Plant Soil (2022) 477:707-723
https://doi.org/10.1007/sl 1104-022-05469-3

RESEARCH ARTICLE

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Shifts in root dynamics along a hillslope in a mixed, mesic temperate forest

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Received: 4 November 2021 / Accepted: 28 April 2022 / Published online: 5 May 2022

Abstract
Aims Complex topography, a common feature of forested areas, generates unique environmental gradients that may shape root dynamics in unexpected ways. Nevertheless, belowground studies rarely capture the environmental gradients imposed by complex topography, such as those found along hillslopes. This begs the question: how much information is lost when complex topography is ignored? Hillslope is a common aspect of complex topography with landscape features that impact water flow, sediment transfer, and water and nutrient storage. We hypothesized that soil water content would have a nonlinear impact on fine-root production, mortality, standing crop, and turnover. Specifically, we expected increased mortality and decreased production, root standing crop, and turnover at the driest and wettest regions of the hillslope.
Methods Using minirhizotron observations from 150 tubes located at 50 sites strategically placed at different hillslope positions across a first-order catchment, we examined how position along a hillslope impacts fine root dynamics.
Results Contrary to our hypotheses, we found no significant hillslope effects on fine root tip production or mortality. Root tip turnover, however, was higher at drier than wetter regions of the hillslope. Additionally, fine root standing crop length was higher in wetter topographic regions.
Conclusions Considering fine root tip turnover and length standing crop in combination with previous research on fine root lifespan suggest two distinct strategies of trees in root deployment along a hillslope: temporal avoidance in drier regions of a landscape (midslope planar and ridgetops) and extended survival of roots in wetter, deeper-soil regions like valley floor and swales.

Keywords Minirlrizotron • Fine root dynamics • Belowground ecology · Critical zone · Temperate forest

Responsible Editor: Timothy J. Fahey.

Supplementary information The online version contains supplementary material available at https://doi.org/10.1007/sl1104-022-05469-3.

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Introduction

Due to the arduous and time-consuming nature of root data collection, researchers often rely on "representative sites" to scale up a plot or several plot observations to a whole forest (e.g., Abramoff and Finzi 2016; Hendricks et al. 2000; Norby et al. 2004). Generally, the usage of representative sites would not be a problem if forest trees grew on landscapes that were relatively homogeneous. However, natural forested systems commonly reside on complex topography. The influence of hillslope on spatial patterns of soil nutrients and water likely strongly impacts root dynamics, which may complicate estimates across the landscape. However, there is a general lack of understanding how environmental gradients imposed by complex topography affects root dynamics.

Topography has been shown to account for a large amount of variation in landscape-level soil moisture. Ridgetops and upper slope areas tend to have shallower soils with relatively less soil volume. These soils typically dry faster when rainfall becomes limiting (Lin et al. 2006; Tromp-van Meerveld and McDonnell 2006). Valley floor regions and some convergent mid slope areas (swales) have deeper soils and are generally wetter through time (Lin et al. 2006; Tromp-van Meerveld and McDonnell 2006). Thus, hillslopes shape the distribution of water across landscapes over time (Li et al. 2018; Lin 2006).

Short-term shifts in soil moisture can impact fine root lifespan in a non-linear fashion. Roots die at faster rates under flooding or "excessively" wet conditions (Drew 1997; Glenz et al. 2006) and, conversely, at very low soil water content (Green et al. 2005; Huang et al. 1997). Thus, root mortality typically exhibits a quadratic response to increasing soil moisture content. However, it is unclear how roots will adapt to non-optimal soil water conditions over longer periods of time or how a tree copes when selective portions of its root system reside in soil that may vary widely in soil moisture across a hillslope.

Fine root mortality is not the only aspect of fine root dynamics that likely responds in a quadratic fashion to increases in soil moisture content. Fine root production has been shown to have a mixed correlation with soil moisture relative to other fine root dynamics. In sandy soils in central Poland, root production was influenced by both current annual precipitation and previous annual precipitation (Withington et al. 2021). Additionally, other studies have shown that fine roots generally proliferate in soils with water or nutrient hotspots (Bilbrough and Caldwell 1995; Eissenstat and Caldwell 1988; Hu et al. 2014; Jackson et al. 1990; Pregitzer et al. 1993). However, time of year may play a large role. In the spring and early summer, fine root production often peaks (McCormack et al. 2014; Ruess et al. 2003; Wells and Eissenstat 2001). Strong seasonal patterns suggest that root production may be more phenologically driven and perhaps less sensitive to soil water conditions in the early growing season; however, later in the growing season root production may be more related to patterns of soil moisture distribution (Withington et al. 2021). Soil water content, therefore, may interact with season and phenological timing to impact fine root production.

Root production and mortality together determine the total population of roots (e.g., standing crop) present in a location. As root production and mortality both respond to soil water content, root standing crop is also likely impacted by soil water conditions. Studies examining the relationship between soil water and root standing crop have been mixed, showing no changes (Santantonio and Hermann 1985), increases (Ruess et al. 1996), and decreases (Jones et al. 2003; Tingey et al. 2005) with increasing soil moisture. Furthermore, one study showed a significant species response to soil moisture, such that one tree species decreased fine root standing crop with increasing water, while another increased fine root standing crop (Lee et al. 2007). Likely the extent that water is limiting in a particular environment partly contributes to differences among studies between fine root standing crop and water. When water is the most limiting resource, we should expect root standing crop to increase to maximize water acquisition (Bloom et al. 1985).

The final aspect of fine root dynamics of interest, root turnover, tends to be somewhat driven by soil moisture. Several studies have concluded that increasing soil moisture can increase fine root turnover Gill and Jackson 2000; Jones et al. 2003; Joslin et al. 2000; Ruess et al. 1996; Zhou et al. 2009, but see Santantonio and Hermann 1985). Root turnover can be estimated in several ways. Root turnover is normally determined by dividing the annual fine root production by the maximum, average, or minimum fine root standing crop (McCormack et al. 2014). Because both production and standing crop of fine roots, determine fine root turnover, the effects of soil moisture on root turnover likely depend on time of year.

Root order matters for fine root dynamics. First order roots, or roots with no other roots branching from them, are typically the most metabolically active roots (Pregitzer et al. 2002; Guo et al. 2004) and the roots most associated with nutrient acquisition (Guo et al. 2004, 2008; Chen et al. 2013; McCormack et al. 2014, 2015). Increased metabolic activity tends to come at a cost though, as first-order roots typically turn over faster than other orders of roots (Wells et al. 2002; Guo et al. 2004; McCormack et al. 2014; McCormack et al. 2015). Additionally, roots of a lower order on a higher order branch must turnover at least as fast as the higher order roots that support them, as roots turnover in a modular fashion (Pregitzer et al. 1997). Because diameter of the finest roots of a plant can vary widely across species (Eissenstat 1992; Ma et al. 2018), using an arbitrary diameter cutoff (e.g., 2 mm) is likely less functionally related to turnover of the absorptive roots than root order (McCormack et al. 2015). Therefore, we confined our study to the examination of only first-order roots.

In Primka IV et al. (2021), we examined the relationship between fine/first-order root lifespan and topographic position. Here we continued our investigation into the role and potential non-linear (quadratic) effects of soil moisture on fine root dynamics across a landscape with spatially structured water content associated with complex topography. We hypothesized that: (1) First-order root production, both in tip number and length, would be lower in topographic regions that were the wettest and driest across the landscape. (2) First-order root tip and length mortality would be high in both the driest and the wettest regions. (3) Standing crop length and standing number of root tips would be highest in the swale topographic regions of the landscape due to higher soil water content but little flooding. Moreover, standing crop length and standing root tip number would decrease moving into wetter or drier topographic regions. (4) First-order root tip and length turnover would increase with increasing soil water content across the topographic regions, until soil moisture conditions approach saturating levels and then turnover would decrease. Hypothesized effects on first-order root dynamics across a hillslope are shown in Fig. 1. First-order root mortality was expected to show an inverse trend of that shown in Fig. 1.

Materials and methods

Watershed

This study was conducted in the Shale Hills Catchment of the Susquehanna-Shale Hills Critical Zone Observatory (SSHCZO), located in Central Pennsylvania, USA (40°40'N 77°54'W). Ridgetop locations and the majority of midslope planar locations were loamy-skeletal, mesic Lithic Dystrudept (Lin et al. 2006). Slopes in the midslope planar region varied substantially, relative to the other topographic regions (Baldwin et al. 2017). Fine-loamy, mesic Aguie Hapludult and fine-loamy, Aguie Fragiudults soils made up the valley floor topographic region (Lin et al. 2006). Concave regions in the midslope planar region, called swales, were generally loamy-skeletal, mesic Typic Dystrochrept (Lin et al. 2006). Soils immediately bordering swales and in other specific locations in the midslope planar region were loamy-skeletal, mesic Typic Dystrudept (Lin et al. 2006). Within the catchment, the elevation gradient ranged from 256 to 310 m (Lin et al. 2006). Maple *(Acer),* hickory *(Carya),* and oaks *(Quercus)* with some evergreen species *(Tsuga canadensis, Pinus strobus,* and *Pinus virginiana)* comprised the majority of tree species composition within the catchment (Naithani et al. 2013). Most of the landscape had closed canopy forest, so generally the understory was sparse, with the exclusion of recent tree falls (Personal observation). For more on the forest composition and species structure, see Smith et al. (2017). Precipitation for the observatory averaged 1115 mm from 2015 to 2018 (data not shown). Mean annual temperature was 9.9 °C in 2008-2010 (Smeglin et al. 2020).

Macroplot sites

In 2014, 250 clear, acrylic minirhizotron tubes were installed across 50 macroplot sites within Shale Hills with 5 tubes installed per site. Macroplot sites were established with varying coverage of the different topographic regions. Midslope planar topographic regions had more macroplot sites established to account for more potential variability within the region. Furthermore, midslope planar locations proportionally occupied more catchment area than the other regions. The topographic regions investigated were valley floor, midslope planar, swale, and ridge

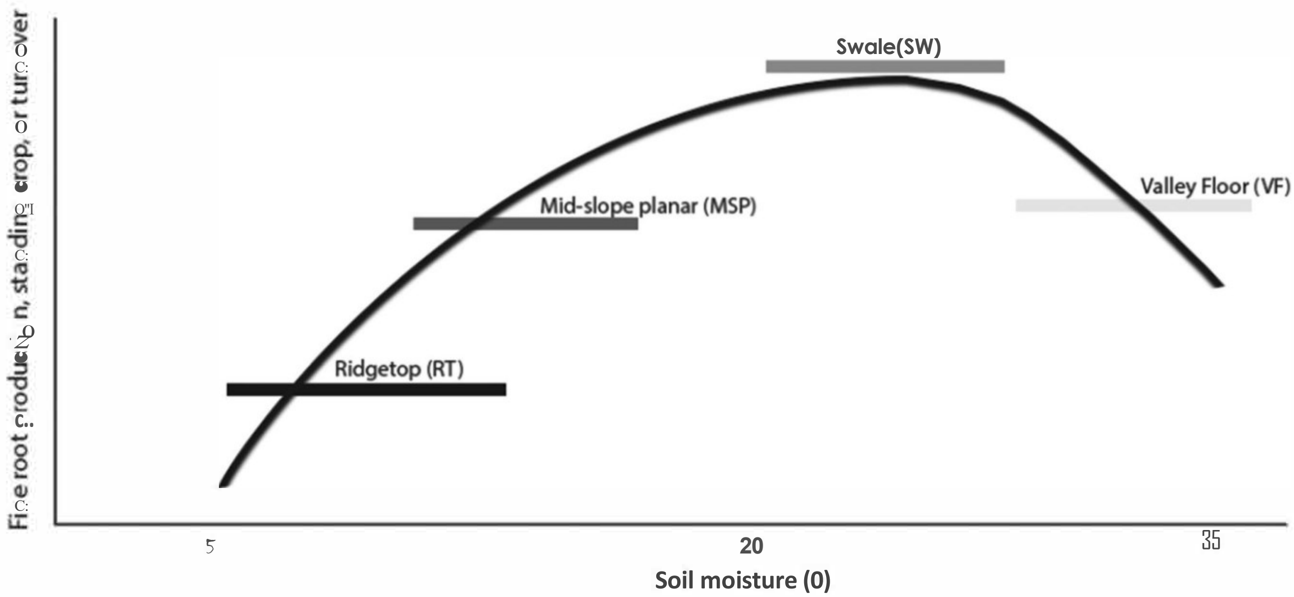

Fig. 1 Hypothesized effects of hillslope on fine root dynamics. A theoretical figure of the response of fine root dynamics (root production, standing crop, or turnover) with increasing soil moisture (E>). The black quadratic line represents the hypothesized overall effect of soil moisture on the various fine root dynamics. The inverse of the effect was expected for fine root mortality. Bars in gray scale represent the soil moisture ranges for the different hillslope regions. Hillslope positions were listed above the bars. Gray scale of bars indicates differences in elevation, with lower elevations in lighter colors

top. These regions had 9, 21, 13, and 7 macroplot sites respectively (See Orr 2016; Primka et al. 2021). Macroplot sites had tubes installed in a "t" shape formation with the shorter leg of 5 m in length and longer leg of 10 m. Three tubes were installed along the longer axis of the "t" and two were installed at the ends of the shorter axis. Tubes were installed at an angle of 30° off the absolute vertical with an installation depth of 1.25 m or to the point of refusal from excessive rock fragments. Exposed ends of tubes were taped and painted white to increase the tubes' albedo. As another form of heat management, foam insulation was inserted into the tubes to reduce heat transfer among soil layers due to the tube. Finally, a hole was drilled in the side of each tube that the minirhizotron camera locked into, to ensure that the same soil face was captured during each imaging session.

Data collection

Root observations

One hundred tubes were initially selected to follow based on root presence and image quality. After the first month, 50 more tubes were additionally sampled based on the same initial survey. The initial 100 tubes were sampled biweekly to a depth of 40 cm. Monthly samples of 150 tubes, which included the initial 100 plus the additional 50, were sampled to the full depth of the tube. As roots tend to have shorter lifespans near the soil surface and the effort of observing tubes to full depth and processing them more than tripled the time to having accessible data, we opted to observe surface roots on a more frequent basis than deeper roots. Full depth observations were collected monthly until the beginning of the growing season of 2018, after which tubes were only observed to 40 cm, but the alternation between 100 and 150 tubes that were sampled was maintained. Two observation periods took place at the beginning of the growing season of 2019 as an end point for the data collection. All 150 tubes had images collected to a depth of 40 cm.

To account for the loss of observations at depths below 40 cm for a subset of tubes (81 out of 150) in 2018 only, we used the proportion of root tips and length at depths below 40 cm in early years to adjust the 2018 root tip and length estimates, respectively. Briefly, we first calculated the mean proportion of first-order root numbers and length of both production and mortality that occurred below 40 cm relative to the shallower soil depths in 2016 and 2017 for the whole catchment (deep root and shallow root dynamics (i.e., production, mortality, etc.) across the CZO were not correlated). We then adjusted estimates of first-order root tip production and mortality in 2018 to include deep roots based on deep-root proportions estimated for 2016--2017. As first-order root tip production number and mortality number were analyzed on a cumulative annual basis, we simply added the missing deep root production or mortality to the annual values for 2018. Only 16 and 5% of the total first-order root tip production and mortality data in 2018 were backfilled data, respectively. First-order root length production and mortality comprised 3.5 and 1.2% backfill, respectively. Backfilled values of first-order root production and mortality were used to adjust the standing tips and length estimates for sites with data missing at depth in 2018 as well. First-order root turnover were calculated based on standing crop and production with backfilled data.

Images from the minirhizotrons were taken with a Bartz digital camera with ICAP version 7.0 (Bartz Technology Corp., Carpinteria, CA, USA). To process the minirhizotron images, root tracing was done using Rootfly version 2.0.2 (Wells and Birchfield, Clemson University, SC, USA). Only first-order roots were tracked through time. If roots became higher order roots later in the season, they were removed from the data set. While only including first-order roots assured that we focused on the most ephemeral roots, we were excluding roots of 2nd and 3rd order that may also be ephemeral and contribute to the dynamic root pool. Species and patch nutrient richness can affect which root orders are ephemeral (e.g., Liu et al. 2015). Thus, while some turnover likely occurred in higher root orders (e.g., 2nd and 3rd), it was likely proportionally related to the turnover of the more numerous first-order roots. To only sample absorptive first-order tree roots, roots with a diameter larger than 2 mm and smaller than 0.2 mm were excluded. To our knowledge, none of the tree species studied should have root diameters less than 0.2 mm (Comas and Eissenstat 2009; McCormack et al. 2012), but roots of herbaceous understory plants can exhibit such first-order roots. Root diameter, length, color, and date of appearance and disappearance were recorded for each individual first-order root in an image. Visible degradation of roots or root disappearance from the soil were indicators of root death.

The date of root birth and death was assumed to be halfway between the image where they were not present (or were last present) and the image when they first appeared (or disappeared) like other studies (e.g., Withington et al. 2006). Standing crop of the roots on the tube for each time period was calculated by adding the number of roots produced and subtracting the number of roots that died to the number of roots present in the last measurement. Annual turnover rate was calculated by dividing the annual root production by the average annual standing crop (McCormack et al. 2014) per macroplot site and then was averaged on a topographic basis for both first-order root length and number. Additionally, attempts were made to identify tree species of roots based on first-order root diameter, as first-order root diameter is phylogenetically conserved by species (Kong et al. 2014). Unfortunately, we could not use our minirhizotron images to reliably identify roots to species or genus because of similarity of root diameters of tree species in our catchment (species-specific root diameters based on estimates from a common garden used nearby) (e.g., McCormack et al. 2012).

Volumetric soil water content

In 2016, at pre-established ground observation (GroundHOG) sites throughout Shale Hills, time domain reflectometry (TOR) sensors were measured on a biweekly basis. GroundHOG sites had TOR waveguides installed at 20, 40, 60, and 100 cm depths in the valley floor. Midslope sites had sensors installed at 20, 40, and 60 cm depths. Ridge top sites TOR sensors were installed at 20 and 40 cm depths. TOR depth locations at the GroundHOG sites were determined by the depth the pit could be dug. In July 2017, 88 TOR probes, 20-cm in length, were horizontally positioned within the soil in 33, spatially-distributed, macroplot locations. TOR installation sites were selected based on topographical region and soil series. Soil series locations were based on the work by Lin et al. (2006). TOR probes were established at 20, 40, and 60 cm depths where rock content permitted. Measurements of the soil moisture sensors (TOR probes) were taken biweekly. Initial TDR readings indicated the presences of some inherent sensor idiosyncrasy, presumably due to variable and often high rock content, so soil water content measurements were relativized. Relativization was accomplished by dividing each observation by the mean of the highest three annual readings per sensor (as rock content reduces the volume available for water) and then multiplying this sensor average by the average water content of the highest three measurements per topographic region. For example, the average of the three highest estimates for the swale region over the course of the study were multiplied by the individual relativized sensor observations in the swales so the general wetness of the swale region could be characterized. Additionally, daily precipitation data from the Shale Hills Catchment in the SSHCZO were utilized for annual precipitation values. Precipitation data from the SSHCZO were calculated for the SSHCZO through a combination of instruments, including an OTT Pluvio weighing rain gauge, a ThiesCLIMA Laser Precipitation Monitor (LPM), hourly tipping bucket gauges, and an external database.

Statistical analysis

Data organization

Root observations were aligned with the closest soil water content sensors. Seasons were split into spring (March or April - May), summer (June - July), and fall (August - November or December). Seasons were chosen as opposed to simply day of year (DOY), because often seasons generally represent similar air temperature and light conditions and the temporal frequency of our root observations was fairly coarse (biweekly).

Other variables tested

Many different variables were tested and found insignificant that were not included in the final model (Tables SI - S3). Root length density, soil organic matter, and soil nitrogen ($N0_3$ and NH_4) were from Buck, et al. (unpublished) (Table Sl). In addition to depth-related soil parameters, we analyzed the potential effects of mass of leaf litter at a site, the neighborhood effect of arbuscular mycorrhizal versus ectomycorrhizal trees of different root thicknesses, and trunk basal area of trees (Table S2). Trunk basal area data was from the Shale Hills Catchment in the SSHCZO (DOI: https://doi.org/10.1594/IEDN100516). For more on how the neighborhood effect of trees was calculated, see Primka et al. (2021). Finally, previous year's annual precipitation and cumulative precipitation were tested (Table S3) because of its potential importance for root production (Withington et al. 2021). Trunk basal area and neighborhood effects of different tree species were found to be insignificant. Site level variation related to different variables were accounted for in the model (see below in the model section).

Testing for spatial autocorrelation

Spatial autocorrelation was tested in the root production and root mortality data via the "variog" function from package geoR (Ribeiro and Diggle 2006). We tested for omni-direction spatial autocorrelation and anisotropic variation using the angles (36, 45, 60, 90, and 180 degrees). We found largely no spatial autocorrelation, except for a minority of tubes. Within the minority of tubes, spatial autocorrelation was confined to tubes within a macroplot site. Therefore, we combined tube data within a macroplot to account for the autocorrelation.

Models

A Bayesian hierarchical modeling framework was used to determine the differences in first-order root dynamics amongst the topographic regions. To account for repeated measures taken across the 50 sites, topographical region (e.g., slope position: ridge top, midslope planar, midslope swale, valley floor) was treated as a fixed factor, while site (macroplot) was treated as a random factor in a crossed statistical manner as suggested by Schielzeth and Nakagawa (2013), for handling random effects nested within fixed effects. However, the interaction term between site and slope position was not significant in these models and consequently was removed, but the random site factor was left in the model as it was significant for some sites. Models for the number of first-order root tips produced or died were analyzed for each year using the following mixed model:

$$Y_{\substack{kl \\ ij}} \sim dpois(mu)$$
$$\ln(mu) = alpha_i + beta_j + betal_k \tag{1}$$

where Y_{ijkl} was either the annual average production or annual average root mortality for observation l in the year k, at macroplot site i in topographic region j. Random effect $alpha_i$ represents site level variability and is part of the random effect structure that describes the effects of the repeated measures. $Alpha_i$ was independent and identically distributed (iid) as $N(0,\sigma)$. Fixed effect $beta_j$ was the mean of the topographic region (j). Fixed effect $beta1_k$ was the mean effect of year (k). R code for this approach can be found in the supplemental (model code 1). Annual models for first-order root standing crop were transformed via the natural log plus 1 in order for the data to meet normality assumptions. Root standing crop and turnover were analyzed using the following mixed model:

$$Y_{ijkl} = alpha_i + beta_j + beta1_k + e_{ijkl} \quad (2)$$

Y_{ijkl} was either the annual average standing crop or annual average turnover for observation l in the year k, at site i in topographic region j. Random effect $alpha_i$ represents site level variability and is part of the random effect structure that describes the effects of the repeated measures. $Alpha_i$ was independent and identically distributed (iid) as $N(0,\sigma)$. Fixed effect $beta_j$ was the mean of the topographic region(j). Fixed effect $beta1_k$ was the mean effect of year (k). Residual error was e_{ijkt} with an iid of $N(0,\sigma)$. R code for this approach can be found in the supplemental (model code 2). Diffuse normal priors were used in all models for the global estimator of $alpha_i$, specifically N[0,100]. Diffuse uniform priors were also used in all models for σ and σ specifically U[0,10]. Corner constraints were used in all models for $alpha_i$ to speed up MCMC convergence (Congdon 2019; Ntzoufras 2011).

Finally, first-order root length for all four root dynamic variables (production, mortality, turnover, standing crop) were run in a model like model 2 above, but with two new slope parameters: $beta2$ and $beta3$. X and xi in the model represent the variables: the number of root tips involved in the root dynamic being modeled (i.e., root production, mortality, etc.) and first-order root diameter of the roots within this first-order root dynamic, respectively. This model equation was:

$$Y_{ijkt} = alpha_i + beta_j + beta1_k + beta2_j * x + beta3_j * x_i + e_{ijkt} \quad (3)$$

Root length production, mortality, and standing crop were natural log+ 1 transformed to meet normality assumptions. Root length for turnover did not require transformations to meet normality assumptions. Parameters found in the previous model were run under the same conditions. R code for this approach can be found in the supplemental (model code 3). Simplified models (codes 1 and 2) were run as comparisons for the more complex model (code 3).

All models were run with three parallel Markov chains beginning with random values. Chains were run for 50,000 iterations with a burn-in of 30,000 and thinning interval of 1 for models 1 and 2. This resulted in 60,000 saved samples for each first-order root dynamic data set. Model three simulations of root length production, mortality, and standing crop were run for 80,000 iterations with a burn-in of 60,000, which generated 60,000 kept samples. Root length turnover was run for 150,000 iterations with a burn-in of 60,000 yielding 270,000 kept samples. Saved samples were used to summarize the posterior distributions and 95% credible intervals. Significant model components were determined using 95% credible intervals of the posterior distributions. Model convergence was determined both visually via traceplots, density plots and through the quantitative measure of the Rubin-Gelman statistic (Brooks and Gelman 1998). Models were fit via calling JAGS (Plummer 2012) by using the "jags.parallel" function from the R2jags R package (Su and Yajima 2020). All statistical analyses were conducted via the program R 4.1.2 (R Core team 2021).

Results

Production

Average cumulative root tip production (number of roots) to full depth of observation ranged from 56 to 107 (or 4.05-4.68 ($\log_e$)±0.11-0.24 SE) root tips produced per site across topographic regions (Fig. S1A). Root tip production did not differ significantly across hillslope positions. Additionally, root tip production only slightly increased first-order root length (range of increase 0.003-0.02 mm per root tip), with no differences among hillslope positions for this trend.

Average cumulative root length production ranged from 17.5 to 55.8 cm(±1.0-24.1 SE) per site annually across regions (Fig. SlB). Root length production did not vary by topographic region. First-order root diameter had a mixed effect on root length production.

Average first-order root diameter of the produced first-order root length ranged from 0.29 to 0.39 mm (0.01-0.02 SE) in diameter. Generally, root diameter had no effect on root length production, except in midslope regions (average increase 0.26 cm with a 0.1 mm increase in root diameter; range of increase 0.04--1.30 cm). However, other hillslope positions were generally not different from midslope planar **(MSP)** regions with the exception of swales **(SW)** (difference range 0.006--12.2 cm with an increase of 0.1 mm in root diameter for MSP vs. SW).

Year of observation was significant, but its effect depended on root trait. Yearly root tip production increased during wetter years(Fig. 2A). In contrast, root length production generally occurred more during drier years(Fig. 2B).

Mortality

Average cumulative root tip mortality (number of roots) to full depth of observation ranged from 22 to 85(or 3.13--4.45 $\log_e \pm$ 0.10-0.30 SE) roots per site annually(Fig. S2A). Over the total observed minirhizotron area, average cumulative root length mortality ranged from 13.7 to 39.3 cm(±2.2-22.5 SE) per site annually across regions(Fig. S2B). Neither root tip nor length mortality were significantly different across topographic regions. Root tip mortality only slightly increased first-order root length mortality (range of increase in length mortality 0.01-0.02 mm per root tip), with no differences among hillslope positions in this trend. Mean first-order root diameter of the dead first-order root length ranged from 0.31 to 0.36 mm(±0.01-0.02 SE) in diameter annually across regions. Increasing root diameter was not linked to higher root length mortality, except at midslope planar locations (0.015-2.46 cm increase in root length mortality with a 0.1 mm increase in root diameter).

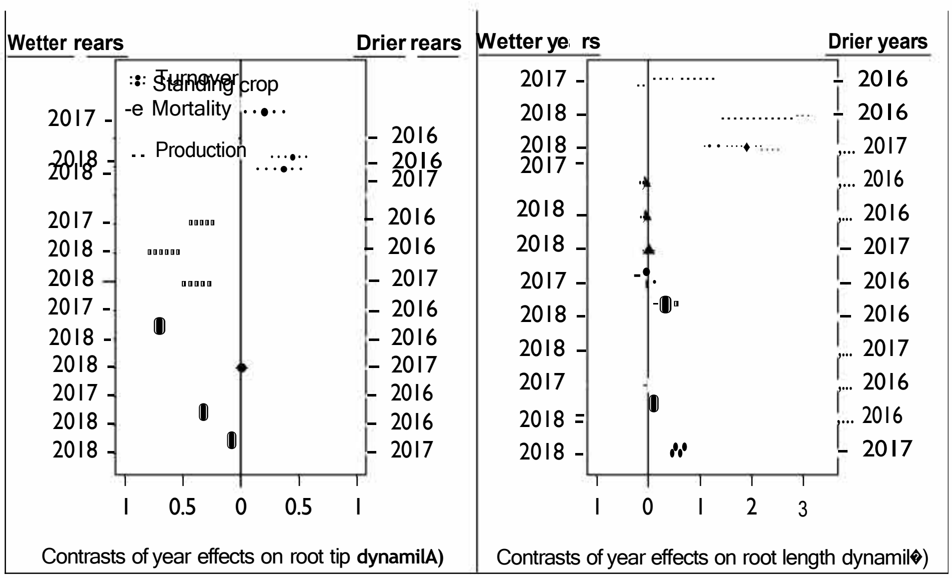

Fig. 2 Contrasts of yearly effects on root tip and length dynamics. (A). Bayesian 95% credible intervals of the contrasts of the posterior differences among years 2016-2018 for fine root tip production, mortality, standing crop, and turnover. Intervals overlapping zero represent non-significant comparisons. X-axis is in absolute units of number of roots year^{-1}, log., (number of roots) year^{-1}, and year^{-1} for fine root production and mortality, standing crop, and turnover, respectively. Intervals on the left side represent dynamics that were significantly higher in wetter years and vice versa for drier years. (B). Bayesian 95% credible intervals of the posterior contrasts among years 2016-2018 for fine root length production, mortality, standing crop, and turnover. Intervals overlapping zero represent non-significant comparisons. X-axis is in absolute units of $\log_e$ (mm) year^{-1}, except turnover, which was in units of year^{-1}. Intervals on the left side represent dynamics that were significantly higher in wetter years and vice versa for drier years

Root mortality was significantly affected by year of observation, with differing effects by root trait. Root tip mortality generally showed higher mortality in wetter years (Fig. 2A). Root length, on the other hand, generally showed increased mortality in drier years (Fig. 2B).

Standing crop

Root tip standing crop (number of roots) to depth of observation ranged from 40 to 125 (or 3.72-4.83 log$_e$ ± 0.13-0.22 SE) per site annually (Fig. 3A). Root length standing crop ranged from 6.7 to 13.4 cm (±0.6-3.1 SE) over the total observed area per site annually across regions (Fig. 3B). Midslope planar regions had significantly fewer root tips than valley floor regions (Fig. 3A). Similar to root tips, differences in first-order root length standing crop due to topographic region were largely split between wet and dry regions. Midslope planar and ridgetop (RT) regions had significantly less first-order root length standing crop than the valley floor (VF) region (VF and RT regions were significantly different at the marginal level $p < 0.1$) (Fig. 3B). Drier hillslope positions generally had more standing root length with more root tips, except for ridges and midslope planar regions which were equivalent (Fig. 4).

Average first-order root diameter of the first-order root length standing crop ranged from 0.31 to 0.40 (mm; ± 0.01-0.05 SE) in diameter annually across regions. First-order root length increased with first-order root diameter at the midslope planar region only (0.14-4.8 mm with a 0.1 mm diameter increase). Despite this, only midslope planar and valley floor regions were significantly different in the effect of first-order root diameter on root length standing (0.009-3.3 cm with a 0.1 mm diameter increase difference between MSP and VF).

Year effects differed between first-order root length and first-order root number models. There were more standing first-order root tips in wetter years than drier years (Fig. 2A). In contrast, there was no difference between wetter and drier years for standing root length (Fig. 2B).

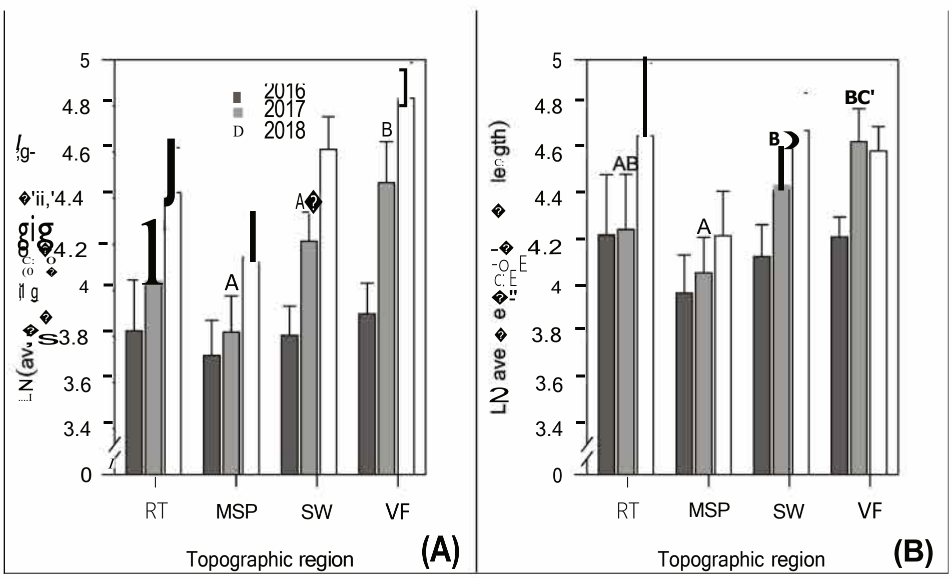

Fig. 3 Average annual cumulative standing crop root length and cumulative root tips standing. (A). Natural log of the average annual cumulative root tips standing across 2016-2018 for the different topographic regions (midslope planar, ridge top, swale, and valley floor). Error bars represent standard error. A, B, C values represent significant differences among topographic regions when letter values were not shared. **(B).** Natural log of the average annual cumulative standing crop root length (mm) across 2016-2018 for the different topographic regions (midslope planar, ridge top, swale, and valley floor). Error bars represent standard error. A, B, C values represent significant differences among topographic regions when letter values were not shared. B C' represents BC for 95% confidence and C only for 90% confidence

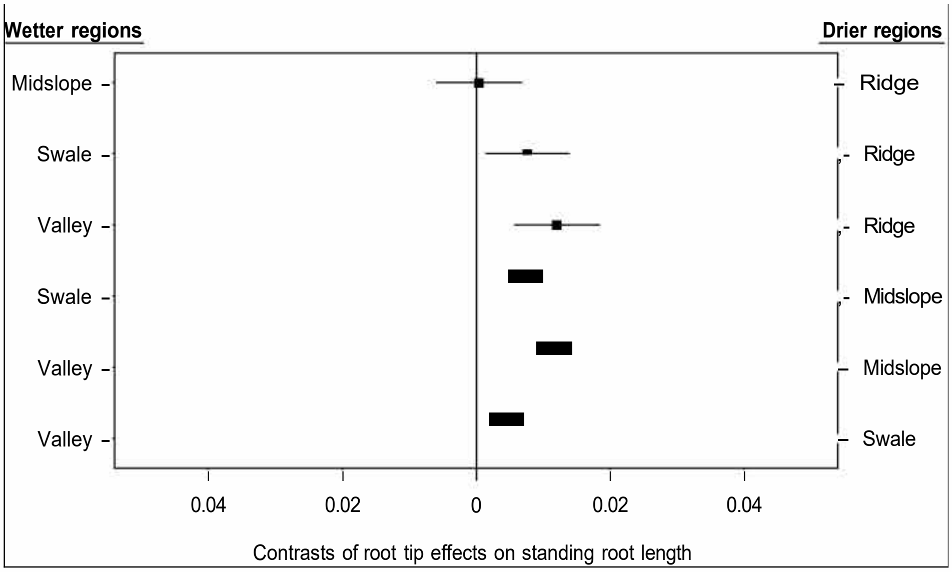

Fig. 4 Contrasts of topographic regions root tip effects on root standing length. (A). Bayesian 95% credible intervals of the contrasts of the posterior differences among topographic regions (ridgetop, midslope planar, swales, and valley floor) for root tip slope effects on root length. Intervals overlapping zero represent non-significant comparisons. X-axis is in absolute units of lo& (mm) root tip-^{1}• Intervals on the left side represent slopes that were significantly higher in wetter regions and vice versa for drier regions

Turnover

Average root tip turnover ranged from 0.83 to 1.67 year-^{1} (±0.06--0.20 SE) annually across topographic regions. Average first-order root length turnover was somewhat higher, ranging from 1.80 to 6.34 year-^{1} (±0.16--1.51 SE) over the entire length of the tube across regions. Root tip turnover showed a wet-dry split with increased root turnover in the drier regions relative to the wetter regions (Fig. 5A). Root length turnover on the other hand was generally not significantly different among hillslope positions, except for a marginally significant difference between valley floors and midslope planar regions ($p < 0.10$; Fig. 5B). There were no significant differences among hillslope positions in the effect of root tip turnover on root length turnover.

As first-order root turnover is calculated by dividing annual first-order root production by annual standing crop (McCormack et al. 2014), the first-order root diameter values were a combination of the previously stated first-order root diameters of production and standing crop. First-order root diameter had no effect on root turnover rate. Additionally, unlike all other dynamics covered so far, root turnover did not differ in response to year of observation between root length and tip models. Both root tip and length turnover were higher in the drier years relative to the wetter years.

Discussion

Generally, none of our hypotheses about quadratic trends proved to be accurate in this study area (Fig. 1). We did find evidence of wet-dry splits in first-order root dynamics. This further corroborates our findings in an earlier paper (Primka et al. 2021), where we examined the effect of topography on first-order root longevity across the catchment and found a wet-dry split in root survivorship, with roots in wetter regions living longer than those in dry regions. Unlike our previous work, we did not find any effects of topographic region on first-order root mortality or production for either root tips or length.

Despite strong aboveground signals in plant growth response due to topography in this forested catchment, specifically increased carbon uptake into wood in swales and higher LAI in swales and the valley floor region Smith et al. 2017; Naithani et al. 2013, respectively), we did not find a continuation of these strong signals in belowground trends. Both tree

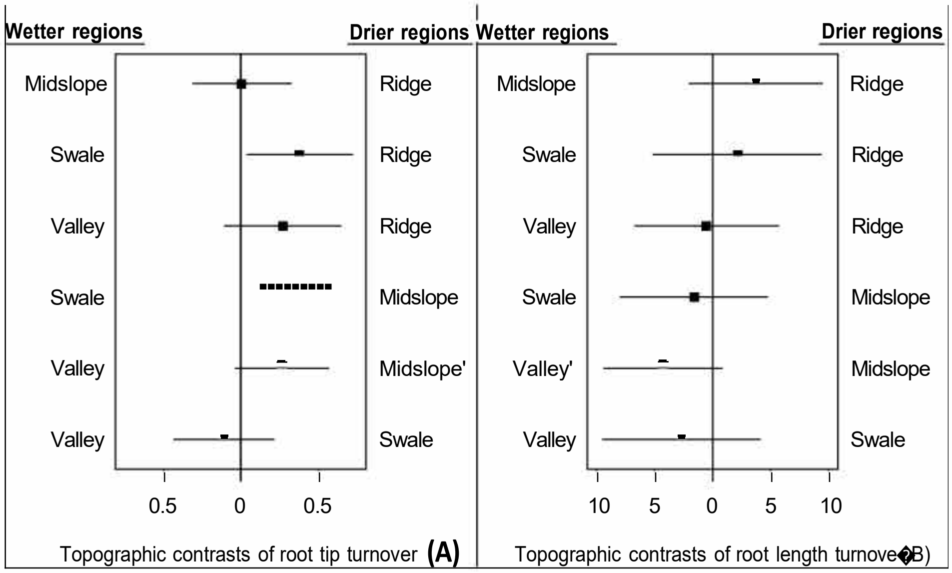

Fig. 5 Topographic contrasts of root tip and length turnover. **(A).** Bayesian 95% credible intervals of the contrasts of the posterior differences among topographic regions (ridgetop, midslope planar, swales, and valley floor) for root tip turnover. Intervals overlapping zero represent non-significant comparisons. X-axis is in absolute units of year^{-1}. Intervals on the left side represent turnover rates that were significantly higher in wetter regions and vice versa for drier regions. ' Indicates significant 90% credible intervals. **(B).** Bayesian 95% credible intervals of the posterior contrasts among topographic regions (ridgetop, midslope planar, swales, and valley floor) for root length turnover. Intervals overlapping zero represent non-significant comparisons. X-axis is in absolute units of year^{-1}. Intervals on left side represent turnover rates that were significantly higher in wetter regions and vice versa for drier regions. ' Indicates significant 90% credible intervals

basal area within sites and the neighborhood effects of tree functional groups (grouped by first-order root diameter and mycorrhizal association) did not significantly affect first-order root dynamics. The catchment is largely dominated by oaks, with some maple, hickory and evergreen species (hemlock and pines) (Smith et al. 2017; Naithani et al. 2013). Despite some variation in tree species across the 50 sites and the four topographic regions, we could not link species composition in a macroplot site to first-order root production, mortality, and standing crop length. Although we did detect modest effects of root diameter on root dynamics in some regions (e.g., midslope planar region), root diameter overall was not a strong contributor to variation in root production, mortality, standing crop or turnover across the catchment.

Minirhizotron tubes to some degree affect first-order root dynamics. Roots may tend to accumulate near the minirhizotron tubes (Vogt et al. 1998), but not if tubes are installed at a 30° angle to the soil surface (Brown and Upchurch 1987). Our minirhizotrons were installed at 30° to the soil surface to avoid artificial root accumulation and observations did not occur for two years after disturbance (see Joslin and Wolfe 1999). We also used acrylic plastic, which was found to be more similar to glass and less inhibitory than butyrate (Withington et al. 2003). Additionally, soil compaction as well as soil temperature and moisture may be increased along the soil/minirhizotron window interface relative to the bulk soil, which will modify rooting patterns (Vogt et al. 1998). To avoid these issues, we coated the tops of our minirhizotron tubes with white tape (to increase albedo), insulated the tubes to reduce temperature differences between the tubes and the soil, and allowed the tubes and the soil around the tubes to settle for a year so that the soil would be closer to normal around the tubes. It is possible that despite our efforts, root dynamics were altered by the presence of the minirhizotrons, but we took great effort to minimize these artifacts.

Backfill

The effects of the data backfilling process were relatively limited. Backfilling roots below 40 cm for year 2018 represented less than 17% of the root tips and less than 5% of the root length estimated for the whole tube for the different first-order root dynamics.

Additionally, backfilling was only done for sites with deeper soils in 2018. Backfilling made the largest differences in swales and valley floor regions where there were a lot of sites with minirhizotron depths below 40 cm. Not including the missing data points in 2018, consequently would affect the wetter topographic regions with the deeper soils more than the drier regions with the relatively shallow soils. Compared to results where 2018 data were not corrected, the overall effects of backfilling was generally modest with first-order root tip production the most impacted (16% backfill), while mortality, standing crop and turnover were less affected (<6%).

Standing crop

Contrary to our predictions, most topographic regions across the landscape did not follow a quadratic response to hillslope differences in soil moisture in standing root tips or length. We did observe that root tips and length were higher in moister hillslope positions (valley floor and swales) relative to drier positions (midslope planar and ridgetop) (Fig. 3). Additionally, valley floor regions had marginally higher first-order tree root standing length relative to the ridgetop region ($p<0.01$; Fig. 3B). While this does not constitute a full wet-dry split, we do provide evidence of topographical differences in standing first-order roots (both tip and length) that are at least partially due to hillslope differences in soil moisture.

The relationship between number of root tips produced and root length may suggest differences in root morphology. Typically, in drier regions across the landscape, first-order root lifespan is shorter (Prirnka et al. 2021). Despite this, more root length was produced per root tip in drier regions along a hillslope (Fig. 4). Increased root length allows roots to access a greater volume of soil and more nutrient pools that may be isolated due to limited soil water in these drier regions. To our knowledge, no other groups have shown this relationship between root tips and length in root standing crop due to soil moisture gradients across a landscape.

Others working in this catchment have shown similar root length effects of topographic region. Root length density measures estimated by soil coring within the CZO corroborate the general difference in standing crop due to topographic region based on wet versus dry regions (Orr 2016). Orr et al. found that the depth of the soil was the driver of the differences between the topographic regions for fine root standing crop from coring measures. It could be that the differences shown here in first-order root length were mostly related to differences in soil depth, as we found no significance of soil moisture dynamics on first-order root dynamics as measured through our TDR sensors. From previous work in this area, we know that the wetter regions tend to have longer first-order root lifespans than roots in drier topographic regions (Prirnka et al. 2021). This would likely drive a difference in first-order root standing crop length, as there were not strong wet-dry region differences in root length production or mortality. Alternatively, some studies have shown an increase in root mass under moderate increases in available soil N (Zhu et al. 2021). Orr (2016) showed that soils in swales and the ridge top regions were much higher in available mineral nitrogen (N) than soils in the midslope planar region. While this does not help explain the results shown here for first-order root length standing crop, it could be that lower N on the midslope drove lower standing root tips and length. However, we did not find an effect of available soil N on first-order root dynamics in our analyses (Table S1). This could be due to available soil N in the Shale Hills catchment being related to topography (Orr 2016), complicating our ability to disentangle the effects of soil N and topography on first-order root dynamics.

Turnover

First-order root length and the simplified tip models showed different topographic effects on first-order root turnover. In the first-order root tip model, there was a split in turnover between trees in wetter and drier topographic regions (Fig. 5A). The wet-dry split in first-order root turnover is likely indicative of a strategy shift of trees between wetter areas of the CZO and drier areas of the CZO. Previous work has shown that valley floor and swale regions tend to have longer tree root lifespans relative to the midslope planar and ridgetop regions (Prirnka et al. 2021). When examining lifespan and tip turnover together, our findings suggest that tree roots in wetter regions with deeper soils tend to persist through challenging seasonal conditions, while roots in ridgetop and midslope planar regions tend to be more frequently replaced during these periods. Plants employing a temporal avoidance strategy will produce roots when soil conditions are favorable such as springtime and allow roots to die faster when conditions are unfavorable in the soil (Santantonio and Hermann 1985). This would result in high root turnover (as found in this study) and low root lifespans (Primka et al. 2021) in unfavorable regions like planar midslopes and ridgetops.

Contrary to results of first-order root tips, topographic region generally did not significantly affect first-order root length turnover (Fig. 5B). Compared to wetter topographical regions, more root tip turnover in drier regions without corresponding high root length turnover might reflect more exploratory roots in drier regions, with short root length. While we did find that trees in drier regions tend to produce more root length per root tip, the effect size was small (range of increase: 0.001-0.019 mm root length per tip for drier regions versus wetter regions; Fig. 4). This may suggest the presence of two pools of first-order roots within the drier regions. One relatively small pool of roots that are more resilient and long, and a second pool of shorter roots that turn over more frequently. This trend was probably not driven by the small amount of variation in tree species across the topographic regions within the study site, based on neighborhood analyses.

It was surprising that first-order root tip turnover was not closely linked to first-order root production and standing crop. Root tip production did not differ across topographic regions (Fig. SI). There were more standing root tips in the valley floor than the midslope planar regions, but the other regions were not significantly different amongst each other (Fig. 3a). Yet, root tip turnover showed a wet-dry split. This was likely due to an underlying coordination of root standing crop and production values among sites, as turnover values were calculated as an average of site values. Contrary to root tips, root length for the most part resembled the combined outcomes of root length standing and production.

Year

Year of observation was linked to changes in annual precipitation that impacted first-order root dynamics. Year fortuitously represented another water gradient in our study area, but through time (years) as opposed to space (along a hillslope). Precipitation values were 719, 1170, and 1680 mm in 2016, 2017, and 2018, respectively. Precipitation in 2016 was at drought-level precipitation conditions for the SSHCZO, while 2017 was a return to normal precipitation levels in the growing season (Hodges et al. 2019). In 2018, precipitation across the whole year increased by approximately 518 mm and reflected substantially higher than normal precipitation conditions for the SSHCZO. Thus, there was an increasing soil water gradient with increasing year across 2016-2018.

The direction of the year effect differed for root tips or root length. First-order root tip production showed increasing tip production with each year, while first-order root length production showed a significant decrease in 2018 relative to 2016 and 2017 (Fig. 2A). Similarly, root tips standing crop and mortality responded positively to wetter years, and root length mortality was higher in drier years (Fig. 2A). Standing root length was not affected by year of observation. Lack of apparent differences across years in standing first-order root length was likely due to similar responses of root production and mortality to increasing annual precipitation.

None of the first-order root dynamics exhibited quadratic trends across 2016-2018 in either root tip nor length models as hypothesized. First-order root tip production increased with each increasing year, consistent with the increase in yearly rainfall. First-order root length production decreased in 2018, the wettest year, but not 2016 or 2017. First-order root tip mortality was lowest under drought conditions and increased under normal precipitation, but then exhibited no increase or decrease with higher-than-normal precipitation conditions relative to normal conditions. First-order root length mortality was generally higher under drier conditions. Gaul et al. (2008) showed that fine root mortality increases with soil freezing. As none of the winters from 2016 to 2018 were especially harsh (Personal Observation), it was unlikely that soil frost impacted a given year's mortality more than any other year. Additionally, despite documented redoximorphic features higher in the soil (0.3-0.5 m) in the valley floor region and other regions showing evidence of these features substantially lower (� 1.1 m) (Lin et al. 2006), there was no increase in first-order root mortality related to anoxic conditions in the valley floor region. Tip turnover showed trends contrary to our expectations with increased turnover in the drier years (Fig. 2). Topographically, this trend held true for root tips, but not root length (Fig. 5). This suggests that length of the individual roots must be changing across topographic regions for root length trends to not match topographic tip and annual turnover trends. When considered as a whole, first-order root length models suggest that more first-order root length were produced and died in drier years relative to wetter years, despite these trends not being shown on a spatial moisture gradient.

Spatial patterns of soil water content, such as topographic region or hillslope, affect root dynamics at different time scales than annual precipitation, which affects the ability of first-order roots to acclimate to the soil water conditions. Patterns of water content across a landscape for different topographic regions were relatively stable over the course of a year (Lin 2006) and likely at least 12 years, as similar patterns were observed 12 years later (Li et al. 2018). This suggests that the timescale that trees have to acclimate to differences in soil water condition based on hillslope position or spatially were at least several years, and likely longer. Annual precipitation reflects changes in soil water conditions that provide trees substantially less time to develop different strategies for variability in soil water conditions, compared to differences in topographic regions. Thus, it is possible that the reason we observed differences in strategy for root tips and length in space versus time is due to differences in the amount of time trees have to acclimate their roots to differences in soil water conditions.

Why did first-order root dynamics generally not show quadratic patterns with increasing soil moisture across hillslope positions? One explanation is that trees could have stabilized their root spatial distribution by hydraulic redistribution. For most roots observed across the Shale Hills catchment, deeper soils were present where roots could take up water when the upper soil layers were dry. This process, termed "hydraulic redistribution", has been shown to keep roots alive under drier soil conditions when adjacent wet soil conditions also exist (Bauerle et al. 2008; Prieto et al. 2012). Additionally, tree roots can spread up to 50 m from the bole (Schenk and Jackson 2002), which would allow trees to spatially distribute their roots within a variety of soil conditions along the hillslope that could stabilize those roots in poor conditions. Ephemeral flooded conditions in valley floor locations were observed during cold periods in the spring (Personal Observation), which did not seem to impact first-order root mortality. This may be because roots were not very metabolically active yet because of low soil temperatures, thus reducing their demand for oxygen, and because relatively few roots may have remained in the soil over winter, relative to other seasons.

Conclusions

First-order root dynamics across a hillslope revealed two distinct general patterns of behavior. In the wetter regions of the catchment, roots had slower tip turnover rates and higher first-order root standing crop length, which suggests a strategy of maintaining roots after their construction. The drier regions of the hillslope on the other hand, generally turned over root tips at a faster rate and had less first-order root standing crop length, which suggests a temporal avoidance strategy during difficult conditions. Unlike the limited responses of first-order roots to spatially structured soil water content, we did see threshold responses in first-order root tip production and mortality associated with increases in annual precipitation (temporally structured) soil water content. Additionally, across both topography and years, there was an effect of more first-order root length produced per root tip with decreasing precipitation or topographic wetness. This reflects a need to be able to take nutrients from a larger soil volume with increasingly dry conditions, regardless of year or landscape position.

Acknowledgements We thank Tyler Wagner for his assistance with Bayesian modeling and Kusum Naithani for deriving spatial orientation of macroplots and minirhizotron tubes. We also thank Jeremy Harper, Molly Pash, and Mitchell Gresock for assistance with TDR construction and installation. Thanks also to Eva Heyen, Kerry Smith, Tiffany Reed, Mitchell Gresock, Myriah Wadley, and Neha Mehta for their assistance in root tracing. Thanks also to Brandon Forsythe for his assistance with precipitation data. The authors would also like to thank Alan Taylor, Erica Smithwick and especially Jason Kaye for suggestions that substantially improved this paper. This manuscript was previously published as part of a dissertation (Prirnka IV 2021). We also would like to thank Timothy Fahey and the two anonymous reviewers who helped improve this manuscript.

Author contributions Conceived and designed study: DE. Contributed to revisions: DE, AB, and TA. Performed the study: EP, AB, and TA. Analyzed the data: EP. Contributed materials: DE. Installed instruments: TA, AB, and EP. Wrote the first draft of the paper: EP. All authors contributed to manuscript revision, read, and approved the submitted version.

Funding Support for this work was through the U.S. Department of Energy, Office of Science, Office of Biological & Environmental Research, under Award Number DE-SC0012003. Work was also facilitated through the NSF Critical Zone Observatory program grants EAR - 0725019 (C. Duffy), EAR - 1239285 (S. Brantley), and EAR - 1331726 (S. Brantley). Logistical support and/or data were provided by the NSF-supported Susquehanna Shale Hills Critical Zone Observatory. We also thank USDA National Institute of Food and Agriculture and Hatch Appropriations for their funding under Project #PEN04744 and Accession #1023222. This research was conducted in Penn State's Stone Valley Forest, which is supported and managed by the Penn State's Stone Valley Forest, which is supported and managed by the Penn State's Forestland Management Office in the College of Agricultural Sciences.

Data availability The datasets generated and analyzed for this study can be found in the Susquehanna Shale Hills Critical Zone Observatory Data Site: http://www.czo.psu.edu/data_geospatial.html.

Declarations

Conflict of interest The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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