Geoderma 435 (2023) 116520

Contents lists available at ScienceDirect

Geoderma

journal homepage: www.elsevier.com/locate/geoderma

Integrating decadal and century-scale root development with longer-term soil development to understand terrestrial nutrient cycling

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A R T I C L E I N F O

Handling Editor: Diego Abalos

Keywords:
Root growth
Phosphorus
Organic matter
Anthropocene
Weathering
Nutrient availability

A B S T R A C T

Nearly 50 y ago, Walker and Syers hypothesized that sources of most terrestrial nutrients shift in dominance from mineral- to organic matter-derived over millennia as soils weather. We investigated how overlaying this soil development framework with vegetation dynamics that can feed back to soil development on relatively short timescales offers insight into ecosystem functioning. To test the hypothesis that forest nutrient economies mediate the nutritional importance of organic matter as mineral weathering proceeds, we paired litterfall decay experiments with soil mineralogical data from diverse forests across the Critical Zone (CZ) Observatory Network, USA. Our findings suggest that dominant sources of tree P may shift from organic matter-bound stocks to minerals as roots expand during the transition from mid to late stages of forest growth and encounter deeper soils that have experienced a lesser degree of weathering. Thus, plants may develop nutritional strategies that do not necessarily rely most heavily on the dominant P form present in an ecosystem, typically driven by stage of soil development, but rather on root proliferation over time, which governs the ability of plants to mine soil volumes at a diversity of depths. Ecosystem P nutrition therefore depends strongly on the interaction between dominant P form and root system growth, particularly as it reflects past land use for both plants and soils. We use these findings to produce a novel framework of vegetative nutrient economics that highlights how root system growth and land use change can influence nutrient transformations and bioavailability, and soil development, across Earth's critical zones.

1. Introduction

The hypothesis that soil nutrient forms transition from mineral to organic as soil development proceeds was introduced in Geoderma nearly 50 years ago with Walker and Syers' (1976) seminal work. Walker and Syers' hypothesis refers specifically to nutrient transformations that occur over the millennial timescales of soil development, defined as alterations in mineralogy and soil textural and hydrological properties that typically accompany pedogenesis (Vitousek and Farrington, 1997; Chorover et al., 2007; Buol et al., 2011). Nutrients indeed vary in form and abundance in different environments (Porder and Ramachandran, 2012), necessitating plant adaptations to a wide range of nutritional conditions (Reich and Oleksyn, 2004; Ordoñez et al., 2009). However, despite extensive research on plants and soils (Bormann and Likens, 1967; Attiwill and Adams, 1993; Vitousek et al., 1997; Lambers et al., 2008), we still lack clarity about the mechanisms by which plants obtain sufficient nutrition in diverse environmental conditions, and under what circumstances their nutrient sources change during ecosystem development. In the Anthropocene, understanding ecosystems' nutritional mechanisms becomes yet more elusive due to often-masked land use histories and patterns of perturbation that alter both soil nutrient stocks and the composition, developmental stage, and

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https://doi.org/10.1016/j.geoderma.2023.116520
Received 17 August 2022; Received in revised form 10 May 2023; Accepted 11 May 2023
Available online 23 May 2023

root system structure of the plants that access them. Consequently, Walker and Syers' hypothesis is still debated and tested across environments (Crews et al., 1995; Richter et al., 2006; Selmants et al., 2010; Lang et al., 2017). Improved understanding of these nutrient cycling phenomena will produce more accurate projections of nutrient bioavailability, ecosystem productivity and vegetation contributions to global change. In spite of the importance of these goals, characterizing soil nutrient dynamics and associated vegetation response has remained a challenge in part due to the difficulties of working across contrasting timescales of soil development and vegetation growth.

While many soils have been developing over thousands to millions of years, forest vegetation grows over decadal- and century-scale timeframes. This growth results in generally increasing root exploration of soil over time, regardless of soil developmental stage. Herein, we define the duration of 'root system development' as the time over which root systems (i.e., roots and their mycorrhizal symbionts) proliferate, a process that typically enables trees to explore increasingly large volumes of soil over time (Doussan et al., 2003; Yan et al., 2006; Wang et al., 2009; Brearley, 2011; Billings et al., 2018). Root development continues until a major disturbance induces tree mortality and re-sets the ecosystem (Odum, 1969; Horn, 1974). The time over which a soil experiences exploration by root systems of the same dominant species can exceed the age of any individual tree if the vegetation can regenerate itself (e.g., late successional stage oak-hickory forests of Eastern North America) and if the time between stand-replacing disturbances is longer than the lifespan of individual trees. In such instances, in spite of isolated tree deaths and canopy gaps permitting sufficient light to support young seedlings (Binkley et al., 2002; Binkley, 2004), the soil will experience continued root exploration by the same dominant tree species until a major disturbance resets the system to an early successional stage. Though tree species vary with forest succession (Connell et al., 1977; Chapin et al., 1994), likely inducing changes in root architectures, we consider time since large-scale perturbation to be a key driver of root system development and thus of the volume of soil roots can access (Billings, 1936; Zangaro et al., 2008; Knops and Bradley, 2009; Devine et al., 2011; Yuan and Chen, 2012; Sun et al., 2015). Because root systems represent the primary mechanism by which trees interact with the developing soil system (Burghelea et al., 2015; Pierret et al., 2016; Billings et al., 2018; Dontsova et al., 2020), concurrently embracing the diversity of timescales over which vegetation and soil profiles interact – decadal, century, and millennial – is critical for understanding how vegetation obtains nutrients, and the ensuing influence of those processes on soil development.

Soil nutrient stocks and their bioavailability vary over these diverse timescales in ways that have been studied independently but have not often been merged into a single paradigm. Most nutrients ultimately are sourced from minerals in rocks, which are renewed on long timescales via orogenic uplift (Carey et al., 2005; Vitousek et al., 2010) and released through the process of rock and mineral weathering (Drever, 1994; Vitousek et al., 1997, Berner and Berner, 2003; Richter and Markewitz, 2000; Burghelea et al., 2015; Dontsova et al., 2020). These processes are typically measured over millennial time scales (Drever, 1994; Brantley, 2008; Ferrier et al., 2010). When taken up by plants, those nutrients are incorporated into biomass in aboveground and root tissues, and subsequently into soil organic matter, comprising a nutrient source that is relatively abundant in more surficial soil horizons (Marschner and Rengel, 2007; Gill and Finzi, 2016). These resources cycle on annual to decadal time scales (Pedersen and Bille-Hansen, 1999; Kavvadias et al., 2001). Walker and Syers' (1976) model of soil development implies that the nutritional relevance of these organic-matter-bound stocks must increase as soils develop over geologic timescales, because weathering processes tend to decrease the abundance of mineral-bound P over millennia (Walker and Syers, 1976). However, this model does not explicitly explore how time-varying nutrient stocks may be exploited by root systems at various stages of development.

Recent work highlighting interactions between soil and root system development (Lambers et al., 2008; Hobbie, 2015) underscores a need for a more detailed assessment of pathways of soil nutrient development. Vegetation is hardly a prisoner of its environment: instead, vegetation develops different nutrient acquisition strategies over time as a consequence of both changing nutrient demands and shifting abilities to tap into different resources, processes that feedback into soil development and subsequent nutrient stocks on comparatively short timescales (Lambers et al., 2008; Bardgett et al., 2014; Hauser et al., 2020). Plants allocate different amounts of fixed C to roots and mycorrhizae at different depths to cope with temporally shifting nutrient forms (Lambers et al., 2008; Hauser et al., 2020; Peixoto et al., 2020), and plant uptake of nutrients can redistribute nutrient forms across the root zone, resulting in deep, mineral-bound nutrients being transferred to surface horizons in organic-matter-bound forms on decadal timeframes (Jobbagy and Jackson, 2001; Austin et al., 2018; Austin et al., 2020, Wang et al., 2022). All of these processes influence metrics of soil development such as mineralogy, soil structure and porosity (Jobbagy and Jackson, 2001; Rasse et al., 2005; Pierret et al., 2016; Austin et al., 2018; Cui et al., 2019; Koop et al., 2020).

Combined, these processes suggest that concepts of nutrient transformations in soil over time require better integration with models of root and vegetation dynamics because plant processes, not just weathering-related soil development processes, influence the relative distribution of nutrient stocks. Such efforts would necessarily acknowledge that, as forest succession proceeds through time (Connell et al., 1977; Chapin et al., 1994), the influence of vegetation on belowground processes likely changes as well. Further, it would offer a novel framework describing the contribution of tree nutritional strategies to critical zone (CZ) development (i.e., development of whole ecosystems, including vegetation and regolith in tandem with each other; Jordan et al., 2001; Richter and Billings, 2015). This effort seems especially apropos in the Anthropocene, when both root depth distributions and soil nutrient distributions are undergoing rapid change due to land cover changes (Richter and Markewitz, 2001; Richter et al., 2006; Haff, 2010; Yoo et al., 2015; Brecheisen et al., 2019; Hauser et al., 2020; Hauser et al., 2022), with implications for weathering in diverse systems (Wen et al., 2020).

Here, we begin to characterize feedbacks between tree nutrition and soil development to better understand how whole, forested CZ nutrient economies develop across diverse timescales. To do this, we estimate the potential dependence of vegetation on organic matter-bound nutrients relative to mineral-bound nutrients as these nutrient sources vary in dominance across forested CZs spanning continua of soil and root system development. We focus our analyses on P because of its essential nature for vegetative growth (Penuelas et al., 2013, Jonard et al., 2015, Hou et al., 2020) and its presence in both rock minerals and organic matter (Walker and Syers, 1976, Vitousek et al., 1997). We discern the potential nutritional relevance of organic matter as mineral P stocks vary and discern the role of expanding root systems in soil developmental processes. We use these data to develop a novel conceptual model describing the development of CZ nutrient partitioning across timescales relevant to contemporary forest root expansion and soil development.

We hypothesize that any increase in the importance of organic matter-derived nutrients for forest nutrition across soil developmental stages is mediated by trees, and specifically that the duration of root proliferation – the stage of root system development – will govern the degree to which trees can access relatively less weathered, mineral-bound nutrient stores deep in soil profiles. Over the timescales relevant to long-term soil development, we would expect that organic matter-bound nutrients have the potential to provide a greater portion of forest nutrition, in agreement with Walker and Syers' (1976) hypothesis (Fig. 1a). However, on the decadal timescales of vegetation growth, we hypothesize that root-mediated access to deep, mineral-bound nutrients generates a relative decline in potential nutrient provisioning from organic matter as aging forests become increasingly able to tap into deep, mineral-bound nutrient stocks via larger rooted volumes (Billings,

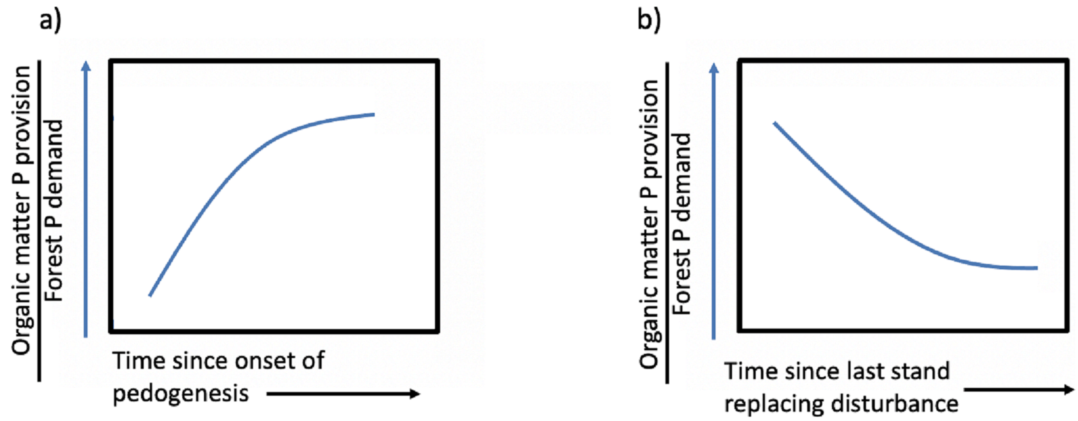

Fig. 1. Predicted relationship between the potential provision of nutrients from organic matter and time as pedogenesis proceeds, as a consequence of Walker and Syers' proposed model (1976; a). In contrast, we offer (b), a hypothesized relationship between provision of nutrients from organic matter and time (on shorter timescales than in (a)) as vegetation root systems develop in the time since the last stand replacing disturbance. Panel b reflects how root system interactions with soil development may lead to increasing provision of nutrients from minerals and reduced potential forest P provision from organic matter as trees age.

1936; Zangaro et al., 2008; Knops and Bradley, 2009; Devine et al., 2011; Yuan and Chen, 2012; Sun et al., 2015; Billings et al., 2018) (Fig. 1b). If true, this finding would suggest that mineral-bound P deep in the subsurface is relevant to forest nutrition even where weathering-induced P losses over time have been substantial, and would suggest that Walker and Syers' (1976) original hypothesis must be considered in the context of root system development. We explore these concepts and examine how different nutrient reservoirs play distinct roles in forest productivity as root systems grow during forest succession, as well as the influence those processes can have on soil development as both forest

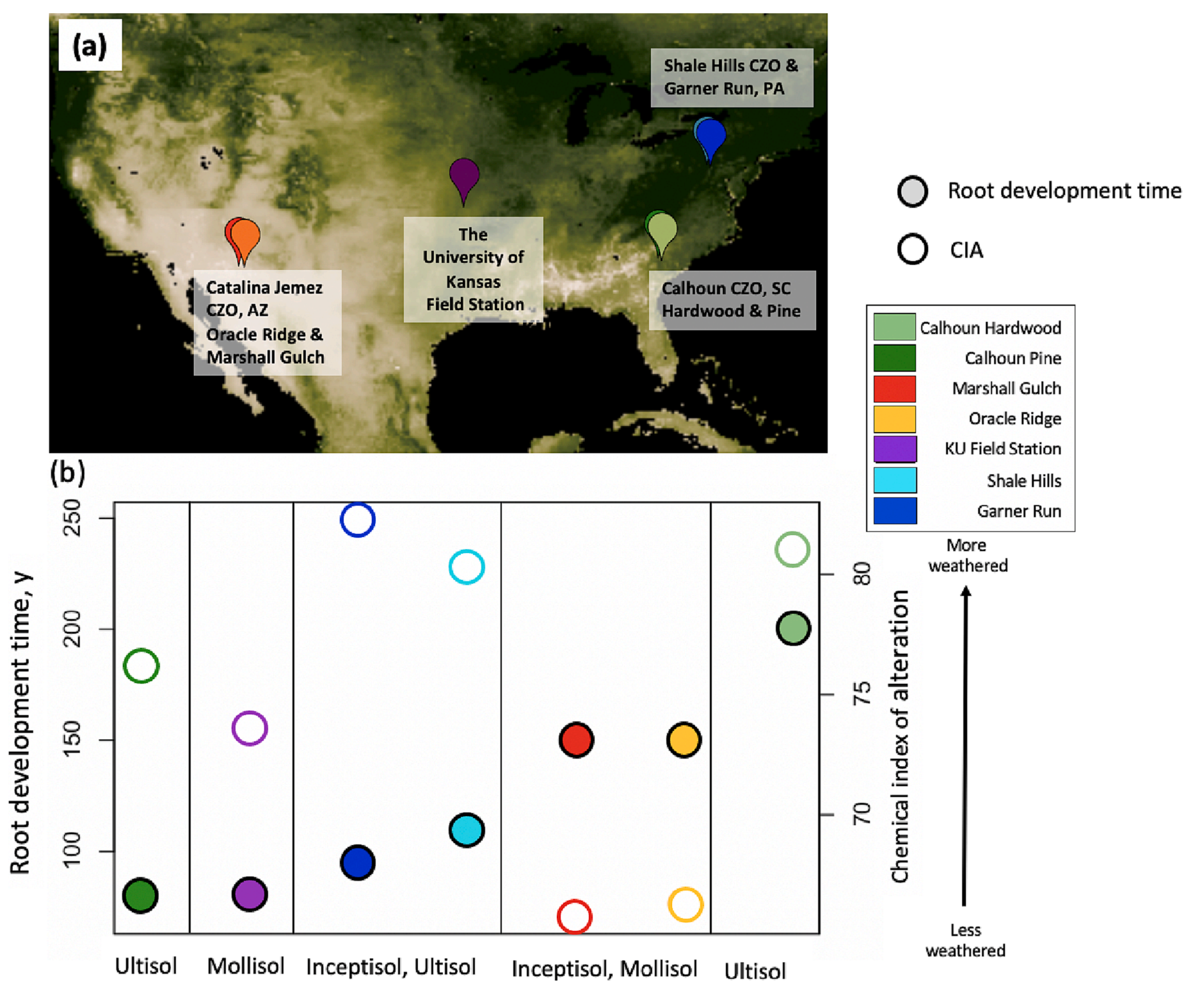

Fig. 2. Field sites across the Critical Zone Exploratory Network (a) representing a gradient of root system development (b, left y axis, filled circles). Sites also represent a gradient of soil mineral development as estimated by the Chemical Index of Alteration (CIA)—a metric of Al, K, Ca, and Na oxide depletion—and soil order (b, open circles, right y axis). Lower CIA values indicate a less weathered material and higher CIA values indicate stronger weathering and elemental depletion.

vegetation and soils change over diverse timescales.

2. Materials and methods

2.1. Study sites

We examined P cycling phenomena in seven forests (Fig. 2a) comprising both Critical Zone Observatory (CZO) and CZ Exploration Network (CZEN) sites (Table 1). These sites represent varied degrees of soil development, indicated by both chemical index of alteration (CIA) — a metric of weathering based on the relative prevalence of mineral Al, Na, Ca, and K calculated as oxides (Price and Vebel, 2003) — and soil taxonomic classification (Fig. 2b). These forests also represent differences in degrees of rooting system development, as defined above (Fig. 2b; see below). Although plant species and thus root architecture (Freschet et al., 2017) and foliar and litterfall nutrient concentrations (Hobbie et al., 2006; Hobbie, 2015) differ across these sites, our focus is on root proliferation over time in diverse forests (i.e., time since stand-replacing disturbance). We recognize that site differences such as bedrock, climate, and plant species present challenges to testing Walker and Syers' (1976) hypothesized relationship; well-controlled, natural ecosystems suitable for testing these ideas are difficult to identify. However, these differences allow us to explore possible, naturally-relevant reasons for deviations from Walker and Syers' (1976) hypothesis as soils develop across diverse ecosystems. Indeed, Walker and Syers (1976) highlight the need for testing their hypothesis broadly—across parent materials, vegetation types, and precipitation regimes. Examining sites with diverse features (Table 1) thus can expand the concepts they began to develop.

2.2. Duration of root system development

We estimated the number of years that each soil has been rooted as one possible factor explaining the relative importance of different nutrient forms to forest nutrition. Many features of roots change over a tree's lifespan. However, we focus on duration of root system development. This metric represents the time that roots in each ecosystem have been growing (i.e., without stand-replacing disturbances) and therefore serves as a first-order estimate of the duration of root expansion and thus of root influence in the soil's development, given that roots proliferate over a greater volume with time (Billings, 1936; Zangaro et al., 2008; Knops and Bradley, 2009; Devine et al., 2011; Yuan and Chen, 2012; Sun et al., 2015; Billings et al., 2018). We leveraged tree surveys and well-characterized disturbance histories at each site to approximate the time period during which roots of species similar to those found today have explored their soil profiles.

At the Calhoun pine forests, KUFS forests, and the Shale Hills and Garner Run forests, known histories of recent land use and tree reestablishment after stand-replacing disturbances determined the amount of time roots of the contemporary vegetation have explored soils at these locations. Both Calhoun pine and KUFS forests are reestablishing after agricultural use ~ 70 and ~ 80 y ago respectively (Richter and Markewitz, 2001; Fitch et al., 2001). Shale Hills and Garner Run sites were subject to widespread logging at the beginning of the 20th century, such that roots in these forests have had ~ 110 and ~ 90 y to develop, respectively (Li et al., 2018). The Catalina and Calhoun hardwood forests represent later successional stages, comprised of self-replacing tree species (Whittaker, 1953), suggesting that these forest soils have been explored by root systems similar to contemporary roots for longer than the age of contemporary trees might suggest. We employ ages of the oldest sampled trees at these sites as a conservative estimate of the amount of time these soils have been explored continually by roots similar to those that exist today, given the self-replacing nature of these mature forests. At Catalina, this is ~ 150 y and at Calhoun, ~200 y (Richter and Markewitz, 2001; Iniguez et al., 2016). These estimates permit a cross-site comparison using a consistently calculated metric derived from the best historical data available from each site. We consider this metric to be particularly conservative at Calhoun because it is likely that these late-successional hardwood forests have maintained themselves for multiple tree generations.

2.3. Data collection

2.3.1. Characterizing forest P nutrition status

We approximated annual vegetation P uptake at each site by estimating net primary productivity (NPP) and converting those values to P

Table 1
Study sites used for the analysis and site characteristics including net primary productivity (NPP), mean annual temperature (MAT), mean annual precipitation (MAP), site elevation (m), dominant vegetation, soil orders, and bedrock types.

Site	NPP ($g_C m^{-2} yr^{-1}$)	MAT (°C)	MAP (mm yr^{-1})	Elevation (m)	Dominant tree species	Soil Order	Bedrock type
Calhoun Pine*	530	16	1250	134–190	*Pinus taeda* and *P. echinata*	Ultisols: Typic Kanhapludults, Typic Hapludults	Granite
KU Field Station****	370	13	940	335	Quercus spp., Carya spp. Juniperus virginiana	Mollisols: Typic Eutrudepts, Lithic and Typic Hapludolls, and Aquic and Typic Argiudolls	Glacial Till and Loess
Garner Run**	440	9.5	1050	256–310	*Quercus* spp., *Carya* spp. and *Pinus spp*	Ultisols/Inceptisols: Typic and Aquic Fragiudults, Typic and Lithic Dystrudepts, and Typic Fragiaquults	Sandstone
Shale Hills**	440	9.5	1050	256–310	*Quercus* spp., *Carya* spp. and *Pinus spp*	Ultisols/Inceptisols: Typic and Aquic Fragiudults, Typic and Lithic Dystrudepts, and Typic Fragiaquults	Rose Hill Shale
Marshall Gulch***	640	10.4	940	2284–2634	*Pinus ponderosa*, *Abies concolor*	Mollisols/Inceptisols: Typic Haplustolls and Typic Humustepts	Granite, Schist, Quartzite
Oracle Ridge***	300	11.9	840	2064 to 2388	*Pinus* and *Juniperus* spp.	Mollisols/Inceptisols: Typic Haplustolls and Typic Humustepts	Granite, Quartz diorite
Calhoun Hardwood*	950	16	1250	134–190	*Quercus alba, Liquidambar styraciflua, Liriodendron tulipifera, Q. rubra,* and multiple *Carya spp*	Ultisols: Typic Kanhapludults, Typic Hapludults	Granite

*Calhoun CZO data for MAT, MAP, and elevation from Critical Zone Observatories, 2020a. Calhoun bedrock characterization from Bacon et al., 2012.
**Garner Run and Shale Hills data from Critical Zone Observatories, 2020b.
*** Marshall Gulch and Oracle Ridge data from Critical Zone Observatories, 2020c.
****KU Field Station bedrock characterization from Klopfenstein et al., 2015 and Hirmas and Mandel, 2017. Climate and elevation data from Kansas Biological Survey, 2020.

demand (NPP_p) via estimates of vegetation stoichiometry. We used annual litterfall biomass (g m^{-2} y^{-1}) to estimate NPP (g C m^{-2} y^{-1}) given its direct linkage to yearly ecosystem NPP (Matthews, 1997). To do this, we converted leaf mass to leaf C approximating leaves to be 48% C (Bowden et al., 1992). We converted these litterfall-based NPP estimates to NPP_p using C:P values specific to the leaves collected from each site, producing values of potential P uptake that reflect the varied P demands of our study sites. Senesced leaf P concentrations were assessed using the methods detailed below. Our approach relies on the assumption that the linkage between litterfall rates and NPP is robust across all forests (Matthews, 1997). While these estimates do not include P in other plant tissues, such as seeds and fruits, these other tissues comprise a relatively small proportion of litterfall (Kaspari et al., 2008) and contribute minimally to P cycling compared to leaves and fine twigs.

We estimated total soil P using bulk elemental data (Jin et al., 2010; Holleran, 2013; Austin and Schroeder, 2019; Brantley, 2019; National Ecological Observatory Network, 2020a). We transformed %P estimates into P contents of each sampled horizon using bulk density distributions (Richter et al., 1994; Herndon, 2012; Holleran, 2013; Bacon, 2014; Brantley, 2019; National Ecological Observatory, 2020a), including O horizons where present. O horizons contain very little mineral-bound P, and therefore represent a large amount of organic material at the soil surface. We summed P contents across horizons to the depth approximating 95% of root biomass to estimate the absolute P content of a square meter soil column in the zone of this majority of roots. We estimated the depth at which 95% of the root biomass is attained (D95) using root distributions from soil profiles sampled at each site (Holleran, 2013; Li et al., 2018; Eissenstat, 2019; Billings et al., 2020; National Ecological Observatory Network, 2020b). Though roots growing below D95 can penetrate into saprolite or bedrock (Hasenmueller et al., 2017) and deep roots can be relatively active in nutrient uptake (Da Silva et al., 2011), our use of D95 captures the majority of roots and the bulk of their absolute activity, while permitting comparison of an analogous metric across sites. Though clay-rich horizons are well-represented at some of these sites, to our knowledge there are no impediments to proliferation of roots as severe as hardpans at any forest studied. We anticipate that the D95 soil depth captures most of the absolute soil volume over which roots may interact with soil P distributions. Our soil P calculations thus estimate the total P present in the rooted zone of each forest. While it is not a measure of different P fractions, it represents the maximum potential P resource with which most tree roots can interact.

2.3.2. P in leaf biomass

We analyzed the P concentration of senesced leaves from each site to generate NPP_P estimates described in the previous section, and to assess leaf P release rates from litter in the incubations described below. Leaves were dried at 60 °C for at least 3 days and ground using a mortar and pestle to pass through a 2 mm mesh sieve before shipment to the Kansas State Soil Testing Lab. There, leaves were further processed using salicylic-sulfuric acid digestion before analysis for bulk elemental concentration using inductively coupled plasma – optical emission spectroscopy (ICP-OES, Varian 720-ES, Palo Alto, USA).

2.3.3. Maximum potential organic P recycling

We developed a metric of the maximum potential rate at which organically-derived P could be provided in each forest by quantifying the release rate of organic P (P_o) from each forest's litterfall and scaling those rates to an annual basis. This approach assumes that P release during litterfall decay represents the fastest rate at which P released from any decaying organic matter, including soil organic matter, could be provided in a bioavailable form. This assumption is likely valid given the generally slower rates of organic matter decay within soil profiles relative to litterfall (Schlesinger and Bernhardt, 2013). We used these annual, litterfall-derived P release rates in conjunction with each forest's NPP estimates to generate an estimate of the fraction of NPP that could potentially be supported by organically-derived P (OM_P:NPP_P). We emphasize that this metric represents the maximum estimate of organically-derived P, and that much of the rooted soil volume at all sites, and indeed in most forests, is dominated by mineral-bound P (Richter et al., 2006, Lang 2017).

To generate our metric, we conducted decomposition experiments using senesced leaves collected from each study site. Conducting these decomposition experiments in the lab instead of the field permitted us to specifically examine annual P release potential without influence from P remaining in soil organic matter, whether particulate or mineral associated, from previous seasons. Additionally, the lab-oriented design made for greater ease of cross-site work, given that sites were widely dispersed geographically. Though our design did not allow litter exposure to soil macrofauna, which can influence soil P distributions (Chapuis-Lardy et al., 2011), we included microbes native to each site (see below) to aid decomposition.

We collected leaf litter at each site with which to conduct the litterfall incubations. At the KUFS and Catalina sites, we deployed 10 to 12 litter baskets in fall 2016 and spring 2017, respectively, for leaf litter collection over the course of the following growing season. At KUFS, litter collection for NPP estimation has continued for 3 additional seasons, but only leaves from 2016 were used for incubations. Previously collected, senesced leaves were available from the prior 2015 and 2016 growing seasons at the Calhoun and Shale Hills CZOs. Upon collection, leaves were dried at 60 °C until a constant weight before grinding with a Wiley mill. We used dried leaves instead of fresh for multiple reasons. First, numerous sites had previously collected leaves and dried them for storage purposes. To make use of readily available samples, we opted to use these leaves to reduce travel and sampling demands at our widely dispersed sites. Additionally, we wanted to be able to control the moisture level of each incubation and needed to start with consistently dried leaves across litter baskets both within and between sites to maintain a consistent starting point for all leaves.

To inoculate these oven-dried, senesced leaves with microbes able to induce decay, we added a small amount of freshly collected, senesced leaves from each site to their respective dried counterpart. During the spring of 2017, we collected a small sample of freshly fallen leaves from each site, which we froze upon return to University of Kansas. We thawed these samples, roughly chopped them with a knife and mixed a small amount with the dried litter. We distributed ~ 0.7 dry g of the mixed litter into six small permeable bags per litter collection trap and placed the bags into a glass jar filled partially with marbles to keep the bags well drained. This resulted in at least six jars per site containing six bags each. We then incubated leaves aerobically in site-relevant conditions (Table 3). We periodically watered the bags in quantities and frequencies mimicking site-specific growing season rainfall (Tables 1 and 3). To mimic the bimodal precipitation regime at the Catalina CZO, we performed two shorter incubations to approximate the amount of decomposition possible over a full year's time course at this site. We periodically subsampled the litter bags and collected the water that had leached through them during rain-mimicking events. These subsamples allowed us to examine P released during organic matter decay and not immobilized in microbial biomass over a time course representative of each site's growing season. We emphasize that the application of temperature and moisture conditions relevant for each forest produce litterfall-derived P release estimates relevant to each site, relative to the others.

At the beginning and end of the incubation, we removed one of the subsample bags and analyzed litterfall P concentration (described above). Using litterfall mass in combination with P concentration, we calculated P content of each leaf subsample. Differences between initial and final P contents in decaying leaves per unit time provide estimates of potential annual P_o release (the numerator in OM_P:NPP_P). We assume that the potential P release from organic matter already present in the upper soil profile is lower than the rates achieved with our combination of fresh and dried litter, so we use these estimates to represent a maximum potential P release from annual organic matter additions. Our incubation approach does not permit knowledge of absolute P release from organic matter decay throughout these soil profiles. However, it provides comparable information about the new P from organic matter that is potentially made plant available at each location on an annual basis.

2.3.4. Metrics of soil development and soil mineral P status

Using previously collected soil mineralogical data (Jin et al., 2010; Holleran, 2013; Austin and Schroeder, 2019; Brantley, 2019; National Ecological Observatory Network, 2020a), we calculated soil weathering indices to numerically characterize the mineral nutrient status of each site, as well as biotic contributions to mineral distributions. We focused on tau_p (τ_p)—a well-established metric of soil development that describes the depletion of P in the soil profile relative to the soil parent material (Ruxton et al., 1968, Price and Vebel, 2003, Oh et al., 2007). This metric offers a means of comparing some features of disparate soil profiles' development relative to others, in spite of different parent materials with contrasting P content. A more negative value of τ indicates that the soil depth examined has been depleted in the element of interest relative to a parent material reference, while a positive value indicates elemental enrichment (Brimhall, 1987).

Calculating τ relies on measurements of a relatively immobile element as a reference to which the more mobile element of interest can be compared. Here, we used Zr as the immobile element. Values of τ vary depending on the soil horizon of interest and the selection of reference parent material. For soils based on alluvium and glacial till, uncertainty about what constitutes the parent material(s) is especially great. However, we calculated τ_P of the root zone given our interest in vegetation influences on soil development metrics, using the ratio of P remaining in the soil surface horizon sampled at each site relative to P at the soil depth where roots have reached ~ 95% biomass (calculation described above). Thus, τ_P as we present it represents relative changes in P across the rooted profile. By replacing parent rock P in the traditional calculations of τ with P of soil where roots are rare, we achieve a metric of Pdepletion across the depth of soil inhabited by the largest proportion of plant roots. (We also report τ values calculated using parent material in Table 2 as τ_P, bedrock). We thus calculate τ_P as follows:

$$\tau_P = \frac{P_t^S * Zr^{RF}}{P_t^{RF} * Zr^S} \tag{1}$$

where P_t^S is total P (mg kg^{-1}) in the uppermost sampled soil horizon, Zr^{RF} is the total Zr (mg kg^{-1}) at the approximated rooting front where roots reach ~ 95% root biomass, Zr^S is the Zr (mg kg^{-1}) in the uppermost soil horizon, and P_t^{RF} is total P (mg kg^{-1}) at the rooting front.

Our use of this metric offers a means of exploring the time-integrated, ecosystem dynamics of P_i and P_o separately. We first focused our analysis on inorganic P (τ_{Pi}) by subtracting estimates of P_o from total soil P values before implementing equation 1. The τ_{Pi} metric thus reflects changes over depth, specific to mineral-bound P. τ_{Pi}, therefore, allows us to estimate the changes to inorganic, mineral-bound P across the depth of the root zone. This produces the following equation:

$$\tau_{Pi} = \frac{P_i^S * Zr^{RF}}{P_i^{RF} * Zr^S} \tag{2}$$

where P_i^S is inorganic P in surface soils estimated by subtracting organic P estimates from total P estimates, and P_i^{RF} is inorganic P at the rooting front estimated by the same method. We generated estimates of soil P_o for this calculation from soil organic C depth distributions available for each site (Rasmussen et al., 2008; Andrews et al., 2011; Holleran, 2013; Hasenmueller et al., 2017; Brantley, 2019; Billings et al., 2020; National Ecological Observatory, 2020c), and organic matter C:P ratios estimated from sites' litter data, the most site relevant C:P ratio we have available for initial inputs of organic matter to soil. There is some evidence that the C:P in roots, a primary soil C source, is comparable to leaf litter C:P, lending greater confidence to use of litter C:P ratios (Zechmeister-Boltenstern et al., 2015). However, this method may underestimate P_o given recent demonstrations that organic matter in mineral soil conserves P_o more effectively than organic C (Spohn, 2020). The difference between τ_P and τ_{Pi} provides us with an estimate of τ_{Po}:

$$\tau_P - \tau_{Pi} = \tau_{Po} \tag{3}$$

The τ_{Po} metric helps us understand the role of P_o in the P status of root zone soils.

2.4. Statistical analyses

We first characterized P demand and P availability across forest sites to better understand the outcomes of our hypothesized relationships. To do this, we regressed NPP_P and site leaf P concentrations on our estimates of root zone P content. These relationships act as an indicator of relative P limitation across the forests examined in our study and characterize forest productivity across a variety of soil conditions. Regression analyses allow us to examine emergent trends across our sites and discuss their possible implications, as well as data limitations.

To test whether our estimates of potential annual organic matter provision of P could meet a greater proportion of forests' NPP_P demands where soils are more depleted in mineral-bound P, we performed regression analyses between the OM_P:NPP_P ratio and $\tau_{Pi,}$ and τ_{Po} metrics. We log transformed the OM_P:NPP_P ratio and τ_{Pi} to meet the assumption of normally distributed residuals. Other metrics did not require transformation to meet assumptions. We also tested for outliers using Cook's Distance and calculated the regression both with and without outlier points. These comparisons discern the maximum capacity for organic matter recycling to sustain forest P uptake in soils of different weathering statuses and, in the case of τ_{Po}, the ways in which soil and stand development display feedbacks as a result of root systems driving P_o distributions.

Table 2
Data used for calculations of potential P provision and τ_P ratios. These include release rate of P from organic matter (OM_p) as determined by litter incubations, estimates of P uptake to meet the demands of NPP at each site (NPP_p), and the depth to 95% root biomass used to determine the soil sample depths for calculating τ_P. We also include an estimate of depth to bedrock at each site for comparison of potential soil volume accessible to roots at each location, as well as τ_P calculated using estimated bedrock P as the parent material. For the KU Field Station, τ_P bedrock is calculated using the deepest sampled soil horizon as the parent material, which approximates the chemistry of glacial loess that underlies the region. The derivation of table values, as well as τ_P values and an explanation of error estimates are outlined in the main text (Methods section) and in captions for figures associated with each dataset. Sites are ordered from shortest to longest duration of root development time.

Site	OM_p ($g_p m^{-2} yr^{-1}$)	NPP_p ($g_p m^{-2} yr^{-1}$)	Depth to 95% Root Biomass (m)	Depth to Bedrock (m)	$\tau_{P,}$ bedrock
Calhoun Pine	0.20	0.20	2.9	5 – 40	−0.49
KU Field Station	0.24	0.65	2.0	0.5 – 2	−0.03
Garner Run	0.31	0.37	1.2	0.7 (ridgetop) to 1.7 (valley floor)	−0.53
Shale Hills	0.16	0.26	0.5	<0.25 (ridgetop) to > 2 (valley floor)	0.01
Marshall Gulch	0.14	0.26	0.6	0.7 – 1.8	1.38
Oracle Ridge	0.09	0.16	0.6	0.7 – 1.8	2.09
Calhoun Hardwood	0.19	0.42	3.2	5 – 40	−0.28

Table 3
Summary of incubation characteristics for each study site. Range of water applied indicates the minimum and maximum amount of water added to incubation jars per forest floor area represented by litterfall in jars. The amount of water applied at each time point was based on the average monthly precipitation for each site corresponding to the month of the incubation. See text for details.

Site	Incubation Length (d)	Incubation Temp (°C)	Range of water applied (mL cm^{-2})	Source of climate and precipitation data
Calhoun CZO, Pine and Hardwood	212	21.5	7.5 – 11	https://criticalzone.org/calhoun/infrastructure/field-areas-calhoun/
Catalina Jemez CZO Marshal Gulch	Incubation 1: 115 Incubation 2: 117	Incubation 1: 7 Incubation 2: 7	0.8 – 15.7	https://criticalzone.org/catalina-jemez/infrastructure/field-areas-catalina-jemez/
Catalina Jemez CZO Oracle Ridge	Incubation 1: 115 Incubation 2: 117	Incubation 1: 10 Incubation 2: 10	0.7 – 10.9	https://criticalzone.org/catalina-jemez/infrastructure/field-areas-catalina-jemez/
University of Kansas Field Station	185	21.5	8.8 – 13.3	https://biosurvey.ku.edu/sites/kbs.drupal.ku.edu/files/docs/Climate%20Synopsis.pdf
Shale Hills CZO	154	19.3	8.8 – 10.4	https://criticalzone.org/shale-hills/infrastructure/
Garner Run	154	19.3	8.8 – 10.4	https://www.hydroshare.org/resource/9535cbe97d5843a788fc7648de39a6e5/

To determine whether OM_P varied in nutritional relevance with forest development, we performed a linear regression between years of root development and the OM_P:NPP_P metric. It is important to note that in these analyses, the years of root development are conservative estimates; if root development has persisted for longer, significance of these statistical tests may change. We again used Cook's Distance and calculated the regression both with and without outlier points. In all analyses we report statistics both with and without outlier points where they alter significance of findings. We also performed a one-way ANOVA using stand ages as categorical variables driving the OM_P:NPP_P metric to discern whether we observed distinct groupings of forests based on their reliance on organic matter- vs. mineral-bound P. We followed t-tests with post hoc Tukey tests to discern which forests exhibited similar OM_P:NPP_P responses, and what response patterns emerged as a function of forest age. Data followed the assumptions of normally distributed residuals.

To assess the degree to which vegetation age was associated with patterns of soil P forms, we analyzed the relationship between stand age and τ_{Po}. We fitted linear and non-linear curves to the data and selected the best fit via Akaike information criterion (AIC) values. In all described analyses, we report every meaningful trend, which embraces P-values < 0.1 given the difficulties inherent in seeking appropriate ecosystem-scale site replicates, as well as the difficulty of collecting comparable ecological data across dispersed sites (Filion et al., 2000; Oren et al., 2001; Bernacchi and Morgan, 2005; Amrhein et al., 2019). Analyses were performed in RStudio v. 1.0.153 (RStudio Team, 2017).

3. Results

Vegetation P demand estimated via NPP (NPP_P) was positively correlated with total root zone P when all points were included in the analysis ($P = 0.013$, $r^2 = 0.7$, Fig. 3a). The removal of an influential point at KUFS altered the significance of the regression ($P = 0.23$, $r^2 = 0.17$, Fig. 3a). Soil depths by which roots have achieved 95% of their biomass, which were used to approximate the depth of most of the rooted zone and determine the rooting front (RF) terms in τ_P calculations, ranged from 3.2 to 0.6 m (Table 2). Leaf [P], though in part dependent on tree species (Reich and Oleksyn, 2004), represents a

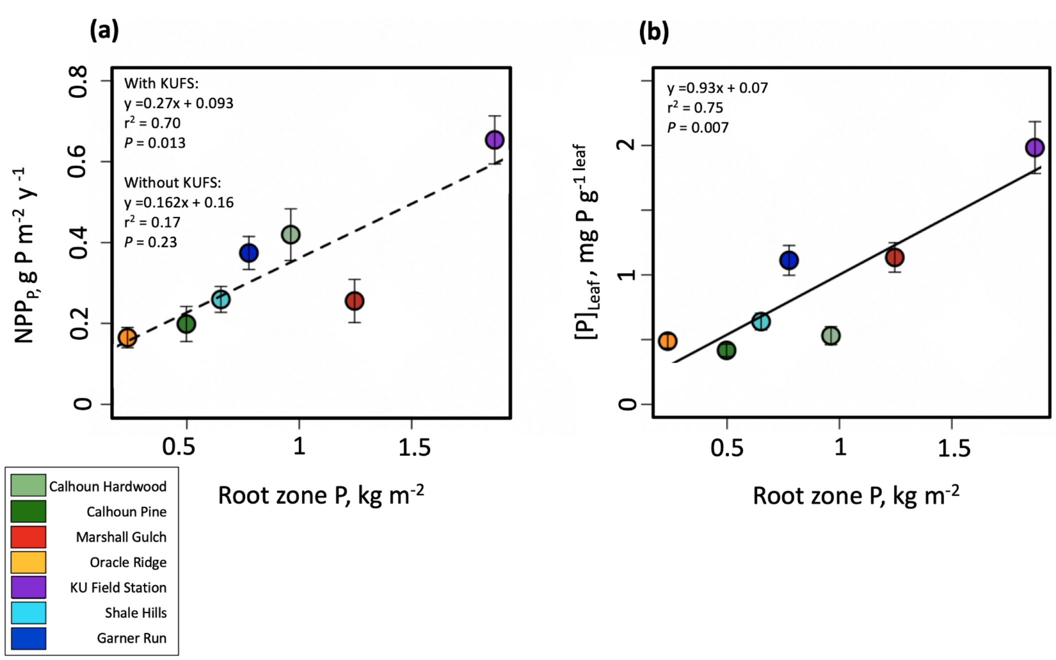

Fig. 3. Vegetation growth characteristics in relation to soil P content. Total P content of a square meter soil profile summed to the depth of ~ 95% root biomass, termed root zone P, displayed positive relationships with both (a) P demand of net primary productivity (NPP_P) estimated from annual leaf litter production ($P = 0.013$, $r^2 = 0.7$) and (b) leaf [P] in forest trees at each study site ($P = 0.007$, $r^2 = 0.75$). Error bars represent one standard error from the mean. In (a), dashed line represents the linear relationship calculated with KUFS site included although KUFS was a significant outlier to the trend. Removal of the KUFS point resulted in non-significant regression ($P = 0.23$, $r^2 = 0.17$).

measure of vegetation P status and was positively correlated with total P of these rooted zones (P = 0.07, r^2 = 0.75, Fig. 3b).

P release from organic matter decay, used to calculate our metric of organic P recycling, ranged from 0.085 to 0.31 g P m^{-2} y^{-1} across sites (Table 2). The relationship between OM_P:NPP_P and τ_{Pi} was best represented by an exponential decay curve (AIC = 1.69), reflecting a steeply negative slope where soils have negative τ_{Pi} values. The AIC values for other tested relationships, including a linear relationship, ranged from 1.82 to 14.43. Where sites were more depleted in inorganic P across the root zone (i.e., low τ_{Pi} values), the OM_P:NPP_P ratio increased, suggesting the potential for organic matter recycling to meet a greater proportion of annual forest P demand (P = 0.017, r^2 = 0.74; Fig. 4). Although the curvilinear relationship fits the data better than a linear fit, we present statistics from the linear relationship in addition to the curved line (Fig. 4) because they are statistically significant and permit a broadly applicable, standardized interpretation of the relationship between potential organic P provision and mineral P depletion. Given the relatively few forests available to contribute data, the statistical metrics offered by the significant linear relationship and the better fit of the exponential equation both hint at increased nutritional relevance of organic matter-bound P where mineral P is depleted.

Forest stands that we estimate to have experienced a longer duration of exploration by roots displayed greater estimated contributions of P_o to total soil P enrichment (i.e., higher values of τ_{Po}). Forests with comparatively younger root systems exhibited less enrichment of soil P by P_o (Fig. 5a). However, with one exception, potential P release from organic matter decay was relatively high for younger root systems and comparatively low where roots had been established for a longer time (Fig. 5b, P = 0.015, r^2 = 0.76). The exception to this finding is the KUFS forest (Cook's Distance = 1.16), where the potential for organic matter P to meet estimated NPP_P demands is lower than the other similarly aged root systems. Compared to the ~ 80 y old Calhoun pine forests and ~ 95 y old Garner Run forests, ~81 y old KUFS forests displayed 0.64 and 0.46 percent less P provision from organic matter as a proportion of NPP_P demands (P < 0.002), respectively. Compared to ~ 110 y old Shale Hills forests, KUFS forest's organic matter provision was 21% less (P = 0.08).

4. Discussion

Our findings highlight the interwoven nature of vegetation and soil dynamics that calls for greater consideration of decadal-scale root system development in metrics of soil development. When examined solely in terms of mineral P status, one metric of long-term pedogenic time (Fig. 1a, X-axis), our data point toward patterns generally consistent with patterns of nutrient bioavailability we might expect under traditional models of soil development (Walker and Syers, 1976, Vitousek et al., 1997; Izquierdo et al., 2013, Fig. 4). Specifically, we observed the highest potential release rate of organic matter-bound P where soils were comparatively mineral-P depauperate and the lowest potential release rate of organic matter-bound P at sites with soils relatively rich in mineral-bound P (Fig. 4). Within the forests studied, where P availability is dominated by either organic matter- or mineral-bound P, vegetation appears to have access to P from the form that is most bioavailable, a feature that varies across geologic timescales (Walker and Syers, 1976, Crews et al., 1995, Hauser et al., 2020). However, when we examine our findings through the decadal-scale lens of root system development, we observe deviations from what we might expect for the role of organic matter- vs. mineral-bound P in forest nutrition if we only considered soil weathering and P losses from the entire system over geologic time (Walker and Syers, 1976).

The relevance of organic matter-derived nutrients for forest nutrition during the course of whole CZ development is a reflection not just of soil elemental losses, but also of the root systems that develop during decades to centuries of vegetation growth. Throughout this shorter timeframe, nutrient demands increase (Mou et al., 1993; Rode, 1993; Vitousek et al., 2010) and root systems expand to explore increasing soil volumes for nutrients (Billings, 1936; Zangaro et al., 2008; Knops and Bradley, 2009; Yuan and Chen, 2012; Sun et al., 2015). We cannot know the functionality of all deep roots (Nippert et al., 2012; Nippert and Holdo, 2015), but as roots reach deeper into soil profiles over the lifetime of forest communities, they have the potential to increasingly access any deep, mineral-bound nutrients that may reside there (Richter et al., 2006; Eger et al., 2018; Hauser et al., 2020; Uhlig et al., 2020; Wang et al., 2022). Trees appear capable of mediating a shift to relatively enhanced mineral reliance through strategic allocation of C to resource exchanges that vary over vegetation's lifespan (Marschner and

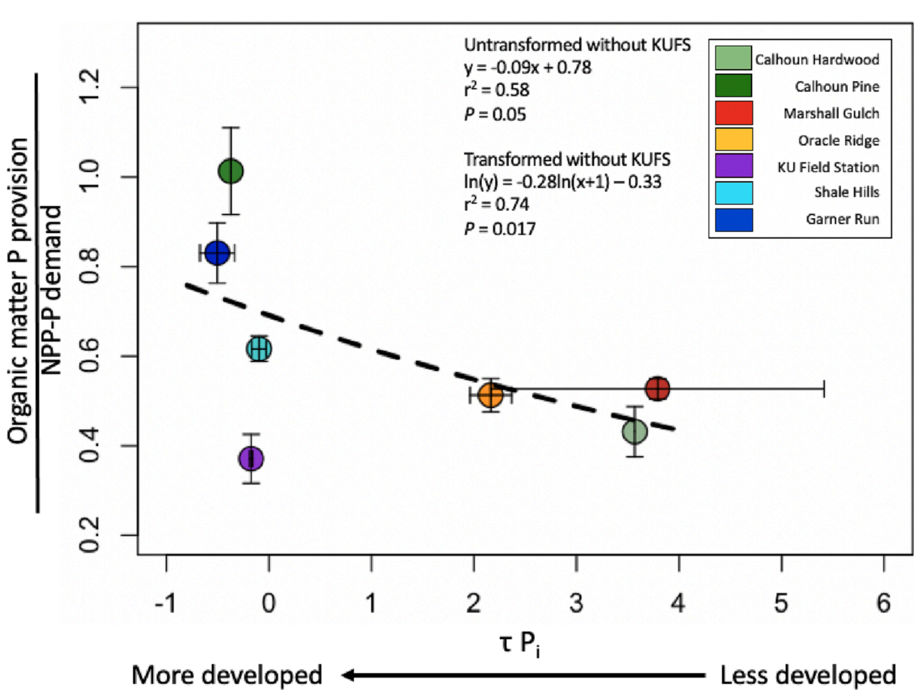

Fig. 4. Estimated proportion of each forest's annual P demand (g P m^{-2} y^{-1}) potentially provided by annual organic matter decay (g P m^{-2} y^{-1}) compared to depletion of inorganic P (τ_{Pi}) across the root zone. Negative τ_{Pi} values represent P depletion through soil depths harboring 95% of the root biomass, while positive values indicate P enrichment. Untransformed data do not demonstrate a significant relationship, but removal of an influential point at KUFS produces a significant linear relationship (P = 0.05, r^2 = 0.58). The log–log relationship omitting KUFS resulted in significant linear results (P = 0.017, r^2 = 0.74). The data are best represented by an exponential decay curve, suggesting a non-linear pattern to organic matter nutrient provision across stages of soil development. The dashed curve represents the relationship calculated with the KUFS forest site included in the analysis. Error bars represent one standard error from the mean, calculated from incubation and soil sampling replicates. Walker and Syers (1976) posited that mineral-bound P becomes increasingly depleted in soils with time; if so, greater organic matter-P provision where soil is more developed might be expected, similar to the trend revealed here.

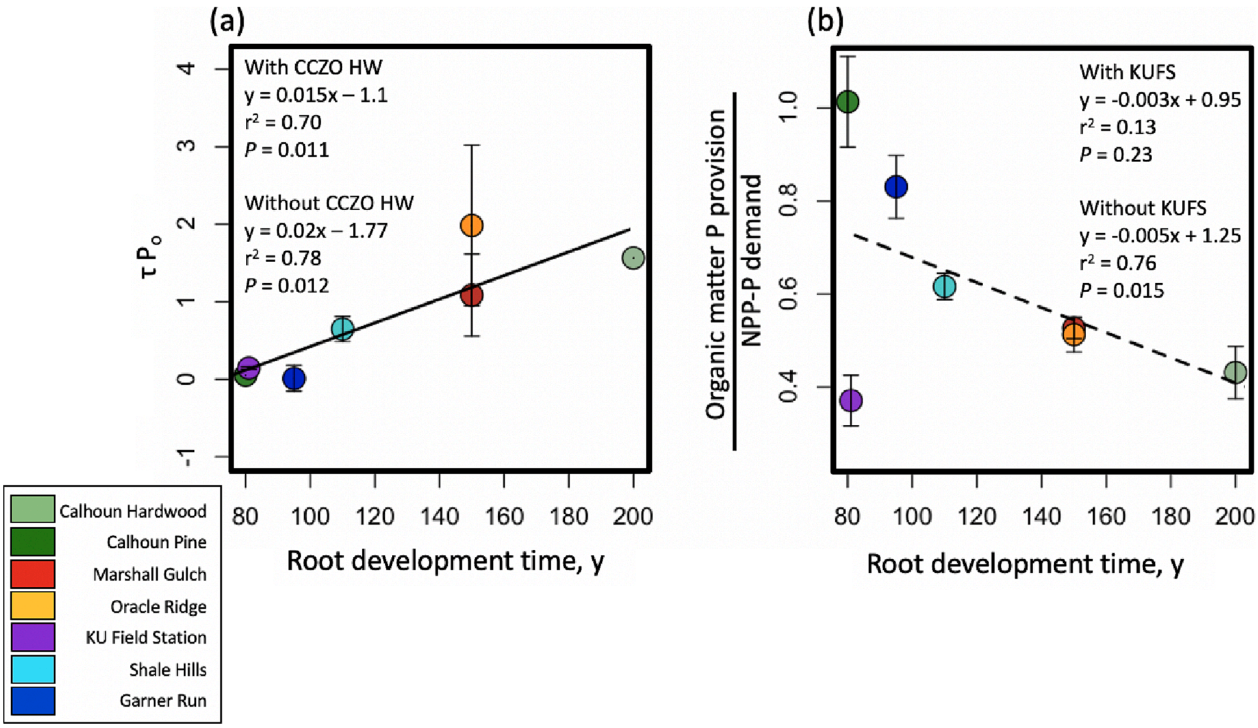

Fig. 5. Demonstrations of the role of forest nutrient economies in subsurface development. (a) Organic P enrichment (τ_{Po}) across the rooted profile vs. root development time (y), indicating the extent to which organic matter stocks and recycling in upper soils can mask evidence of soil P_i loss throughout the profile. (b) Estimated proportion of each forest's annual P demand (g P m^{-2} y^{-1}) potentially provided by annual organic matter decay (g P m^{-2} y^{-1}) vs. root development time. Statistics in (a) are calculated both with (solid line) and without inclusion of the Calhoun hardwood forest, an influential point (Cook's Distance = 1.85; see discussion in text for details). Statistics in (b) are calculated both before (dashed line) and after removal of the KUFS site, which is a significant outlier (Cook's Distance = 1.16). Error bars in both plots represent one standard error from the mean, calculated from incubation replicates (n = 6 with one exception of n = 5 and one of n = 7).

Rengel, 2007; Lambers et al., 2008; Bardgett et al., 2014; Hauser et al., 2020). These dynamics can alter soil profiles in ways that feed back into the distribution of mineral and organic matter-bound nutrient stocks (Austin et al., 2018; Brantley et al., 2012), thereby contributing to distinct soil developmental patterns on root-growth driven timeframes.

The results from the forests we examined point toward a shift in the relative reliance on organic nutrient sources to mineral nutrient sources as forest root systems age (Fig. 5), regardless of the degree of development of the underlying substrate. This finding contrasts with some contemporary conceptual models (Lambers et al., 2008), which suggest that forests trend toward organic matter-provided supplies over time. We observed mineral P depletion where the bulk of roots are present in the youngest root systems (Fig. 4, sites with $\tau_{Pi} < 0$) as well as relatively high potential P_o input rates (Table 2), suggesting that aboveground biomass has accumulated sufficiently in younger systems such as CCZO pine forests and KUFS forests to provide a readily available organic matter-rich nutrient pool to the upper soil horizons (Crews et al., 1995; Balogh-Brunstad et al., 2008). However, root systems in these still comparatively young forests likely have relatively limited proliferation below the organic matter-rich horizons (Dupouey et al., 2002; Mobley et al., 2013; Billings et al., 2018; Hauser et al., 2020). This prompts an organic matter-dominated nutrient economy, apparently across a span of soil developmental time, as evidenced by the high potential for organic matter to provide P to vegetation in multiple forests where root systems have been developing for ~ 80 to 110 y, even across a diversity of soil developmental stages (Fig. 1b; Fig. 4, values below 0 on the X-axis; Fig. 5b).

As root system development proceeds, a greater abundance of roots extends past the organic rich horizons to the weathering front (Knops and Bradley, 2009; Yuan and Chen, 2012; Pierret et al., 2016; Billings et al., 2018), where they are in contact with less weathered mineral surfaces (Brantley et al., 2012; Hasenmueller et al., 2017). In part because mineral-bound P is less C-expensive to liberate than organic matter-bound P (Smith, 1976; Hauser et al., 2020), it seems especially beneficial for deep roots to mine this mineral nutrient source. This could prompt a shift to a mineral-focused P supply at these depths, with decreased potential P provision from organic matter in sites with the oldest forest vegetation even where substrate development was advanced (Fig. 2b & 5). Thus, forests with older vegetation and older root systems appear able to develop a mineral-focused P economy even where soils are well-developed and, presumably, primary mineral P is depleted in the rooted zone.

Primary mineral P stocks traditionally are not strongly implicated in the P nutrition of highly-developed CZs due to their oft-observed decline across the soil development continuum (Walker and Syers, 1976, Fig. 6). We thus expand Walker and Syers' (1976) idea to incorporate root development over time, demonstrating that even where mineral bound P is scarce, if present, it is likely still relevant to ecosystem P nutrition (Fig. 6, red arrow 2). Note that none of our sites are true endmembers of Walker and Syers' (1976) concept (i.e., Entisols or Oxisols), so there may be an increase in the nutritional relevance of organic matter-bound P in very developed systems that we did not observe in this study (Fig. 6, red arrow 3). It also is important to note that our test of Walker and Syers' (1976) concept could be improved with reduced variation in multiple site characteristics (Table 1), such as conducting our analyses across sites with the same parent material, climate, land use history, or plant species. However, available sites that match in all qualities except soil development are limited, reducing our capacity to test Walker and Syers' hypothesis (1976) and variations on it in the natural world. We selected sites that at least allow us to begin probing Walker and Syers' (1976) hypothesis by examining some features of their patterns of soil development. Our observations across the studied forests suggest that

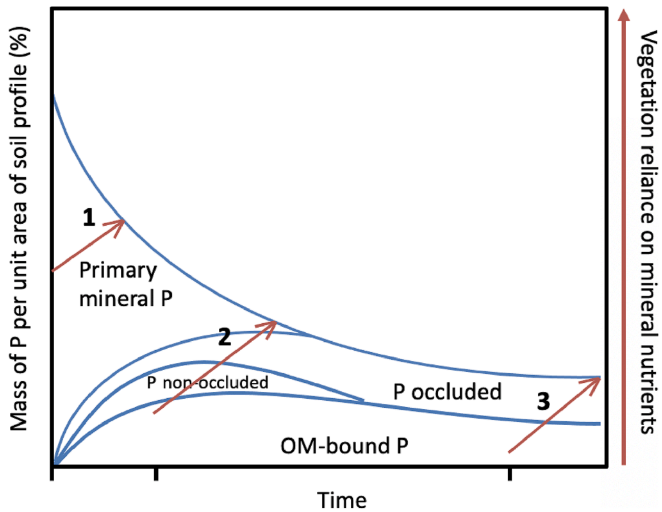

Fig. 6. Conceptual diagram reframing Walker and Syers' 1976 hypothesis. Within a given, relatively short, time frame (e.g., within but not across regions 1, 2, and 3), as root systems develop nutrient economies will develop that are more mineral focused (right-hand Y-axis) and less organic matter focused (red arrows). The sites in this study are most likely representative of region 2. Both natural and human-induced disturbances that induce secondary succession can reset the system in terms of P forms and root system development. When disturbance occurs, ecosystems can be pushed to the left along the X-axis such that the proportion of nutrients available as soil minerals and as organic matter shifts with the degree of perturbation. The vertical lines on the X-axis represent timepoints when stand replacing disturbance might occur throughout many years of CZ development, re-setting the vegetation to an early successional stage. As root systems develop after disturbance, (moving upslope on red arrows), ecosystem reliance on deep, mineral sources of P increase (right Y-axis) even as total system P declines over soil development timescales.

root system proliferation drives forest nutrient economies despite a soil's status within the soil development continuum (Fig. 6). These observations also remind us that, like any instance of Simpson's paradox (Simpson, 1951; Ellenberg, 2022), it is important to think across a multitude of timescales to understand an ecosystem's functioning.

Any nutritional transition of trees from organic matter to mineral forms represents the resource tradeoff that root systems face when confronted with different forms of the same nutrient. Perhaps as a consequence of the relatively low C cost for acquisition of mineral-bound nutrients (Smith, 1976; Hauser et al., 2020; Reichert et al., 2022; Raven et al., 2018; Wang and Lambers, 2020; Lynch et al., 2005), vegetation may preferentially utilize mineral-bound forms. The KUFS forest, an outlier to many of the patterns detailed above (Fig. 3a, Fig. 4 & Fig. 5b), hints at the potential for roots to economize C for P. In contrast to other similarly-aged systems in this study, our estimates of P provision from organic matter recycling suggest that organically-derived P does not provide a large portion of KUFS trees' nutrient demands (Figs. 4 & 5b). These lands have been subjected to human activity linked to altered metrics of soil development (Amundson and Jenny, 1991; Haff, 2010; Yoo et al., 2015) and vegetation development (Ellis et al., 2010; Mcdowell et al., 2020), and likely exhibit modified nutrient and rooting depth distributions compared to pre-agricultural times (Billings et al., 2018; Hauser et al., 2020). Both KUFS soil P contents and leaf [P] values are high (Fig. 2), suggesting a lack of P limitation (Ordoñez et al., 2009; Hou et al., 2020). The soils likely contain mineral P from past fertilizer applications, effectively pushing the system to the left on Walker and Syers' (1976) X-axis (Fig. 6, black lines on X-axis), but are rich in organic P as well due to their tallgrass prairie legacy (Balesdent et al., 1988). Our results hint that when both nutrient forms are readily available, vegetation may preferentially implement a less C-intensive, mineral-based P economy belowground (Hauser et al., 2020).

While differences among our sites in parent material, biota, and land use history challenge our ability to conduct a controlled test of Walker and Syers' (1976) venerated hypothesis, they do permit us to examine potential variability and mechanisms that allow or prevent the hypothesis from being revealed in Earth's ecosystems. This strategy is unique from the template of chronosequence studies and allows more axes of variation to be explored and identified for future, more controlled statistical tests. Here we identify one of those mechanisms – root system development – which likely warrants further attention in chronosequence and soil nutrient development frameworks. It is beyond the scope of this study to fully test a hypothesis focused on land use history, nutrient economies, and soil development. However, given pervasive, global-scale land use changes that modify rooting depth (Hauser et al., 2022) and fertilization of organic-rich soils that once supported native grasslands (Brye and Pirani, 2005; Ellis et al., 2010), shifts of ecosystems toward selective, mineral-based economies such as that observed at the KUFS forest in our study may occur in many systems, with yet unseen soil development feedbacks.

5. Conclusion

This work illuminates how vegetation growth through time and land use history can influence whether hypothesized patterns of dominant nutrient sources over soil developmental timeframes (Walker and Syers, 1976) are realized in Earth's critical zone. We suggest that a high degree of root system development can heighten the importance of mineral-bound nutrients for forest vegetation even where soils are highly weathered, and thus more than might be predicted by Walker and Syers' original hypothesis (1976). The feedbacks we observed between geologic and biologic drivers of soil development allude to the strength of biotic processes in geologic phenomena that can occur meters below Earth's surface. Further advancement of these ideas requires additional work across a yet-greater diversity of ecosystem ages and forest successional stages. In the Anthropocene, human alterations to both plants and soils produce novel alterations to soil developmental patterns through their influence on root system economies. Thus, incorporating root system development into concepts of plant nutritional strategies across soil developmental time will help us more accurately forecast regolith nutrient dynamics and forest C sink strength.

6. Statement of authorship

EH and SAB conceived of the idea and designed the study. EH carried out the study and wrote the first draft of the manuscript. EH and SAB both contributed substantially to subsequent drafts and revisions of the manuscript. JC, CC, DM, CR, and DDR assisted with site dataset development and manuscript edits.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are available at http://doi.org/10.5281/zenodo.4428967. Previously collected data are available through the Critical Zone Observatory Network data archive, https://www.hydroshare.org/community/1/

Acknowledgements

We are grateful for the help of many colleagues who served important roles while conducting this research, including Dr. Sue Brantley, Nate Abramson, Jennifer Williams, Dr. Margot Kaye, Warren Reed, Dr. Pam Sullivan, Dr. Daniel Hirmas, Dexter White, and Armeliz Romero.

We also greatly appreciate the help of the Critical Zone Observatory Network's many contributors who have been a part of establishing study sites and maintaining the Network's database. We are also grateful to the staff at the University of Kansas Field Station, including Vaughn Salisbury and Dr. Dean Kettle. Funding for this work was provided by the Critical Zone Observatory's Science Across Virtual Institutes Summer Interns program and National Science Foundation grant EAR-1331846. This material is also based upon work supported by the National Science Foundation under Award OIA-1656006 and matching support from the State of Kansas through the Kansas Board of Regents.

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