Asynchrony in shoot and root phenological relationships in hybrid walnut

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Abstract

Understanding the processes driving plant phenology is crucial for assessing how shifts in climate affect plant productivity and species' distribution. Despite the key role of fine roots in carbon and nutrient cycling, root phenology is less well characterized than shoot phenology, due largely to methodological problems when measuring root systems at depths > 1.0 m. Fine root demography is also poorly related to the better established patterns of aboveground primary and secondary growth. We examined the influence of climatic factors on the dynamics of fine root elongation rate (RER), to a depth of 4.7 m, and assessed relationships with shoot phenology of walnut trees (*Juglans nigra* × *J. regia*) in a Mediterranean agroforestry system. Rhizotrons and minirhizotrons were installed for 21 months to monitor RER. Dendrometers were used to measure trunk and lateral root radial growth during the same period. Results showed that RER was not synchronous with budbreak and leaf unfolding (occurring from April to May) at any soil depth. However, during phase 2 of the growing season (June–November), daily RER in the upper soil (0.00–1.70 m) was synchronous with both trunk and lateral root radial growth, which were themselves positively correlated with the mean monthly soil and air temperatures and the mean monthly solar irradiance. Mean daily RER was not correlated to mean monthly soil and air temperatures at any soil depth during phase 2 of the growing season. However, during this period, mean daily RER of very shallow roots (0.00–0.85 m) was significantly and positively correlated with both mean monthly soil water content and solar irradiance. Maximal daily RER occurred during phase 2 of the growing season for the three upper soil layers (June–October), but peaked during the aerial dormant season (December) in the deepest soil layer (4.00–4.70 m). We conclude that drivers of phenology for different tree organs and between shallow and deep roots are not the same. This spatial plasticity in growth throughout a tree enables it to maximize resource uptake, even throughout the winter months, and thus is a highly useful mechanism for increasing tree resistance to abiotic stresses.

Keywords Phenology · *Juglans nigra* × *J. regia* · Root elongation rate · Deep roots · Trunk growth · Secondary growth

Introduction

In the current context of a changing climate, predicting the responses of ecosystems and vegetation to variations in temperature has become a major challenge for research (Casassa et al. 2007). Modifications in the timing of plant developmental stages are considered a reliable indicator of climate change (Donnelly et al. 2006; Slaney et al. 2007). Most studies to date have focused on shoot phenology (Bigras et al. 1996), largely because of the methodological difficulties encountered when measuring root growth, especially for deep roots (Norby and Jackson 2000; Maeght et al. 2013; McCormack et al. 2014). It is now necessary to better understand the environmental drivers of belowground phenology and relate them to patterns of aboveground phenology (McCormack et al. 2014).

The triggering of plant phenological phases can be affected by both biotic and abiotic factors. Air temperature is considered the most important environmental factor controlling the timing of aboveground growth (Wielgolaski 1999; Menzel 2003; Radville et al. 2016). Factors controlling root phenology are poorly understood, especially in different soil horizons (Laclau et al. 2013; Germon et al. 2017; Erktan et al. 2018). Roots growing near the soil surface are more likely to be in synchrony with aboveground growth and surface micro-climate, whereas deeper roots are influenced by water table dynamics (Canham et al. 2012), and their functioning can help maximize survivorship if environmental conditions deteriorate (Maeght et al. 2015; Germon et al. 2016). However, even when soil depth is considered, relationships between daily root elongation rate (RER) and abiotic factors can be contradictory. For example, Germon et al. (2016), studying hybrid walnut (*Juglans nigra × J. regia*) in a Mediterranean climate found that RER in shallow fine roots was most strongly correlated with soil temperature, but measuring the same trees 1 year later, Mohamed et al. (2017a, b), found that RER was principally driven by increasing soil water potential. In a meta-analysis of data on root demography, Abramoff and Finzi (2015) further suggested that endogenous factors and allocation of stored carbohydrates are important drivers of superficial root growth in a Mediterranean climate. Therefore, RER is influenced by a variety of abiotic and endogenous factors, the strength of each depending on the local micro-environment and dynamics of tree functioning. Disentangling the different factors is challenging, especially for adult trees, and requires a detailed study of root demography with soil depth and in relation to aboveground growth.

As shoots and roots are dependent on each other for resources (Steinaker et al. 2010), an understanding of the synchrony between shoot and root growth should improve our understanding of whole plant functioning (Du and Fang 2014). Several studies showed that shoot and superficial root growth were synchronous (Misson et al. 2006; Germon et al. 2016), whereas other studies indicated the existence of an asynchronous relationship. For example, shoot growth was shown to precede root growth by several weeks or months, e.g., in Mediterranean, arctic, boreal and temperate biomes (Abramoff and Finzi 2015). In contrast, root growth may precede shoot growth in subtropical biomes (Abramoff and Finzi 2015). The possible reason for asynchrony in root and shoot phenology can be because above- and belowground organs are either under different controls or they are both competing for photosynthates (Radville et al. 2016). Investigating environmental factors and source–sink relationships controlling both root and shoot growth is fundamental to understanding how plants may acclimate to a changing climate. Hence, synchronous measurements of the phenology of different plant organs (i.e., leaf, trunk structural roots and fine roots) are essential to better understand the seasonal carbon (C) allocation within a plant and therefore whole plant responses to shifts in climate (Steinaker and Wilson 2008; Sloan et al. 2016).

Agroforestry systems associating trees with farming practices (Somarriba 1992; Cardinael et al. 2015) may play an important role in climate change mitigation (Ramachandran Nair et al. 2009). The alley cropping system is one of the most established agroforestry practices in temperate regions (Cardinael et al. 2015), and offers a number of ecosystem services (Jose 2009; Newaj et al. 2016). Trees contribute to soil C enrichment through an increase in leaf litter, and a greater water infiltration and retention in the soil profile as soil porosity is improved (Gyssels et al. 2005; Newaj et al. 2016). In addition, tree roots are able to expand over a large volume of soil for water and nutrient uptake and in doing so, improve soil structure, thus deep fine roots can also play a crucial role in soil C sequestration (Maeght et al. 2015). Yet, there are still major uncertainties about the mechanisms that control fine root phenology in these systems, especially in deep soil horizons.

We measured RER of fine roots at different soil depths (down to 4.70 m) of walnut trees (*Juglans nigra × J. regia*) growing in an alley cropped Mediterranean agroforestry system. We focused on relating fine root phenology to leaf, trunk and structural root phenology. We asked whether shoot phenology reflects or differs from fine root phenology at different depths. Root phenological measurements were performed using rhizotrons and minirhizotrons installed in a 4.0 m deep pit. We hypothesized that (1) shoot and root growth is asynchronous and under different drivers, (2) the drivers of fine root elongation are not the same between soil depths.

Materials and methods

Study site

The agroforest was located at the Restinclières experimental site, 15 km north of Montpellier, Department Hérault, France (43°43′N, 4°01′E, elevation 54 m a.s.l.) (Fig. S1). The climate is sub-humid Mediterranean with a mean annual temperature of 15.4 °C and a mean annual rainfall of 873 mm. The study plot comprised hybrid walnut trees (*Juglans nigra × J. regia*. cv. NG23) (at 13 × 4 m tree spacing) intercropped with durum wheat [*Triticum turgidum* L. subsp. *durum* (*Desf.*) Husn]. However, rapeseed (*Brassica napus* L.) was also cultivated in 1998, 2001 and 2006, and pea (*Pisum sativum* L.) in 2010 and 2016 (Mohamed et al. 2017b). All walnut trees were planted in 1995 in lines oriented east–west, and the density at the time of this study (2014–2015) was 110 trees ha^{-1}. The annual crop was fertilized with approximately 150 kg N ha^{-1} year^{-1} (Cardinael et al. 2015). The soil is a silty clay deep alluvial soil (25% clay and 60% silt) (depth > 4 m) and slope angle is negligible within the site (Mulia and Dupraz 2006). The average pH is 8.0 (Dupraz et al. 1999). The site is near the Lez river watershed and the depth from the soil surface to the water table usually oscillates between 5 m in winter and 7 m in summer (Cardinael et al. 2015). More details about the experimental site are available in Dupraz et al. (1999), Mulia and Dupraz (2006) and Cardinael et al. (2015). Mean DBH of all walnut trees at the site was 0.24 ± 0.13 m and mean height was 11.09 ± 2.50 m.

Rhizotron installation

To measure walnut root elongation, we installed rhizotrons and minirhizotrons in the same stand (Reich et al. 1980; Misra 1999; Germon et al. 2016). In November 2011, six minirhizotron tubes (105 cm length × 7.6 cm diameter) were installed. Each tube was placed
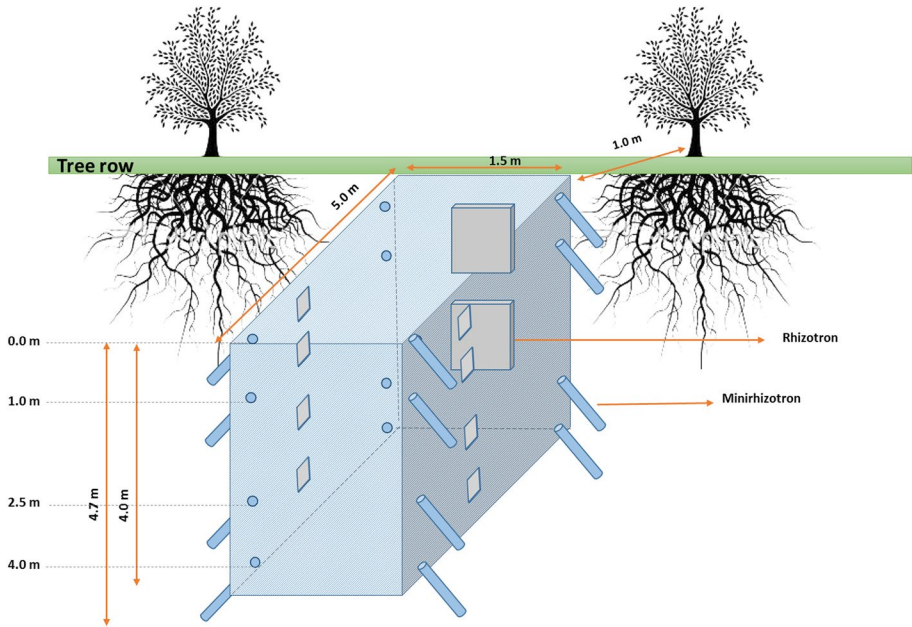
Fig. 1 The 4 m deep pit was situated between two walnut (*Juglans nigra* × *J. regia*. cv. NG23) trees, with rhizotrons (windows) and minirhizotrons (tubes) installed at different depths. Minrhizotrons at depths of 0.0, 1.0, 2.5 and 4.0 m and rhizotrons at depths of 0.2, 1.1, 2.0 and 2.8 m

between two trees in different lines of trees and each tube was inserted into the soil at an angle of 45°. The top of the tube was situated at the soil surface. In March 2012, one pit (5 m length × 1.5 m width × 4 m depth) was dug between two walnut trees on the same tree row (Cardinael et al. 2015). The pit was reinforced with wooden beams to avoid collapse of the pit walls. In June 2012, 16 minirhizotron tubes identical to those installed in the field were installed in the pit. Tubes were inserted into the soil wall of the pit at an angle of 45°, and the tube window covered a surface area of 0.7 m² of soil. Tubes were installed at different depths, with the uppermost end of the tube located at depths of 0.00, 1.00, 2.50 and 4.00 m. Each tube was closed with a black cap to prevent light entering (Cardinael et al. 2015).

Rhizotrons comprised transparent polyvinylchloride (PVC) sheets placed against the soil profile. In June 2014, two larger rhizotrons (100 cm long × 80 cm wide × 0.5 cm thick) were installed, as well as eight smaller rhizotrons (50 cm long × 30 cm wide × 0.5 cm thick) at depths of 2.00, 1.10, 2.00 and 2.80 m (Fig. 1). To prepare the soil surface for rhizotron installation, we gently removed soil and cut all roots on the soil wall with secateurs. The soil removed during the digging of the trenches was kept aside, and then sieved through a 5 mm sieve and air-dried for several hours (Mao et al. 2013; Wang et al. 2018). Panes of Plexiglas© were placed against the soil profile at an angle of 15° from the vertical so that roots would grow downwards along the pane (Huck and Taylor 1982). The sieved and air-dried soil was then poured into the space between the plexiglas© and the soil profile and compacted using a wooden plank. Each rhizotron was covered with foil backed felt insulation and black plastic sheeting to protect roots from light and temperature variations. The pit was then covered with a metallic roof to avoid damage from passing animals and to prevent direct rainfall and sunlight

on both rhizotrons and minirhizotrons (Fig. S2) (Cardinael et al. 2015). In September 2014, the trench was flooded due to exceptionally strong rainfall (Fig. S3), therefore, all rhizotrons were reinstalled in March 2015. Root growth and initiation data from March to June 2015 were not used in statistical analyses because when roots are cut during rhizotron installation, subsequent root growth is greater than usual for at least 3 months (Strand et al. 2008). Monthly measurements of root elongation rate (RER) were carried out immediately after root initiation and until June 2015.

Measurements of root growth

To measure fine root growth and initiation, we scanned rhizotrons and minirhizotrons and then analyzed images (Mohamed et al. 2017a, b). A scan of each rhizotron (between two and four images per window depending on the size of the window) was taken at monthly intervals over 12 months using an Epson Perfection V370 flatbed scanner with a high optical resolution of 4800 dpi (Fig. S4a). Similarly, a scan of each minirhizotron (five images of 21.59×19.56 cm per tube) was taken at monthly intervals over 21 months using a circular scanner (CI-600 Root Growth Monitoring System, CID, USA, Fig. S4b) (Graefe et al. 2008). We standardized the surface area of minirhizotrons and rhizotrons and combined data from both to calculate mean root number and mean RER for a given surface area. The total surface area of the rhizotron and the total number of growing roots differed between soil depths: 74 roots were measured over a surface area of 1.58 m^2 at a depth of 0.00–0.85 m; 49 roots were measured over a surface area of 1.54 m^2 at a depth of 0.85–2.00 m; 24 roots were measured over a surface area of 2.12 m^2 at a depth of 2.00–3.30 m and 22 roots were measured over a surface area of 0.84 m^2 at a depth of 4.00–4.70 m. Roots were classified into three diameter classes: 0–1 mm, 1–2 mm, and 2–5 mm (Mohamed et al. 2017b).

Image analysis

We analysed images of roots using the semi-automated SmartRoot software (Lobet et al. 2011) (Fig. S5). SmartRoot is an operating system independent freeware based on ImageJ and using cross-platform standards (RSML, SQL, and Java) for communication with data analysis softwares (Lobet et al. 2011; Mathieu et al. 2015). Before analyzing roots, it was necessary to stitch images together (e.g. with Adobe Photoshop CS3 software), if several were taken for the same rhizotron or minirhizotrons (because the window surface area was greater than the field of the scanners). We transformed all images to 8 bit gray scale and then inverted them using ImageJ software so that roots were darker than the background of the image. The length and diameter of each root produced during one interval time (i.e. 1 month) were calculated for each window. Before analyzing a new sequence of images, SmartRoot provides the user with an icon to import the previous data file on this new image, which helps the estimation of the evolution of root length. This preceding image also helps determine whether the root is live (usually cream in color) or dead (turning black) (Huck and Taylor 1982; Mao et al. 2013).

Aboveground phenology and trunk growth

We assessed the timing of shoot production through changes in the phenological phases of leaves throughout the year (Mohamed et al. 2017b). We divided the year into three phenological periods, phase 1 of the growing season (from budbreak to 100% leafing out of early green leaves), phase 2 of the growing season (100% leafing out to leaf-fall) and dormancy (leaf-fall to budbreak). From here on, unless otherwise specified, "growing season" refers to that of the aboveground parts of the tree, not the root system. Shoot phenological periods were recorded visually and weekly using binoculars. During the budbreak period, visual measurements were made daily. The number of days between the beginning and the end of each phenological stage was calculated to determine the duration in days of each phenological stage.

We also measured the radial growth of tree trunks by installing dendrometers (Increment Sensor DB20) on the trunk of eight trees. The dendrometers were girth bands, comprising a steel band, spring and nonius scale. Bands were placed on the trunk; at a height of 1.3 m. Measured values are read at the nonius scale with 0.1 mm precision (Fig. S6). We also installed five dendrometers near the base of five excavated structural roots of two trees. These structural roots were second order lateral roots initiated on the taproot (Fig. S6). Readings were made monthly. Tree height was recorded annually after leaf shedding using a hypsometer Vertex (Haglôf, Sweden).

Root growth dynamics

We used the following methods to estimate daily root elongation rate (RER) (Mohamed et al. 2017a, b):

1. Individual root growth was calculated as the difference between root length at $t-1$ and at t. To determine daily RER, the mean of all individual root lengths produced between time t and $t-1$ was divided by the duration of the corresponding period

$$RER_{t-1,t} = \frac{len._t - len._{t-1}}{P_{t-1,t}} \tag{1}$$

where RER $t-1$, t is the daily RER (in mm day^{-1}) from inventory time $t-1$ to t; len_{t-1} and len_t are the lengths of the root n at inventory time $t-1$ and t, respectively; $P_{t-1,t}$ is the period in days between inventory time $t-1$ and t.

Climatic measurements

Global precipitation and air temperature data were obtained from a weather station located at the field site. In April 2013, eight volumetric soil water (θ) sensors (CS 616, Campbell Scientific, USA) and eight temperature sensors (Campbell 107, Scientific, USA) were installed in the pit at four depths (0.5 m, 1.2 m, 3.0 m and 4.0 m) (two sensors per depth at distances of 1.5 m and 6 m from the tree row) (Cardinael et al. 2015). Soil temperature and θ were recorded every hour for 21 months from September 2014 to May 2016, using a datalogger (CR1000, Campbell Scientific, USA). Shortwave

radiation (total solar irradiance incident) was recorded hourly for 21 months, using a pyranometer (SP-110, Apogee Instruments Inc., USA) installed at a height of 2.0 m from the soil surface (Germon et al. 2016; Cardinael et al. 2015).

Statistical analysis

A Shapiro–Wilk test was performed before each statistical test to ensure if the investigated indicator followed a normal distribution, and homogeneity of variances was checked using Levene's test. For data not normally distributed, analyses were performed using a Kruskal–Wallis Test. Effects of season, soil depth, diameter classes were tested on RER. A post hoc analysis was performed when Kruskal–Wallis result was significant using Nemenyi test of Kruskal–Wallis at $p < 0.05$ to determine which levels of the independent variable differ from each other level. Box plots were used to describe daily RER depending on soil depth and root diameter class. Data shown are mean ± standard error. Spearman's rank correlations were performed to determine the relationships between mean daily RER and the climatic variables (mean soil and air temperatures and mean soil θ of the month preceding the measurement of RER). Monthly RER is the daily growth that has cumulated during the period preceding the new measurement (i.e., the current growth period). This growth rate therefore occurred between two measurement intervals and so was correlated to the climate data for the same period.

Severe flooding occurred from October to December 2014, and soil θ data from this period were not considered in the statistical analysis.

All analyses were performed using R software, Version 2.15.3 at a significance level of < 0.05.

Results

Climate data

Mean monthly soil temperatures were significantly higher in the upper soil layers (0.00–0.85 m and 0.85–1.70 m) (14 °C and 13.7 °C respectively) compared to the two deeper soil horizons (2.00–3.30 m and 4.00–4.70 m) (13.5 °C and 13.4 °C respectively). There were no significant differences in soil temperature between the two upper soil horizons (0.00–0.85 m, 0.85–1.70 m), nor between the two deeper soil horizons (2.00–3.30 m, 4.00–4.70 m) during phase 2 of the growing season (Fig. 2). Soil θ increased significantly with soil depth ($p < 0.001$, Fig. 2) and was 27.9% (at 0.00–0.85 m), 29.2% (at 0.85–1.70 m), 31.9% (at 2.00–3.30 m) and 33.2% (at 4.00–4.70 m). However, no significant differences were found in θ between soil depths of 2.00–3.30 m and 4.00–4.70 m. Total precipitation was highly variable between the 2 years, with 1264 mm in 2014 (severe flooding occurred from October to December 2014) and only 613 mm in 2015. During the entire study, the sum of precipitation during phase 2 of both growing seasons was 1053 mm and 654 mm in the dormant seasons. Mean global annual solar irradiance was 0.18 kw m^{-2} in 2015 and was 0.19 kw m^{-2} during phase 2 of the growing season over both years.
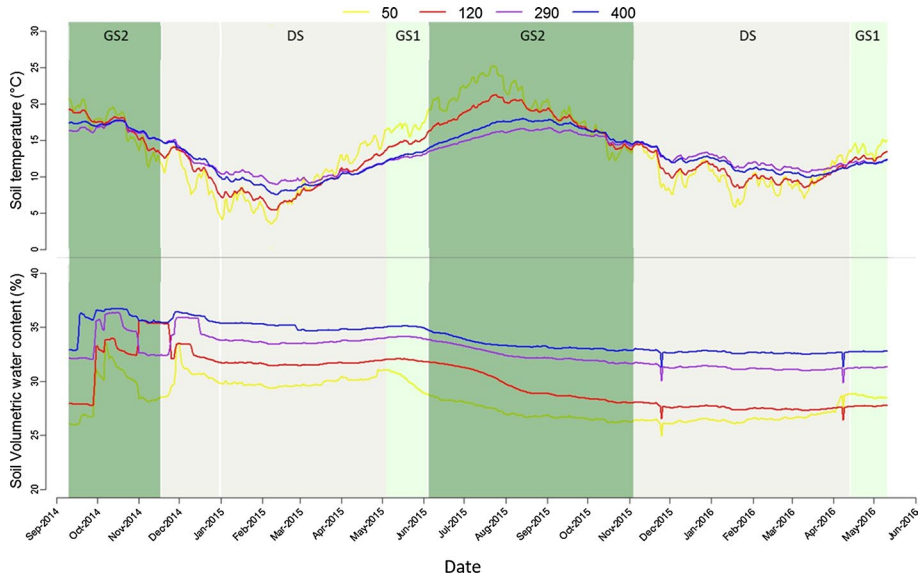
Fig. 2 Soil temperatures and volumetric water content from September 2014 to May 2016 at the four soil layers: 50 cm depth (yellow line), 120 cm depth (red line), 290 cm depth (purple line), and 400 cm depth (blue line). Different background colors correspond to different phenological periods: GS2 is phase 2 of the growing season (green); GS1 is phase 1 of the growing season (light green); DS is the dormant season (gray). (Color figure online)

Leaf, trunk and lateral root phenology

Budbreak occurred on 18 and 14 April in 2015 and 2016, respectively. 100% of leaf unfolding occurred by 02 June 2015, and leaf shedding (more than 80% of leaves were shed) occurred by 18 and 12 November in 2014 and 2015, respectively. Trunk radial growth preceded root radial growth by 1 month and both peaked in June or July before decreasing, and then increasing to a greater extent in September. Root radial growth started when 100% of green leaves had unfolded, corresponding to the onset of phase 2 of the growing season (02 June 2015). Both trunk and lateral root radial growths decreased sharply with leaf fall. Lateral root radial growth followed a similar pattern to that of trunk radial growth with a strong, positive correlation ($p < 0.001$, $\rho = 0.88$, Fig. 3). Both trunk and lateral root radial growth were significantly correlated with both mean monthly soil and air temperatures, and mean monthly solar irradiance (Table 1). However, no significant correlations were found between either trunk and lateral root radial growth and mean monthly soil θ ($p = 0.52$, $\rho = 0.07$) and ($p = 0.60$, $\rho = 0.07$), respectively.

Fine root elongation rate

Mean daily RER for growing roots differed significantly between soil depths over the year ($p < 0.001$, Fig. 4). Mean daily RER was significantly higher at a depth of 0.85–1.70 m (3.2 ± 2.6 mm day^{-1}) than at depths of 0.00–0.85 m (1.3 ± 1.4 mm day^{-1}) and 4.00–4.70 m (1.4 ± 1.6 mm day^{-1}) during phase 2 of the growing season only.
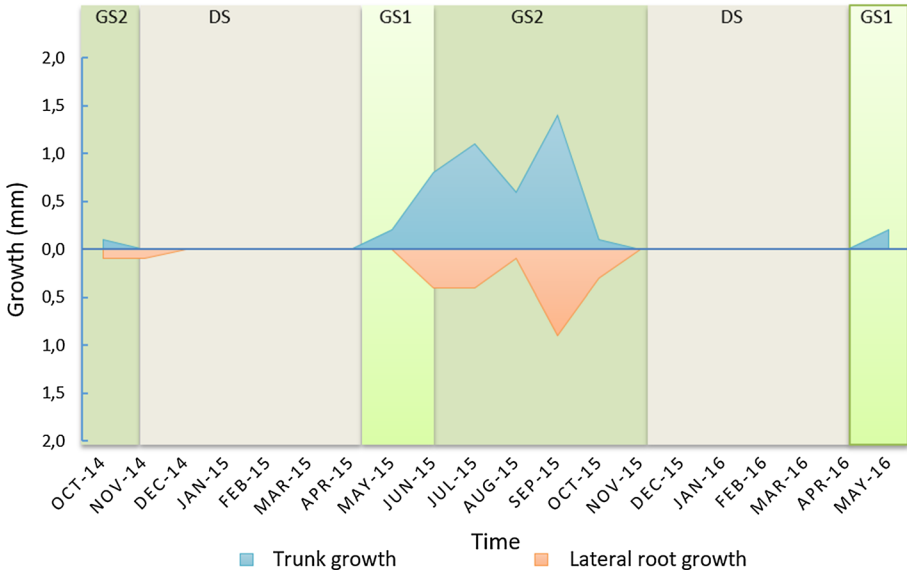
Fig. 3 Comparison of mean trunk radial growth (blue shading) and mean root radial growth (orange shading) from October 2014 to May 2016. Different background colors correspond to different phenological periods: GS2 is phase 2 of the growing season (green); GS1 is phase 1 of the growing season (light green); DS is the dormant season (gray). (Color figure online)

Table 1 Spearman correlation coefficients (ρ) between trunk radial growth and lateral root radial growth and mean monthly soil and air temperatures, mean monthly soil volumetric water content (θ) and mean monthly solar irradiance

Growth	Probability	ρ
Trunk radial growth		
Soil temperature (°C)	<0.001	0.57
Air temperature (°C)	<0.001	0.70
Soil θ (%)	0.52	0.07
Solar irradiance (kw/m^2)	<0.001	0.72
Root radial growth		
Soil temperature (°C)	<0.001	0.54
Air temperature (°C)	<0.001	0.55
Soil θ (%)	0.60	0.07
Solar irradiance (kw/m^2)	<0.001	0.53

The climatic data were measured in the month preceding the new measurements of radial growth

However, no significant differences were found in mean daily RER between depths during the dormant season. Shallow fine roots (in the depth class 0.00–0.85 m) continued to grow almost all the year around and daily RER peaked in June and August (Fig. 5). In the second soil layer (0.85–1.70 m), budbreak preceded root growth by 69 days. RER in this soil layer peaked 2 months later than the uppermost soil layer 0.00–0.85 m reaching a maximal rate in August and October, before dropping sharply to zero in December. However, small peaks in growth rate occurred during the dormant and early growing seasons at the two uppermost soil layers. At a depth of 2.00–3.30 m,
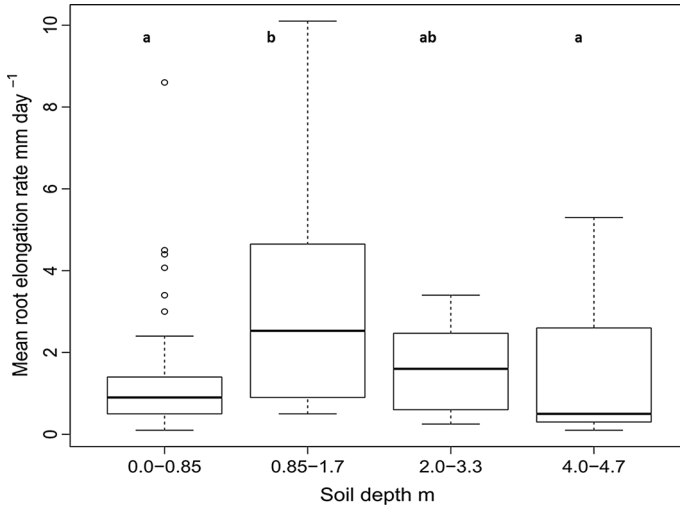
Fig. 4 Comparison of mean daily RER (mm day^{-1}) of the growing roots between soil depths (m) during the entire observation period. In each boxplot, the lower edge of the box corresponds to the 25th percentile data point, while the top edge of the box corresponds to the 75th percentile data point. The line within the box represents the median and the hollow points indicate outliers. Different letters above the boxplots indicate statistically significant differences ($p < 0.05$) between soil depths according to HSD Tukey tests

root growth preceded budbreak by 31 days, peaked 2 months earlier than the second soil layer (0.85–1.70 m) in April or June, before decreasing and then peaking again in September, before dropping to zero in January. However, mean daily RER in the deepest soil (4.00–4.70 m), started 94 days after budbreak, peaked 1 month later (in July) than in the soil layer just above (2.00–3.30 m), before decreasing and then peaking again in December, and dropping to zero in February (Fig. 5). The first peaks of root growth in the two upper most layers were greater than the subsequent peaks of growth later in the year. However, at depths of 2.00–3.30 m and 4.00–4.70 m, the autumnal peaks of root growth were greater than the peaks earlier in the year.

Mean daily RER was significantly higher during phase 2 of the growing season compared to the dormant season ($p = 0.03$) with much less root growth recorded in phase 1 of the growing season. A significant effect (Fig. 6, $p = 0.003$) of root diameter classes was found on mean daily RER for shallow roots only. However, differences in RER were found between the 0–1 mm and both 1–2 mm ($p = 0.03$) and 2–5 mm ($p = 0.008$) diameter classes (Fig. 6). Positive correlations were found between mean daily RER and mean monthly soil temperature at depths of 0.00–0.85 m ($p = 0.04$, $\rho = 0.27$, Table 2, Fig. S7) and 0.85–1.70 m ($p = 0.04$, $\rho = 0.40$, Table 2, Fig. S7). However, mean daily RER was not correlated with either soil or air temperatures during phase 2 of the growing season. Mean daily RER was significantly and positively correlated with both mean monthly solar irradiance and mean monthly soil θ ($p = 0.02$, $\rho = 0.39$, Table 2, Fig. S8) and ($p = 0.02$, $\rho = 0.43$, Table 2, Fig. S9), respectively in the uppermost soil layer (0.00–0.85) during phase 2 of the growing season only. However, mean daily RER in deeper soil layers was not significantly correlated with any climatic factors.

Fig. 5 Mean daily root elongation rate of fine roots at depths of **a** 0.00–0.85 m (blue line), **b** 0.85–1.70 m (orange line), **c** 2.00–3.30 m (violet line), **d** 4.00–4.70 m (red line) over the observation period from October 2014 to June 2016. Different background colours correspond to different phenological periods: GS2 is phase 2 of the growing season (green); GS1 is phase 1 of growing season (light green); DS is the dormant season (gray). Vertical bars represent standard errors (not shown when smaller than the symbol size). (Color figure online)
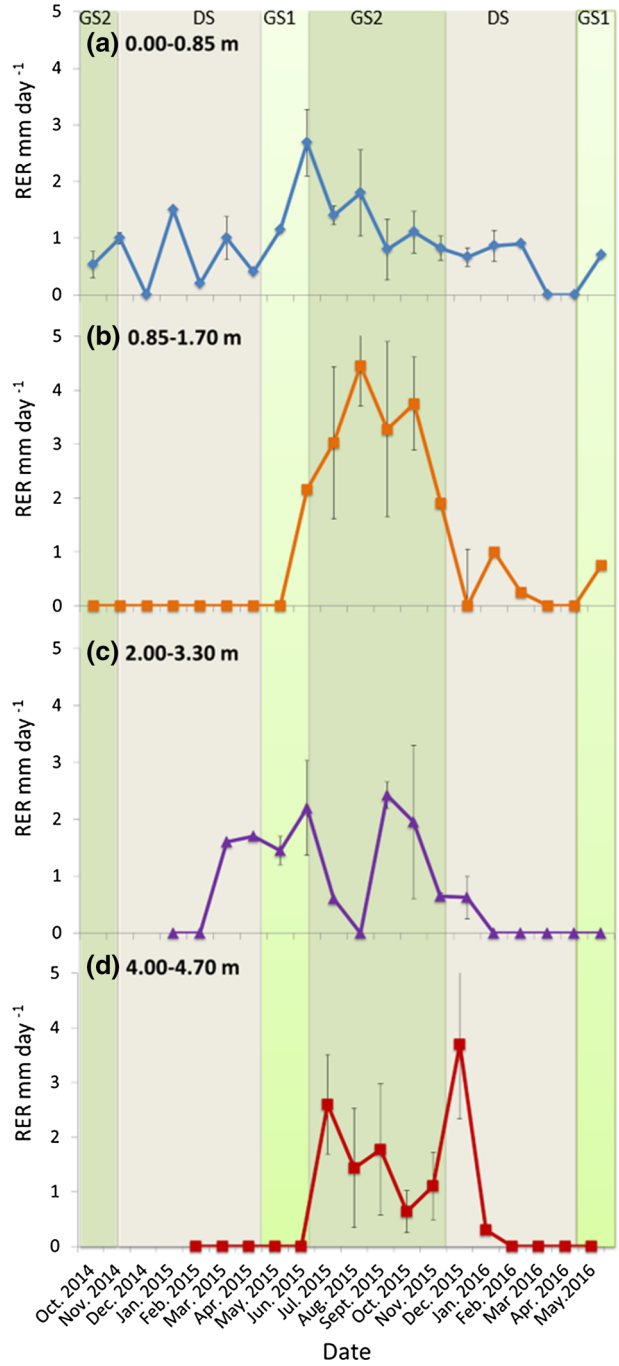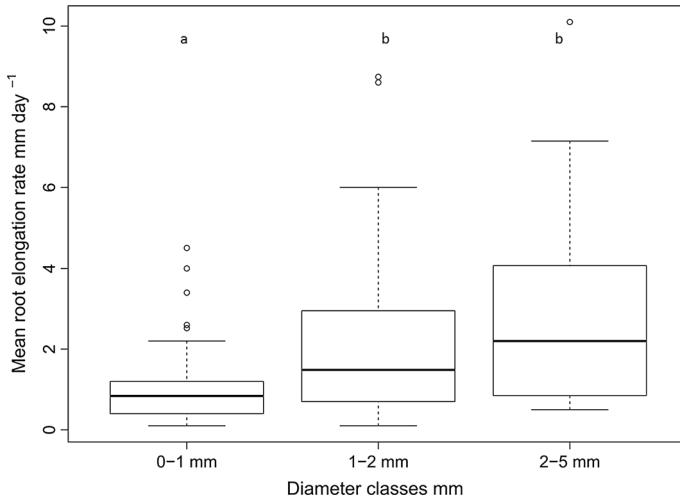
Fig. 6 Comparison of the mean daily root elongation rate (RER) between diameter classes (mm) at a depth of 0.00–0.85 m over the year. The lower edge of the box corresponds to the 25th percentile data point, while the top edge of the box corresponds to the 75th percentile data point. The line within the box represents the median and the hollow points indicate outliers. Different letters above the boxplots indicate statistically significant differences ($p < 0.05$) between soil depths according to Tukey HSD tests

Comparing above and belowground phenology

Leaf phenology and fine root growth were not synchronous at any soil depth (Fig. 7, Fig. S10), RER always peaked to maximal rate after budbreak: by 2 months (at 0.00–0.85 m), 4 months (at 0.85–1.70 m), 5 months (at 2.00–3.30 m) and 8 months (at 4.00–4.70 m).

The timing of fine root growth in the two uppermost soil layers 0.00–0.85 m and 0.85–1.70 m was synchronous with that of both trunk and lateral root radial growth during phase 2 of the growing season only (Fig. 7, Fig. S10). However, the growth patterns were antagonistic, with peaks of fine root growth occurring inversely to those of trunk and lateral root radial growth during phase 2 of the growing season. However, fine RER at depths of 2.00–3.30 m and 4.00–4.70 m followed similar patterns to those of trunk and lateral root radial growth during phase 2 of the growing season (Fig. 7, Fig. S10). In 2015, roots did not stop growing over the year in the uppermost soil (0.00–0.85 m), and the length of the root growing season was greater at depths of 2.00–3.30 m (9 months) than at 0.85–1.70 m (6 months) and 4.00–4.70 m (6 months).

Discussion

Effects of climatic factors on root elongation rate

Mean daily RER over the whole year (including the winter months), was significantly correlated with mean monthly soil temperature in the topsoil, confirming that soil temperature

Table 2 Spearman correlation coefficients (ρ) between daily RER and mean monthly soil temperatures, mean monthly soil volumetric water content (θ) and mean monthly solar irradiance, at the four soil depths

Environmental variables	Soil depth (m)							
	0.00–0.85		0.85–1.70		2.00–3.30		4.00–4.70	
	Probability	ρ	Probability	ρ	Probability	ρ	Probability	ρ
Mean soil temperature over the year (°C)	0.04	0.27*	0.04	0.4*	n.s	0.23	n.s	−0.06
Mean soil θ (%) during phase 2 of growing season	0.02	0.43*	n.s	0.04	n.s	0.45	n.s	0.2
Mean solar irradiance during phase 2 of growing season	0.02	0.39*	n.s	0.008	n.s	0.29	n.s	0.2

The climatic data were measured in the month preceding the new measurements of fine root elongation
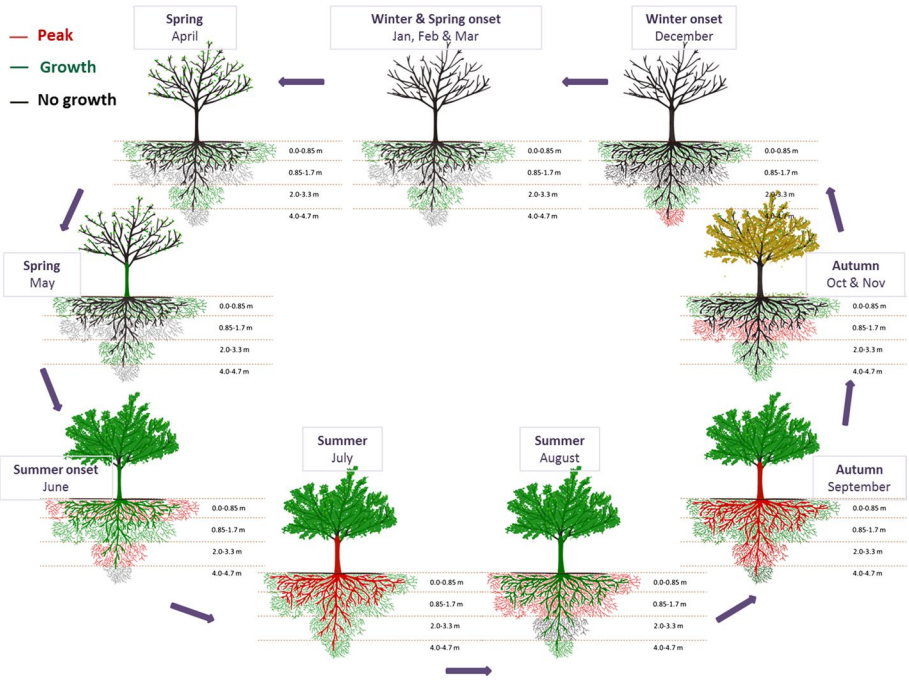
Fig. 7 Above and belowground phenological stages of hybrid walnut *Juglans nigra×J. regia*. cv. NG23 at four soil depths over the year

is a major driver of growth in these trees (Germon et al. 2016), but in superficial roots only. Topsoil is colder and more humid in the winter and warmer and drier in the summer compared to the deeper layers, where temperature and θ are less variable (Waisel et al. 2002). However, when we investigated mean daily RER during phase 2 of the growing season only, we showed that no significant relationships existed between RER and soil/ air temperature at any depth. As soil temperature (for all soil depths) remained between 13 and 23 °C during phase 2 of the growing season, when RER was at its highest, it is likely that this range of temperatures is optimal for walnut root growth (Mohamed et al. 2017b). Therefore, significant relationships between RER and soil temperature only occur when the range of temperatures is more variable, as also found by Contador et al. (2015).

The absence of correlations of daily RER with soil or air temperatures during phase 2 of the growing season is also in conflict with other studies that indicate air and soil temperatures as prominent factors driving RER in superficial roots (Riedacker 1976; Lopushinsky and Max 1990; Lyr 1996; Gill and Jackson 2000; Hendricks et al. 2006; McCormack and Guo 2014), especially during the growing season in temperate climates. However, our results showed a decrease in RER with the decline of soil θ at the uppermost soil layer, demonstrating that soil water is a limiting factor for root growth in climate characterized by dry summers, as also found by Misson et al. (2006) studying *Pinus ponderosa* in a Mediterranean climate. These results are likewise in accordance with the findings of Germon et al. (2016) and Mohamed et al. (2017b), who studied walnut tree root growth at the same stand, but in 2013–2014 and 2015–2016. Surprisingly, we found that in the shallowest soil (0.00–0.85 m), daily

RER was correlated with mean monthly solar irradiance during phase 2 of the growing season, as also found by Joslin et al. (2001), studying *Q. prinus* and *Q. alba* in a subtropical climate. Joslin et al. (2001) found that daily root elongation intensity was related mainly to leaf phenology and soil water potential and not soil temperature. These results could be interpreted in terms of increased carbon assimilation from photosynthesis (Mahmoud and El-Gindy 2016), as the energy needed to produce photosynthates depends on the number of photons from solar irradiance, thus the fraction of incident solar irradiance intercepted depends on total leaf area (Amthor 2010). As leaves have expanded during the late growing period, photosynthates will be produced rapidly, reaching the superficial roots within hours or days (Keel et al. 2012). In deeper soil layers, where roots are more distal and hence need more time to receive photosynthates, any relationship between solar irradiance and root growth is probably masked, as several factors potentially combine to influence root growth.

Mean daily RER and root diameter were significantly and positively correlated in shallow roots only, where a greater number of roots in different diameter classes existed compared to deeper soil layers. Thaler and Pages (1996) suggested that the growth potential (or sink strength) of an elongating tree root is related to the size of its apical meristem, which in turn is determined at the primordium stage. Therefore, the largest meristems will be the strongest sinks in the root system, explaining why RER was higher in thicker roots, as also found in other studies (e.g., Wang et al. 2018). The high number of roots in the topsoil horizon may be due to the production of very fine ephemeral roots that are produced under suitable conditions to optimize the capture of e.g., rainfall and/or nutrients when the intercrop is fertilized (Eissenstat and Caldwell 1988).

Effects of climatic factors on trunk and lateral root radial growth

Both trunk and lateral root radial growths were correlated with climatic factors (soil and air temperatures and solar irradiance) as also found in previous studies, e.g. Oribe et al. (2001), studying *Abies sachalinensis*, who reported that cambial reactivation in spring was highly dependent on air temperature. However, in our study, trunk and lateral root radial growth were not correlated with mean monthly soil θ. The absence of a significant relationship between trunk radial growth, fine root growth and soil θ is contradictory to previous results found in Mediterranean climates, where trunk radial growth was mainly limited by soil water availability, and precipitation of the current year played a major role in determining cambial activity (e.g., Cartan-Son et al. 1992; Cherubini et al. 2003). Nevertheless, several studies have showed that in Mediterranean species, trunk radial growth was correlated with precipitation from the previous autumn and winter months, which are the seasons with highest precipitation and when most soil water recharge occurs (Campelo et al. 2007; Żywiec et al. 2017). The lack of correlation between trunk and lateral root radial growth with soil θ in our study during phase 2 of growing the season is possibly because precipitation was high from September 2014 to January 2015 (987 mm), and thus water accumulated in the soil during autumn and winter, when the aerial parts of trees were dormant. Therefore, autumnal/winter rainfall, rather than summer rainfall, may be a key factor influencing trunk and lateral root radial growth in the subsequent growing season in a Mediterranean climate.

Comparing above and belowground phenology

The initiation of fine root growth was asynchronous with that of budbreak at all soil depths. Both budbreak and root emergence are very sensitive to local temperatures (Du and Fang 2014; McCormack et al. 2014), thus a rapid increase in air temperature in April would stimulate the budbreak quickly as well as reactivate cambial activity in the trunk. As topsoil buffered against any rapid changes in air temperature, the subsequent cambial activity in fine and structural roots took longer to occur deeper in the soil (Pregitzer et al. 2000). Root initiation in both the shallowest roots and at 2.00–3.00 m began *before* budbreak, and was likely fueled by non-structural carbohydrates (NSC) produced during photosynthesis and stored in the roots during the previous dormant season (Dyckmans and Flessa 2002; Vizoso et al. 2008; Najar et al. 2014; Villar-Salvador et al. 2015; Wang et al. 2018). Soil temperature decreased significantly with depth, resulting in root initiation *after* budbreak in the deepest roots as well as those at a depth of 0.85–1.70 m. It is not known why root initiation occurred after budbreak in roots at a depth of 0.85–1.70 m, unlike roots above and below this soil layer. Possibly, the presence of the intercrop (durum wheat), that grows throughout the winter and is harvested in April/May, was in competition with walnut roots, delaying root emergence (Mulia and Dupraz 2006). The initiation of both trunk and root radial growth also occurred *after* budbreak and peaked during phase 2 of the growing season, when levels of freshly produced NSC would be high (Uscola et al. 2015; Villar-Salvador et al. 2015; Martínez-Vilalta et al. 2016).

The peak of maximal fine root growth occurred 2–4 months after budbreak and a delay in peak growth occurred with increasing soil depth. Very shallow roots (0.00–0.85 m) continued growing over almost the entire year and elongation peaked in June (during the leaf expansion phase) and August (the end of leaf expansion and total canopy cover), as also found by Bauerle et al. (2008), studying winter root growth of *Vitis* spp. in a Mediterranean climate. As the main control of C allocation between roots and shoots is thought to be related to sink activity (Friend et al. 1994; Pallas et al. 2013; White et al. 2015), the decrease in fine root elongation in the two upper soil layers in July and August may be due to NSC being used primarily for trunk and lateral root radial growth. If the position and strength of NSC sinks along the vertical profile of a tree does influence the quantity of NSC that reaches a sink, then deep roots will acquire less NSC when superior sinks are undergoing intense activity. When other tree organs and shallow roots are dormant, more NSC will be available for deep root growth, as long as abiotic factors are favorable for growth. By having deeper roots growing and so capturing resources in the winter, water and nutrient uptake will be optimized (Maeght et al. 2015; Germon et al. 2016).

In conclusion, our results highlight that root initiation and budbreak were asynchronous and that the phenology of different organs was influenced by a variety of drivers throughout the year. Root elongation over the whole year (including the winter months), was correlated with monthly soil temperature in the topsoil only. During the growing season however, soil water content and solar irradiance were strongly related to shallow root elongation. As very shallow roots were initiated *before* budbreak, we suggest that stored NSC are important to fuel root emergence in deciduous species that cannot photosynthesize until budbreak occurs. Trunk and lateral root radial growth peaked in the summer, to the detriment of shallow fine root growth. As superficial soil dried out in the summer, and shallow fine root elongation decreased, slightly deeper root growth increased, thus improving overall water and nutrient uptake. In the deepest roots, a time lag existed between budbreak and maximum deep root elongation. Deeper soil layers are colder and wetter after the winter,

and roots may receive less NSC than superior organs in periods of intense activity. More focus is now needed on how the growth of different tree species, in a variety of climates, interact with abiotic factors to influence the phenology of different organs. In particular, how deep roots function to capture resources when aboveground organs are dormant would permit a better understanding of tree resistance to abiotic stress.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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