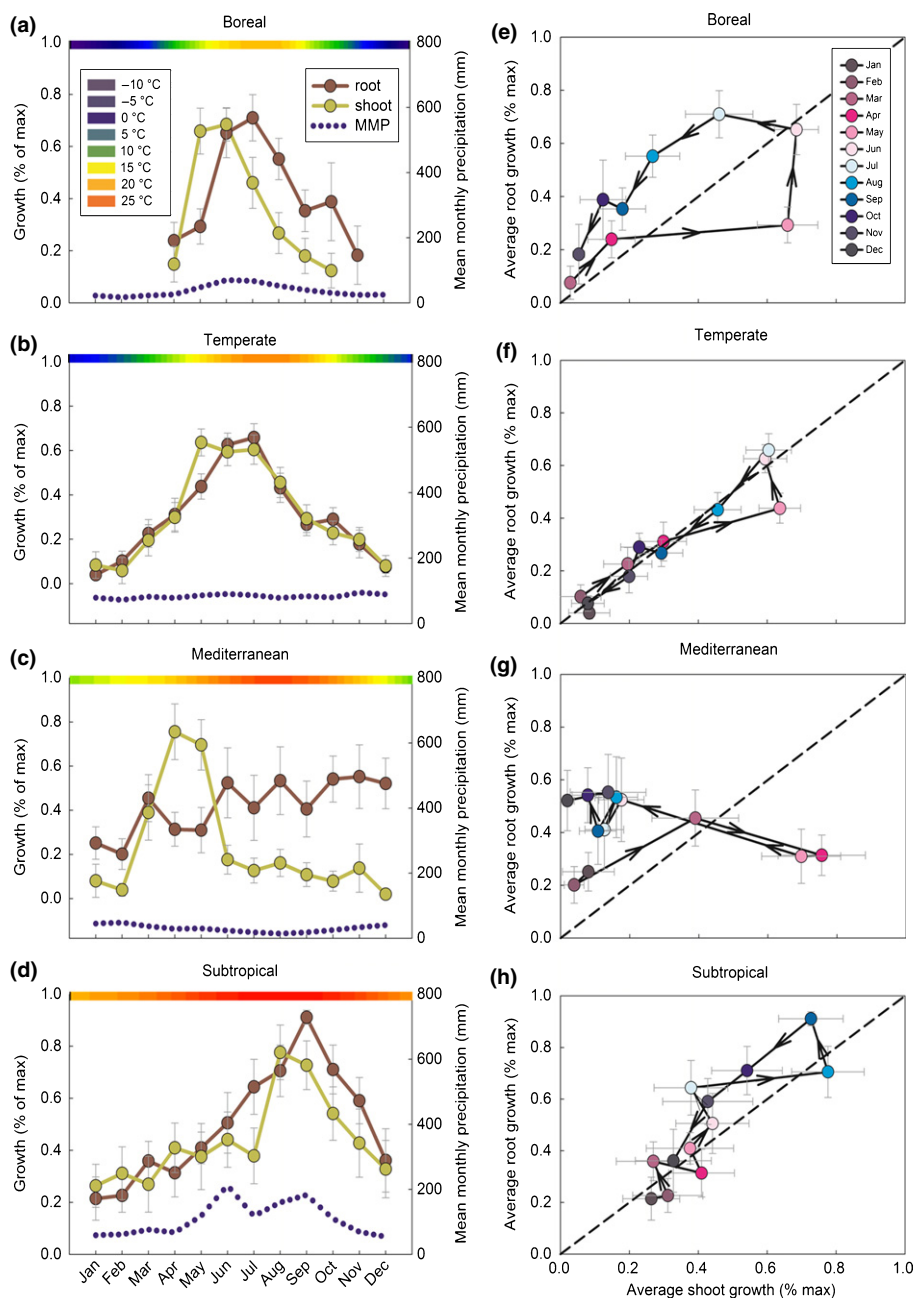

Fig. 3 The proportion of maximum monthly root and shoot growth for each month in: (a) boreal, (b) temperate, (c) Mediterranean, and (d) subtropical biomes (Table S3). In panels (a)–(d), dark brown corresponds to root growth and light green is shoot growth. The blue dotted line is mean monthly precipitation (mm, right-hand side y-axis). The color bar across the top is a heat map showing seasonal temperatures ranging from −10°C (purple) to 25°C (red), with 0°C as bright blue. Panels (e)–(h) plot the proportion of maximum monthly root vs shoot growth. In these panels, black lines join consecutive months and the direction of the arrowheads indicates time from January to December. This approach assumes that shoot growth is a suitable proxy for the initiation of photosynthesis. Calculating the proportion of peak root or shoot growth rather than absolute growth rates enables us to plot the different types of data on the same y-axis (i.e. minirhizotron vs soil coring). Note that these proportions are not a probability distribution function (i.e. area under the curve ≠ 1) and that no point equals 1, because multiple studies with differently timed maximum growth were averaged.

Wilson (2008), air temperature rises more rapidly than soil temperature in the spring and hence root growth is delayed later into the spring or summer (Fig. 3a–d). The boreal dataset supports this hypothesis. A corollary to this observation is that thermal buffering allows soils to remain warm through the autumn and, as a result, the duration of root production can be 40% longer than shoot production (Steinaker & Wilson, 2008; Steinaker *et al.*, 2010). Once again, this observation is strongly supported by the boreal zone data set (Fig. 3a).

There is, however, at least as much variation in the offset between peak root and shoot growth within and between biomes as that explained by climate variables (Table 2). This leads to the ecologically interesting hypothesis that endogenous control of plant C allocation is an important driver of root phenology. What evidence is there in support of this hypothesis?

For the purposes of this paper, we define endogenous cuing as any factor that influences the growth of roots other than direct effects of temperature and precipitation. One of the clearest examples of endogenous root cuing is the production, storage and transport of photoassimilate (Pregitzer *et al.*, 2000; Palmroth *et al.*, 2006). There are important stores of carbohydrates in plants that can fuel production (Richardson *et al.*, 2013), and root growth depends on these stores as well as newly fixed C from above-ground organs. Isotopic labeling studies have confirmed that substantial C used in root biomass is newly fixed (Keel *et al.*, 2006; Trumbore *et al.*, 2006). Root growth stops or is greatly reduced in response to experimental manipulations such as girdling and stem chilling that cut off the supply of photoassimilates from the canopy (Högberg *et al.*, 2001; Johnsen *et al.*, 2006), and thus below-ground phenology must be in part regulated by above-ground phenology (Litton *et al.*, 2007).

Does the difference in root growth phenology implicate the supply of photoassimilate? It does appear to provide a parsimonious explanation. Leaf area and photosynthetic rates in temperate deciduous forests tend to be highest in the spring and decline through late summer and rapidly in autumn as a consequence of canopy senescence (Wu *et al.*, 2010). This seasonality is highly synchronous with the most active period of root growth, and the progressive summer decline in photosynthesis and autumnal leaf senescence correlates with reductions in root growth (Fig. 3f). The prolonged autumnal root growth in the boreal zone may also reflect photoassimilate control in that the retention of live needles in the canopy sustains the supply of photoassimilate even as temperatures cool and day length declines (but soils stay warm). Additional support for photoassimilate-regulated autumnal root growth is observed when separating the boreal dataset into evergreen trees vs deciduous woody and herbaceous species. Doing so shows that autumnal root growth in evergreen trees dominates the hysteresis (Fig. S2a) in Fig. 3(f). Autumnal root growth in the deciduous plants follows that found in the temperate biome data (i.e. maximum root growth in the spring and very little in the autumn; Fig. S2b). Boreal evergreen trees may also utilize stored C during late-season root growth (Nordgren *et al.*, 2003).

The subtropical and Mediterranean data are challenging to interpret. The subtropical data come from evergreen species, largely palms, in a consistently warm environment, yet there is a distinct phenology in shoot and root production, with the peak in both following the wettest months of the year (Fig. 3d). We speculate that the distinct phenology may be analogous to observations from seasonally dry Amazonian rainforests where evapotranspiration rates are highest in the dry season (Hutyra *et al.*, 2007) because of reductions in cloudiness and light limitation of photosynthesis (Restrepo-Coupe *et al.*, 2013). It is possible that the reduction in late summer and autumnal precipitation is sufficiently large that photosynthetically active radiation does not limit photosynthesis during this period of time and peak growth occurs.

The Mediterranean observations are the most challenging to interpret under the assumption that the majority of C used for root growth is newly fixed. Shoot growth and root growth are not correlated with MMT or MMP and root growth is apparently decoupled from shoot growth (Fig. 3g). The one exception is a concentrated pulse of vernal shoot growth following winter precipitation and the delay in peak root relative to shoot growth (Fig. 3c). The strong asynchrony between shoot and root growth that extends across the year, however, suggests that endogenous cuing and subsequent allocation of stored carbohydrates are dominant drivers of root growth in Mediterranean plants. Root and stem nonstructural carbohydrates generally decline during the growing season and reaccumulate in autumn (Loescher *et al.*, 1990; Richardson *et al.*, 2013), as stored carbohydrates are allocated to respiration and growth during the growing season. However, limited data availability in this biome may prevent any meaningful conclusions.

Finally, we note that the timescale of the data analysis here cannot address the occurrence of alternating above- and below-ground growth, for example, as found in *Quercus* spp. (Reich *et al.*, 1980; Cardon *et al.*, 2002). Whether this is common is not well known, but at least these data suggest coordination of C allocation across the growing season, which may be mediated by both above- and below-ground plant organs. For example, roots produce and transport several shoot-regulating hormones acropetally, such as abscisic acid, cytokinin and strigolactone, that can affect stomatal closure, shoot and bud growth, respectively (Sharp, 2002; Domagalska & Leyser, 2011). Roots may also control photoassimilate transport by modifying the rate that photoassimilates in the phloem are taken up by root tissues (Patrick, 1997) that feed back to genetic regulatory networks (Koch, 1996). Numerous studies provide support for shared control of C allocation (Farrar & Jones, 2008; Davidson & Holbrook, 2009).

Moving forward

At the extreme, root and shoot phenology can be offset by ± 200 d, and both are mechanistically linked by temperature, water, and C allocation. This dataset establishes possible generalizations regarding root and shoot phenology based on biome and growth form (evergreen, deciduous). Temperature and moisture are positively correlated with the phenology of both shoot and root growth in three of four biomes, suggesting that abiotic factors affect root physiology, both directly and indirectly. Endogenous factors (allocation of photoassimilate, source–sink dynamics, hormonal control) are also likely to be important drivers of phenology, but as

yet we are not able to draw any broad conclusions, with the possible exception that photoassimilate supply, storage and transport are key drivers of root growth phenology. The temperature hysteresis in Fig. 3 provides support for endogenous controls – particularly the boreal and Mediterranean datasets. At the present time, there are few data available in the literature, probably because of the difficulty in making measurements of seasonal root growth. Current datasets are derived from techniques that are relatively indirect (soil respiration), often destructive (coring), labor-intensive (minirhizotrons) and hence expensive to implement. In addition to the paucity of data, many methods are difficult to compare, often with known biases (e.g. minirhizotron vs isotopic methods, Guo *et al.*, 2008), and suffer from chronic undersampling (Taylor *et al.*, 2013). However, for our purposes these methods capture temporal change in root length or biomass well enough to characterize its timing, although perhaps not its magnitude. We hope that improved scaling methods (Taylor *et al.*, 2014) and standardization across large networks (Keller, 2010) will alleviate sampling difficulties and allow for more accurate and generalizable data to emerge over time. Root growth is an important conduit for photosynthetically fixed C into the soil, with well-established feedbacks on C and N cycling (Drake *et al.*, 2011; Schmidt *et al.*, 2011; Brzostek *et al.*, 2013; Averill *et al.*, 2014). Quantitative models assume that the phenology of root growth is synchronous with that of above-ground phenology, despite empirical evidence to the contrary. Whether the addition of below-ground phenology will affect total C efflux in terrestrial biosphere models is presently unknown. In the temperate biome, where phenology is largely in sync, such a change may be unnecessary, but in boreal biomes, late-season root allocation may explain observed fall increases in soil respiration that are currently poorly explained by temperature and soil moisture (Davidson *et al.*, 2006; Giasson *et al.*, 2013). As both root growth and decomposition are known to be temperature-sensitive, and the latter also substrate-limited, understanding the phenology and drivers of above- vs below-ground C allocation is important for estimating ecosystem C fluxes under global change.

Acknowledgements

References

Averill C, Turner BL, Finzi AC. 2014. Mycorrhiza-mediated competition between plants and decomposers drives soil carbon storage. *Nature* **505**: 543–545.

Bevington KB, Castle WS. 1985. Annual root growth pattern of young citrus trees in relation to shoot growth, soil temperature, and soil water content. *Journal of the American Society for Horticultural Science* **110**: 840–845.

Broschat TK. 1998. Root and shoot growth patterns in four palm species and their relationships with air and soil temperatures. *HortScience* **33**: 995–998.

Brzostek ER, Greco A, Drake JE, Finzi AC. 2013. Root carbon inputs to the rhizosphere stimulate extracellular enzyme activity and increase nitrogen availability in temperate forest soils. *Biogeochemistry* **115**: 65–76.

Cardon ZG, Czaja AD, Funk JL, Vitt PL. 2002. Periodic carbon flushing to roots of *Quercus rubra* saplings affects soil respiration and rhizosphere microbial biomass. *Oecologia* **133**: 215–223.

Cox PM. 2001. Description of the TRIFFID dynamic global vegetation model. *Hadley Centre Technical Note* **24**: 1–16.

Davidson EA, Holbrook NM. 2009. Is temporal variation of soil respiration linked to the phenology of photosynthesis? In: Noormets A, ed. *Phenology of ecosystem processes*. New York, NY, USA: Springer, 187–199.

Davidson EA, Janssens IA, Luo Y. 2006. On the variability of respiration in terrestrial ecosystems: moving beyond Q10. *Global Change Biology* **12**: 154–164.

Domagalska MA, Leyser O. 2011. Signal integration in the control of shoot branching. *Nature Reviews Molecular Cell Biology* **12**: 211–221.

Drake JE, Gallet-Budynek A, Hofmockel KS, Bernhardt ES, Billings SA, Jackson RB, Johnsen KS, Lichter J, McCarthy HR, McCormack ML et al. 2011. Increases in the flux of carbon belowground stimulate nitrogen uptake and sustain the long-term enhancement of forest productivity under elevated CO_2. *Ecology Letters* **14**: 349–357.

Drew A, Ledig FT. 1980. Episodic growth and relative shoot: root balance in loblolly pine seedlings. *Annals of Botany* **45**: 143–148.

Farrar J, Jones D. 2008. The control of carbon acquisition by roots. *New Phytologist* **147**: 43–53.

Friend AD, Stevens AK, Knox RG, Cannell MGR. 1997. A process-based, terrestrial biosphere model of ecosystem dynamics (Hybrid v3.0). *Ecological Modelling* **95**: 249–287.

Friend AD, White A. 2000. Evaluation and analysis of a dynamic terrestrial ecosystem model under preindustrial conditions at the global scale. *Global Biogeochemical Cycles* **14**: 1173–1190.

Fukuzawa K, Shibata H, Takagi K, Satoh F, Koike T, Sasa K. 2013. Temporal variation in fine-root biomass, production and mortality in a cool temperate forest covered with dense understory vegetation in northern Japan. *Forest Ecology and Management* **310**: 700–710.

Giasson M-A, Ellison AM, Bowden R, Crill PM, Davidson E, Drake J, Frey S, Hadley J, Lavine M, Melillo J. 2013. Soil respiration in a northeastern US temperate forest: a 22-year synthesis. *Ecosphere* **4**: 140.

Grier CC, Vogt KA, Keyes MR, Edmonds RL. 1981. Biomass distribution and above-and below-ground production in young and mature *Abies amabilis* zone ecosystems of the Washington Cascades. *Canadian Journal of Forest Research* **11**: 155–167.

Guo DL, Li H, Mitchell RJ, Han WX, Hendricks JJ, Fahey TJ, Hendrick RL. 2008. Fine root heterogeneity by branch order: exploring the discrepancy in root turnover estimates between minirhizotron and carbon isotopic methods. *New Phytologist* **177**: 443–456.

Harris JR, Bassuk NL, Zobel RW, Whitlow TH. 1995. Root and shoot growth periodicity of green ash, scarlet oak, turkish hazelnut, and tree lilac. *Journal of the American Society for Horticultural Science* **120**: 211–216.

Hendrick RL, Pregitzer KS. 1996. Temporal and depth-related patterns of fine root dynamics in northern hardwood forests. *Journal of Ecology* **84**: 167–176.

Högberg P, Nordgren A, Buchmann N, Taylor AFS, Ekblad A, Högberg MN, Nyberg G, Ottosson-Löfvenius M, Read DJ. 2001. Large-scale forest girdling shows that current photosynthesis drives soil respiration. *Nature* **411**: 789–792.

Hutyra LR, Munger JW, Saleska SR, Gottlieb E, Daube BC, Dunn AL, Amaral DF, de Camargo PB, Wofsy SC. 2007. Seasonal controls on the exchange of carbon and water in an Amazonian rain forest. *Journal of Geophysical Research-Biogeosciences* **112**: G03008.

Jackson RB, Mooney HA, Schulze ED. 1997. A global budget for fine root biomass, surface area, and nutrient contents. *Proceedings of the National Academy of Sciences, USA* **94**: 7362–7366.

Johnsen K, Maier C, Sanchez F, Anderson P, Butnor J, Waring R, Linder S. 2006. Physiological girdling of pine trees via phloem chilling: proof of concept. *Plant, Cell & Environment* **30**: 128–134.

Joslin JD, Wolfe MH, Hanson PJ. 2001. Factors controlling the timing of root elongation intensity in a mature upland oak stand. *Plant and Soil* **228**: 201–212.

Keel SG, Siegwolf RTW, Korner C. 2006. Canopy CO_2 enrichment permits tracing the fate of recently assimilated carbon in a mature deciduous forest. *New Phytologist* 172: 319–329.

Keller M. 2010. NEON Scientific Data Products Catalog. [WWW document] URL http://www.neoninc.org/science/data [accessed 25 August 2014]

Koch K. 1996. Carbohydrate-modulated gene expression in plants. *Annual Review of Plant Biology* 47: 509–540.

Krám P, Santore RC, Driscoll CT, Aber JD, Hruška J. 1999. Application of the forest–soil–water model (PnET-BGC/CHESS) to the Lysina catchment, Czech Republic. *Ecological Modelling* 120: 9–30.

Krinner G, Viovy N, de Noblet-Ducoudré N, Ogée J, Polcher J, Friedlingstein P, Ciais P, Sitch S, Prentice IC. 2005. A dynamic global vegetation model for studies of the coupled atmosphere–biosphere system. *Global Biogeochemical Cycles* 19: GB1015, doi: 10.1029/2003GB002199.

Lahti M, Aphalo P, Finér L, Ryyppö A, Lehto T, Mannerkoski H. 2005. Effects of soil temperature on shoot and root growth and nutrient uptake of 5-year-old Norway spruce seedlings. *Tree Physiology* 25: 115–122.

Landsberg J, Waring R. 1997. A generalised model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning. *Forest Ecology and Management* 95: 209–228.

Levy P, Cannell M, Friend A. 2004. Modelling the impact of future changes in climate, CO_2 concentration and land use on natural ecosystems and the terrestrial carbon sink. *Global Environmental Change* 14: 21–30.

Litton CM, Raich JW, Ryan MG. 2007. Carbon allocation in forest ecosystems. *Global Change Biology* 13: 2089–2109.

Loescher WH, McCamant T, Keller JD. 1990. Carbohydrate reserves, translocation, and storage in woody plant roots. *HortScience* 25: 274–281.

McCormack ML, Adams TS, Smithwick EAH, Eissenstat DM. 2014. Variability in root production, phenology, and turnover rate among 12 temperate tree species. *Ecology* 95: 2224–2235.

McGuire AD, Sitch S, Clein JS, Dargaville R, Esser G, Foley J, Heimann M, Joos F, Kaplan J, Kicklighter DW et al. 2001. Carbon balance of the terrestrial biosphere in the Twentieth Century: Analyses of CO_2, climate and land use effects with four process-based ecosystem models. *Global Biogeochemical Cycles* 15: 183–206.

Medvigy D, Wofsy SC, Munger JW, Hollinger DY, Moorcroft PR. 2009. Mechanistic scaling of ecosystem function and dynamics in space and time: Ecosystem Demography model version 2. *Journal of Geophysical Research-Biogeosciences* 114: G01002.

Mickelbart MV, Robinson PW, Witney G, Arpaia ML. 2012. 'Hass' avocado tree growth on four rootstocks in California. II. Shoot and root growth. *Scientia Horticulturae* 143: 205–210.

Misson L, Gershenson A, Tang J, McKay M, Cheng W, Goldstein A. 2006. Influences of canopy photosynthesis and summer rain pulses on root dynamics and soil respiration in a young ponderosa pine forest. *Tree Physiology* 26: 833–844.

Noguchi K, Nagakura J, Konôpka B, Sakata T, Kaneko S, Takahashi M. 2013. Fine-root dynamics in sugi (*Cryptomeria japonica*) under manipulated soil nitrogen conditions. *Plant and Soil* 364: 159–169.

Nordgren A, Ottosson Löfvenius M, Högberg M, Mellander PE, Högberg P. 2003. Tree root and soil heterotrophic respiration as revealed by girdling of boreal Scots pine forest: extending observations beyond the first year. *Plant, Cell & Environment* 26: 1287–1296.

Oleson KW, Lawrence DM, Bonan GB, Flanner MG, Kluzek E, Lawrence PJ, Levis S, Swenson SC, Thornton PE, Dai A et al. 2010. *Technical description of version 4.0 of the Community Land Model (CLM)*. Boulder, CO, USA: NCAR Tech.

Palacio S, Montserrat-Marti G. 2007. Above and belowground phenology of four Mediterranean sub-shrubs. Preliminary results on root-shoot competition. *Journal of Arid Environments* 68: 522–533.

Palmroth S, Oren R, McCarthy HR, Johnsen KH, Finzi AC, Butnor JR, Ryan MG, Schlesinger WH. 2006. Aboveground sink strength in forests controls the allocation of carbon below ground and its CO_2-induced enhancement. *Proceedings of the National Academy of Sciences* 103: 19362–19367.

Patrick J. 1997. Phloem unloading: sieve element unloading and post-sieve element transport. *Annual Review of Plant Biology* 48: 191–222.

Ploetz RC, Ramos JL, Parrado JL, Lovatt C. 1992. Shoot and root growth phenology of grafted avocado. In: Lovatt CJ, Holthe PA, Arpaia ML, eds.

Proceedings of Second World Avocado Congress. Riverside, CA, USA: University of California, 215–220.

Pregitzer KS, King JS, Burton AJ, Brown SE. 2000. Responses of tree fine roots to temperature. *New Phytologist* 147: 105–115.

Reich PB, Teskey RO, Johnson PS, Hinckley TM. 1980. Periodic root and shoot growth in oak. *Forest Science* 26: 590–598.

Restrepo-Coupe N, da Rocha HR, Hutyra LR, da Araujo AC, Borma LS, Christoffersen B, Cabral OM, de Camargo PB, Cardoso FL, da Costa ACL. 2013. What drives the seasonality of photosynthesis across the Amazon basin? A cross-site analysis of eddy flux tower measurements from the Brasil flux network. *Agricultural and Forest Meteorology* 182: 128–144.

Richardson AD, Carbone MS, Keenan TF, Czimczik CI, Hollinger DY, Murakami P, Schaberg PG, Xu X. 2013. Seasonal dynamics and age of stemwood nonstructural carbohydrates in temperate forest trees. *New Phytologist* 197: 850–861.

Scagel CF, Bi G, Fuchigami LH, Regan RP. 2007. Seasonal variation in growth, nitrogen uptake and allocation by container-grown evergreen and deciduous rhododendron cultivars. *HortScience* 42: 1440–1449.

Schmidt MW, Torn MS, Abiven S, Dittmar T, Guggenberger G, Janssens IA, Kleber M, Kögel-Knabner I, Lehmann J, Manning DA. 2011. Persistence of soil organic matter as an ecosystem property. *Nature* 478: 49–56.

Sharp R. 2002. Interaction with ethylene: changing views on the role of abscisic acid in root and shoot growth responses to water stress. *Plant, Cell & Environment* 25: 211–222.

Sitch S, Smith B, Prentice IC, Arneth A, Bondeau A, Cramer W, Kaplan J, Levis S, Lucht W, Sykes M. 2003. Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model. *Global Change Biology* 9: 161–185.

Sloan JL, Jacobs DF. 2008. Carbon translocation patterns associated with new root proliferation during episodic growth of transplanted *Quercus rubra* seedlings. *Tree Physiology* 28: 1121–1126.

Smith B, Wårlind D, Arneth A, Hickler T, Leadley P, Siltberg J, Zaehle S. 2013. Implications of incorporating N cycling and N limitations on primary production in an individual-based dynamic vegetation model. *Biogeosciences Discussions* 10: 18613–18685.

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.

Taylor BN, Beidler KV, Cooper ER, Strand AE, Pritchard SG. 2013. Sampling volume in root studies: the pitfalls of under-sampling exposed using accumulation curves. *Ecology Letters* 16: 862–869.

Taylor BN, Beidler KV, Strand AE, Pritchard SG. 2014. Improved scaling of minirhizotron data using an empirically-derived depth of field and correcting for the underestimation of root diameters. *Plant and Soil* 374: 941–948.

Thornton PE, Zimmermann NE. 2007. An improved canopy integration scheme for a land surface model with prognostic canopy structure. *Journal of Climate* 20: 3902–3923.

Trumbore S, Da Costa ES, Nepstad DC, Barbosa De Camargo P, Martinelli LA, Ray D, Restom T, Silver W. 2006. Dynamics of fine root carbon in Amazonian tropical ecosystems and the contribution of roots to soil respiration. *Global Change Biology* 12: 217–229.

Weinstein DA, Beloin RM, Yanai RD. 1991. Modeling changes in red spruce carbon balance and allocation in response to interacting ozone and nutrient stresses. *Tree Physiology* 9: 127–146.

Whittaker RH. 1970. *Communities and ecosystems*. New York, NY, USA: Macmillan.

Willaume M, Pagès L. 2006. How periodic growth pattern and source/sink relations affect root growth in oak tree seedlings. *Journal of Experimental Botany* 57: 815–826.

Woodward F, Lomas M. 2004. Vegetation dynamics—simulating responses to climatic change. *Biological Reviews* 79: 643–670.

Woodward FI, Smith TM, Emanuel WR. 1995. A global land primary productivity and phytogeography model. *Global Biogeochemical Cycles* 9: 471–490.

Wu C, Munger JW, Niu Z, Kuang D. 2010. Comparison of multiple models for estimating gross primary production using MODIS and eddy covariance data in Harvard Forest. *Remote Sensing of Environment* **114**: 2925–2939.

Supporting Information

Additional supporting information may be found in the online version of this article.

Fig. S1 Proportion of root and shoot growth for data in all biomes plotted against median monthly temperature (°C).

Fig. S2 The relationship between root growth and MMT in boreal evergreen tree roots, and the relationship between root growth and MMT in boreal deciduous tree, shrub and herbaceous plant roots.

Table S1 Phenological relationships between above-ground and below-ground processes as well as potential drivers of below-ground phenology, their direction and strength of effect, if given

Table S2 Measurements from the literature used to quantify the offset between above-ground and below-ground growth peaks in Figs 1 and 2

Table S3 Monthly root and shoot growth rates for each biome estimated from the literature with temperature and precipitation data

Notes S1 Description of (1) paper selection criteria, statistical tests associated with (2) gross and net root production, (3) offset, and (4) monthly root and shoot growth, and (5) sources of temperature and precipitation data.

Please note: Wiley Blackwell are not responsible for the content or functionality of any supporting information supplied by the authors. Any queries (other than missing material) should be directed to the *New Phytologist* Central Office.

About *New Phytologist*

- *New Phytologist* is an electronic (online-only) journal owned by the New Phytologist Trust, a **not-for-profit organization** dedicated to the promotion of plant science, facilitating projects from symposia to free access for our Tansley reviews.

- Regular papers, Letters, Research reviews, Rapid reports and both Modelling/Theory and Methods papers are encouraged.
  We are committed to rapid processing, from online submission through to publication 'as ready' via *Early View* – our average time to decision is <25 days. There are **no page or colour charges** and a PDF version will be provided for each article.

- The journal is available online at Wiley Online Library. Visit **www.newphytologist.com** to search the articles and register for table of contents email alerts.

- If you have any questions, do get in touch with Central Office (np-centraloffice@lancaster.ac.uk) or, if it is more convenient, our USA Office (np-usaoffice@lancaster.ac.uk)

- For submission instructions, subscription and all the latest information visit **www.newphytologist.com**