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Impacts and Legacies of Extreme Precipitation on Temperate Forests During Critical Ecological Windows

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Abstract

Within seasonal temperate forests, changes in precipitation structure—its form, duration, and seasonal timing—is a dominant characteristic of climate change. While past research has focused primarily on annual precipitation totals, emerging evidence shows that short-duration extreme precipitation can impact ecosystem carbon, water, and biogeochemical cycling when it coincides with key phenological and physiological transitions. These impacts are mediated by the responses of plant and microbial physiology, aboveground–belowground interactions, and lagged feedbacks as organisms and communities adjust to these extremes. This review focuses on shifts (*a*) within ecosystem water cycling, (*b*) within tree growth dynamics (carbon uptake and aboveground–belowground allocation and coordination), (*c*) within soil biogeochemical cycling, (*d*) from the loss of winter snow, and (*e*) in forest structure and community composition. Together, these concepts highlight the urgent need to understand how changes in all aspects of precipitation structure reshape the functioning and resilience of mesic temperate forests.

1. INTRODUCTION

The even temporal distribution of abundant precipitation, particularly during the growing season, is a key climate characteristic of temperate regions that support broadleaf mesic forest ecosystems. Changes in the structure of precipitation; the timing of delivery; the duration or frequency of dry spells, hot droughts, snowpack quantity and timing; the intensity of rainfall events; or even the frequency of small rain events can affect these forests under current and future climate change.

Across many regions of the temperate broadleaf mesic forest biome, shifts in seasonal precipitation patterns are a dominant characteristic of climate change. For example, the northeastern United States has experienced a strong increase in total precipitation and an even faster rise in extreme precipitation events (Huang et al. 2017). Up until 2014, part of the region showed a significant increase in the number of days with measurable rainfall during the growing season (Bishop & Pederson 2016). Since then, hotter and more intense flash droughts have become more common in various regions of the eastern United States (US), indicating how changes in the structure of precipitation delivery varies by region. Despite overall increases in annual precipitation, there is strong evidence that mesic temperate forests respond to intense and episodic drought and pluvial conditions, especially when these events intersect with critical ecological windows.

The timing of a critical ecological window can vary depending on the ecosystem process under consideration (**Figure 1*a***). For most aspects of deciduous tree physiology, spring is a critical period due to the mobilization of carbon and nutrient reserves for leaf out, and within the Northern Hemisphere, June through July is a key period for radial growth (D'Orangeville et al. 2018). The late growing season is important for bud development, seed production (depending on the tree species), and building nonstructural carbohydrate (NSC) reserves (Richardson et al. 2013). Autumn is an important period for the resorption of nutrients from leaves (Chapin et al. 1990) and early decomposition of labile nutrients within leaf litter. In seasonally snow-covered temperate forests, tree roots are damaged when warmer winters result in less insulating snowpack and thus greater soil freezing, which can impact the uptake of nutrients, water, and carbon during the growing season (Campbell et al. 2014, Reinmann et al. 2019). Either spring or autumn drought can reduce the duration of carbon uptake by trees, reducing gross primary productivity. Additionally, extreme late summer and autumn drought can advance and hasten leaf senescence and reduce nutrient resorption with potentially important implications for tree nutrient economies and productivity (Wu et al. 2022).

Although changes in annual precipitation are important for characterizing long-term patterns, some of the strongest ecosystem impacts from extreme precipitation in mesic systems occur when events during shorter time periods intersect with critical ecological windows. For example, the cooccurrence of low precipitation and high air temperatures that coincides with leaf out of deciduous trees can damage leaves, resulting in reduced canopy leaf area and lower carbon uptake for the remainder of the growing season (**Figure 2*a***). This type of short-lived episodic drought does not fall into the traditional framework of drought forecasting and characterization but is the type of extreme precipitation event that is likely to lead to significant shifts in ecosystem function for the duration of the growing season. Similar climatic events late in the growing season can

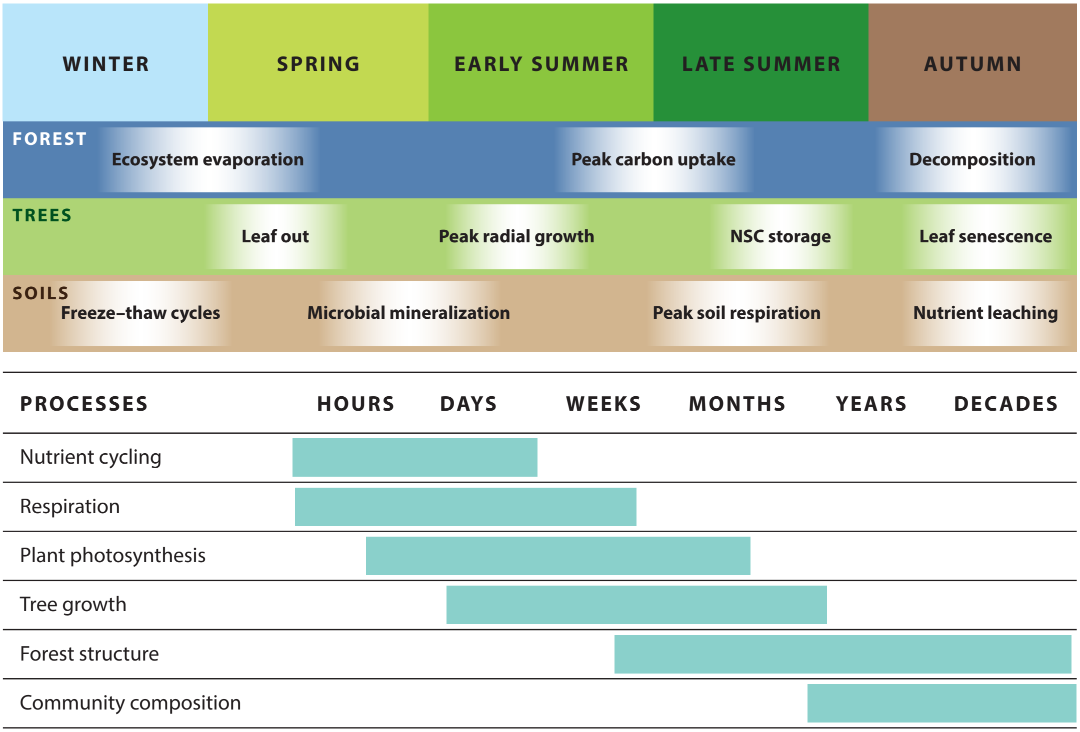

Figure 1

(*Top*) Changes in precipitation structure create the strongest impacts on plant, soil, and ecosystem physiology when events coincide with critical ecological windows, which are highlighted by the shaded white boxes and discussed in this review. Gradations in shading reflect variation in the timing of plant, soil, and ecosystem physiological events that can be impacted by changes in precipitation (both high and low precipitation extremes). (*Bottom*) Impacts on physiology during the critical ecological windows shown in the top panel can have cascading effects across timescales from near-term shifts in physiology to changes in forest structure and community composition that play out over hours to decades in response to both extreme wet and extreme dry conditions. Abbreviation: NSC, nonstructural carbohydrate.

impair bud development and substantially advance leaf senescence (**Figure 2*b***) with potentially important implications for NSC accumulation and leaf and wood production during the following growing season.

Although some critical ecological windows make it easier to establish cause-and-effect relationships in response to precipitation extremes, many ecological responses vary in both timing and magnitude. Ecosystems react to precipitation extremes over timescales ranging from seconds to centuries, making it difficult to distinguish between short-term fluctuations that may balance out over time and lasting changes that drive prolonged ecosystem shifts.

There are also a growing number of observations and increased concern regarding extreme precipitation events that intersect with extreme temperature events [e.g., hot droughts (Adams et al. 2017)]. The 2003 hot drought in Europe led to elevated tree mortality and significantly reduced forest productivity (Ciais et al. 2005), and more broadly, excess mortality has been associated with drought across Europe since 1987 (Senf et al. 2020). In the northwestern US, the 2021 Heat Dome event caused widespread tree mortality (Still et al. 2023), and a late flash drought in 2019 advanced leaf senescence by nearly one month in southeastern New York's seasonal deciduous forests (**Figure 2*b***).

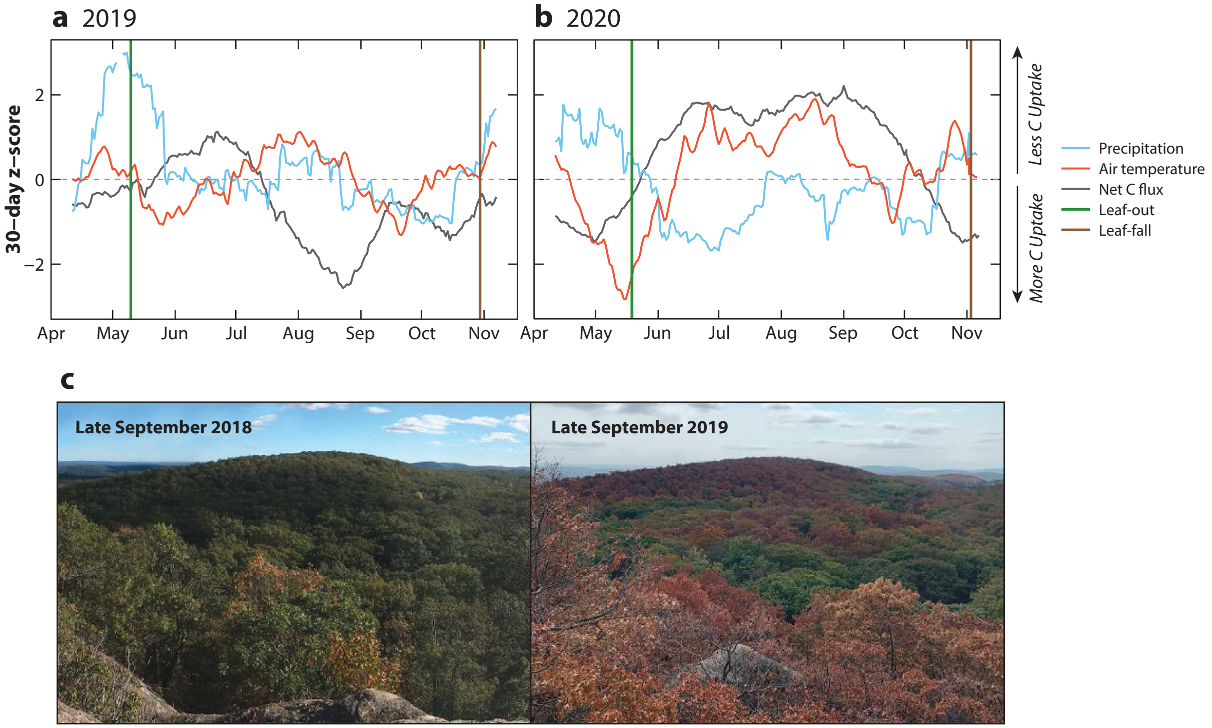

Figure 2

At Harvard Forest in Petersham, Massachusetts, USA, differences in patterns of net ecosystem–atmosphere carbon (C) flux between 2019 and 2020 were strongly controlled by precipitation after leaf out. (*a*) Slightly higher than average temperature and precipitation caused an increase in net C uptake in 2019, and (*b*) hot and dry conditions in 2020 caused lower net C carbon uptake. Z-scores represent the departure from the 1992–2023 mean conditions for each day (in units of standard deviation), calculated as a rolling 30-day sum for daily precipitation or rolling 30-day mean for daily net C flux and daily mean air temperature (Munger 2023). These responses to seasonal drought sensitivity impact annual net C budgets, despite only small differences in annual precipitation of 1,424 mm in 2019 and 1,148 mm in 2020 (mean annual precipitation = 1,150 mm from 1971–2023) (Boose & Gould 2024). (*c*) Contrasting late–growing season leaf phenology between a year with a late–growing season flash drought (2019) and a year with near average conditions (2018). The photographs collected from the same vantage point are of an oak-dominated temperate forest at Black Rock Forest in Cornwall, New York, USA. Photos copyright by A. Reinmann.

Intersections between extreme precipitation and other disturbances [i.e., compound disturbances sensu Buma (2015)], such as coincidence with defoliating pests or frost events, can magnify the physiological and ecological responses to drought. For example, in a recent outbreak of the defoliating spongy moth during a period of drought in central Massachusetts, USA, trees with higher defoliation severity were more likely to die due to depletion of carbon stores (Barker Plotkin et al. 2021). At long timescales, compound disturbances have been implicated in structuring much of the eastern US over different periods of the twentieth century (Druckenbrod et al. 2019) and also European temperate forests (Gazol & Camarero 2022).

Alterations in precipitation regimes have impacts across timescales from hours to decades in connection with shifts in organismal physiology, ecological community composition, and ecosystem processes. Working across these biological scales is essential for untangling the mechanisms that cause ecosystem processes to change in order to understand and predict future change. In this review, we focus on the impacts of high and low precipitation extremes and their timing and form (e.g., rain versus snow) on ecosystem water cycling, ecosystem carbon uptake and sequestration, soil biogeochemistry, and tree community composition and ecosystem structure.

We first review the literature on the role of soil structure and evapotranspiration (ET) as fundamental controls on the ecosystem water balance. We then focus on how precipitation extremes influence leaf and canopy ecophysiology and the uptake of carbon dioxide (CO_2) through gross primary productivity, followed by tree carbon allocation to aboveground woody biomass and belowground roots. We then assess broader impacts on soil biogeochemistry and shifts in forest community composition and structure. Through all of these sections, we acknowledge that the scientific literature on this topic is much more detailed with respect to drought than for extreme precipitation, with a few exceptions for soil biogeochemistry and the impacts of extreme storms and declining winter snowpack.

2. ECOSYSTEM WATER BALANCE

Extremes in precipitation create impacts on ecosystem water cycling through shifts in infiltration, runoff, and ET. The flow of precipitation into an ecosystem is a primary factor controlling ecosystem water availability, while soil texture and soil depth are fundamental controls on soil water-holding capacity. Whether a soil reaches a saturated state that sustains runoff is strongly regulated by soil texture. For example, relatively coarse soils that experienced recent glaciation or reflect alluvial deposition have a relatively low water-holding capacity and are common in many temperate forests across the northeastern US, Canada, Europe, and Asia (European Commission et al. 2023, Soil Survey Staff 2024). Low water-holding capacity can create a primary control on ET that creates dry land–atmosphere feedbacks during drought periods despite overall increasing annual precipitation (Jurado & Matthes 2025). However, trees that are adapted or acclimated to these conditions can fulfill water needs through deeper rooting depths that tap water sources inaccessible to the atmosphere or by adaptive traits that produce low rates of ET, for example, evergreen leaves. Conversely, species adapted to wetter landscapes can sustain higher transpiration and photosynthetic rates in normal or high rain conditions.

Extreme rainfall events that exceed the soil water-holding capacity can create runoff that drives the physical transport of dissolved forms of carbon, nitrogen, and other particulates and solutes from soils into streams and rivers along hydraulic flow paths. A meta-analysis of small watersheds in mesic temperate forests found that large discharge events comprised only 4.8% of annual flow velocities but were responsible for transporting 57% of total annual dissolved organic carbon to streams (Raymond & Saiers 2010). Topography is another important control on sediment runoff, where thin soils on steep slopes are likely to be more vulnerable to erosion and landslides with extreme rain events. Snowmelt runoff in spring is disproportionately responsible for the export of nutrients and carbon from seasonally snow-covered temperate forests during these peak streamflow periods (Fuss et al. 2015). Increased flow events also transport CO_2, methane, and nitrous oxide from soils into streams, particularly in watersheds influenced by wetlands, and higher stream velocities cause more turbulent mixing, creating a higher flux of greenhouse gases from streams into the atmosphere (Aho & Raymond 2019).

Increased rainfall and runoff transport nutrients, particularly nitrogen, a common limiting resource in mesic temperate forests (Geng et al. 2020). Nutrient losses through rainfall-induced leaching can occur even during periods of high plant demand within ecosystems (Neff et al. 2003, Ren et al. 2017b). Total precipitation outside of the growing season can cause nitrogen leaching from ecosystems, which can induce nitrogen limitation and remove increases in primary productivity from elevated CO_2 (Hovenden et al. 2014). There are also potential interactions between drought conditions and nitrogen leaching by rainfall, where increased leaf litter inputs to soil during drought lead to higher rates of nitrogen leaching in subsequent years (Leitner et al. 2020).

ET is closely connected to soil water content and atmospheric vapor pressure deficit (VPD), the difference between maximum atmospheric water vapor concentrations and the actual water vapor concentration. Rates of ET are amplified by high soil water availability and high VPD, whereas ET rates are dampened by drier soil moisture conditions and a more humid atmosphere. Increasingly high VPD conditions, which indicate low atmospheric humidity, are impacting ET rates in temperate deciduous forests (Novick et al. 2016). In a global analysis, increasing ET was identified as a key mechanism contributing to declining soil moisture in temperate ecosystems (Qing et al. 2023). ET during high rainfall years is an ecosystem service that could reduce runoff and the severity of floods in downstream systems (Collentine & Futter 2018).

ET is linked to the opening of leaf stomata, which take up CO_2 for photosynthesis. Water-use efficiency (WUE) measures how much carbon is fixed during photosynthesis per unit of water evaporated in transpiration. Studies of tree rings from the northeastern US indicate that rising atmospheric CO_2 concentrations during the first half of the twentieth century led to an increase in WUE (Belmecheri et al. 2021). However, since 1975, the effect of rising CO_2 on WUE has diminished where summer moisture was the most important factor predicting WUE (Belmecheri et al. 2021). Other studies indicate that in mature North American temperate forests, the rise in WUE is mainly due to increased photosynthesis rather than decreasing stomatal conductance (Guerrieri et al. 2019). Stomatal dynamics create close coupling between ET and carbon uptake, linking soil water availability, atmospheric humidity, and canopy carbon uptake. The timing of both wet and dry hydrological extremes is critical in regulating soil water availability and atmospheric drought, affecting carbon flow into leaves and ecosystems.

The distribution of tree community composition between needleleaf and broadleaf plant functional types, the stomatal behavior of a tree species and community, the timing of leaf out and leaf off, physical canopy structure and interactions with atmospheric turbulence, and physiological conditions during the growing season can interactively influence water demand and ET rates. A warming climate is lengthening the growing season and increasing annual gross primary productivity (Keenan et al. 2014), but this extended leaf-on period is likely to elevate water demand (Yang et al. 2023) and intensify late-season water stress.

3. LEAVES AND CANOPIES

The interaction between soils and trees affects how gross primary production and transpiration respond to precipitation extremes. In temperate broadleaf forests, nearly all transpiration and carbon uptake occur through leaves, and both tree canopy and stand-level transpiration generally increase with increasing leaf area index (LAI) (Yang et al. 2023). This increase in LAI can accelerate soil drying and exacerbate water stress during droughts. Stomatal behavior also influences transpiration at leaf to canopy scales, with tree species ranging along a continuum from isohydry, where stomata respond dynamically to drought, to anisohydry, where stomata are less responsive to water stress. Species-level responses are the product of interactions among soil moisture, atmospheric demand for water, and wood hydraulic characteristics. Isohydric trees such as maples (*Acer* spp.) tend to close their stomata earlier under lower levels of water stress than anisohydric trees such as oaks (*Quercus* spp.) (Meinzer et al. 2013). As such, anisohydric trees are tolerant of relatively low water potentials and maintain higher rates of transpiration and photosynthesis during periods of high water stress, albeit with a higher risk of hydraulic failure due to xylem cavitation (Huber et al. 2015).

In a Pennsylvania, USA, temperate broadleaf forest, transpiration (and presumably photosynthesis) of oak trees was up to three times higher and two times less sensitive to drying soils than that in cooccurring sugar maple trees (*Acer saccharum*) (Meinzer et al. 2013). Oaks' deeper rooting, compared to other temperate forest trees (e.g., maples; see Section 5), allows them to access water from deeper soil, sustaining transpiration despite declines in surface soil moisture. However, during prolonged severe droughts, anisohydric trees are more susceptible to hydraulic failure, delayed recovery, and potentially higher mortality rates compared to isohydric trees (Gu et al. 2015). The less conservative water-use strategies of anisohydric trees might amplify drought effects on soil moisture by depleting water through high transpiration rates.

While stomatal closure can decrease carbon assimilation during droughts, it is reversible with increased water availability. However, extreme droughts can cause early leaf senescence, preventing photosynthesis recovery once the soil is rewetted. Hot and dry conditions can cause the rapid development of a hydrological drought (i.e., flash drought) that may not register as an extreme drought using standard metrics like the Standardized Precipitation Evapotranspiration Index. These conditions can significantly affect leaf phenology and tree mortality in temperate forests (Still et al. 2023) (for an example of early senescence, see **Figure 2*b***). In the extreme 2003 European drought, early leaf senescence was widespread, with beech trees shedding green leaves, indicating that little or no nutrient resorption occurred (Bréda et al. 2006), potentially exacerbating nitrogen limitation.

Hot droughts are increasingly common in many temperate broadleaf forests (Mazdiyasni & AghaKouchak 2015). Heatwaves that cooccur with droughts limit foliar cooling through transpiration, resulting in leaf temperatures slightly higher than air temperatures (Still et al. 2022). In a European hot drought, leaf temperatures were nearly 5°C above ambient air temperature for many common tree species (Scherrer et al. 2011). Such temperature increases exacerbate water stress–related declines in canopy carbon uptake by exceeding the leaves' optimum temperature for photosynthesis. Although the effects of increases in precipitation are understudied in comparison to drought, it is plausible that increases in water availability could bolster transpiration and keep leaf temperatures closer to their photosynthetic optimum during heat waves, thereby mitigating declines in carbon uptake.

Gross primary production is the key ecosystem-scale process for carbon uptake and sequestration in temperate forests. Sugars produced during photosynthesis are transported within the tree to support growth, to build biomass, to maintain mycorrhizal symbionts, and to build NSC reserves for times of stress. The ecophysiological processes regulating carbon flows in temperate forests are tightly coupled to water availability, significantly linked by the frequency, intensity, and timing of extreme precipitation events. There is also variation in temporal coupling between carbon allocation and extreme precipitation events.

Trees maintain NSC pools as metabolic reserves against short-term resource constraints (Dietze et al. 2014). Prolonged or repeated moisture stress can deplete these reserves, making trees more vulnerable to future stress. Under adequate moisture, trees allocate carbon not only to immediate growth but also to build reserves for maintenance, osmotic regulation, and future leaf and wood production. During droughts, trees often prioritize maintenance over new growth, using NSC stores for vital physiological processes. In times of sufficient water, more carbon may go to wood growth, while in droughts, it may support leaf function and root survival (He et al. 2020).

4. WOOD GROWTH AND ABOVEGROUND BIOMASS

A growing body of literature points to growing season precipitation and soil moisture as important drivers of tree growth and net carbon sequestration, even in humid regions like the eastern US (Brzostek et al. 2014, Martin-Benito & Pederson 2015). Although temperate forest regions are experiencing longer growing seasons, these benefits can be offset by drought-induced declines in photosynthesis. For example, Brzostek et al. (2014) found that in a temperate broadleaf forest in

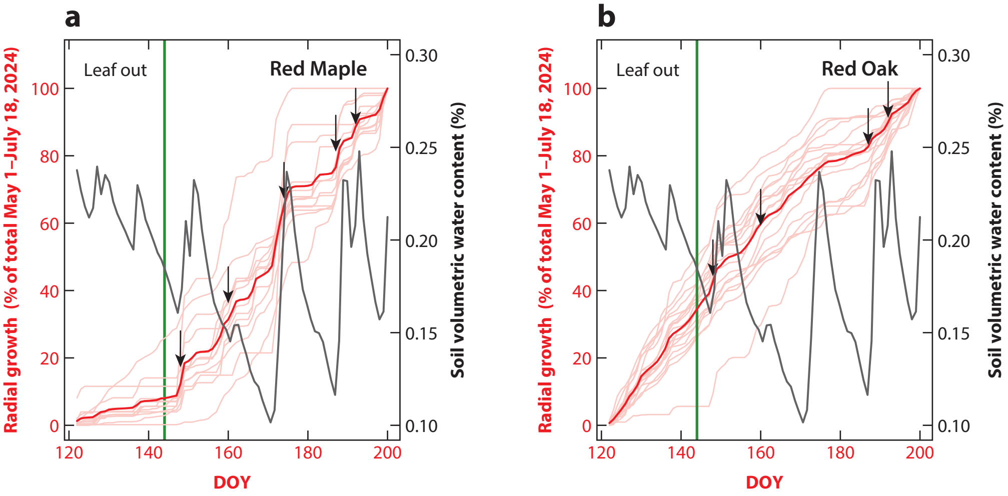

Figure 3

Temporal patterns of soil moisture (*dark gray lines*) and radial growth (*red lines*) for (*a*) red maple and (*b*) red oak trees at Harvard Forest in Petersham, Massachusetts, USA, during the growth period from May 1 to July 18. Arrows indicate growth spurts that are synchronized with spikes in soil moisture associated with precipitation events during the 2024 growing season. Radial growth data were collected using automated point dendrometers, and soil moisture data are from 30-min measurements at 10 cm soil depth. Growth patterns of individual trees are represented by thin red lines, while the mean across trees is represented by the thick red line. The vertical green line indicates the approximate date of full leaf expansion. Abbreviation: DOY, day of year.

Indiana, USA, a warmer-than-average year resulted in 26 more days with canopy carbon uptake. However, drought conditions that year shortened wood production by 42 days and reduced overall carbon sequestration in biomass by 41% compared to nondrought years. These findings mirror those from a temperate Asian region where end-of-season water availability limited or extended radial growth under seasonal temperatures (Zhang et al. 2020).

During the growing season, there is evidence that the timing of radial tree growth is closely connected to soil moisture patterns in some temperate tree species (Etzold et al. 2022). At fine temporal scales, radial growth of diffuse porous, shallow-rooted red maple trees at Harvard Forest in Massachusetts tends to exhibit growth spurts timed with episodic spikes in soil moisture (**Figure 3**). In contrast, cooccurring red oak trees exhibit more constant growth patterns throughout the early growing season, with less pronounced growth spurts during wetting events. This interspecific difference is likely because red oaks, which are comparatively deeply rooted and anisohydric, can access a more stable water supply. This ability allows them to maintain higher rates of transpiration and photosynthesis even when soil moisture is reduced near the surface. On a larger temporal scale, moisture stress during peak radial growth often limits cell division and elongation, directly reducing annual wood increment (Cuny et al. 2015). Later in the growing season, moisture deficits can limit cambial activity and cell expansion, leading to narrower tree rings, reduced wood increment, and ultimately lower carbon sequestration in biomass.

The response of ring-porous and diffuse-porous tree species to water availability varies. A 6-year study of 15 tree species in an eastern US forest revealed that diffuse-porous species began growing 16–18 days earlier than ring-porous and conifer species. However, despite this early start, diffuse-porous trees reached maximum growth rates a few weeks later, making them more susceptible to mid-summer drought (D'Orangeville et al. 2022). Compared to ring-porous trees, diffuse-porous species exhibit greater year-to-year variation in wood growth. In an Appalachian deciduous forest region with near temperate rainforest conditions, diffuse-porous species showed a stronger relationship with water variability and a greater range in wood production between wet and dry years than ring-porous species (Elliott et al. 2015). Ring-porous species start producing new wood earlier in the growing season (D'Orangeville et al. 2022), likely relying more on carbon reserves from the previous growing season (Richardson et al. 2013). This makes them sensitive to late-season droughts, which can affect NSC storage.

At annual to multiannual temporal scales, there are often strong lags between precipitation events and wood production, with late-season droughts reducing growth in the following year across multiple species in the temperate mesic region of eastern North America (D'Orangeville et al. 2018). Such droughts during bud development can decrease leaf numbers (Bréda et al. 2006) and thereby reduce LAI in future growing seasons, limiting canopy photosynthetic capacity. This effect is more pronounced in trees with determinate growth (e.g., *A. saccharum*) than those with indeterminate or semideterminate growth (e.g., *Quercus* spp.), although the LAI of trees with indeterminate growth can be heavily impacted by a current-year summer drought (Bréda et al. 2006).

During the late growing season, many temperate broadleaf trees shift allocation of photosynthate from growth to NSC accumulation (Richardson et al. 2013). Therefore, late-season droughts can reduce the NSC pool for wood production in the following year, particularly in genera that begin radial wood production before leaf budbreak, like oaks (*Quercus* spp.). The impact of climate on radial growth in subsequent years has been used to reconstruct past climate and shows variability from stand to regional scales (Kannenberg et al. 2019, Tang et al. 2024). Curiously, the lagged effects between precipitation and radial growth have become more important during a strong wetting trend. In recent decades, water availability from the prior growing season has become a stronger constraint on radial growth (Helcoski et al. 2019).

Research on the impacts of extreme precipitation events on tree growth is limited, partly due to the logistical challenges of in situ manipulation experiments and the stochastic nature of these events, which may include extended dry periods or occur amid wetter than normal conditions. In a 10-year analysis of the enhanced vegetation index across several temperate broadleaf forest sites, Zhang et al. (2013) found that extreme precipitation events resulted in less than a 10% decline in vegetation production, compared to years with similar total annual precipitation but few extreme precipitation events. They also found that extreme precipitation events reduced the sensitivity of vegetation production to total annual precipitation and led to a 24% reduction in rainwater use efficiency. More mechanistic studies on the impact of seasonally high rainfall are needed to better understand these effects on tree growth.

5. ROOTS AND BELOWGROUND ALLOCATION

Belowground, changes in precipitation patterns influence root dynamics, mycorrhizal interactions, and soil microbial activity. In most upland temperate forests, fine-root biomass is concentrated near the soil surface where nutrient concentrations are highest (Schenk & Jackson 2002). Maximum rooting depths are generally less than 2 m with considerable spatial heterogeneity related to the depth to bedrock (Fan et al. 2017). With well-timed precipitation events, trees may allocate more carbon belowground, fueling root production and rhizosphere microbial communities.

Rooting depth and fine-root surface area determine the volume of soil from which trees can access water, playing an important role in how temperate trees respond to precipitation. Shallow soils found on ridgetops and hillslopes limit both rooting depth and water retention capacity, making trees in these topographic locations shorter and more prone to hydrologic drought (Hawthorne & Miniat 2018). However, tree species can vary widely. Deep-rooted species like oak can maintain high transpiration rates and are less affected by the interplay between topography (and related soil depth) and precipitation than cooccurring hickories (*Carya* spp.) (Hawthorne & Miniat 2018). Deeply rooted species can sustain higher rates of transpiration during drought by varying the depth of water acquisition between surface and deeper soils as surface soils dry, in turn exerting a strong control on the vertical profile of soil moisture (Bréda et al. 2006). By contrast, shallow-rooted temperate forest tree species such as birches (*Betula* spp.) and maples (*Acer* spp.) are generally more likely to incur declines in transpiration and photosynthesis earlier in a drought than cooccurring tree species with deeper root systems (Coble et al. 2017, Matheny et al. 2017). Changes in precipitation structure, with more high-intensity rain events, could increase the frequency of rapid fluctuations in water availability and the rate of water infiltration through the soil. Even if total precipitation increases, such changes in the pattern of water availability could overwhelm the capacity of shallow-rooted species to take up water when it is available and thus hinder their performance while potentially benefiting deeply rooted species. Nonetheless, trees may acclimate by extending their rooting depth by increasing fine-root elongation deeper into the soil, potentially reducing the long-term effects of species differences in rooting depth (Lanning et al. 2020, Zhang et al. 2019).

Trees also exhibit plasticity in their rooting traits, responding over time to persistent changes in precipitation. Optimum partitioning theory suggests trees should increase resource allocation to roots when water is scarce, and root biomass tends to follow soil moisture depth profiles (Fan et al. 2017). However, in a global meta-analysis, fine-root biomass within a site decreased with reductions in precipitation and increased with increases in precipitation (Zhang et al. 2019). Declines in fine-root production in response to drought appear to be ubiquitous across the temperate broadleaf forest biome, having been observed in Asia (Dong et al. 2022), Europe (Fuchs et al. 2020), and North America.

Root traits can also respond to drought; some studies suggest a drought might reduce fine-root diameter, maintaining high root surface area even with declines in total fine-root biomass (Zhang et al. 2019). Mycorrhizal associations can extend plant root connectivity to small soil pores that contain water during drought and improve plant osmolytes that lower plant matric potential (Phillips et al. 2016). While these associations have shown drought resistance in photosynthetic capacity and water retention, their effectiveness depends on the specific mycorrhizal symbionts and tree species involved (Kannenberg & Phillips 2017) and could deplete tree carbon reserves during drought, affecting future growth and resilience (Phillips et al. 2016). While less studied, precipitation addition experiments suggest that increases in water availability can stimulate fine-root production in both surface and deeper soils in temperate broadleaf forests, possibly in response to changes in water availability and greater nitrogen leaching during high precipitation events (Li et al. 2021, Zhang et al. 2019).

NSC availability also influences how trees allocate carbon belowground. Variability in moisture can drive shifts toward increased root production and increased carbon allocation to mycorrhizal symbionts to improve water uptake. On the other hand, severe droughts may reduce fine-root production and turnover, limiting the tree's future ability to access soil moisture and nutrients. These allocation strategies vary among species, leading to divergent responses among tree communities, ultimately affecting forest structure and composition over time.

6. RESPONSES OF SOIL BIOGEOCHEMISTRY OUTSIDE OF WINTER

Soil water, in combination with biological, physical, and chemical factors, influences how carbon, nutrients, and contaminants are transformed and persist in soils. Soil type, along with infiltration and matric processes, governs microscale geochemistry. The way these processes scale up to entire watersheds depends on the amount, form, and temporal distribution of precipitation. Responses to precipitation can vary based on soil horizon, the quantity of soil organic matter present, and soil drainage status.

Seasonal moisture limitations can inhibit soil respiration in temperate deciduous forests. During warm periods, well-drained soils may experience reduced water availability, leading to lower soil respiration rates and higher carbon storage compared to poorly drained upland soils (Raymond et al. 2013). Extreme droughts can severely decrease soil respiration, as evidenced by a 10–30% reduction with 200 mm less annual rainfall at Harvard Forest, Massachusetts (Borken et al. 2006b). Prolonged droughts have caused extremely low soil matric potentials (below −150 kPa) that inhibited soil respiration across New England forests (Savage & Davidson 2001).

Antecedent soil moisture, rather than total rainfall, is a better predictor of soil respiration pulses in response to precipitation following drought, with responses influenced by organic content and drainage status. Postdrought rainfall can briefly boost soil respiration, predominantly in the organic soil horizon (Wu & Lee 2011), with a smaller effect in mineral soil (Borken et al. 2006b, Courcot et al. 2024). Well-drained mineral soils increased respiration in response to precipitation more than poorly drained soils, and moist organic-rich soils (e.g., Histosols) often experience respiration limitation following precipitation events (Wu & Lee 2011). Extreme flash droughts and inconsistent storms have transient effects on soil respiration that are small relative to annual budgets when integrated over time (Herberich et al. 2023). If the soil respiration response to drought and rewetting occurs predominantly within the forest floor organic horizons in less-developed soils, at regional scales this response should depend heavily on organic layer depth and topographic position.

The impact of drought on soil carbon dynamics varies. In a Bavarian forest, an experimental drought caused by a 70% throughfall reduction increased soil organic carbon by over 80% but only at 0–5 cm depths due to an increase in less stable organic matter in the water-extractable and free, light particulate fractions (Brunn et al. 2023). This outcome might result from slower microbial respiration, as microbes become dormant with drought, yet extracellular enzymes continue breaking litter down into substrates that are rapidly mineralized upon rewetting (Fierer & Schimel 2003). However, other studies postdrought have found lower dissolved organic matter production (Orme et al. 2022) and global decreases in litter decomposition (Deng et al. 2021). This suggests decomposition responses may vary depending on drought extent, soil water retention, and other soil and site characteristics.

In contrast to the effect of precipitation following drought, consistently high precipitation might enhance mineral soil respiration and microbial activity, whereas in organic soil layers respiration and microbial activity could be suppressed. Soil moisture fosters connectivity among microorganisms, their organic substrates, and nutrients, enhancing their activity (Tecon & Or 2017). Thus, while organic soils typically do not see increased microbial activity with more rainfall, younger soils over sandy or rocky substrates require higher precipitation to connect macropores and promote microbial functions (Davis et al. 2010). When macropore connectivity is sufficient, additional moisture limits decomposition and respiration by creating small oxygen-limited sites within pore spaces called anoxic microsites (Lacroix et al. 2023). These microsites occur across upland soils with varying texture (Lacroix et al. 2022) and are likely enhanced by moisture-retaining particulate organic matter (Li et al. 2022).

The first oxygen-dependent limitation hinges on microbial enzymes: Oxygen limitation inhibits extracellular oxidative enzymes that depolymerize plant-derived compounds. Particularly in peatlands, drainage or aeration are associated with increased activity of extracellular oxidative enzymes (Fenner & Freeman 2011), whereas flooding inhibits oxidative depolymerization (Burns et al. 2013). During high precipitation and in poorly drained temperate forest areas, decreased extracellular oxidative enzyme activity (Ren et al. 2017a), litter turnover, and decomposition are expected.

The second oxygen-dependent limitation on soil carbon cycling relates to microbial energetics. Anaerobic conditions slow microbial respiration due to poor energy yields of anaerobic metabolisms driven by both less favorable electron acceptors and less favorable organic substrates (Keiluweit et al. 2016, Naughton et al. 2021). This process can happen in both well-drained (Lacroix et al. 2022) and poorly drained mineral soils (Keiluweit et al. 2017). Furthermore, anaerobic dissimilatory respiration of iron oxides may supply dissolved iron that can reprecipitate and protect organic carbon from mineralization (Wen et al. 2019).

However, particularly in the litter horizon, abiotic depolymerization mediated by redox-active metals (i.e., manganese, iron) and associated microbial enzymes (e.g., manganese peroxidase) might thrive with increased moisture and redox variability (Jones et al. 2020, Ren et al. 2017a). Oxygen limitations lead microbes or soil chemical species to reduce oxidized forms of these metals (Hall & Silver 2013, Naughton et al. 2023), often solubilizing the metals. A constant recycling of reduced metal species like manganese(II/III) and iron(II) provides more fuel for abiotic depolymerization and oxidation of phenolic and lipid compounds in litter because these metals generate reactive oxygen species, radicals that efficiently breakdown and oxidize organic matter (Keiluweit et al. 2015). Such mechanisms would likely enhance plant nutrient availability under wet conditions, which could lead to greater losses through leaching. Ultimately, within temperate forests, the impact of increased precipitation on decomposition and soil respiration depends on the balance of organic and mineral soils and whether the forest floor retains enough moisture to limit oxygen availability.

7. RESPONSES OF WINTERTIME ABOVE- AND BELOWGROUND PROCESSES TO CHANGING WINTER PRECIPITATION IN SNOW-COVERED ECOSYSTEMS

Seasonal snow cover, which insulates the underlying soil from subfreezing winter air temperatures and limits the depth and duration of soil freezing, impacts ecosystem processes in northern temperate broadleaf forests. Snow is often not classified as extreme precipitation, but conditions such as dry winters, increased ratios of rain to snow, and/or frequent thawing events that prevent snowpack accumulation can impact both above- and belowground forest processes. Studies manipulating snowpack and examining soil freeze–thaw cycles in these forests find that losing snow and experiencing freeze–thaw cycles result in higher dormant season nitrogen mineralization (Hosokawa et al. 2017) and higher nitrogen mineralization and nitrification in the following growing season (Urakawa et al. 2014). The lasting effects of these changes include higher nitrogen turnover and oxidative enzyme activity, especially in higher-latitude forests (Kreyling et al. 2020, Sorensen et al. 2016, Urakawa et al. 2014). In cold-adapted climates, freeze–thaw cycles can increase inorganic nitrogen up to 250%, compared to a global average increase of approximately 37% for dissolved nitrogen (Song et al. 2017), and elevate available phosphorus by 400% (Kreyling et al. 2020). These cycles appear to lower microbial biomass nitrogen (Sorensen et al. 2016) and winter nitrification (Hosokawa et al. 2017), possibly explaining the higher levels of available nitrogen and phosphorus in soils. Some studies report that fungal abundance and diversity either remain unaffected or decline after multiple soil freeze–thaw cycles (Sang et al. 2021). Overall, reduced snowpack and intensified freeze–thaw cycles could increase nitrogen mineralization, allowing it to be quickly absorbed by plants or lost through leaching, affecting nutrient cycling in forests.

Changes in snowpack and soil freeze–thaw dynamics also influence oil trace gas fluxes. A review of 338 studies found that fluxes of greenhouse gases, such as CO_2, CH_4, and N_2O, often rise after soil thawing and rewetting, although results varied widely across studies (Kim et al. 2012). In different field settings, N_2O fluxes can increase up to 95% in response to freeze–thaw cycles, although lab microcosms show opposite trends, likely due to the absence of root inputs (Song et al. 2017). Temperature, extremity of freeze–thaw temperatures and swings, and microbial biomass control the N_2O pulse after freeze–thaw cycling (Yao et al. 2010), and water content often dominates other factors in predicting N_2O flux (Koponen & Martikainen 2004). In a mesocosm experiment with temperate forest organic horizon soils, severe soil freezing delayed and reduced losses of carbon and nitrogen in leachate and trace gases during a simulated snowmelt, while mild soil freezing had no impact (Campbell et al. 2014, Reinmann et al. 2012). Soil respiration, which accounts for CO_2 flux from both autotrophic and heterotrophic sources, responds weakly to freeze–thaw cycles, during which water content and temperature may exert stronger control over longer timescales than gaseous nitrogen loss (Koponen & Martikainen 2004). CH_4 fluxes may be lower as a result of freeze–thaw cycles, possibly reflecting a changing microbial community (Ren et al. 2018) or enhanced CH_4 uptake as a result of reduced snowpack and drier soils (Borken et al. 2006a). Despite higher N_2O emissions and potentially higher CH_4 uptake, the overall impact of changing winter precipitation on forest greenhouse gas dynamics remains unclear.

Perhaps nowhere have the effects of changing snowpack and soil freezing dynamics on feedbacks between above- and belowground processes been more studied than in the northern hardwood forests at Hubbard Brook Experimental Forest in New Hampshire, USA. This research reveals that reduced snowpack increases soil freezing (Hardy et al. 2001), which in turn damages and kills fine roots (Comerford et al. 2013) and sets off a chain of ecosystem responses that persist into the next growing season. Root damage from freezing also results in reduced nitrogen uptake by trees (Campbell et al. 2014) and alters soil biogeochemistry and nutrient uptake in ways that increase the aluminum-to-calcium ratios of tree leaves (Comerford et al. 2013). Soil freezing–induced damage to roots also results in reduced water uptake and transpiration during the growing season (Harrison et al. 2020). Collectively, these impacts of declining winter snowpack and increasing soil freezing result in reduced radial growth of dominant tree species, like sugar maple (*A. saccharum*) (Reinmann et al. 2019). Winter snowpack is expected to decline across large areas of temperate forest, and the frequency of soil freezing is expected to increase as the climate continues to warm (Campbell et al. 2010, Reinmann et al. 2019). Although not explicitly tested, the damage to tree roots and reduced water uptake due to soil freezing may also reduce tree drought tolerance during the following growing season.

8. PHYSICAL FOREST STRUCTURE AND TREE COMMUNITY COMPOSITION RESPONSES TO PRECIPITATION EXTREMES

Species characteristics associated with LAI, stomatal behavior, and rooting dynamics interact to influence feedbacks between extreme precipitation events and forest hydrology. Changes in soil moisture and atmospheric water demand alter hydraulic resistance and water potential along the soil–root–atmosphere continuum, thereby controlling transpiration. The balance between atmospheric conditions and soil moisture in controlling transpiration rates varies with soil moisture. For example, Bréda et al. (2006) suggest a soil moisture threshold below which transpiration rates in temperate forests decline. Above this threshold, transpiration is less affected by increasing soil moisture and is instead driven by humidity and sunlight. However, this soil moisture threshold, along with absolute transpiration rates and their response to environmental conditions, is influenced by tree hydraulic traits and forest community composition (Yang et al. 2023). Temperate forest stands with high LAI and a high proportion of anisohydric and deeply rooted tree species may accelerate long-term hydrologic drought development or exacerbate soil moisture drawdown during a short-term precipitation deficit. Such stands maintain high rates of photosynthesis during brief droughts but may be more vulnerable to catastrophic and irreversible hydraulic failure, crown dieback, and tree mortality during extended droughts.

Changes in precipitation timing and intensity can significantly affect forest tree community composition and structure, from subtle shifts in competition and recruitment to large mortality events. Young seedlings and saplings, with their less-developed root systems, are generally more sensitive to soil moisture conditions than mature trees, making the regenerating layers of the forest most susceptible to changes in precipitation patterns. A precipitation manipulation experiment in a temperate forest gap in Vermont, USA, found that small-seeded moisture-sensitive species, such as maples and birches *(Betula* spp.), have survival rates 10 times higher under normal and above-average precipitation compared to episodic drought or episodic drought punctuated by extreme precipitation events. By contrast, large-seeded species like red oak (*Quercus rubra*) and American beech (*Fagus grandifolia*) exhibited consistent survival across different moisture treatments. Although specific aspects of precipitation affecting survival were not pinned down, the extent of soil drying between precipitation events appeared to be the biggest factor in species survival rates. This suggests that future precipitation patterns resembling historic totals but with less frequent events with extended dry periods could favor drought-tolerant, large-seeded species, altering forest community dynamics.

Shifts in precipitation structure can also affect tree species interactions, such as competition for resources or facilitation, through the creation of microenvironments, leading to changes in species composition and structure over time. These complex interactions under new climate conditions will take years to decades to play out, and few studies have documented them. Some conceptual hypotheses might include (*a*) an increase in the frequency of growing season drought could favor deeply rooted oak trees over other, more shallowly rooted species such as maples and shift the belowground structure of the forest toward deeper rooting depths and (*b*) an increase in the duration of dry periods during the growing season could reduce forest LAI, creating opportunities for drought-resilient understory species recruitment with more light resources.

Tree mortality and extensive canopy dieback can induce abrupt changes in forest structure and composition. Even though temperate mesic regions typically receive evenly distributed precipitation, drought has been linked to tree mortality. A metanalysis of 22 mortality events in the eastern US during the twentieth century found that summer precipitation two years prior to mortality was ≥ 2 standard errors less than the 120-year mean (Druckenbrod et al. 2019). Drought-induced mortality has historically coincided with other stressors, like fungal diseases and early frost (Druckenbrod et al. 2019) and now also occurs alongside newer disturbances like invasive species (Seidl et al. 2017). As such, it is difficult to detangle the specific impacts of drought from other factors (Haavik et al. 2015), requiring a comprehensive framework (Manion 1981). Observations suggest that drought will be a major factor shaping tree mortality in temperate, mesic regions around the world (Gazol & Camarero 2022, Ma et al. 2023, Rodríguez-Catón et al. 2016, Suarez et al. 2024), with the potential to change both recruitment and forest structure if increased water stress and hot droughts become more common (Allen et al. 2015, Cook et al. 2015).

Understanding shifts in forest structure and tree species communities is challenging because precipitation extremes rarely occur in isolation (Buma 2015, Seidl et al. 2017). Compound disturbances, like drought combined with insect defoliation or pathogen outbreak, can exacerbate forest carbon stress and often target specific tree taxa. For example, in the northeastern US, drought-weakened oak trees with low NSC reserves were more susceptible to defoliating pests and thus had a reduced capacity to recover, leading to elevated mortality rates (Barker Plotkin et al. 2021). Such compound interactions can catalyze or accelerate shifts in species composition and ecosystem structure, although long-term observations and further studies are needed to understand and predict these interactions.

9. CONCLUSIONS AND SYNTHESIS

Many studies on ecosystem responses to changes in precipitation have focused on annual precipitation extremes within nonforested systems, with considerably more research conducted in semiarid forests than mesic forests (Feldman et al. 2024, Zeppel et al. 2014). Yet emerging evidence strongly indicates that alterations in the precipitation structure—including timing, intensity, duration, frequency, and spatial distribution—are fundamentally transforming ecosystem processes in mesic temperate forests. The effects of these changes are most profound when they intersect with critical ecological windows that control phenology, resource allocation, and biogeochemical cycling. (**Figure 1**).

Most research in temperate forests has concentrated on the effects of drought, rather than extreme rain events. This could reflect the complex ways ecosystems respond to seasonal extremes (**Figure 4**). Drought impacts on plants are often intense and immediately observable, such as wilting leaves, early leaf drop, and even rapid widespread mortality. In contrast, the impacts of higher rainfall can be more subtle but equally transformative. High rainfall extremes, especially outside of the growing season, can cause high nutrient leaching from soils and microbial immobilization and can create anoxia that further slows decomposition. This slow loss of soil nutrients could potentially create a feedback loop that reduces plant nutrition and productivity, further reducing the carbon supply belowground. These lagged and indirect feedbacks from changes in precipitation extremes deserve more study through long-term observations and experimental manipulations to mechanistically describe their complex processes.

Another important area for research is the potential for plants to acclimate to oscillating wet and dry conditions. Although the plant traits literature often describes traits as being adapted to particular hydrologic conditions, this may overlook the plasticity of responses like rooting depth and fine-root biomass. Many studies use space-for-time approaches to assess response variation, while fewer studies examine long-term variation where traits might acclimate to increased moisture variability. Investigating the degree of that plasticity could inform our understanding of the

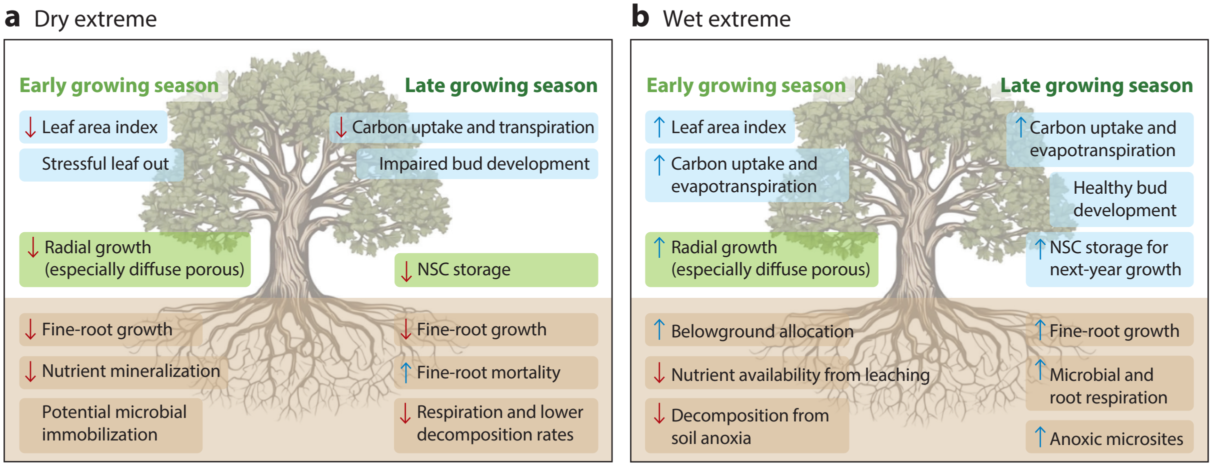

Figure 4

Key processes that shift within critical ecological windows in the early and late growing seasons under (*a*) dry and (*b*) wet seasonal extremes. Abbreviation: NSC, nonstructural carbohydrate.

resilience and resistance of temperate mesic forests to hydrological variability. Ultimately, the complex interactions between aboveground and belowground ecological processes, along with the potential for resistance, resilience, acclimation, and plasticity of organisms within these environments, warrant further long-term observations and experiments to understand novel disturbances from precipitation extremes within mesic temperate forests.

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The authors are not aware of any affiliations, memberships, funding, or financial holdings that might be perceived as affecting the objectivity of this review.

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