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Review

Patterns in Root Phenology of Woody Plants Across Climate Regions: Drivers, Constraints, and Ecosystem Implications

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Abstract

Root phenology significantly influences ecosystem processes yet remains poorly characterized across biomes. This study synthesized data from 59 studies spanning Arctic to tropical ecosystems to identify woody plants root phenological patterns and their environmental drivers. The analysis revealed distinct climate-specific patterns. Arctic regions had a short growing season with remarkably low temperature threshold for initiation of root growth (0.5–1 °C). Temperate forests displayed pronounced spring-summer growth patterns with root growth initiation occurring at 1–9 °C. Mediterranean ecosystems showed bimodal patterns optimized around moisture availability, and tropical regions demonstrate seasonality primarily driven by precipitation. Root-shoot coordination varies predictably across biomes, with humid continental ecosystems showing the highest synchronous above- and belowground activity (57%), temperate regions exhibiting leaf-before-root emergence (55%), and Mediterranean regions consistently showing root-before-leaf patterns (100%). Winter root growth is more widespread than previously recognized (35% of studies), primarily in tropical and Mediterranean regions. Temperature thresholds for phenological transitions vary with climate region, suggesting adaptations to environmental conditions. These findings provide a critical, region-specific framework for improving models of terrestrial ecosystem responses to climate change. While our synthesis clarifies distinct phenological strategies, its conclusions are drawn from data focused primarily on Northern Hemisphere woody plants, highlighting significant geographic gaps in our current understanding. Bridging these knowledge gaps is essential for accurately forecasting how belowground dynamics will influence global carbon sequestration, nutrient cycling, and ecosystem resilience under changing climatic regimes.

Keywords: root phenology; belowground phenology; soil temperature; winter root growth; climate regions; root dynamics

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1. Introduction

Knowledge of plant phenology, the timing of key life cycle events in plants, is critical for understanding ecosystem functions and responses to environmental change [1,2]. While aboveground phenological patterns are well-documented across climate gradients, belowground phenology remains poorly understood, often described as a "black box" in ecosystem dynamics [3]. Root phenology, encompassing the seasonal timing of root growth initiation, peak mass, and cessation, significantly influences ecosystem processes such as

carbon sequestration [4], nutrient uptake [5], and plant-water relations [6]. Despite their critical role, roots remain underrepresented in global vegetation models and climate change predictions [7].

Terrestrial plants allocate approximately half of the 120 Pg C fixed annually through photosynthesis belowground [8]. These resources drive soil organic matter formation [9], microbial community dynamics [10], and biogeochemical processes that regulate ecosystem carbon and nutrient fluxes [11]. However, the temporal patterns of this significant carbon flow remain poorly understood, restricting our ability to forecast terrestrial ecosystem responses to climate change [12]. In contrast to aboveground phenology, which benefits from scalable monitoring via remote sensing and citizen science [13–15], root phenology relies on labor-intensive techniques like minirhizotrons, soil coring, or rhizotrons, which are challenging to standardize across studies [16–18]. As a result, root phenological patterns lack the spatial and temporal resolution of aboveground processes. While leaf phenology closely tracks photoperiod and temperature cues [19], root phenology appears driven by more complex, potentially region-specific environmental factors [3]. It has been suggested that root phenology exhibits distinct regional variations due to differing climatic limitations [20–22]. In temperate and boreal forests, following winter dormancy, spring root growth typically initiates at threshold soil temperatures [20], whereas precipitation patterns often govern root development in water-limited tropical and Mediterranean ecosystems [21,22]. The interplay between root and shoot phenology further complicates our understanding of belowground seasonal dynamics [23].

The fragmented nature of root phenology research, due to geographic and methodological disparities, has impeded the development of a unified perspective on belowground seasonal dynamics. To address these knowledge gaps, we synthesized data from 59 studies across arctic to tropical ecosystems to examine five key questions: (1) how root phenology varies across climate regions and what general patterns emerge; (2) which environmental factors are associated with root phenological stages and how these associations vary geographically; (3) the patterns of temporal coordination between root and aboveground phenology across climate gradients; (4) the prevalence and ecological significance of winter root growth across different ecosystems; and (5) how root phenological patterns might respond to climate change and the implications for ecosystem functioning. Through this synthesis, we seek to provide a clearer perspective on belowground seasonal dynamics, enhance our understanding of terrestrial ecosystem processes, and highlight critical knowledge gaps for future research.

2. Materials and Methods

2.1. Literature Search and Selection Criteria

We conducted a systematic literature search using Web of Science (Clarivate Analytics, London, UK) to identify studies examining root phenology across diverse ecosystems. The search employed combinations of the terms 'root phenology' or 'roots' with 'growth', 'dynamics', 'production', 'leaf', or 'shoot'. We restricted our search to peer-reviewed articles published in English until October 2024, resulting in an initial pool of 217 publications. From this initial pool, we applied several inclusion criteria to select relevant studies. We specifically focused on research featuring observations of root growth dynamics under natural conditions, excluding studies with experimental manipulations such as fertilization, thinning, or other anthropogenic interventions. Studies were required to concentrate on woody plant species or forest ecosystems and utilize non-destructive observation methods, primarily minirhizotrons or root windows. Furthermore, selected research needed to quantitatively report at least one root phenological parameter, including initiation, peak growth, or cessation. Finally, we ensured that all included studies maintained tempo-

ral resolution sufficient to identify seasonal patterns, with a minimum requirement of monthly observations.

After applying these criteria, 59 studies were retained for analysis (Table S1). The selected studies spanned 24 countries across six continents, with publication dates ranging from 1994 to 2024. The majority of studies (97%) were conducted in the Northern Hemisphere, reflecting a geographical bias in the current literature.

2.2. Data Extraction and Standardization

For each selected study, we extracted several categories of information. This included study location details such as city, country and climate classification, as well as vegetation characteristics including dominant species, ecosystem type. We documented root phenological parameters, recording the day of year (DOY) of root growth initiation, peak root growth, and cessation, along with the presence or absence of winter root growth. When available, we also extracted leaf phenological parameters, noting the DOY of budburst or leaf emergence, full leaf expansion, and leaf senescence. Additionally, we compiled environmental correlates, including soil temperature at phenological transitions, air temperature at phenological transitions, and soil moisture conditions when reported. When studies reported data for multiple years, species, or sites, each distinct dataset was recorded separately, resulting in a total of 124 individual observations across the 59 studies. To standardize the data across hemispheres, we adjusted DOY values for Southern Hemisphere studies by adding 182 days, aligning them with Northern Hemisphere seasonality. We quantified the temporal offset between root and shoot developmental timing by calculating the difference in days between corresponding phenological stages (initiation, peak activity, cessation). Positive values indicate that root phenological stages (initiation, peak activity, or cessation) occur after the corresponding leaf phenological stages, while negative values indicate that root phenological stages precede their leaf counterparts.

Climate Classification

Studies were categorized into climate regions based on their reported location using the Köppen-Geiger climate classification system [24]. For analysis purposes, we grouped the studies into five major climate categories: Temperate (including cold temperate), tropical (including subtropical), continental (including humid continental), Mediterranean, arctic (including subarctic). Detailed information about specific subcategories and their characteristics is provided in Table S1. When studies crossed climate boundaries or contained multiple sites across different climate zones, they were categorized according to the predominant climate of their research sites or split into separate entries when distinct data were available for each climate zone.

2.3. Analysis Approach

We analyzed patterns in root phenology across climate regions using both quantitative and qualitative approaches. For quantitative analysis, we calculated descriptive statistics (mean, median, range) for each phenological parameter within climate categories. We assessed the relationship between environmental variables (primarily soil temperature) and phenological transitions using the reported threshold values. To evaluate root-shoot phenological coordination, we analyzed temporal offset patterns both within and across climate regions. We calculated the proportion of studies showing synchronous patterns (defined as root and shoot phenology occurring within $\pm$14 days of each other) versus asynchronous patterns (>14 days offset). The completeness of phenological reporting varied substantially across studies. Only 47% documented the timing of root growth initiation, and 37% identified drivers of root growth onset (Table S1). While 85% of studies reported peak root growth timing (predominantly in summer), fewer (53%) measured root growth

during winter months, with only 35% actually observing winter growth. Although 54% of studies established connections between root and leaf phenology, just 15% comprehensively monitored complete phenological cycles of both roots and leaves within the same annual period. Due to this reporting heterogeneity, we employed a weight-of-evidence approach in our synthesis, giving greater consideration to studies with more complete phenological documentation. For climate regions with limited representation (fewer than three studies), we present their findings but exercise caution in drawing broad conclusions.

Statistical Analysis

Due to the non-normal distribution of data and relatively small sample sizes, a combination of parametric and non-parametric statistical methods was employed. Initial differences in soil temperature among climate zones were analyzed using one-way ANOVA for variables where assumptions could be reasonably met, and Kruskal-Wallis tests for variables with more severe departures from normality. All statistical analyses were performed using Python (version 3.8). Only climate zones with sample sizes ≥ 3 were included in the statistical analysis. When tests indicated significant differences ($p < 0.05$), pairwise *t*-tests were conducted between all possible climate region combinations to identify specific group differences. Different letters were assigned to climate regions based on these pairwise comparisons, with regions sharing the same letter not differing significantly from each other. Due to small sample sizes in some climate regions (particularly those with only 1–2 data points), more stringent multiple comparison correction methods (such as Tukey HSD or Bonferroni correction) were not applied. The letter notation approach reflects groupings based on pairwise *t*-test results, which was deemed appropriate given the sample size limitations. Readers should exercise caution when considering results from climate regions with limited samples.

3. Results

3.1. Patterns in Root Phenology Across Climate Regions

3.1.1. Temperate Regions

Root phenological patterns show distinct regional variations across climate zones (Figure 1a). Temperate forests exhibit pronounced seasonality with a clear annual cycle characterized by spring initiation, summer peak activity, and autumn cessation. Across temperate studies ($n = 20$), root growth initiates between DOY 91–140 (range; early April to mid-May), with a median onset at DOY 105. This spring initiation consistently follows soil temperature thresholds of 1–9 °C in temperate and 2–14 °C in cold temperate zones. The timing of root growth initiation followed a clear latitudinal gradient, with earlier onset in mild temperate regions (range; DOY 90–100) compared to cold temperate forests (range; DOY 120–140) (Table S1).

Peak root growth in temperate regions occurs predominantly during summer months (range; DOY 121–244, May to August), with 82% of temperate studies reporting maximum growth rates during this period. This summer peak coincides with warmer soil temperature conditions (15–20 °C) and generally favorable moisture availability. Cold temperate forests (e.g., those in northeastern China, Finland, and northern Japan) showed a narrower window of peak activity (range; DOY 152–214) compared to mild temperate forests, suggesting adaptation [25] to shorter growing seasons (Table S1).

Root growth cessation in temperate regions occurs between DOY 243–305 (range; September to October), with variation across sites and species. This variation is driven by the interaction between declining soil temperatures and species-specific cessation thresholds. Studies from New York [20] and Japan [26] found that temperate deciduous species

ceased root growth when soil temperatures dropped below 7–18 °C, while some evergreen conifers-maintained growth at lower temperatures.

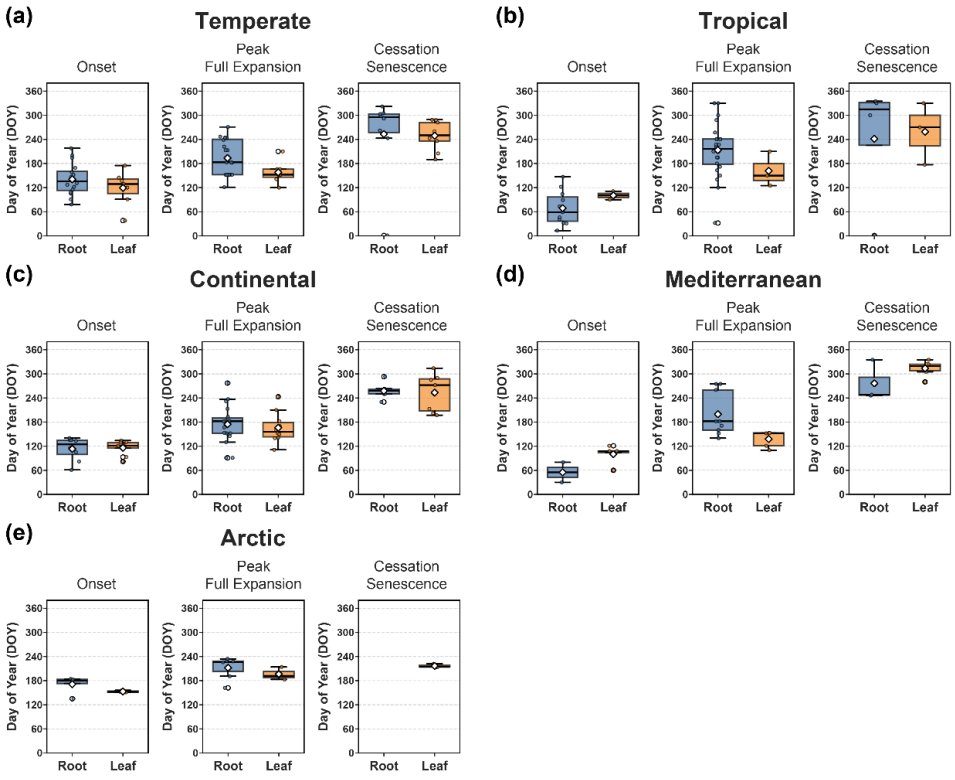

Figure 1. Patterns in root and leaf phenology timing across climate regions. (**a**) Temperate; (**b**) Tropical; (**c**) Continental; (**d**) Mediterranean; (**e**) Arctic. Bars represent the median values. White circles represent the mean values. Error bars indicate variability among observed data points. Absence of error bars signifies fewer than three data points were available from the surveyed researches. Missing data points indicate that the specific information was not reported in the surveyed researches.

3.1.2. Tropical and Subtropical Regions

In tropical and subtropical regions (n = 13), root phenological patterns vary considerably based on local moisture regimes (Figure 1b). The majority of studies (79%) across tropical forests revealed seasonal fluctuations in root growth intensity, with periods of higher and lower activity rather than complete cessation. After accounting for hemispheric differences, consistent patterns related to regional precipitation cycles emerged. The Darwin, Australia savannah study [27], when adjusted for hemispheric differences, showed peak root growth during DOY 241–273 (range; early August to late August), occurring during the wet season in Northern Australia. Similarly, the Central Chile study [28], after hemispheric adjustment, revealed root growth onset at DOY 147 (April) with first peak activity around DOY 172–202 (range; late May to late June) during the season of highest precipitation. The same pattern was shown in Costa Rica [29]. These values demonstrate how root phenology in these regions synchronizes with seasonal moisture availability rather than temperature.

Studies in tropical savannas and seasonally dry forests [27,30] have shown that peak root growth typically coincided with the onset of rainy seasons, implicating soil moisture as the primary driver. In contrast, studies in evergreen tropical forests [31,32] reported multiple growth peaks throughout the year, suggesting more complex environmental cues. These findings showing that tropical woody species maintain greater year-round growth activity, with 71% of studies reporting active root growth during cooler months, the highest prevalence among all climate regions studied.

Subtropical ecosystems showed intermediate patterns between tropical and temperate systems (Table S1). Studies from subtropical China [22] and the eastern Japan [33] documented root growth initiation as early as DOY 13–59 (range; January to February), substantially earlier than in temperate regions. Unlike tropical systems, these regions generally exhibited a more defined peak growth period (range; DOY 163–288, June to October) and occasional growth cessation during cooler months in some species.

3.1.3. Continental Regions

Continental climate regions (n = 13), characterized by greater seasonality and temperature extremes, exhibited shorter growing seasons relative to temperate regions (Figure 1c). Root growth initiation in continental forests typically occurred later (median DOY 140, late May) compared to temperate regions, possibly reflecting adaptation [25] to delayed soil warming. Studies from northeast and mid-west United States [34,35] reported root growth onset when soil temperatures reached 11–15 °C, substantially higher than the 1–9 °C thresholds observed in temperate regions.

Peak root growth in continental regions was concentrated in a narrower time window (range; DOY 167–237, mid-June to late August) compared to temperate forests. This compressed period of peak activity coincides with the brief summer window when both temperature and moisture conditions are favorable. Steinaker et al. (2010) and McCormack et al. (2014) reported that continental forest species exhibited higher root elongation rates during summer compared to other seasons [36,37]. According to these studies, this growth pattern differs from the more extended, moderate growth patterns observed in temperate forests. However, these observations are based on limited studies and further research would be needed to establish whether this represents a consistent regional pattern.

Root growth cessation in continental regions occurs relatively early (range; DOY 250–293, September to early October), driven by rapidly declining autumn soil temperatures. Studies from Minnesota [35] and Quebec [38] found that root growth ceased when soil temperatures dropped below 13–20 °C, higher thresholds than those observed in temperate regions. This earlier cessation further compresses the annual root growth window in continental compared to temperate ecosystems.

3.1.4. Mediterranean Regions

Mediterranean ecosystems (n = 10) displayed distinctive bimodal root growth patterns possibly reflecting adaptation [25] to seasonal drought conditions (Figure 1d). Root growth in these regions typically initiates early (range; DOY 30–80, January to March) during the wet, mild winter season, decreases or ceases during summer drought periods, and shows a second growth peak in autumn when moisture conditions improve, but temperatures remain favorable. Studies from France [39], Spain [40,41], and California [21] consistently reported bimodal peaks in root growth during spring (range; DOY 152–182, May to June) and autumn (range; DOY 275–304, October to November), with altered growth strategies during summer drought months (range; DOY 213–274, July to September). This response was particularly evident in Mediterranean oak forests [42], where *Quercus ilex* maintained root production during summer drought by shifting to an intensive resource acquisition strategy, increasing specific root length while developing thinner fine roots, thereby maximizing soil volume exploration per unit of invested biomass despite suboptimal moisture conditions. With this drought adaptation strategy prioritizing resource allocation during dry periods [25], Mediterranean woody species showed a lower prevalence of winter root growth, with 36% of studies reporting active root growth during winter months.

3.1.5. Arctic and Subarctic Regions

Arctic and subarctic ecosystems (n = 7) displayed the shortest roots phenological cycles, with extremely restricted growing seasons (Figure 1e). Root growth in these regions initiates remarkably late (range; DOY 171–184, late June to early July), coinciding with rapid soil warming after snowmelt. Studies from Sweden [43] found that root growth initiated at soil temperatures as low as 1–3 °C in *Betula pubescens* and 0.5–1 °C in *Eriophorum vaginatum*, substantially lower than thresholds in all other climate regions.

Peak root growth in arctic regions was tightly concentrated around DOY 191–229 (range; mid-July to mid-August), the brief period when soil temperatures reach their annual maximum. Research from Alaska [44] and Sweden [43] documented soil temperature of 5–11 °C for peak root growth, considerably lower than the 15–20 °C reported in temperate and continental regions. This change to function at lower temperatures enables arctic plants to complete their growth cycles within extremely compressed growing seasons.

In arctic region studies, observations of root growth typically ended by DOY 244–259 (range; late August to mid-September), primarily due to research teams concluding their field campaigns before the onset of harsh winter conditions rather than necessarily reflecting biological cessation of growth. This methodological limitation is important to consider when interpreting apparent patterns of root growth cessation in arctic regions, as the actual timing of biological growth cessation might differ from reported observation endpoints.

3.2. Environmental Controls on Root Phenology

3.2.1. Temperature Effects

Our synthesis suggests an association between temperature and root growth patterns across climate regions, with regional differences in the temperature conditions at which phenological events occur (Figure 2). The data indicate that root growth initiation was associated with different soil temperature ranges across climate regions: 0.5–1 °C in arctic regions, 1–3 °C in subarctic regions, 1–9 °C in temperate regions, 11–15 °C in continental regions, 2.5–6 °C in humid continental regions and 18–21 °C in Mediterranean regions (Table S1). While these associations are consistent within regions, they do not necessarily indicate that temperature alone triggers these transitions, as other factors such as photoperiod, soil nutrient availability, and biological interactions may also play important roles.

The remarkably low temperature thresholds in arctic and subarctic regions possibly represent critical adaptations that allow plants to initiate growth immediately following snowmelt [45], maximizing utilization of the brief growing season. In contrast, the higher thresholds in continental and Mediterranean regions may reflect adaptation to greater temperature extremes and the presence of additional limiting factors beyond temperature [25].

Temperature thresholds for peak root growth showed less variation across climate regions (Figure 2), with temperatures generally between 15–20 °C in temperate and continental regions. However, significant variations were evident in extreme environments. Arctic species exhibited peak growth at just 5–11 °C, while Mediterranean and tropical species showed peak growth at 11–15 °C and 19–24 °C, respectively. These temperature ranges align closely with the prevailing soil temperatures during periods of otherwise favorable conditions, for instance, N mineralization rates increase exponentially with temperature when soil temperatures ranged between 7 and 26 °C annually in the Southern San Joaquin Valley [46]. This suggests that root growth responds to the available temperature conditions within each environment. For example, Arctic plant roots may grow much faster under conditions that are warmer than the typical annual temperatures in their native habitat.

Temperature thresholds for root growth cessation showed the greatest variability across both regions and species. In temperate regions, root growth typically ceased when

soil temperatures declined to 7–18 °C, while continental species stopped growth at higher thresholds (13–20 °C).

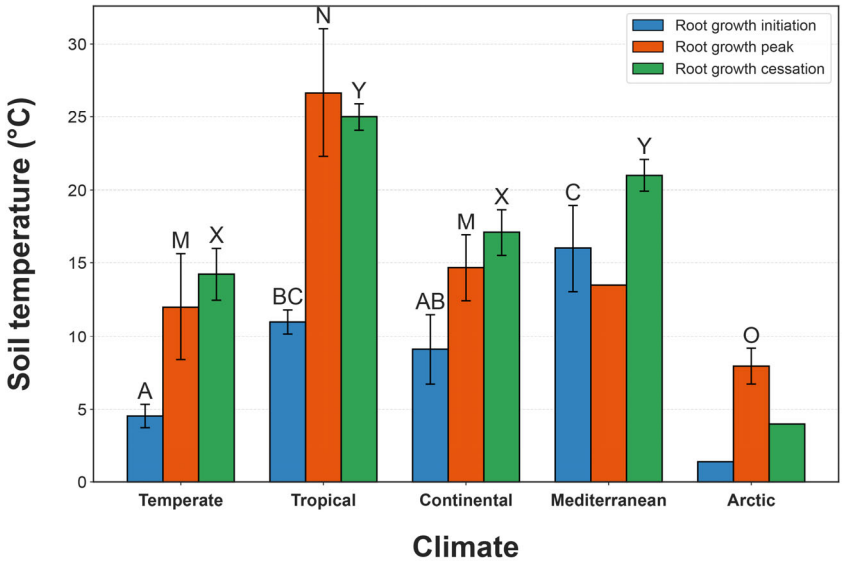

Figure 2. Distribution of mean soil temperature at critical root phenological events across different climate regions. Error bars indicate variability among observed data points. Missing values indicate that the surveyed researches did not contain this specific data; absence of error bars indicate fewer than three data points were available from the surveyed researches. Note: Mediterranean (n = 2, 3), and Tropical (n = 3) climate zones have small sample sizes, which may affect the reliability of significance tests. Different letters (A–C root growth initiation; M,O root growth peak; X,Y, root growth cessation) indicate significant differences between climate zones ($p < 0.05$).

3.2.2. Water Availability Effects

While temperature regulates root phenology in temperature-limited ecosystems (temperate, continental, and arctic), moisture availability dominates as the primary control in water-limited regions. In Mediterranean and seasonally dry tropical ecosystems, observed root growth patterns coincided more closely with seasonal changes in soil moisture than with temperature fluctuations. This association suggests that water availability might be an important factor related to root phenology in these regions, although the precise mechanisms and potential interactions with other environmental variables require further investigation. Studies in Mediterranean oak forests [42] documented clear seasonal patterns in soil moisture, with volumetric soil water content (SWC) increasing from 20% in early September to 35% by mid-November, remaining stable until early May, then declining to 19% by early July during peak summer drought, before recovering to 25% by early September. These soil moisture dynamics corresponded with bimodal fine root growth, with significant peaks occurring during the transitions between wet and dry seasons. While not included in our primary analysis due to different life forms or the use of experimental manipulation, studies from arid ecosystems reinforce and add complexity to this principle. In some cases, fine root growth shows a strong quantitative dependency on water availability, increasing directly with irrigation intensity [47]. However, the pattern of precipitation can be more influential than the total volume; for example, one study found that desert plant growth remained stable with rainfall variations of up to 30% as long as the frequency of rainfall events was consistent [48].

In tropical savannas and seasonally dry forests, root phenology showed strong synchronization with precipitation patterns. Studies from Burkina Faso [30] and China [22] found that root production peaked during the rainy season, suggesting that soil water content triggers growth responses in these ecosystems. The adjusted data from Darwin,

Australia [27] provides a clear example of moisture-driven phenology in savannah ecosystems. With peak root growth during the adjusted DOY 214–241 (August in Northern Hemisphere equivalent), this corresponds to the transition from dry to wet season in Northern Australia monsoonal climate, further supporting the primacy of moisture as a phenological cue in water-limited systems. The interaction between temperature and moisture controls was particularly evident in Mediterranean and subtropical regions, where studies documented temperature control during moist periods and moisture control during dry periods [22,49].

3.2.3. Other Environmental Factors

Beyond associations with temperature and moisture, studies on *Pinus halepensis* Mill. [41] and *Pinus resinosa* Ait. [50] observed relationships between photosynthetic activity and root growth, suggesting potential connections between current photosynthate supply and root development in specific contexts, though experimental manipulations would be needed to establish causal linkages.

Soil nutrient availability showed a decoupling between root biomass and phenological timing. Contrary to expectations, comparative studies found that while fertilization significantly increased root biomass production, it did not alter the timing of root phenological events (initiation, peak growth, or cessation) [41,51,52]. This important distinction demonstrates that soil nutrient status primarily influences the magnitude of root growth rather than its seasonal timing, which remains controlled by temperature and moisture cues.

Biotic interactions, particularly mycorrhizal associations, emerged as potentially important modifiers of root phenology. Studies examining both mycorrhizal colonization and root growth dynamics [53,54] documented temporal coordination between fungal activity and fine root production. Pioneer roots colonized by mycorrhizal fungi demonstrated notably different temporal patterns compared to fibrous roots, initiating growth earlier in the season, maintaining extended growth periods, and exhibiting remarkable resilience during drought conditions [53].

3.3. Patterns of Root-Shoot Temporal Offsets

It is important to note that conclusions about root-shoot coordination are inherently limited by the small number of studies that comprehensively track both above- and belowground cycles; thus, the patterns presented here should be interpreted with constraint. The temporal relationship between root and shoot phenology varied substantially across climate regions, revealing diverse resource allocation strategies (Figure 3). Approximately 54% of studies made some comparison between root and leaf phenology, though most focused on limited aspects of phenological cycles. Only a small number (n = 15) comprehensively examined the onset of both root and shoot growth throughout complete annual cycles. Among these more complete studies, 40% reported synchronous patterns (root and shoot phenology within ±14 days), 33% reported root growth lagging behind shoot growth (by >14 days), and 27% reported root growth preceding shoot activity (by >14 days). The limited number of studies with complete phenological data highlights a significant research gap and suggests that our understanding of root-shoot coordination patterns is preliminary and would benefit from more comprehensive year-round observations.

Temperate deciduous forests predominantly exhibited sequential phenology with leaf emergence preceding root growth by 14–28 days [20,26,55]. However, studies by Schenker et al. (2014) found cases where root growth initiated before leaf emergence in temperate species, attributable to warmer soil temperatures during winter [56]. Malyshev et al. (2023) conducted a study to investigate how warming non-dormant tree roots affects aboveground spring phenology in temperate trees, suggested that temperate species have

the capacity to opportunistically resume root growth under favorable soil conditions, whereas more northern species may possess some form of true root dormancy that prevents such early activation [57]. In contrast, Mediterranean and some seasonally dry tropical ecosystems frequently displayed the opposite pattern, with root growth preceding leaf emergence [29,58]. This strategy may enable plants to secure belowground resources, particularly water, before investing in transpiring leaf tissues. The Central Chile study of *Prunus avium* [28], after hemispheric adjustment, shows a different pattern than originally reported. With adjusted values (root onset at DOY 147, leaf budburst at DOY 111), the offset becomes +36 days (roots following leaves) rather than −146 days (roots before leaves). This adjusted pattern aligns with temperate deciduous strategies where leaf growth precedes root growth, consistent with the deciduous nature of sweet cherry. The strongest root-shoot synchronization occurred in humid continental forest ecosystems, where 57% of studies reported simultaneous root and shoot growth (within ±14 days). This coordination possibly reflects adaptation to moderate growing seasons, where balanced resource acquisition above- and belowground optimizes productivity within seasonal constraints [25]. However, studies from arctic and subarctic regions showed strong asynchronization, with 100% of arctic observations displaying root growth lagging behind shoot growth (>14 days) and subarctic regions showing a 50-50 split between root lagging and root preceding patterns. Studies from Alaska [44] and Sweden forest systems [43] documented varying DOY for leaf emergence and root growth initiation, with processes responding differently to snowmelt and soil thawing. It is worth noting that non-forest arctic systems such as heathlands and meadows [43] may exhibit different coordination patterns, with root growth sometimes preceding leaf emergence by up to 31 days, suggesting potential species-specific strategies even within the same climate region.

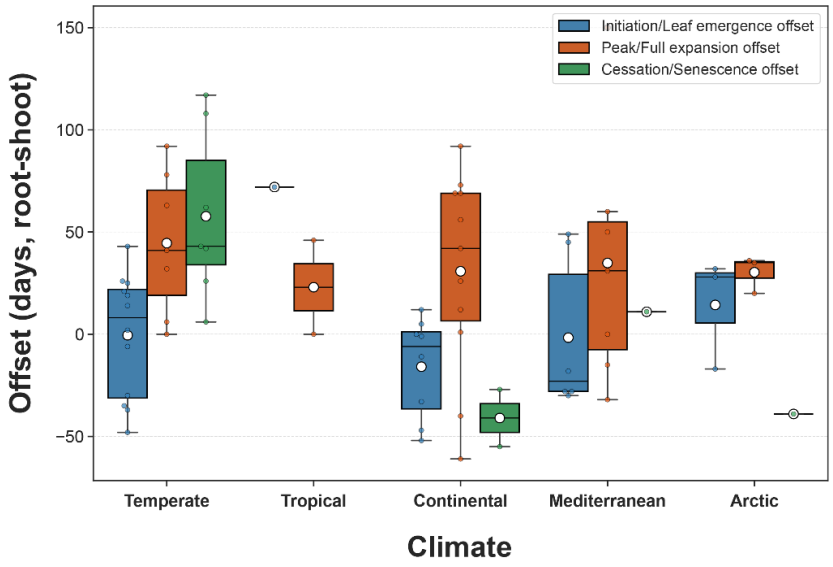

Figure 3. Temporal offset between root and leaf phenological events. Bars represent the median values; white circles represent the mean values. Positive values indicate that root phenological stages (initiation, peak activity, or cessation) occur after the corresponding leaf phenological stages, while negative values indicate that root phenological stages precede their leaf counterparts. Error bars indicate variability among observed data points. Missing values indicate that the surveyed researches did not contain this specific data; absence of error bars indicate fewer than three data points were available from the surveyed researches.

Evergreen species across climate zones showed substantially different coordination patterns compared to deciduous species. Evergreen conifers in temperate and boreal

regions generally exhibited more continuous root growth patterns with weaker correlation to aboveground phenology [26,53,59].

3.4. Winter Root Growth

Winter root growth, defined as active root production during the meteorological winter period, emerged as a widespread, but regionally variable phenomenon. Of the 59 studies analyzed, 35% reported active winter root growth, although this phenomenon was distributed unevenly across climate regions: It was most prevalent in tropical studies (71%), followed by Mediterranean (36%) and temperate (25%) regions (Figure 4). No winter root growth was reported in arctic regions as measurements were not conducted during winter period. However, it is essential to note that a substantial number of studies (marked as 'ND' in Figure 4) did not include winter measurements at all. The complete lack of winter data in the reviewed continental studies and the majority of arctic studies means no conclusions can be drawn about winter root dynamics in these cold climates. These studies with no winter data were still included in our overall dataset, but cannot inform our understanding of winter root dynamics. This methodological limitation restricts our ability to draw comprehensive conclusions about winter root growth patterns and highlights a critical gap in our understanding, particularly for ecosystems with prolonged soil freezing.

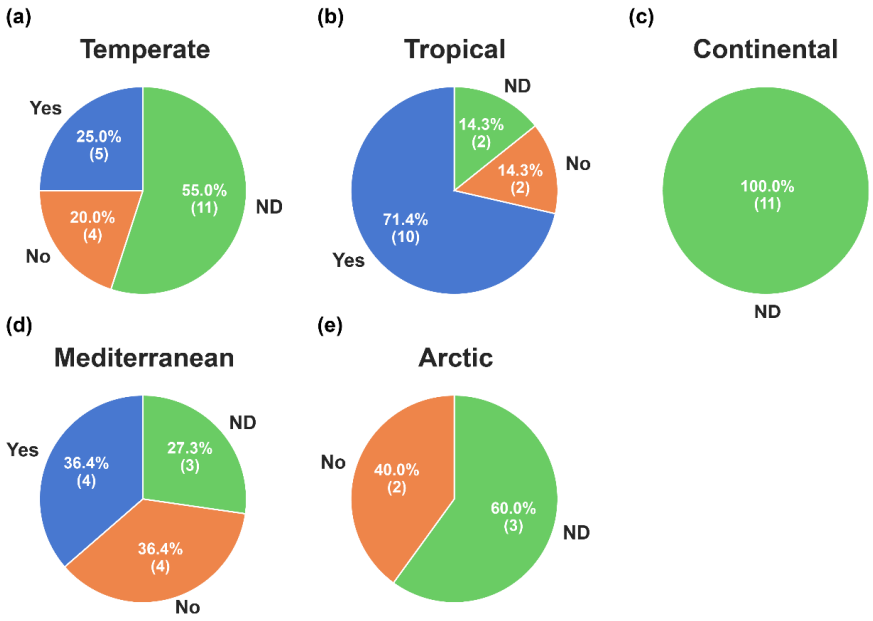

Figure 4. Winter root growth patterns across different climate regions. (**a**) Temperate; (**b**) Tropical; (**c**) Continental; (**d**) Mediterranean; (**e**) Arctic. Bars show the percentage of studies within each climate region that observed winter root growth (Yes), did not observe winter root growth despite monitoring (No), or did not determine winter growth because measurements were not conducted during winter months (ND).

The high prevalence of winter growth in tropical regions (Figure 4b) reflects their stable, warm soil conditions throughout the year. Studies from Thailand [31], Malaysia [32], and Australia [27] documented continuous root production when consistent soil temperatures and moisture availability supported year-round growth, even during what would be considered winter months in other regions. In Mediterranean regions, winter root growth (36% prevalence) coincides with favorable moisture conditions that characterize Mediterranean climates. Studies from Spain [41], Italy [42], and California [60] found substantial winter root growth when soil temperatures remained above 18–21 °C, and both carbon and moisture were available, even when aboveground tissues were dormant. This winter

growth appears critical for annual resource budgets in these ecosystems, allowing resource acquisition during the brief favorable moisture window. In temperate regions, winter root growth occurred primarily in mild maritime climates and in evergreen species. Studies from coastal Europe [56] and Japan [26] documented winter root production when soil temperatures remained above 4–5 °C.

We observed a decline in winter growth prevalence along the gradient from tropical to arctic ecosystems, which corresponds with regional winter soil temperature patterns. Winter root growth was rarely reported in regions where soils routinely freeze. This geographic pattern suggests a possible relationship between soil freezing and root growth limitations, though other factors such as carbon allocation priorities, or methodological differences between studies may also contribute to these observations.

4. Discussion

4.1. Comparative Analysis of Root Phenological Patterns Across Climate Regions

4.1.1. Phenological Variations in Temperate Regions

Seasonal root growth patterns in temperate forests show distinct relationships with local climate conditions. Spring initiation occurs at different soil temperatures along a latitudinal gradient (1–5 °C in mild temperate regions, 2–14 °C in colder ones), with this variation potentially reflecting different strategies for timing root growth within the available growing season [61–63].

In temperate regions, summer root growth peaks often coincide with periods following canopy expansion, supporting observations related to carbon availability for root growth [64,65]. For instance, Burke & Raynal (1994) study in a New York temperate forest found root growth peaking approximately 30 days after leaf expansion [20]. While carbon translocation from leaves to roots occurs within 1–4 days [66], the 30-day lag may reflect the sufficient photosynthetic carbon accumulation to support peak root growth rates. Additionally, this lag could also result from the time required for soil temperatures to warm adequately, as soil temperature changes much more slowly than air temperature [67,68].

Temperate deciduous species were observed to cease root growth at higher soil temperatures (7–18 °C) compared to arctic species. This difference could potentially reflect adaptation to regional growing season characteristics, where temperate species may benefit from concentrating growth during more favorable conditions. However, multiple alternative explanations are possible, including differences in root physiological adaptations, carbon allocation strategies, or methodology differences between studies.

4.1.2. Resource-Driven Phenology in Tropical and Subtropical Systems

In tropical and subtropical regions, root growth patterns align closely with precipitation cycles, highlighting a shift in limiting factors compared to temperate ecosystems. Temperate root phenological patterns appear to coincide closely with seasonal temperature changes, while tropical systems show stronger associations with precipitation patterns. This difference in apparent environmental relationships may reflect regional adaptations to different limiting factors, though we cannot rule out the influence of other variables such as light regimes, soil properties, or biotic interactions [69]. Evergreen tropical forests exhibit multiple root growth peaks [32], reflecting an opportunistic strategy that contrasts with the rigid annual cycles of temperate systems. This flexibility possibly evolved to cope with less predictable resource availability, where light and temperature remain stable but rainfall varies [70]. Subtropical ecosystems display intermediate phenological patterns, with earlier spring initiation than temperate forests but more pronounced seasonality than tropical systems, illustrating a continuum from temperature-driven (arctic, temperate) to moisture-driven (Mediterranean, tropical) phenological strategies.

4.1.3. Bimodal Patterns in Mediterranean Ecosystems

Mediterranean ecosystems show a distinctive bimodal root growth pattern, a sophisticated adaptation to wet spring, autumn and dry summers [71]. This strategy enables plants to exploit two distinct growth windows separated by the limitation of summer drought. The pattern diverges from the single, temperature-driven growth peak typical of other temperate-latitude ecosystems. The prominence of moisture as a limiting factor in Mediterranean regions overrides temperature signals that dominate in non-water-limited systems at similar latitudes. Winter root activity, supported by mild, wet conditions, allows Mediterranean plants to efficiently utilize seasonal moisture, even at suboptimal temperatures, maximizing resource acquisition in a drought-constrained environment [72].

4.1.4. Compressed Phenology in Continental and Arctic Regions

The compressed root growing seasons in continental and arctic regions show distinct patterns related to temperature constraints. Arctic ecosystems exhibit remarkably late root initiation (DOY 171–184) and early cessation, resulting in growing seasons roughly half as long as those in temperate regions, and is associated with frozen soils and brief summers [73]. Arctic species showed root initiation at remarkably low soil temperatures (0.5–1 °C), coinciding with the period shortly after soil thawing. In contrast, continental species were observed to initiate root growth at higher soil temperatures (11–15 °C). These regional differences in root growth initiation temperatures could potentially reflect different physiological constraints or adaptations, though experimental studies would be needed to test this hypothesis. Alternative explanations could include methodological differences between studies or variations in other environmental factors that coincide with temperature changes.

These regionally distinct phenological patterns have implications for how different ecosystems may respond to climate change [74]. As warming shifts soil thaw timing and extends growing seasons, the observed differences in temperature-phenology relationships between regions suggest that root systems may respond differently to temperature changes. For example, arctic species that currently show root growth at near-freezing temperatures may respond differently to warming compared to continental species where root growth occurs at much warmer temperatures. However, the specific nature and magnitude of these responses remain unclear and require further investigation.

4.2. Hierarchical Control of Environmental Factors

The observed patterns suggest that moisture and temperature may have different relative associations with root phenology across regions, possibly reflecting a "limiting factor principle", where plant responses appear most strongly related to the most limiting resource. However, these relationships are correlative, and multiple environmental factors possibly interact to influence root phenological patterns. Other potential influencing factors include photoperiod, soil chemistry, microbial associations, and plant carbon status [75,76]. In moisture-abundant temperate and continental climates, temperature predominantly governs root phenology, whereas in moisture-limited Mediterranean and tropical ecosystems, precipitation patterns take precedence. This hierarchical control has critical implications for predicting climate change impacts [3,77]. As temperature and precipitation patterns shift concurrently, ecosystems may experience "control switches", where the dominant environmental driver of root phenology transitions from one factor to another.

Temperature thresholds for root growth vary across climate regions (0.5 °C in arctic to 18–21 °C in Mediterranean ecosystems), possibly reflecting adaptations to regional climate histories rather than universal physiological limits [78,79]. This variability challenges the use of uniform temperature thresholds in global vegetation models [80] and underscores

the need for regionally parameterized phenological responses. In transitional ecosystems, such as Mediterranean regions, species exhibit a dynamic interplay between temperature- and moisture-driven growth, switching cues based on seasonal moisture availability, which highlights a sophisticated environmental sensing mechanism.

4.3. Ecological and Evolutionary Significance of Root-Shoot Coordination

Root-shoot coordination patterns vary across climate regions (Figure 3), possibly reflecting evolutionary adaptations to distinct environmental constraints. Three primary strategies emerge: (1) sequential root-then-leaf growth in Mediterranean ecosystems, where 100% of studies showed root growth preceding shoot growth by >14 days [30]; (2) sequential leaf-then-root growth in temperate and arctic regions, where 55% and 100% of studies respectively showed root growth lagging behind shoot growth [59]. This lag possibly reflects the fact that while canopy tissues can warm rapidly from direct sunlight to enable photosynthesis, soil temperatures remain low or frozen, preventing root growth; and (3) synchronous root and shoot growth in humid continental regions, where 57% of studies reported simultaneous development (within $\pm$14 days) [81]. These strategies entail ecological trade-offs with implications for resource economics [82]. The leaf-first pattern observed in temperate and arctic ecosystems may enhance early-season carbon gain, but could increase vulnerability to spring droughts. Isotopic tracing studies in these ecosystems suggest that early-season root growth primarily utilizes recently fixed rather than stored carbon [64,65]. This observation supports the carbon limitation model, which proposes that root growth depends on current photosynthate supply rather than stored reserves, though the relative importance of current versus stored carbon possibly varies by species and environmental conditions. This dependence on current photosynthates creates a physiological link between canopy development and subsequent root expansion. In contrast, Mediterranean ecosystems exhibit root-first patterns reflecting greater reliance on stored carbon reserves. This investment strategy reduces drought risk during leaf development by establishing water uptake capacity beforehand [42,83]. Such change may become increasingly advantageous as climate change intensifies seasonal drought patterns in these regions. Humid continental ecosystems demonstrate the highest root-shoot synchrony (57% of studies), possibly reflecting adaptation to balanced seasonal constraints. With moderate growing seasons, simultaneous investment in above- and belowground structures may optimize resource acquisition and utilization. This synchronous strategy balances the trade-offs between early carbon gain and water acquisition, potentially providing resilience to variable environmental conditions.

4.4. Ecosystem Implications of Winter Root Growth

The widespread occurrence of winter root growth, particularly in tropical and Mediterranean ecosystems, has important implications for terrestrial carbon cycle models. Most current Earth system models assume complete root dormancy during winter months, which may lead to underestimation of annual carbon allocation to belowground components [84,85]. The sharp gradient in winter growth prevalence across climate regions (from 71% in tropical to 0% in arctic ecosystems) suggests that winter root activity is tightly linked to soil temperature regimes rather than photoperiod or other seasonal cues. This temperature dependence explains why winter growth occurs primarily in regions where soils rarely freeze [86]. Winter root growth may confer significant competitive advantages in ecosystems where it occurs [57]. Species capable of winter root production can expand their resource capture range during periods when competitors remain dormant, potentially altering community composition over time. This strategy may become increasingly important as climate warming extends potential growing seasons in many regions. This

difference in winter activity highlights a fundamental divergence in strategy between leaf habits. The persistence of winter growth, observed almost exclusively in evergreen species within a given temperate climate (e.g., [26]), demonstrates how their capacity for winter photosynthesis supports year-round root activity. This strategy allows evergreens to acquire resources outside the main growing season, a strategy generally unavailable to their deciduous counterparts.

4.5. Limitations and Future Research Directions

Despite providing a perspective on root phenology, several key limitations remain in this synthesis. Geographic coverage shows substantial bias toward Northern Hemisphere temperate regions, with limited representation from tropical, arid, and Southern Hemisphere ecosystems. This imbalance limits our understanding of global patterns, particularly in predicting climate change responses. Several methodological limitations of this synthesis should be acknowledged. Our literature search was restricted to English-language publications, potentially overlooking relevant research published in other languages, particularly from regions underrepresented in our dataset. Additionally, inclusion criteria required quantitative reporting of root phenological parameters, which may have excluded studies with valuable qualitative observations. The disparate methodologies employed across studies—ranging from direct observation techniques (rhizotrons, minirhizotrons) to indirect methods (soil coring, isotope tracing)—introduce varying levels of precision and temporal resolution that complicate direct comparisons. Future meta-analyses would benefit from establishing standardized reporting protocols for root phenological studies to facilitate more robust cross-ecosystem comparisons. Furthermore, publication bias may favour reporting of distinct seasonal patterns over continuous growth dynamics, potentially skewing our understanding of phenological strategies, particularly in regions with less pronounced seasonality. Future research should prioritize coordinated networks of standardized root observations across climate gradients and long-term monitoring spanning multiple years to capture interannual variability in root phenological responses, including targeted comparisons between evergreen and deciduous species within the same ecosystems to better separate the influence of leaf habit from broad climatic drivers. The integration of root phenology with soil microbial dynamics represents a critical frontier for future research [87]. The observed seasonal patterns in root growth possibly drive corresponding cycles in rhizosphere processes, including carbon exudation, nutrient cycling, and microbial community succession. Understanding these belowground interactions will be essential for predicting ecosystem responses to climate change. Climate change offers both challenges and opportunities for understanding root phenology. As warming advances spring thaw in cold regions and alters precipitation patterns in water-limited ecosystems, we can observe responses in root phenological timing. Specifically, future research should establish monitoring networks at climate-sensitive ecotones (e.g., arctic-boreal transitions, temperate-Mediterranean boundaries) where species may experience novel seasonal cues. Experiments manipulating soil temperature and moisture, alongside continuous root observations, would help disentangle complex environmental interactions and identify thresholds where phenological responses might shift dramatically. The contrasting temperature thresholds we observed across regions (0.5–1 °C in arctic vs. 11–15 °C in continental systems) suggest potentially different sensitivities to warming that deserve explicit experimental testing. Finally, the inclusion of root phenological dynamics in Earth system models remains underdeveloped. Our synthesis reveals systematic variation in temperature thresholds and root-shoot coordination across climate regions that should be incorporated into next-generation vegetation models to improve predictions of terrestrial carbon cycling under climate change [88].

5. Conclusions

Our synthesis of root phenology in woody plants reveals distinct, climate-specific strategies that challenge simple assumptions in ecosystem models. We found that root growth timing is highly adapted to regional limitations: arctic ecosystems initiate growth at near-freezing soil temperatures (0.5–1 °C), temperate forests follow predictable seasonal temperature thresholds (1–9 °C), Mediterranean systems exhibit bimodal growth driven by moisture availability, and tropical patterns are governed by precipitation. These regional differences extend to root-shoot coordination, with strategies ranging from root-first growth in Mediterranean climates (100% of studies) to leaf-first growth in temperate regions (55%) and synchronous growth in continental zones (57%). Furthermore, winter root growth is a significant phenomenon, observed in 35% of all studies and most prevalent in tropical (71%) and Mediterranean (36%) ecosystems, indicating that belowground activity is often decoupled from aboveground winter dormancy. Collectively, these findings demonstrate that a universal approach to modeling root phenology is inadequate. Incorporating these regionally-specific phenological patterns and the reality of winter root growth is crucial for accurately predicting how nutrient cycling, carbon sequestration, and overall ecosystem resilience will respond to ongoing climate change.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/f16081257/s1, Table S1: List of literature reviewed with citation, location, climate, vegetation type, species, methods, whether the study measured the onset, peak and cessation of root growth, whether the study found evidence of winter root growth and whether the study link to leaf or shoot phenology.

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