

Title: Walker and Syers enter the critical zone: Integrating decadal scale root development with longer term soil development to understand terrestrial nutrient cycling

Short title: Integrating root and soil development

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Abstract:

Most terrestrial nutrient sources are hypothesized to shift in dominance from mineral- to organic matter (OM)-derived over millennia. We investigated how overlaying this hypothesis with plant rooting dynamics that can feedback to soil development offers insight into ecosystem functioning. To test the hypothesis that the nutritional importance of OM as mineral weathering proceeds is mediated by rooting system nutrient economies that vary with vegetation development, we paired litterfall decay experiments with soil mineralogical data from diverse forests across the Critical Zone (CZ) Observatory Network. We demonstrate that sources of phosphorus shift from OM-bound stocks to minerals as the rooting zone expands during the transition from mid to late stages of forest growth. Root-driven, plant-soil feedbacks thus can prompt inconsistencies with soil development models that posit a unidirectional transition from mineral to organic nutrient dominance, and illuminate how forest growth and land use influence nutrient bioavailability in Earth's CZ.

Introduction

Nutrients 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). 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. This lack of understanding hinders accurate projections of future nutrient bioavailability, ecosystem productivity and vegetation contributions to global change.

Characterizing soil nutrient dynamics and vegetation responses to them has remained a challenge partly due to the mismatched timescales of soil development and vegetation response. Here, we use the term soil development to refer to the alterations in mineralogy, texture, and structure that typically accompany pedogenesis (Vitousek and Farrington 1997; Chorover et al. 2007). We use the term vegetation development to refer to forest growth, and specifically focus on rooting system proliferation during vegetation development (Doussan et al. 2003; Yan et al. 2006; Wang et al. 2009; Brearley 2011; Billings et al. 2018). 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; Burghel 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 (OM) in aboveground and root tissues, and subsequently into soil organic matter (OM), comprising a nutrient source that is relatively

abundant in surficial soil horizons (Marschner and Rengel 2007; Gill and Finzi 2016). These resources are replenished on annual to decadal time scales (Pedersen and Bille-Hansen 1999; Kavvadias et al. 2001).

A decades-old, now-iconic hypothesis proposes that the nutritional relevance of OM-bound P increases as soils develop over geologic timescales because weathering processes decrease the abundance of mineral-bound P (Walker and Syers 1976). This transition to an increasingly OM-bound nutrient stock, relevant for many elements excepting N (cf. Houlton et al. 2018), inherently blends the millennial and decadal processes just described. Though multiple studies report exceptions and caveats to the Walker and Syers (1976) hypothesis (Crews et al. 1995; Vitousek et al. 1997; Richter et al. 2006; Porder and Ramachandran 2012; Gu et al. 2019), the paradigm has gained general support over the past ~40 y.

Recent work highlighting interactions between soil and vegetation development (Lambers et al. 2008; Hobbie et al. 2015) underscores a need for a more detailed assessment of pathways of soil nutrient development over time. Vegetation develops different nutritional strategies over time as a consequence of both changing nutrient demands and shifting abilities to tap into different resources, processes which feedback into soil development and subsequent nutrient stocks (Lambers et al. 2008; Bardgett et al. 2014; Hauser et al. 2020). Many of these changing strategies accompany increasing root extension over time, which typically enables plants to explore increasing volumes of soil (Billings 1936; Doussan et al. 2003; Yan et al. 2006; Wang et al. 2008; Brearley 2011, Billings et al. 2018) and thus helps satisfy vegetation's increased nutrient demand as biomass accrues (Hasenmueller et al. 2017; Uhlig et al 2017; Dawson et al. 2020).

Plants allocate different amounts of fixed C to roots at different depths to cope with temporally shifting nutrient forms (Lambers 2008, Hauser et al. 2020; Peixoto et al. 2020). Preferential uptake of different nutrient sources can redistribute nutrient forms across the rooting zone, resulting in deep, mineral-bound nutrients being transferred to surface horizons in OM-bound forms on decadal timeframes (Jobbagy and Jackson 2001; Austin et al. 2018; Austin et al. 2020). 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, they also suggest that models of nutrient partitioning require better integration with models of vegetation dynamics because vegetation feedbacks influence the relative distribution of nutrient stocks. Such work would produce a novel framework describing the contribution of plant 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).

Here, we begin to characterize feedbacks between plants' nutrient exchanges and soil development to better understand how whole CZs develop across diverse timescales. To do this, we estimate the potential dependence of vegetation on OM-bound nutrients relative to mineral-bound nutrients as these nutrient sources vary in dominance across diverse, forested CZs. We focus our analyses on P because of its high demand by vegetation (Penuelas et al. 2013, Jonard et al. 2015, Hou et al. 2020) and its presence in both rock minerals and OM (Vitousek et al. 1997). We discern the potential nutritional relevance of OM as mineral P stocks vary, and discern the role of expanding rooting 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 root expansion and soil development.

We hypothesized that any increase in the importance of OM-derived nutrients for forest nutrition across soil developmental stages is mediated by rooting systems and their changing interactions with soil minerals as trees age. We note that this hypothesis assumes that nutrient inputs from the atmosphere (Porder et al. 2007; Menge et al. 2012) remain constant over time. If Walker and Syers' concept is correct, OM-bound nutrients must comprise a greater proportion of vegetation nutrient uptake over the timecourse of soil development (Fig 1a). However, we hypothesize that root-mediated uplift of deep, mineral-bound nutrients made possible by the greater rooting volumes explored in later stages of forest vegetation development generates a relative decline in potential nutrient provisioning from OM as aging forests become increasingly able to tap into deep, mineral-bound nutrient stocks (Fig. 1b). If true, this hypothesis suggests that late in vegetation development, forests may rely less on OM than predicted, and that mineral-bound P is relevant to vegetation nutrition even where weathering-induced P losses over time have been substantial.

Methods

Study Sites

We examined P cycling phenomena in multiple forests (Fig. 2a) comprising both the CZ Observatory (CZO) and CZ Exploratory Networks (CZEN) that represent varied degrees of soil development and rooting system development (Fig. 2b). We use the chemical index of alteration (CIA) — a metric of weathering based on the presence of Al, Na, Ca, and K oxides (Price and Vebl, 2003) — and soil orders as soil development metrics (Fig. 2b). Although plant species

and thus rooting 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 development over time in diverse forests and the distinct strategies they develop for obtaining nutrients. Our approach thus integrates these species differences.

The site with the most well-developed soils is the Calhoun CZO, SC, USA, which supports hardwood forests with ~100-200 y old trees and re-growing pine forests with ~50-90 y old trees on highly weathered Ultisols derived from granitic gneiss bedrock (Bacon et al. 2012). The dominant vegetation at the hardwood sites is comprised of *Quercus alba*, *Liquidambar styraciflua*, *Liriodendron tulipifera*, *Q. rubra*, and multiple *Carya spp.* The pine sites are dominated by *Pinus taeda* and *P. echinata*. This site ranges in elevation from 134 to 190 m, has a mean annual precipitation (MAP) of 1250 mm y⁻¹ and mean annual temperature (MAT) of 16°C (Critical Zone Observatories 2020a).

Sites with moderately developed Inceptisols and more highly weathered Ultisols support middle-aged, ~95-110 y old hardwood forests at the Shale Hills CZO, PA. Sites here range in elevation from 256 to 310 m and have a MAP of 1050 mm y⁻¹ and MAT of 9.5°C (Critical Zone Observatories 2020b). Within this site, there are two subsites with differing underlying lithologies: Rose Hill Shale regolith at the Shale Hills watershed site, and sandstone at the Garner Run watershed site. Vegetation at these sites is dominated by multiple *Quercus spp.*, *Carya spp.* and *Pinus spp.*

At the Catalina CZO, AZ, USA, forests grow on Mollisols and Inceptisols formed predominantly from granite at the high elevation Marshall Gulch (2284-2634 m) and mid-elevation Oracle Ridge (2064 to 2388 m) sites. Marshall Gulch forests are dominantly ponderosa pine (*Pinus ponderosa*) and white fir (*Abies concolor*), while Oracle Ridge sites span a

vegetation transition from oak-dominated to the pinyon-juniper community type (dominated by *Pinus* and *Juniperus spp.*) to ponderosa pine stands. The MAP at these sites is 940 mm y⁻¹ and 840 mm y⁻¹, and MAT is 10.4°C and 11.9°C, respectively (Critical Zone Observatories 2020c).

These soils support relatively old, mixed conifer vegetation averaging ~150 y in age.

Finally, the University of Kansas Field Station (KUFS) is comprised of Mollisols formed from glacial till and loess that are relatively rich in both mineral nutrients and organic matter (Klopfenstein et al. 2015, Hirmas and Mandel 2017) and that support a ~90 y old oak-hickory forest growing on former agricultural lands that had replaced the tallgrass prairies. In regions of the forest that experienced particularly heavy degradation under agricultural use, red cedar (*Juniperus virginiana*) is also a dominant species. Elevation at KUFS is 335 m, MAP is 940 mm y⁻¹ and MAT is 13°C (Kansas Biological Survey 2020).

Rooting system development time

We relied on site histories and tree surveys to estimate the amount of time roots at each site could have been exploring the soil profiles, a metric that we term rooting system development time. Each site's unique history prompted individual site assessments to develop age estimates representative of the time over which roots 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 may 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 explore, 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 rooting 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 today's. At Catalina, this is ~150 y and at Calhoun, ~200 y (Richter and Markewitz 2001; Iniguez et al. 2016).

Data Collection

Characterizing forest P nutrition status

We approximated vegetation P uptake at each site by estimating net primary productivity (NPP) and converting those values to P demand (NPP_p) via estimates of vegetation stoichiometry. We used annual litterfall biomass (g m² y⁻¹) to estimate NPP (g C m² y⁻¹) given its direct linkage to yearly ecosystem NPP (Matthews 1997). To do this, we converted leaf mass to leaf C assuming leaves to be 48% C (Bowden et al. 1992). We converted these litterfall-based NPP estimates to NPP_p using C:P in leaves collected from each site. 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).

We estimated total soil P using bulk elemental data (Jin et al. 2010; Holleran 2013; Austin & Schroeder 2019; Brantley 2019; National Ecological Observatory Network 2020a). We transformed P_2O_5 and %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). We summed P contents across horizons to the depth approximating 95% rooting biomass to estimate the absolute P content of a square meter soil column in the rooting zone. We estimated the depth at which 95% of the rooting biomass is attained (D95) using rooting 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) our use of D95 captures most root activity and permits comparison of an analogous metric across sites.

P in Leaf Biomass

We analyzed the P concentration of leaves from each site to generate NPP_P estimates and to assess leaf P release rates. 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).

Maximum potential organic P recycling

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271 To examine comparable potentials for annual OM recycling that could potentially meet plant
272 P uptake in these forests, we developed a metric of the maximum release rate of organic P (P_o)
273 from the OM (OM_p) produced in a year in each forest, normalized by annual plant P uptake
274 ($OM_p:NPP_p$). To estimate sites' potential annual P_o release rates, we conducted decomposition
275 experiments using leaves collected from each study site.

276 At the Catalina and KUFS sites, we deployed 10 to 12 litter baskets in fall 2016 and
277 spring 2017, respectively, for leaf litter collection over the course of the following growing
278 season. Previously collected, senesced leaves were available from the prior 2015 and 2016
279 growing seasons at the Calhoun and Shale Hills CZOs. Upon collection, leaves were dried at
280 60°C for up to a week before grinding with a Wiley mill.

281 To inoculate these oven-dried, senesced leaves with microbes able to induce decay, we
282 added a small amount of freshly collected, senesced leaves from each site to their respective
283 dried counterpart. During the spring of 2017, we collected a small sample of freshly fallen leaves
284 from each site, which we froze upon return to University of Kansas labs. We thawed these
285 fresher samples, roughly chopped them with a knife and mixed a small amount with the dried
286 litter. We distributed ~0.7 dry g of the mixed litter into six small permeable bags per litter
287 collection trap and placed the bags into a glass jar filled partially with marbles to keep the bags
288 well drained. This resulted in at least 6 jars per site containing 6 bags each. We then incubated
289 leaves aerobically in site-relevant conditions (Table 1). We periodically watered the bags in
290 quantities and frequencies mimicking site-specific growing season rainfall (Table 1). To mimic
291 the bimodal precipitation regime at the Catalina CZO, we performed two shorter incubations to
292 approximate the amount of decomposition possible over a full year's time course at this site.

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 over time, we calculated P content of each leaf subsample over time. 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 OM already present in the upper soil profile is lower than rates observed with litterfall, and that these estimates thus represent maximum potential P release from annual OM additions. Our approach provides comparable information about each location's annual potential to offer P from OM in plant available forms.

Metrics of soil mineral P status

Using previously collected soil mineralogical data (Jin et al. 2010; Holleran 2013; Austin & Schroeder 2019; Brantley 2019; National Ecological Observatory Network 2020a), we calculated a modified version of τ_p (τ_p) — a metric describing depletion of P in the soil profile relative to the soil's parent material (Ruxton et al. 1968, Price and Vebel 2003, Oh et al. 2007) — to numerically characterize the mineral nutrient status of each site. We calculated τ_p of the rooting zone given our interest in vegetation influences on soil development metrics, using the ratio of P remaining in the soil surface horizon relative to P at the soil depth where roots have reached ~95% biomass. We thus replaced parent rock %P in the traditional calculations of τ with %P of soil where roots are rare, achieving a metric of P depletion across the depth of soil inhabited by the largest proportion of plant roots. We determined the depth of ~95% rooting biomass for the rooting front components in each equation from site data (Holleran 2013; Li et al. 2018;

Eissenstat 2019; Billings et al. 2020; National Ecological Observatory Network 2020b). We thus calculate τ_p as follows:

$$\tau_p = \frac{P_t^S * Zr^{RF}}{P_t^{RF} * Zr^S} - 1 \quad (\text{Eqn. 1})$$

where P_t^S is total %P the uppermost soil horizon, Zr^{RF} is %Zr at the approximated rooting front, Zr^S is %Zr in the uppermost soil horizon, and P_t^{RF} is total %P at the rooting front.

We can further focus our analysis on inorganic P (τ_{pi}) by subtracting estimates of P_o from total soil P values before implementing equation 1. 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:

$$\tau_{pi} = \frac{P_i^S * Zr^{RF}}{P_i^{RF} * Zr^S} - 1 \quad (\text{Eqn. 2})$$

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. This allows us to examine the P status of inorganic, mineral-bound P separate from organic P. We generated estimates of soil P_o 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 OM C:P ratios estimated from sites' litter data. Though root C:P can be comparable to leaf litter C:P (Zechmeister-Boltenstern et al. 2015), this method may underestimate P_o given recent demonstrations that OM 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} , which helps us understand the role of P_o in the P status of root zone soils.

Statistical Analyses

We first characterized P demand and P availability across forest sites to more fully understand the outcomes of our hypothesized relationships. To do this, we regressed NPP_P and site leaf P concentrations on our estimates of rooting 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.

To test whether our estimates of potential annual OM provision of P could meet a greater proportion of forests' NPP_P demands where soils are more depleted in mineral-bound P (as hypothesized by Walker and Syers' model), we performed regression analyses between the $OM_P:NPP_P$ ratio and τ_{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. These comparisons discern the maximum capacity for OM 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 rooting systems driving P_o distributions.

To determine whether OM_P varied in nutritional relevance with forest development, we performed a linear regression between stand age and the $OM_P:NPP_P$ metric. We tested for outliers using Cook's Distance and calculated the regression both with and without outlier points. 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 OM- vs. mineral-based 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 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).

Results

Vegetation P demand estimated via NPP (NPP_p) was positively correlated with total rooting zone P ($P = 0.013$, $r^2 = 0.7$, Fig. 3a). Soil depths by which roots have achieved 95% of their biomass, which were used to approximate the depth of the rooted zone and determine the rooting front (RF) terms in τ_p calculations, ranged from 3.2 to 0.6 m (Table S1). Leaf [P], a measure of vegetation P status, was significantly correlated with total P of these rooted zones ($P = 0.07$, $r^2 = 0.75$, Fig. 3b).

P release from OM decay, used to calculate our metric of OM recycling, ranged from 0.085 to 0.31 g P m⁻² y⁻¹ across sites (Table S1). The relationship between OM_P:NPP_p and τ_{Pi} was best represented by an exponential decay curve (AIC = 1.146507), reflecting its steeply negative

slope where soils have negative τ_{pi} values. The AIC values for other tested relationships, including a linear relationship, ranged from 1.65 to 16.22. Where sites were more depleted in inorganic P across the rooting zone, OM recycling exhibited a near-significant rise, suggesting the potential to meet a greater proportion of annual forest P demand ($P = 0.07$, $r^2 = 0.41$ Fig. 4). Given the relatively few forests available to contribute data, the marginally significant linear relationship they exhibit, and the better fit of the exponential equation, the fitted curved hints at increased nutritional relevance of OM-bound P where mineral P is depleted.

Stands that experienced longer duration of exploration by contemporary roots displayed greater contributions of P_o to total soil P enrichment (i.e., higher values of τ_{po}). Comparatively younger root systems exhibited less enrichment of soil P by P_o (Fig. 5a). However, with one exception, potential P release from OM decay was relatively high for less well-developed rooting 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 OM P to meet estimated NPP_p demands is lower than the other similarly aged forests. Compared to the ~80 and ~95 y old forests, ~81 y old KUFS forests displayed 0.64 and 0.46 percent less P provision from OM as a proportion of NPP_p demands ($P < 0.002$), respectively. Compared to ~110 y old forests, KUFS forest's OM_p provision was 21% less ($P = 0.08$).

Discussion

Our findings demonstrate the interwoven nature of vegetation and soil dynamics that calls for a reframing of Walker and Syers' iconic 1976 hypothesis. When examined solely in terms of

mineral P status, one metric of pedogenic time (Fig. 1a, x-axis), our data are consistent with Walker and Syers' model: we observed the highest potential release rate of OM-bound P where soils were comparatively mineral-P depauperate and the lowest potential release rate of OM-bound P at sites with soils relatively rich in mineral-bound P (Fig. 4). Where P availability is dominated by either OM- or mineral-bound P, vegetation rooting systems likely leverage a nutrient strategy based on the P form that is most bioavailable (e.g., Hauser et al. 2020). However, when we examine our findings through the lens of rooting system development, we observe deviations from what we might expect in models of OM- vs. mineral-bound P development for forest nutrition.

Observed deviations from Walker and Syers' hypothesis in OM dominance with CZ development are a consequence of the rooting systems that develop during decades to centuries of vegetation growth. Throughout this timeframe nutrient demands increase (Mou et al. 1993; Rode 1993; Vitousek et al. 2010) and rooting 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). These dynamics alter soil profiles in ways that feedback into the distribution of mineral- and OM-bound nutrient stocks, thereby contributing to distinct soil developmental patterns on root-growth driven timeframes.

Our findings suggest a root-promoted shift in the relative dominance from organic to mineral nutrient sources as forests age (Fig. 5), regardless of the degree of development of the underlying substrate. This finding is in contrast to current conceptual models (Turner 2008; Lambers et al. 2008; Phillips et al. 2013), which suggest that forests trend toward relatively OM-dominant 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 P_o input

rates (Table S1), suggesting that aboveground biomass has accumulated sufficiently to provide a readily available OM-rich nutrient pool in the upper soil horizons (Crews et al. 1995; Turner et al. 2007; Turner and Laliberté 2015). However, root systems in these forests are still comparatively young and likely have relatively limited proliferation below the OM-rich horizons (Dupouey et al. 2002; Mobley et al. 2013; Billings et al. 2018; Hauser et al. 2020). This prompts an OM-dominated nutrient economy, regardless of the amount of soil developmental time, as evidenced by the high potential for OM to provide P to vegetation in multiple forests where rooting systems have been developing for ~80 to 110 y, even across a diversity of soil developmental stages (Fig. 4, values below 0 on the x axis, Fig. 5a).

As rooting 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 more nutrient-rich mineral surfaces (Brantley et al. 2012; Hasenmueller et al. 2017). Deep roots mine this mineral nutrient source, in part because mineral-bound P is less C expensive to liberate than OM-bound P (Smith 1976, Hauser et al. 2020). This prompts the observed shift to a mineral focused P supply, signified by decreased potential P provision from OM in sites with the oldest forest stands despite varied degrees of underlying substrate development (Fig. 2b & 5). Thus, in direct contrast to what we might expect given Walker and Syers' proposed model, forests comprised of older vegetation and well-developed rooting 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. These observations lend support to our proposition that rooting systems drive forest nutrient economies despite a soil's status within the soil development continuum (Fig. 6).

A primary mechanism underlying the nutritional transition from OM to mineral forms likely is the resource tradeoff rooting systems face when confronted with different forms of the same nutrient. Perhaps as a consequence of relatively low C cost for acquisition of mineral-bound nutrients (Smith 1976; Hauser et al. 2020), we demonstrate that vegetation may preferentially utilize mineral-bound forms. The KUFS forest, an outlier to many of the patterns detailed above (Fig. 4 & Fig. 5b), highlights the potential for roots to economize C for P. In contrast to other similarly-aged systems in this study, P provision from OM recycling does not appear able to 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). The soils likely contain mineral P from past fertilizer applications, and are rich in organic P as well due to their tallgrass prairie legacy (Balesdent et al. 1988). Indeed, 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). This hints that when both nutrient forms are readily available, roots preferentially implement a less C-intensive mineral-based P economy.

Conclusion

This work demonstrates the complexities that sometimes result in inconsistencies with Walker and Syers' soil development model, and highlights how vegetation growth through time and land use history influence whether hypothesized patterns are realized in Earth's ecosystems. The feedbacks we observed between geologic and biologic drivers of soil development demonstrate the strength of biotic processes in geologic phenomena that occur many meters within Earth's subsurface. These processes sometimes result in the dominance of unanticipated nutrient sources

for forest vegetation and metrics of elemental depth distributions in soils that can mask the degree of soil development. In the Anthropocene, human alterations to both plants and soils produce novel soil developmental patterns through their influence on rooting system economies. Thus, incorporating rooting system development into concepts of vegetation nutrition across soil developmental time, and in the context of anthropogenic change, will help us more accurately project regolith nutrient dynamics and forest C sink strength in the Anthropocene.

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935 Figure 1. Predicted relationship between the potential provision of nutrients from OM as
936 pedogenesis proceeds, as a consequence of Walker and Syers' proposed model (1976; a). In
937 contrast, we offer (b), a hypothesized relationship between provision of nutrients from OM as
938 vegetation rooting systems develop, reflecting how rooting system interactions with soil
939 development may lead to increasing provision of nutrients from minerals and reduced potential
940 forest P provision from OM as trees age.

941

942 Figure 2. Field sites across the Critical Zone Exploratory Network (a) representing a gradient of
943 soil mineral development as estimated by the Chemical Index of Alteration (CIA)—a metric of
944 Al, K, Ca, and Na oxide depletion—and soil order (b, open circles). Lower CIA values indicate a
945 less weathered material and higher CIA values indicate stronger weathering and elemental
946 depletion. These sites also represent a gradient of rooting system development (b, right y axis,
947 filled circles) overlaying the diverse soil environments.

948

949 Figure 3. Characterization of vegetation growth characteristics in relation to soil P content. Total
950 P content of a square meter soil profile summed to the depth of ~95% rooting biomass, termed
951 root zone P, displayed positive relationships with both (a) P demand of net primary productivity
952 (NPP_p) estimated from annual leaf litter production ($P = 0.013$, $r^2 = 0.7$) and (b) leaf [P] in forest
953 trees at each study site ($P = 0.007$, $r^2 = 0.75$). Error bars represent two standard errors from the
954 mean.

955

956 Figure 4. Estimated proportion of each forest's annual P demand ($\text{g P m}^{-2} \text{y}^{-1}$) potentially
957 provided by annual organic matter decay ($\text{g P m}^{-2} \text{y}^{-1}$) compared to depletion of inorganic P (τ_{Pi})
958 across the rooting zone. Negative τ_{Pi} values represent P depletion across the rooting zone, while
959 positive values indicate P enrichment. Log transformed data display a marginally significant
960 correlation ($P = 0.07$, $r^2 = 0.41$) and are best represented by an exponential decay curve,
961 suggesting a non-linear pattern to organic matter nutrient provision across stages of soil
962 development. Error bars represent two standard errors from the mean, calculated from incubation
963 and soil sampling replicates. Walker and Syers (1976) posited that mineral-bound P becomes
964 increasingly depleted in soils with time, which should result in greater OM-P provision where
965 soil is more developed, similar to the trend revealed here.

966

967 Figure 5. Demonstrations of the role of forest economies in subsurface development. (a) Organic
968 P enrichment (τ_{Po}) across the rooted profile vs. root development time (y), indicating the extent
969 to which OM recycling in upper soils can mitigate the appearance of soil P loss. (b) Estimated
970 proportion of each forest's annual P demand ($\text{g P m}^{-2} \text{y}^{-1}$) potentially provided by annual OM
971 decay ($\text{g P m}^{-2} \text{y}^{-1}$) vs. root development time. Statistics are calculated after removal of the KUFS
972 site, which is a significant outlier (Cook's Distance = 1.16; see discussion about this site in text
973 for details). Error bars in both plots represent two standard errors from the mean, calculated from
974 incubation replicates.

975

976 Figure 6. Conceptual diagram reframing Walker and Syers' 1976 hypothesis. For any point along
977 the originally hypothesized P development timeline, indicated by red circles, vegetation will

978 develop nutrient economies that are more mineral focused and less OM focused as rooting
979 systems develop over time (red lines). Disturbances, both natural and human-induced, that
980 induce secondary succession can reset the system in terms of P forms and rooting system
981 development. As rooting systems develop (moving upslope on red lines), ecosystem reliance on
982 deep, mineral sources of P increases (right Y axis) even as total system P declines over soil
983 development timescales.

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985 Table 1. Summary of incubation characteristics for each study site.

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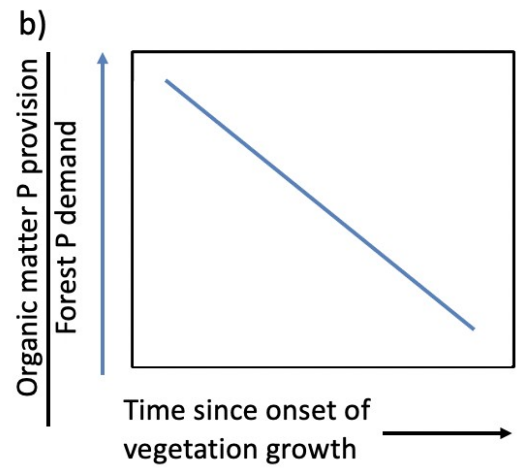
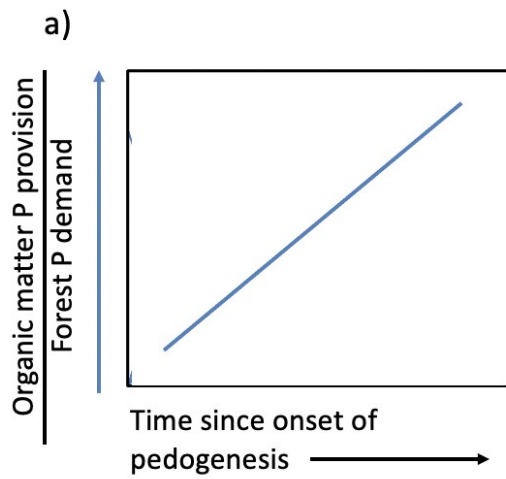


Figure 1.

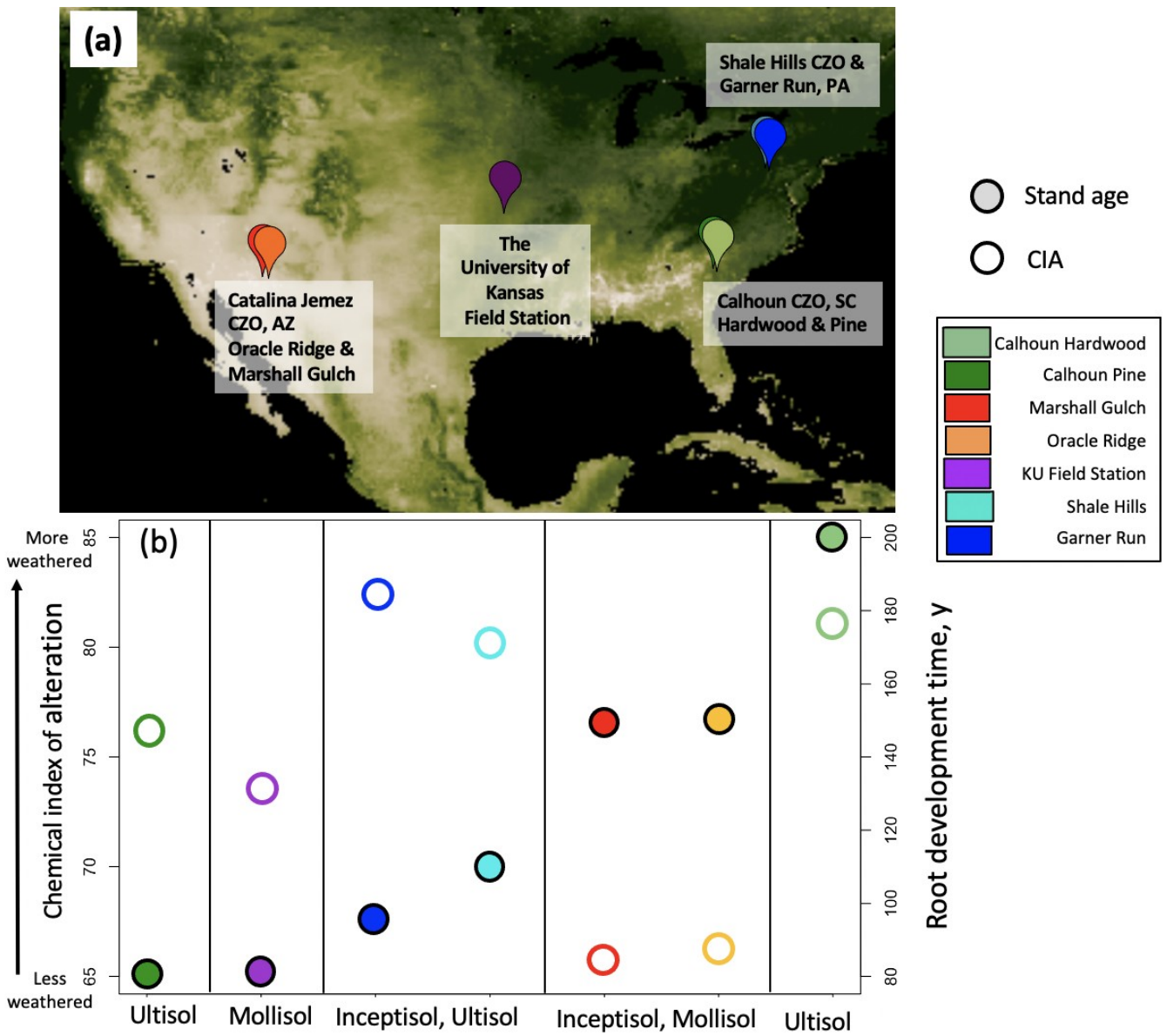


Figure 2.

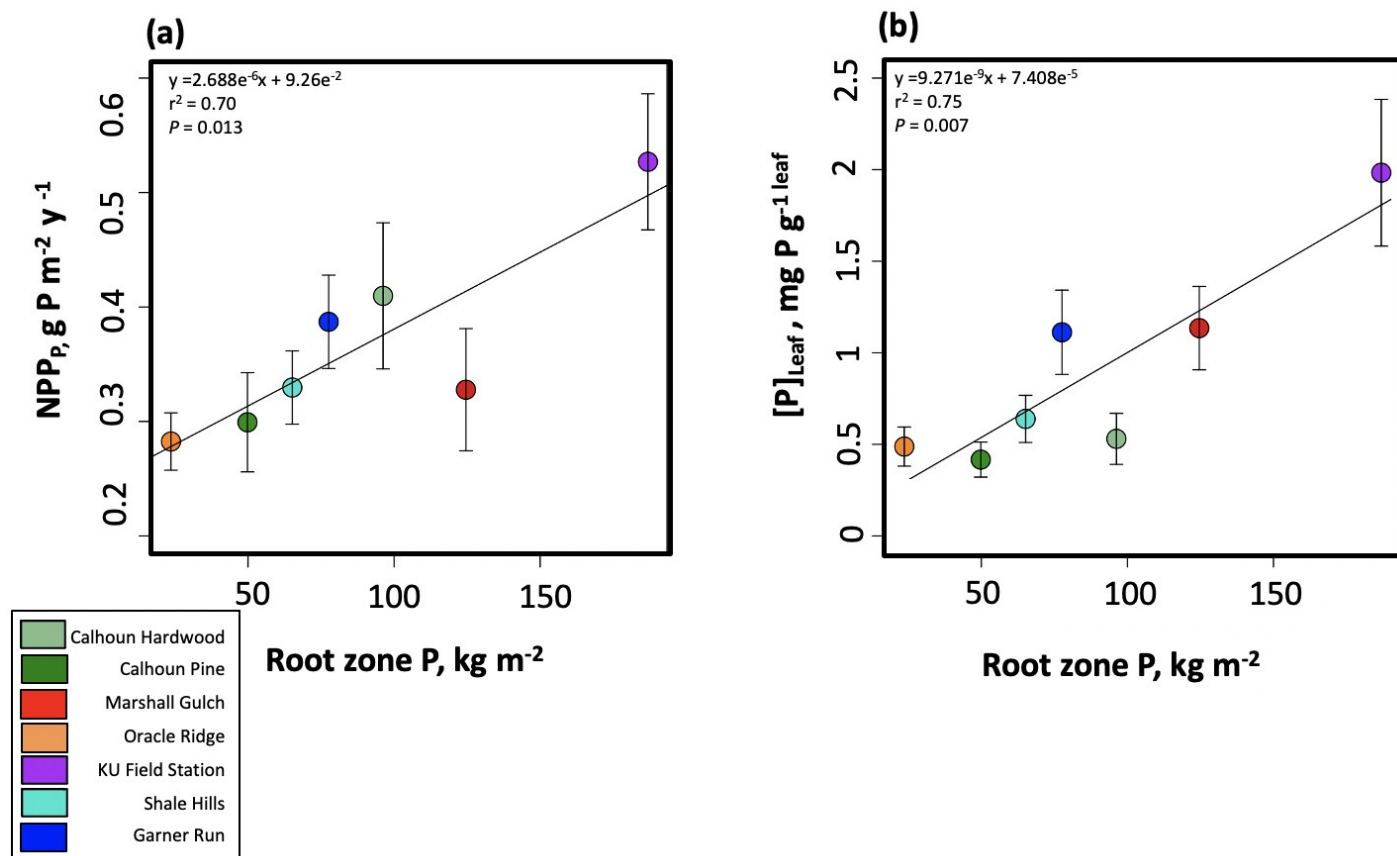


Figure 3.

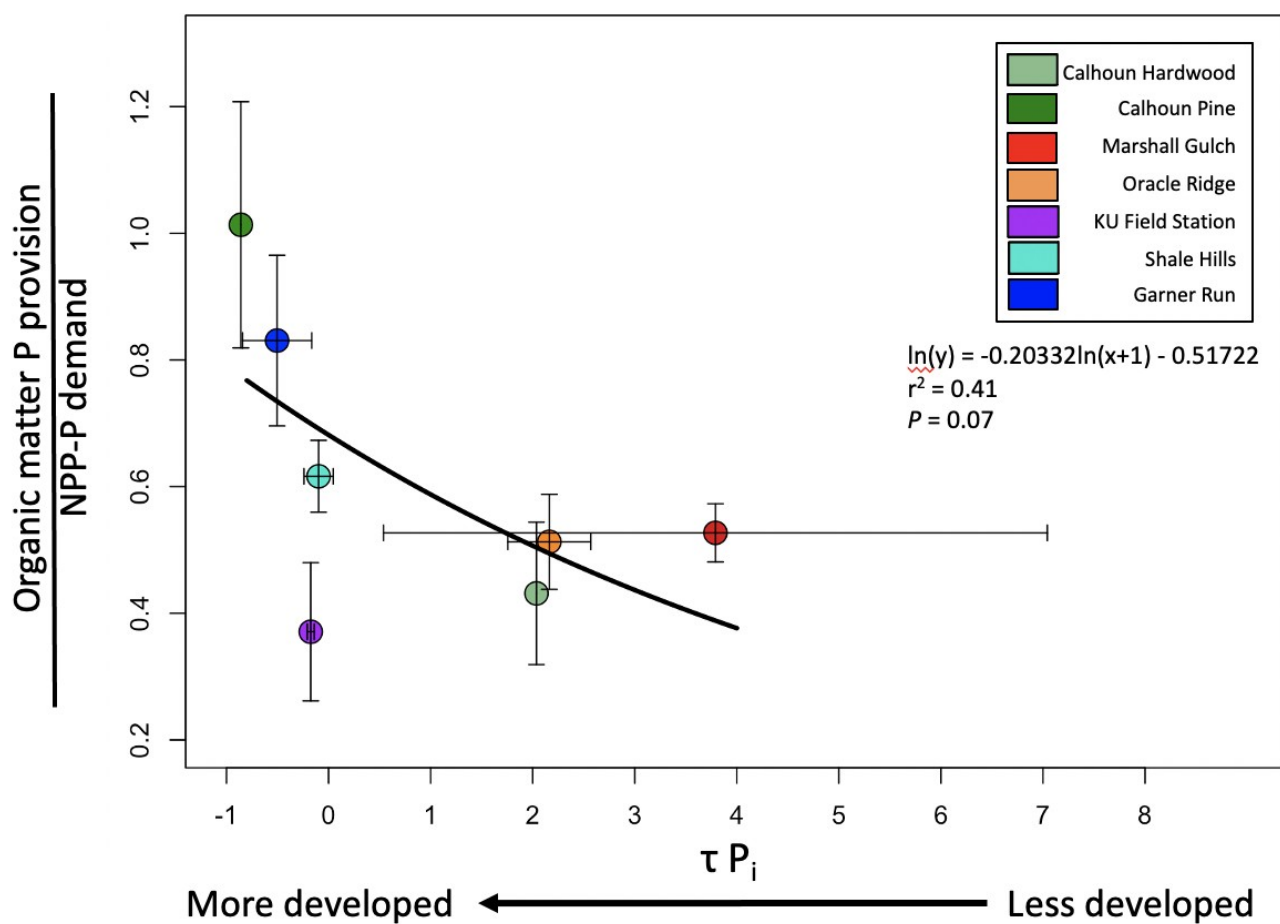


Figure 4.

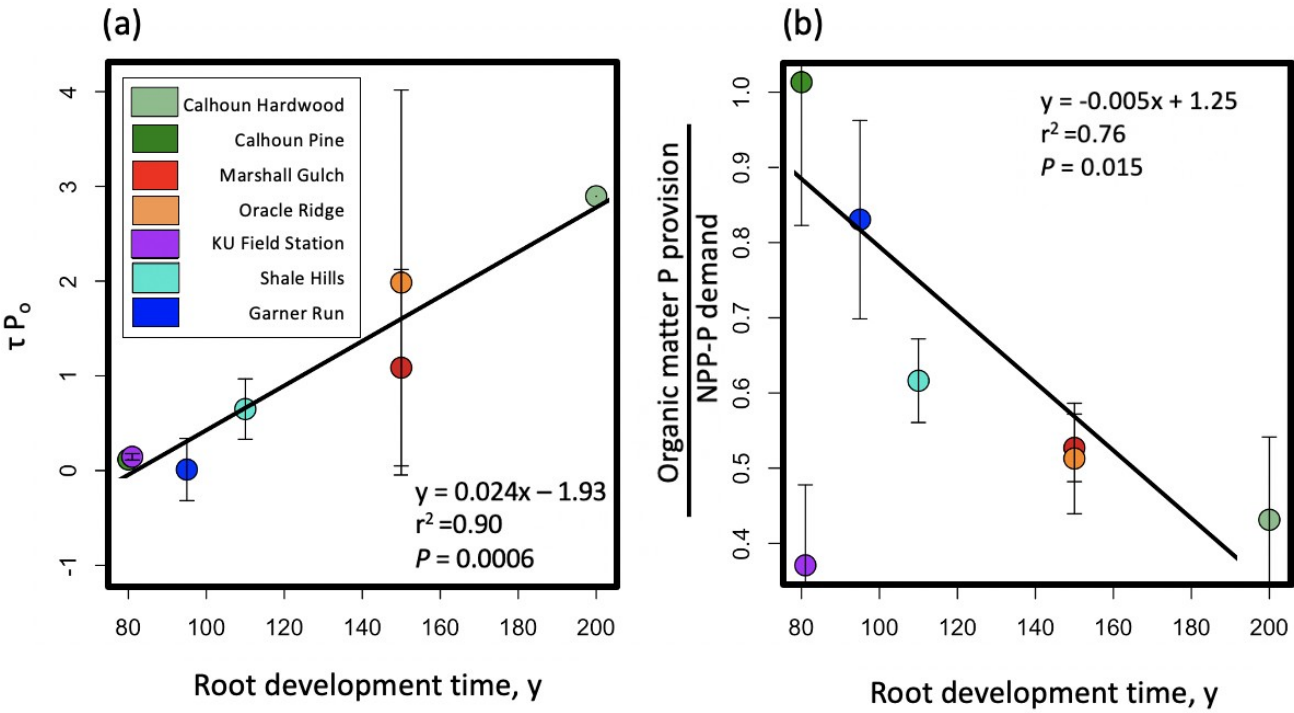


Figure 5.

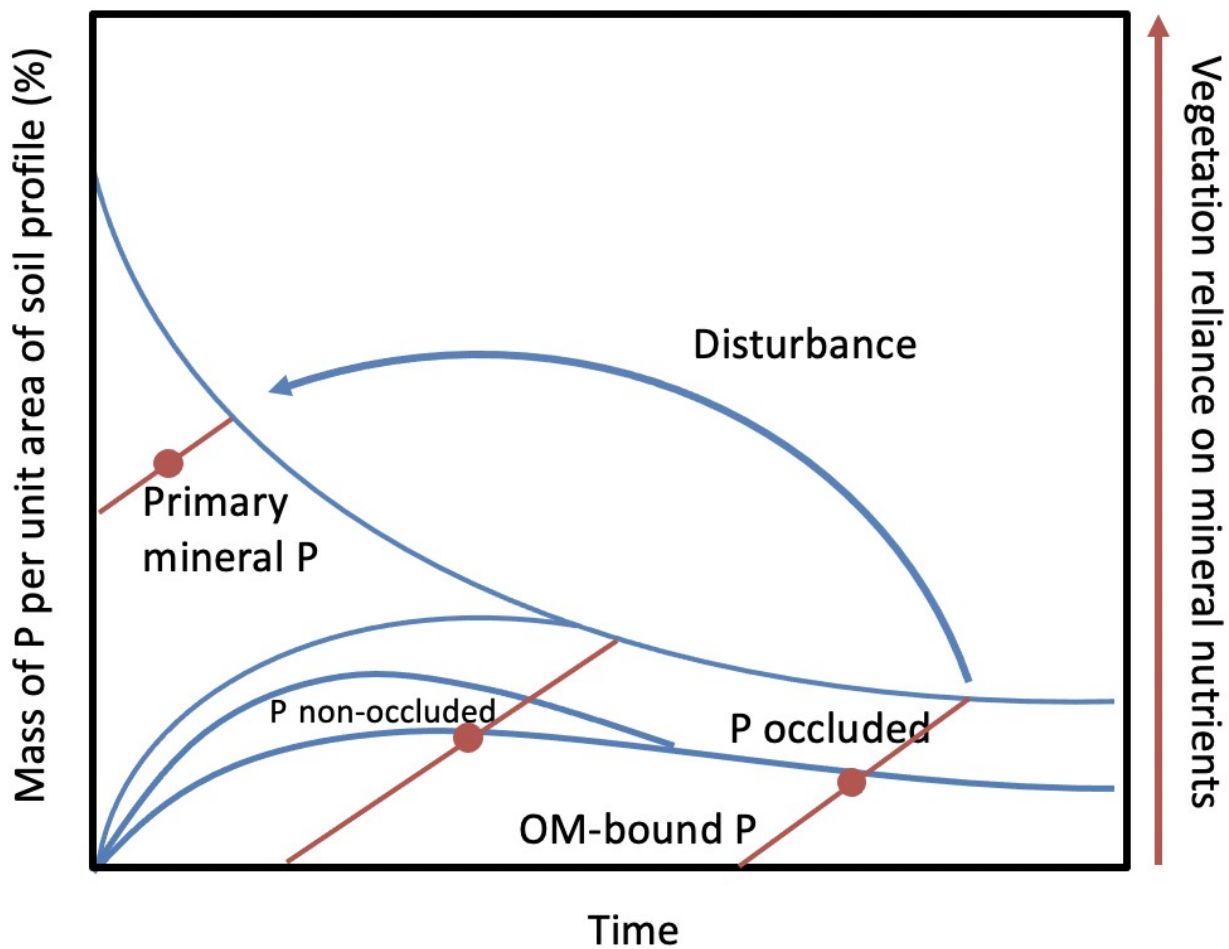


Figure 6.

Table 1.

Site	Incubation Length (d)	Incubation Temp (C)	Precipitation (mm/y)	Source
Calhoun CZO	212	21.5	1250	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	940	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	840	https://criticalzone.org/catalina-jemez/infrastructure/field-areas-catalina-jemez/
University of Kansas Field Station	185	21.5	940	https://biosurvey.ku.edu/sites/kbs.drupal.ku.edu/files/docs/Climate%20Synopsis.pdf
Shale Hills CZO	154	19.3	1050	https://criticalzone.org/shale-hills/infrastructure/
Garner Run	154	19.3	1050	https://www.hydroshare.org/resource/9535cbe97d5843a788fc7648de39a6e5/