

Woody plant encroachment amplifies spatial heterogeneity of soil phosphorus to considerable depth

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Abstract. The geographically extensive phenomenon of woody plant encroachment into grass-dominated ecosystems has strong potential to influence biogeochemical cycles at ecosystem to global scales. Previous research has focused almost exclusively on quantifying pool sizes and flux rates of soil carbon and nitrogen (N), while few studies have examined the impact of woody encroachment on soil phosphorus (P) cycling. Moreover, little is known regarding the impact of woody encroachment on the depth distribution of soil total P at the landscape scale. We quantified patterns of spatial heterogeneity in soil total P along a soil profile by taking spatially explicit soil cores to a depth of 120 cm across a subtropical savanna landscape that has undergone encroachment by *Prosopis glandulosa* (an N₂-fixer) and other tree/shrub species during the past century. Soil total P increased significantly following woody encroachment throughout the entire 120-cm soil profile. Large groves (>100 m²) and small discrete clusters (<100 m²) accumulated 53 and 10 g P/m² more soil P, respectively, compared to grasslands. This P accumulation in soils beneath woody patches is most likely attributable to P uplift by roots located deep in the soil profile (>120 cm) and transfer to upper portions of the profile via litterfall and root turnover. Woody encroachment also altered patterns of spatial heterogeneity in soil total P in the horizontal plane, with highest values at the centers of woody patches, decreasing toward the edges, and reaching lowest values in the surrounding grassland matrix. These spatial patterns were evident throughout the upper 1.2 m of the soil profile, albeit at reduced magnitude deeper in the soil profile. Spatial generalized least squares models indicated that fine root biomass explained a significant proportion of the variation in soil total P both across the landscape and throughout the profile. Our findings suggest that transfer of P from deeper soil layers enlarges the P pool in upper soil layers where it is more actively cycled may be a potential strategy for encroaching woody species to satisfy their P demands.

Key words: landscape scale; P uplift; soil profile; soil total P; spatial heterogeneity; subtropical savanna; woody encroachment.

INTRODUCTION

In terrestrial ecosystems, nitrogen (N) and phosphorus (P) are generally the most limiting nutrients for primary production and other major biological processes (Vitousek et al. 2010). Although P stocks and dynamics are relatively well studied in humid ecosystems (i.e., Walker and Syers 1976, Hobbie and Vitousek 2000, Cleveland et al. 2002, Vitousek 2004), the P cycle in more water-limited arid and semiarid ecosystems remains poorly understood (Selmants and Hart 2010), particularly with respect to responses to anthropogenic disturbances such as woody encroachment and climate change. Given that drylands cover about 41% of Earth's land surface (Reynolds et al. 2007) and play a major role in global biogeochemical cycles (Poulter et al. 2014), a more thorough understanding of P distribution patterns and dynamics in these ecosystems is essential for the development of integrated

climate-biogeochemical models that incorporate P cycle properties and processes (Yang et al. 2013, Reed et al. 2015, Achat et al. 2016, Sun et al. 2017).

Arid and semiarid ecosystems around the world have experienced woody plant proliferation during the past 100 years due to overgrazing, fire suppression, rising atmospheric CO₂ concentrations, and/or long-term climate change (Van Auken 2009, Eldridge et al. 2011, Stevens et al. 2017). In these ecosystems, vegetation patchiness serves as a key regulator of P redistribution during soil and ecosystem development, often resulting in islands of fertility beneath tree/shrub canopies (Schlesinger et al. 1996). This is especially true for ecosystems dominated or encroached by symbiotic N₂-fixing trees or shrubs with high canopy area (e.g., *Prosopis* in North America and *Acacia* in Africa), which generally have a high P requirement and accumulate significant amounts of P in their biomass (Vitousek et al. 2002, Houlton et al. 2008). Unlike N, which accumulates rapidly from the atmosphere via biological N₂-fixation, P in terrestrial ecosystems is derived ultimately from weathering of parent material (Walker and Syers 1976, Vitousek 2004, Schlesinger and Bernhardt 2013). Since ecosystems begin their existence with a fixed

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amount of P from soil parent materials (Walker and Syers 1976) and new atmospheric inputs are relatively low (Mahowald et al. 2008), significant accumulation of P in plant biomass could lead to depletion of P within the soil.

More recently, some field studies have shown that N₂-fixing woody plants encroaching into grasslands actually increase P storage in topsoil beneath their canopies (e.g., Kantola 2012, Sitters et al. 2013, Blaser et al. 2014). This increase in surface soil is likely a consequence of P acquisition from root activity in deeper portions of the soil profile (Kantola 2012, Sitters et al. 2013, Blaser et al. 2014), or from lateral roots in the surface soil that spread beyond the woody canopy (Scholes and Archer 1997). Sitters et al. (2013) and Blaser et al. (2014) found no evidence of depletion of either total or extractable P in topsoil beyond the boundaries of woody patches in grasslands, suggesting P accrual in the topsoil underneath woody patches is almost certainly derived from P acquisition by roots located deep in the soil profile. Since trees/shrubs typically have much deeper rooting systems than herbaceous species (Jackson et al. 1996, Schenk and Jackson 2002), it is reasonable to presume that amplified P dynamics are occurring not only in topsoil, but also deeper in the soil profile following shifts in plant functional composition. However, with most studies focused solely in surface soils (≤ 15 cm), there is a knowledge gap regarding the potential for changes in soil P stocks in deeper portions of the soil profile following grassland to woodland transitions in drylands around the world.

Woody encroachment into grass-dominated ecosystems has been shown to alter patterns of spatial heterogeneity in surface soil C and N storage at scales ranging from the patch to the landscape (Jackson and Caldwell 1993, Schlesinger et al. 1996, Throop and Archer 2008, Liu et al. 2011, Zhou et al. 2017a). The fact that the biogeochemical cycles of C, N, and P are interlinked by their strong stoichiometric relationships (Finzi et al. 2011, Reed et al. 2015), together with observed accrual of topsoil total P underneath woody patches (e.g., Kantola 2012, Sitters et al. 2013, Blaser et al. 2014), suggests that spatial patterns of total P in surface soil are likely altered by woody plant encroachment into grasslands, though this has not been explicitly investigated. Deep soil cores at the ecosystem level (e.g., forestland, grassland, and cropland) have shown that soil total P decreases gradually with soil depth (McCulley et al. 2004, Yang et al. 2012, Li et al. 2016), implying that potentially strong spatial gradients of soil total P may exist throughout the soil profile at the landscape scale in complex ecosystems with different plant life forms. However, no study has assessed the extent to which woody encroachment into grasslands alters the spatial pattern of soil total P in deeper portions of the profile at the landscape scale.

The primary purpose of this study was to assess how woody encroachment into grasslands alters the direction, magnitude, and patterns of spatial heterogeneity in soil total P across the landscape and throughout the soil profile. To this end, we collected spatially explicit soil

cores to a depth on of 120 cm and analyzed them for total P across a 100 × 160 m subtropical savanna landscape, which has undergone encroachment by *Prosopis glandulosa* (an N₂ fixer) and other trees/shrubs during the past century. Our specific objectives were to (1) estimate changes in direction and magnitude of soil total P throughout the soil profile after woody encroachment, (2) quantify patterns of spatial heterogeneity in soil total P across this landscape and throughout the soil profile, and (3) elucidate factors responsible for the variance in soil total P across this landscape and throughout the soil profile. We hypothesized that woody plant encroachment would (1) increase soil total P only in surface soils, with no changes or even a decrease in deeper portions of the soil profile, and correspondingly (2) alter spatial patterns of soil total P only in surface soils, with marginal to no effects in subsurface soils.

METHODS AND MATERIALS

Study site

This study was conducted at the Texas A&M AgriLife La Copita Research Area (27°40' N, 98°12' W), 65 km west of Corpus Christi, Texas, USA. The climate is subtropical (mean annual temperature is 22.4°C; mean annual precipitation is 680 mm), and rainfall peaks occur in May and September. Topography is relatively flat, with gentle slopes (<3%) where well-drained uplands transition to lower-lying drainage woodlands. Elevation ranges from 75 to 90 m above sea level.

Upland soils are sandy loams with non-argillic inclusions embedded within a laterally continuous subsurface argillic horizon (Bt; Fig. 1; Loomis 1989, Watts 1993, Archer 1995, Zhou et al. 2017c). Vegetation is characterized by a two-phase pattern consisting of woody patches interspersed within a matrix of remnant C₄ grasslands (Fig. 1). Studies using historical aerial photos, tree rings, coupled $\delta^{13}\text{C}$ and natural ^{14}C measurements on soil organic carbon, and simulation models have all indicated that woody plant encroachment into these grasslands, which were once almost exclusively dominated by C₄ grasses, occurred over the past 100 years (Archer 1995, Boutton et al. 1998, 1999, Bai et al. 2009). Woody encroachment is initiated when grasslands are colonized by *Prosopis glandulosa* (honey mesquite), an N₂-fixing tree legume. As mesquite trees grow, they serve as nurse plants, facilitating the recruitment and establishment of other woody plant species in their understory to form discrete clusters (generally <100 m²; Fig. 1; Archer et al. 1988, Archer 1995, Bai et al. 2012). If discrete clusters occur on non-argillic inclusions, they expand laterally and ultimately fuse to form large groves (generally >100 m²; Fig. 1; Archer 1995, Bai et al. 2012, Zhou et al. 2017c). Clusters occurring where the argillic horizon is present remain as small isolated patches and do not fuse with other clusters to form groves. Though large groves are restricted to non-argillic inclusions, they also

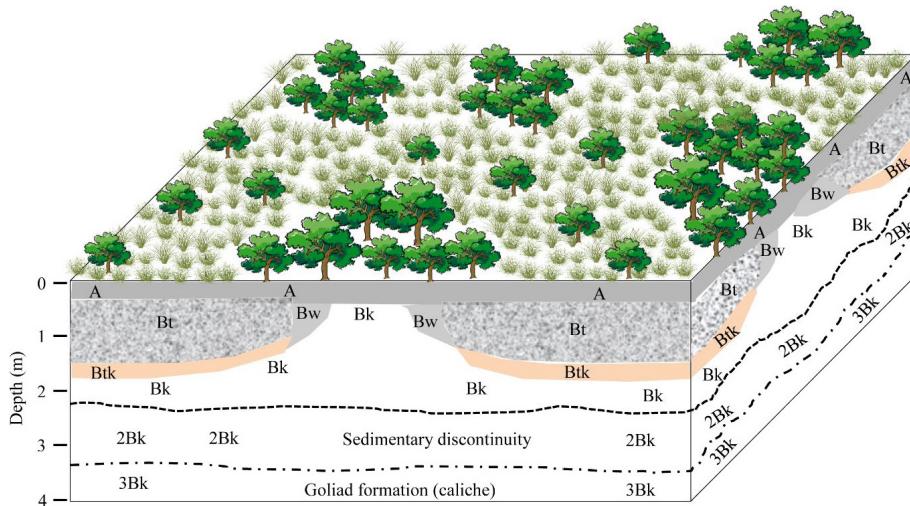


FIG. 1. Conceptual model of vegetation cover in relation to soil horization on upland portions of the landscape (adapted from Archer 1995). Small discrete clusters are dispersed within the herbaceous matrix where the argillic horizon (Bt) is present, whereas groves occupy non-argillic inclusions and expand laterally to the non-argillic/argillic boundary.

expand their canopies laterally beyond these inclusions to soils with subsurface argillic horizon (Fig. 1) (Archer 1995, Zhou et al. 2017c). Species composition can be found in Appendix S1: Table S1.

Field sampling

On an upland portion of this study site, a 100 × 160 m landscape consisting of 10 × 10 m grid cells was established in January 2002 (Bai et al. 2009, Liu et al. 2011), and included all three of the upland

landscape elements: grasslands, clusters, and groves (Fig. 2). The corners of each 10 m × 10 m grid cell were georeferenced (UTM 14 N, WGS 1984) using a GPS unit (Trimble Pathfinder Pro XRS; Trimble Navigation, Sunnyvale, California, USA). A color-infrared aerial photograph (6 × 6 cm resolution) was acquired for this landscape in July 2015, and used to create a classified vegetation map for the site.

In July 2014, two points were selected randomly within each 10 × 10 m grid cell, yielding a total of 320 sample points (Fig. 2). The distance from each sample

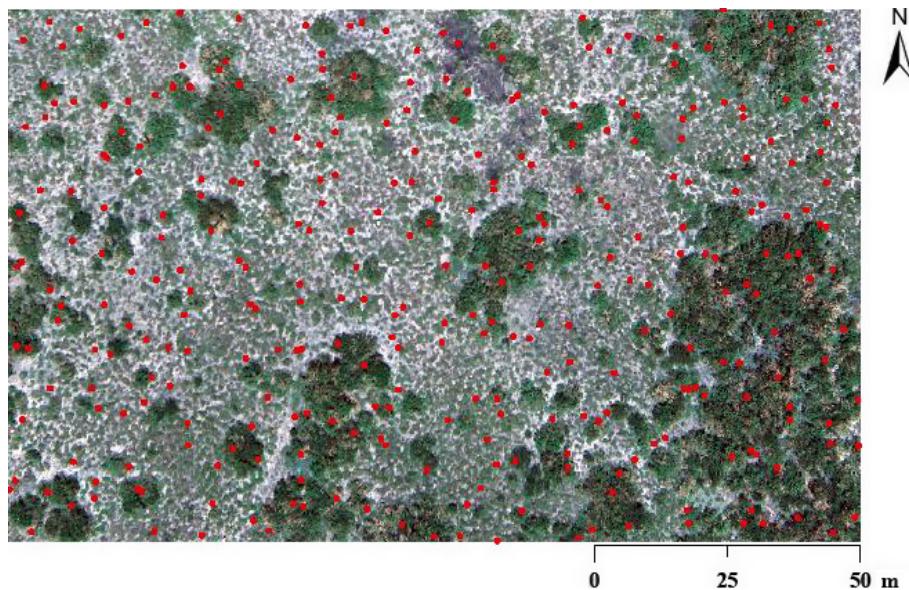


FIG. 2. Aerial photograph of the 100 × 160 m study area and locations of 320 random soil samples (red dots). Green patches are woody clusters and groves, and light gray color indicates open grassland.

point to two georeferenced cell corners were recorded. At each sample point, the landscape element was classified as grassland, cluster, or grove based on the vegetation type and size of woody canopy area, and two adjacent soil cores (2.8 cm in diameter \times 120 cm in length) were collected using the PN150 JMC Environmentalist's Subsoil Probe (Clements Associates, Newton, Iowa, USA). Each soil core was subdivided into six depth increments (0–5, 5–15, 15–30, 30–50, 50–80, and 80–120 cm). One soil core was oven dried (105°C for 48 h) to determine soil bulk density. The other core was air-dried prior to subsequent analyses. In September 2015, fine roots from each plant species occurring on this landscape were collected by careful soil excavations that confirmed linkages to identified plant species.

Lab analyses

Soils used to determine bulk density were subsequently used to estimate fine (<2 mm) and coarse (>2 mm) root biomass by washing through sieves. Soils from the air-dried cores were passed through a 2 mm sieve; roots and other coarse organic fragments not passing through the sieve were discarded (Boone et al. 1999, Pierzynski 2000). No soils contained rock or gravel-sized particles. Soil pH was determined on a 1:2 (10 g soil: 20 mL 0.01 mol/L CaCl₂) mixture using a glass electrode. Soil texture was determined by the hydrometer method (Sheldrick and Wang 1993). An aliquot of air-dried, sieved soil was dried at 60°C for 48 h and pulverized in a centrifugal mill (Angstrom, Belleville, Michigan, USA) in preparation for subsequent chemical analyses. Fine roots from each species were washed carefully to remove soil particles, dried, and pulverized.

Total P concentrations in pulverized soils and fine roots were determined using the lithium fusion method (Lajtha et al. 1999). Briefly, 0.25 g of pulverized soil or root tissue was mixed with 0.75 g of pure lithium metaborate (LiBO₂; Spex Sample Prep, Metuchen, New Jersey, USA) in precombusted graphite crucibles, and heated to 1050°C in a muffle furnace. The molten flux was poured into a 150-mL beaker containing a magnetic spin bar and 50 mL of 10% HNO₃, placed on a stir plate, and a watch glass was placed over the beaker while the flux was stirred and completely dissolved. The dissolved solution was filtered (Whatman 42 ashless filters), transferred to a volumetric flask, and made up to 100 mL with Type 1 water. Then, 30 mL of the solution was pipetted into a 50-mL volumetric flask and its pH was adjusted by adding 4 mol/L NaOH. The P concentration of the solution was determined by the molybdenum blue colorimetry method (Murphy and Riley 1962). The concentration of P was measured on a Spectronic 20D⁺ spectrophotometer (Thermo Fisher Scientific, Waltham, Massachusetts, USA) and referenced with a standard curve of potassium phosphate solution (KH₂PO₄ at 0, 0.125, 0.25, 0.375, 0.5, and 0.625 μ g P/mL). To control the quality of soil total P concentration analysis, one method blank was included within each batch of samples (1 blank + 11 samples). A

NIST-certified standard reference material (San Joaquin soil, NIST SRM 2709a with certified total P concentration 688 mg P/kg) was analyzed periodically to check the accuracy of this method (678.71 ± 1.57 mg P/kg [mean \pm SE], $n = 25$). In addition, we developed an internal lab soil standard that was analyzed with each batch of 11 samples to verify the repeatability of this method (103.10 ± 0.14 mg P/kg, maximum = 108.39 mg P/kg, minimum = 98.20 mg P/kg, $n = 151$).

Data analyses

Since soil P is derived primarily from weathering of parent material, soil development exerts strong control over the status of P in an ecosystem. Pedogenic formation of non-argillic inclusions embedded into the laterally continuous subsurface argillic horizon across this landscape may leave a legacy effect on the distribution pattern of total P in soil prior to the encroachment of woody plants. At this site, groves occur exclusively on non-argillic inclusions and expand laterally to soils with a subsurface argillic horizon (Fig. 1); however, some non-argillic inclusions in the remnant grassland matrix are still not occupied by groves across this landscape (Zhou et al. 2017c). Thus, we subdivided soil cores from grasslands into those on non-argillic inclusions and those on argillic horizons to address potential differences in soil total P that might be inherited from soil development. Across this study site, clay illuviation generally starts at approximately 30 cm below the surface soil (Archer 1995). According to horizons and characteristics diagnostic for the higher categories in USDA Soil Taxonomy (Soil Survey Staff, 1999), we used the following modified criteria to test whether there is clay illuviation (or argillic horizon) in the 30–50 cm depth increment: (1) if the clay content in the prior depth increment (i.e., 15–30 cm) is <15%, the 30–50 cm depth increment must contain at least 3% (absolute) more clay, or (2) if the clay content in the prior depth increment (i.e., 15–30 cm) is between 15–40%, the 30–50 cm depth increment must have at least 1.2 times more clay. These criteria were also used to test the 50–80 and 80–120 cm depth increments. If one or more of these three depth increments from a soil core have clay illuviation, then we considered the argillic horizon to be present at that point. Where the argillic horizon was present, it generally began within the 30–50 cm depth increment; in a few cases, it did not begin until the 50–80 cm increment.

Mixed models were used to compare total P concentrations (g P/kg soil), stocks (g P/m²), cumulative stocks, and fine root biomass (g/m²) in different landscape elements within each depth increment. In mixed models, spatial autocorrelation of a variable was considered as a spatial covariance component for adjustment. Post hoc comparisons of these variables in different landscape elements were conducted with Tukey's test. An unpaired *t* test was performed to compare total P concentration in grasslands occurring on argillic vs. non-argillic soils within each depth increment. A cut-off value of $P < 0.05$

was used to indicate significant differences. All these statistics were performed using JMP pro 12.0 (SAS Institute, Cary, North Carolina, USA).

A sample variogram fitted with a variogram model was constructed to quantify the spatial structure of soil total P stocks based on 320 random samples for each soil depth increment using R statistical software (R Development Core Team 2014; Appendix S1: Table S2 and Fig. S1). Ordinary kriging was used to predict soil total P stocks at unsampled locations based on the best fitting variogram model using ArcMap 10.1 (ESRI, Redlands, California, USA), and kriged maps of soil total P stocks with a 0.5×0.5 m resolution were generated for each soil depth increment. Lacunarity was used to assess the spatial heterogeneity of soil total P concentration across this landscape and throughout the soil profile. Lacunarity is a scale-dependent measurement of spatial heterogeneity or the “gappiness” of a landscape structure (Plotnick et al. 1996), with a higher value indicating a more heterogeneous distribution pattern across the landscape. Briefly, lacunarity was determined using a gliding box algorithm based on kriged maps of soil total P concentration. The gliding box of a given size (side length of the gliding box, r) was first placed at one corner of the kriged map and the box mass $S(r)$ (the sum of total P concentration of each pixel within the box) was determined. The box was then moved through the kriged map one pixel at a time and the box mass was determined at each location. The lacunarity value $\Lambda(r)$ for box size r is calculated by adding one to the ratio of variance and the mean square of the box mass: $\Lambda(r) = \text{var}[S(r)]/E[S(r)]^2 + 1$. A log-log plot of lacunarity against box size was used to quantify spatial heterogeneity of soil total P at different scales. Lacunarity was calculated using R statistical software (R Development Core Team 2014). More details can be found in Zhou et al. (2017a).

Within each soil depth increment, a spatial generalized least squares (GLS) model that incorporated spatial structure in the error term of the regression model (Beale et al. 2010) was used to analyze the relationships between soil total P concentration and explanatory variables, including fine root biomass, soil bulk density, soil clay and silt contents, and soil pH. Values for these explanatory variables have been presented elsewhere (Zhou et al. 2017a,c). Different models of spatial structure (i.e., linear, spherical, exponential, Gaussian structure) and non-spatial structure were tested, and the best fitting model was selected using the Akaike information criterion (AIC). Parameters were estimated based on restricted maximum likelihood (REML). In each full regression model for each soil depth increment, t values for explanatory variables were used to indicate their relative importance in explaining the response variable (Diniz-Filho et al. 2003). Analyses were performed using R statistical software (R Development Core Team 2014).

RESULTS

Phosphorus concentrations in fine roots were 65% higher in woody species (447.4 ± 31.7 mg P/kg, $n = 15$)

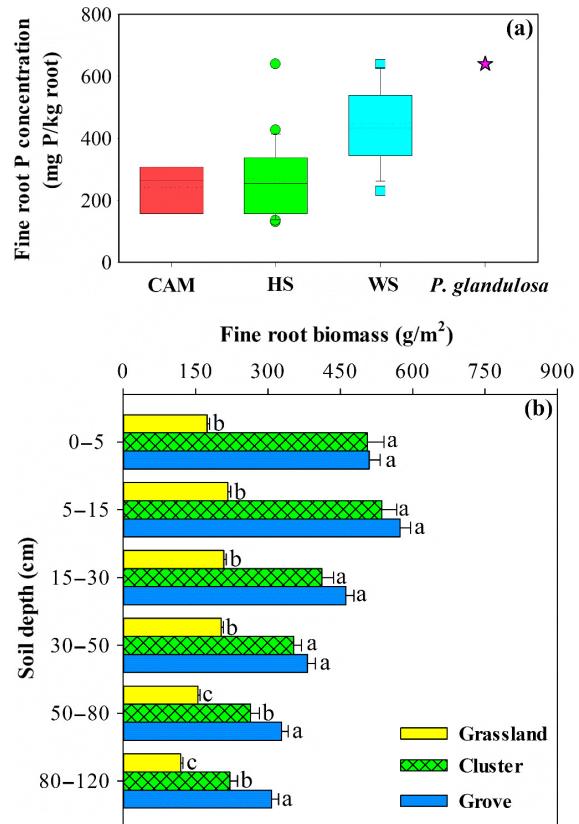


FIG. 3. (a) Phosphorus concentrations of fine roots from different plant functional group and *Prosopis glandulosa*. The central box shows the inter-quartile range, and the horizontal line within the box is the median. Lower and upper error bars indicate 10th and 90th percentiles, and points above and below the error bars are individuals above the 90th or below the 10th percentiles. CAM, crassulacean acid metabolism species, $n = 3$; HS, herbaceous species (forbs and grasses), $n = 21$; WS, woody species (including *P. glandulosa*), $n = 15$. (b) Fine root biomass (mean and SE) for different landscape elements throughout the soil profile. Significant differences ($P < 0.05$) between means for landscape elements are indicated with different letters. Number of samples: grassland, 200; cluster, 41; grove, 79. Panel b was adapted from publicly available archived data (Zhou et al. 2017b) derived from Zhou et al. (2017a).

than in herbaceous species (270.5 ± 26.0 mg P/kg, $n = 22$) (Fig. 3a). It is worth noting that the dominant woody species, *P. glandulosa*, had the highest fine root P concentration (640.1 mg P/kg) among all species collected across this landscape (Fig. 3a and Table S1).

Fine root biomass in soils beneath woody patches (both groves and clusters, hereafter) ranged from >500 g/m² in upper portions of the profile to approximately 220 g/m² in the deepest portions (Fig. 3b). In contrast, fine root biomass in grassland soils ranged from approximately 200 g/m² in the upper profile to 120 g/m² in deeper portions of the profile (Fig. 3b).

Both woody patch types had remarkably higher soil total P concentrations than those of grasslands for all soil depth increments, and groves had significantly higher soil

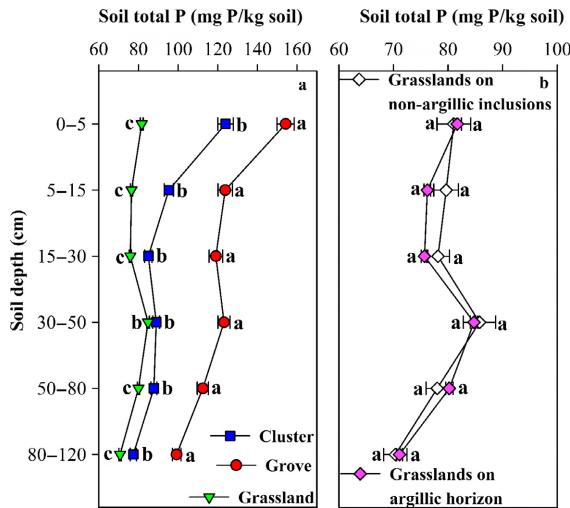


FIG. 4. Soil total P concentrations (mean ± SE) for different landscape elements (a) throughout the soil profile and (b) for grasslands on non-argillic inclusions and on argillic horizon. Significant differences ($P < 0.05$) between means for landscape elements are indicated with different letters. Number of samples: grassland, 200; cluster, 41; grove, 79; grasslands on non-argillic inclusions, 17; grasslands on argillic horizon, 183.

total P concentrations than those of clusters throughout the soil profile (Fig. 4a). Soil total P concentrations of grasslands on non-argillic inclusions were not significantly different from those on argillic horizon throughout the soil profile (Fig. 4b). Soil total P concentrations decreased with depth throughout the soil profile for all landscape elements, and showed slight enrichment in the 30–50 cm soil depth increment where the argillic horizon begins (Fig. 4a). Woody patches had higher soil total P stocks (g P/m^2) than those of grasslands throughout the soil profile (Table 1a), with groves and clusters

accumulating 52.88 and 9.59 g/m^2 more P, respectively, than grasslands in the full 120-cm soil profile (Table 1b).

The spatial patterns of soil total P stocks revealed in the kriged maps for each soil depth displayed strong resemblance to aboveground vegetation spatial patterns readily discernable in the classified vegetation map derived from the aerial photograph of this landscape (Fig. 5). This coincidence of vegetation and soil P spatial patterns is particularly strong where groves occur. Soil total P stocks were highest at the centers of woody patches, decreased toward the canopy edges of woody patches, and reached lowest values within grassland matrix. Though this pattern was clearly evident in each depth increment throughout the entire 1.2 m profile (Fig. 5), lacunarity analysis indicated that spatial heterogeneity of soil total P across this landscape decreased with soil depth, with topsoil (0–30 cm) having higher spatial heterogeneities than those of subsoil (30–120 cm) (Fig. 6). Spatial GLS models revealed that fine root biomass explained a significant portion of the variation in soil total P concentrations across this landscape and throughout the soil profile, especially for the 0–5 cm and 5–15 cm depth increments (Table 2). In addition, soil pH also emerged as an important factor explaining variation in soil total P across this landscape at soil depths >15 cm (Table 2). Soil bulk density was negatively correlated with soil total P throughout the profile, reflecting the fact that woody patches had lower bulk densities than grasslands (Zhou et al. 2017a), whereas soil silt and clay concentrations were not consistently related to soil total P (Table 2).

DISCUSSION

Increases in total P throughout the soil profile

The lack of significant differences in soil total P concentrations between grasslands on non-argillic inclusions

TABLE 1. Soil total P stocks within each depth increment (a), and cumulative soil total P stock in different landscape elements across this subtropical savanna.

Soil depth (cm)	Grassland	Cluster	Grove
a) Soil total P stock (g P/m^2)			
0–5	5.44 ^c ± 0.05	6.74 ^b ± 0.19	8.36 ^a ± 0.23
5–15	10.97 ^c ± 0.08	12.21 ^b ± 0.23	16.14 ^a ± 0.48
15–30	16.09 ^b ± 0.13	17.33 ^b ± 0.35	24.45 ^a ± 0.73
30–50	24.79 ^b ± 0.19	25.39 ^b ± 0.46	35.19 ^a ± 0.87
50–80	36.53 ^c ± 0.27	39.13 ^b ± 0.62	49.54 ^a ± 1.17
80–120	45.99 ^c ± 0.33	49.16 ^b ± 0.89	63.12 ^a ± 1.34
b) Cumulative soil total stock (g P/m^2)			
Surface to 5 cm	5.44 ^c ± 0.05	6.74 ^b ± 0.19	8.36 ^a ± 0.23
Surface to 15 cm	16.41 ^c ± 0.11	18.95 ^b ± 0.37	24.50 ^a ± 0.65
Surface to 30 cm	32.50 ^c ± 0.21	36.28 ^b ± 0.63	48.95 ^a ± 1.32
Surface to 50 cm	57.28 ^c ± 0.36	61.67 ^b ± 0.95	84.14 ^a ± 2.13
Surface to 80 cm	93.81 ^c ± 0.58	100.80 ^b ± 1.44	133.68 ^a ± 3.21
Surface to 120 cm	130.34 ^c ± 0.83	139.93 ^b ± 2.00	183.22 ^a ± 4.34

Notes: Values are mean ± SE. Number of samples: grassland = 200, cluster = 41, and grove = 79. Significant differences ($P < 0.05$) between means for landscape elements are indicated with different superscript letters.

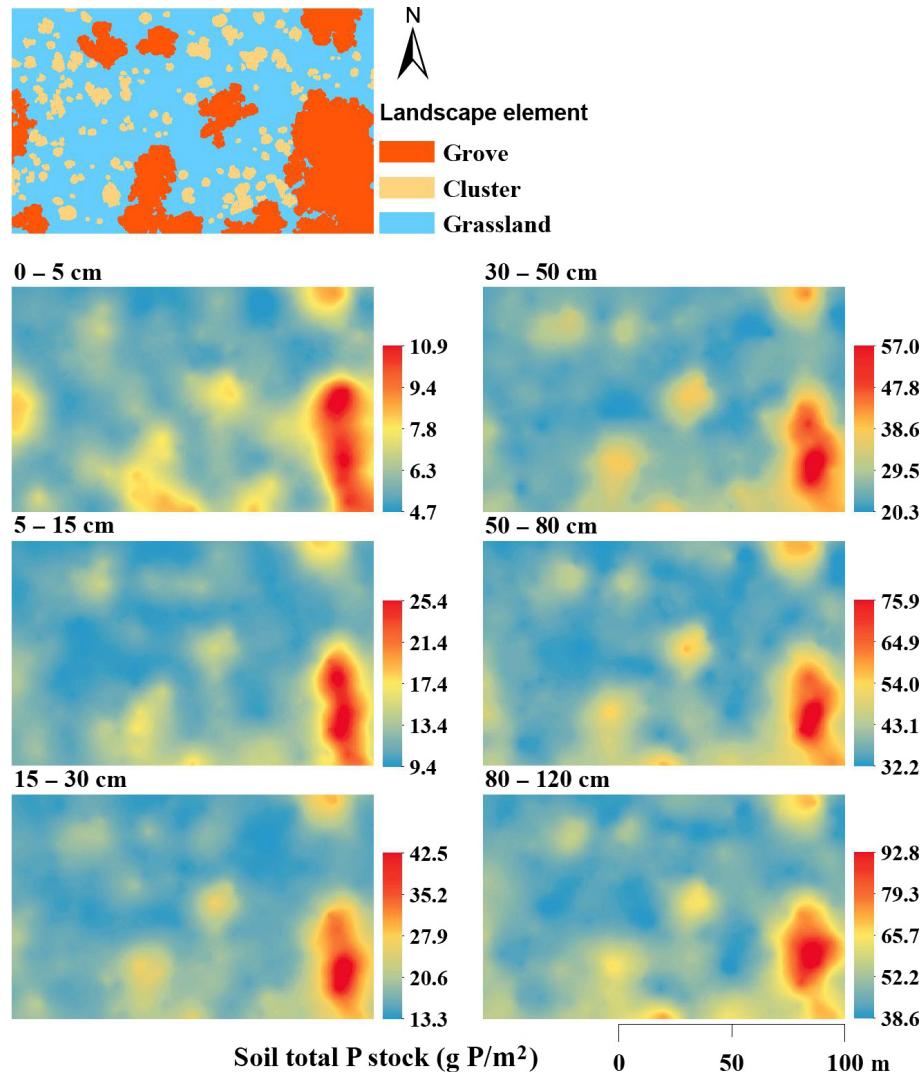


FIG. 5. Classified vegetation map derived from aerial photo and kriged maps of soil total P stock (g P/m^2) throughout the soil profile for this 100×160 m landscape in a subtropical savanna based on 320 randomly located sampling points.

and those on argillic horizons (Fig. 4b) excludes the possibility of spatially non-homogeneous distribution of soil P due to pedogenic processes, suggesting that observed accumulation of P in soils beneath woody patches (both clusters and groves) results from woody plant encroachment into areas that were once grassland. More importantly, this accumulation of soil P underneath woody patches is occurring throughout the upper 1.2 m of the soil profile (Figs. 4a and 5, Table 1). Thus, our first hypothesis that increases in soil total P would occur only in surface soils was rejected.

Since there is no gaseous component of the P cycle (Walker and Syers 1976, Schlesinger and Bernhardt 2013), the accumulation of P in soils beneath woody patches must be derived from the addition or redistribution of P from other potential sources including (1) atmospheric deposition, (2) faunal activities (e.g., large

animals, termites, ants), (3) horizontal transfer from adjacent soils beyond the woody canopy, and/or (4) uplift by roots located deeper than 1.2 m. Atmospheric P deposition rates in this study area located in south-central USA range from 0.5 to 1.0 $\text{mg P}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ (Mahowald et al. 2008), which is a small fraction of the soil P accumulation rate (~ 100 $\text{mg P}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$ in the 0–10 cm soil depth increment) under woody patches estimated for this ecosystem using a chronosequence approach (Kantola 2012). Livestock grazing has been excluded from this study area for at least the past 30 years (Liu et al. 2011) and is probably not responsible for the soil P patterns described here. Although desert termites (*Gnathamitermes perplexus*) are present across this landscape, their activities are confined to grassland areas, they feed only on grasses and forbs, and they are absent from wooded portions of the landscape.

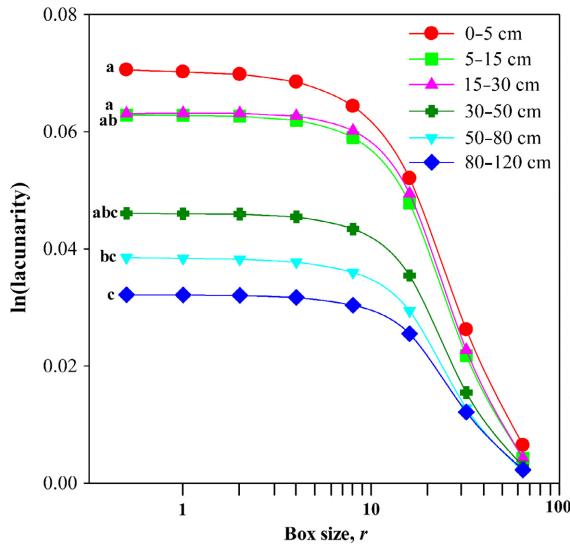


FIG. 6. Lacunarity curves throughout the soil profile derived from spatial patterns of soil total P concentrations (mg P/kg). Significant differences ($P < 0.05$) between different soil depth increments were detected based on one-way ANOVA (Student's t test) and indicated with different letters.

Thus, faunal activity is an unlikely determinant of P spatial patterns. Soil total P concentrations in grasslands are similar regardless of their proximity to woody patches, suggesting that the woody plants are not using lateral roots to mine P from the surrounding grasslands.

These results are consistent with other studies reporting no depletion of either total or extractable P in grassland soils adjacent to woody patches (Kantola 2012, Sitters et al. 2013, Blaser et al. 2014).

Given that atmospheric deposition, faunal activity, and lateral mining of P from surrounding grasslands by woody plant roots are unlikely scenarios, we propose that P increases in the upper 1.2 m of the soil profile beneath woody patches are due to translocation of deep soil P via root uptake, and, to a lesser extent, from hydraulic redistribution of dissolved P. Considerable potential for nutrient acquisition from deeper soil layers by deep-rooting plants has been reported in a variety of ecosystems (Scholes and Archer 1997, Jobbágy and Jackson 2001, McCulley et al. 2004, Kautz et al. 2013, Sardans and Peñuelas 2014). For example, McCulley et al. (2004) used $^{87}\text{Sr}/^{86}\text{Sr}$ isotope ratios of soils and plant tissues to show that roots were able to acquire and translocate Sr from deep in the profile to aboveground plant parts in five semiarid and arid sites across the southwestern USA, demonstrating strong potential for the acquisition of nutrients by deep roots. Similarly, at our study site, $\delta^2\text{H}$ values of plant and soil water have shown that woody species are able to acquire water located 2–4 m below the soil surface, whereas herbaceous species utilize water exclusively from the upper soil layers (<1.2 m) (Midwood et al. 1998, Boutton et al. 1999). Thus, woody plant roots at this site have demonstrated potential to access and acquire P located in deeper portions of the soil profile that are inaccessible to

TABLE 2. Best fit regression models for prediction of soil total P concentration (mg P/kg, \log_{10} -transformed) by vegetation and soil variables using spatial generalized least squares (GLS) models with Akaike information criterion (AIC) as model selection for each depth increment.

Parameters	Fine root biomass	Soil physical variables			
		SBD	Clay	Silt	pH
0–5 cm depth					
Coefficient	0.20	–0.23	0.003	0.017	0.005
t	10.98***	–6.70***	0.089	4.04***	0.35
5–15 cm depth					
Coefficient	0.09	–0.17	0.002	0.0059	0.003
t	5.77***	–5.17***	0.64	1.54	3.41***
15–30 cm depth					
Coefficient	0.045	–0.081	0.002	0.005	0.051
t	3.15**	–2.18*	1.23	1.21	6.17***
30–50 cm depth					
Coefficient	0.04	–0.10	0.005	0.009	0.11
t	2.63**	–2.54*	4.11***	2.58*	11.95***
50–80 cm depth					
Coefficient	0.28	–0.10	–0.005	0.001	0.099
t	2.49*	–2.68**	–4.29***	0.19	9.17***
80–120 cm depth					
Coefficient	0.04	–0.17	–0.0019	0.007	0.13
t	3.79***	–2.72**	–2.07*	2.11*	4.79***

Note: Explanatory variables are fine root biomass (g/m^2) and soil physical variables, including soil bulk density (g/cm^3) (SBD), soil clay (%) and silt (%) content, and soil pH.
 * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

herbaceous species that dominate the grassland portions of the landscape. This additional P derived from deep soils by woody species is initially incorporated in plant tissues and ultimately delivered to upper portions of the soil profile via root turnover and aboveground litterfall. Since fine root biomass is the primary source of soil organic matter input (Rasse et al. 2005) and is significantly higher underneath woody patches than grasslands throughout the entire 1.2-m soil profile (Fig. 3b), more P should accumulate underneath woody patches via root turnover. In addition, *P. glandulosa* trees at this study site have been shown to transfer deep soil water upward into drier portions of the soil profile by hydraulic redistribution (Zou et al. 2005). This could create favorable moisture conditions in the surface soil for organic matter decay and subsequent biogeochemical processes that mineralize plant nutrients (including P) and enable plant uptake (Sardans and Peñuelas 2014). Alternatively, when deeper portions of the soil profile are dry but surface layers are relatively moist, downward siphoning (the opposite of hydraulic redistribution) via roots may translocate water from surface soils into deep soils, solubilizing P in the soil matrix and facilitating its uptake by deep roots (McCulley et al. 2004, Lambers et al. 2006, Sardans and Peñuelas 2014).

In addition, groves accumulated significantly more soil total P than clusters even though they are composed of the same woody species (Fig. 4a, Table 1). This is probably due to the fact that clusters in this landscape are constrained in size (mean canopy area = 13.4 m², $n = 121$; Zhou et al. 2017c) and are relatively young compared to groves (cluster mean age = 22 yr, grove mean age = 48 yr; Boutton et al. 1998). Since P and other nutrients in soils accumulate linearly with age or size of woody patches (e.g., Liao et al. 2006, McClaran et al. 2008, Throop and Archer 2008, Kantola 2012, Blaser et al. 2014), the generally younger and size-constrained clusters have accrued less soil P than the older and larger groves. Although the formation of discrete clusters is initiated by the colonization of N₂-fixing *P. glandulosa* trees (Archer et al. 1988, Archer 1995, Bai et al. 2012), many of these mesquite trees in clusters have died (Archer 1995, Boutton et al. 1998). Since the process of N₂ fixation requires a substantial supply of P (Treseder and Vitousek 2001, Vitousek et al. 2002, Houlton et al. 2008), the death of *P. glandulosa* in discrete clusters may significantly reduce P demand and its rate of accumulation in cluster soils as other woody species have lower P concentrations in their tissues (433.6 ± 30.7 mg P/kg, $n = 14$) than *P. glandulosa* (640.1 mg P/kg; Fig. 3a).

Could the increase in soil P in woody patches be influenced by the fact that *P. glandulosa* is an N₂ fixer? As mentioned above, fast growing N₂ fixers have a high P demand (Treseder and Vitousek 2001, Vitousek et al. 2002, Houlton et al. 2008), and this demand can be fulfilled via deep acquisition. Alternatively, N₂-fixing species maintain higher root phosphatase activity than non-N₂ fixers (Houlton et al. 2008, Boutton et al. 2009, Blaser

et al. 2014), which may influence their ability to acquire P and concentrate it within the rooting zone. At our site, acid phosphatase activity is four to eight times greater in soils beneath woody patches with *P. glandulosa* than in grassland soils (Boutton et al. 2009). This difference in enzyme activity results in plant-available P pools (i.e., resin-extractable P) of 3.4 mg P/kg in grasslands vs. 9.0 to 14.6 mg P/kg in clusters and groves (Kantola 2012). This is consistent with the hypothesis of Houlton et al. (2008), that symbiotic N-fixation may be a mechanism for plants to acquire additional N for investment in the production of N-rich root phosphatase enzymes that can increase the P availability in P-limited environments. If correct, this may be another important mechanism that leads to P accumulation where N₂-fixing woody plants are encroaching into grassland. Regardless of the exact mechanism by which P accumulates following woody encroachment, our findings suggest that transfer of P from deeper soil layers enlarges the P pool in upper soil layers where it is more actively cycled may be a potential strategy for encroaching woody species to satisfy their P demands and enable their ongoing encroachment into areas that were once grass dominated.

Patterns of spatial heterogeneity in soil total P

Kriged maps revealed that woody encroachment into grasslands altered patterns of spatial heterogeneity in soil total P throughout the upper 1.2 m of the soil, albeit at reduced magnitude in deeper portions of the profile (Figs. 5 and 6). Therefore, we reject our second hypothesis that spatial patterns of total P would be altered only in surface soils. Although spatial patterns of soil total P displayed strong resemblance to the distribution of grove vegetation, the same was not true for the smaller woody clusters (Fig. 5). One possible reason for this is that clusters accumulated less P due to their smaller sizes and younger ages, as discussed above. However, the more likely reason is that our sampling intensity may not have been sufficient to capture the spatial heterogeneity of soil total P beneath clusters (Liu et al. 2011). Approximately 80% of clusters are <20 m² (Zhou et al. 2017c), while only two soil samples were collected randomly within each 100-m² grid cell. Kriged maps also revealed that soil total P decreases gradually from the centers of groves to the edges (Fig. 5). These strong within-grove spatial gradients illustrate that the accumulation of soil P is time dependent. Woody plants near the centers of groves are generally older (>100 yr) than those closer to the grove/grassland interface (Bai et al. 2012), and have had more time to concentrate P in soils beneath their canopies.

The influence of woody encroachment on patterns of spatial heterogeneity in soil total P diminishes gradually with soil depth across this landscape (Fig. 6). Root distribution plays an important role in shaping vertical patterns of soil total P (Jobbágy and Jackson 2001) since much of the P in the soil profile is derived from root turnover, although surface soils also receive additional inputs from

litterfall. As shown in this study (Fig. 3b) and many others (e.g., Jackson et al. 1996, Arora and Boer 2003, Laio et al. 2006), root distribution generally decreases exponentially with soil depth. Coupled with the fact that deeper roots have greater longevity and slower turnover than roots near the surface (e.g., Hendrick and Pregitzer 1996, Joslin et al. 2006), this suggests that the rate of P accrual will be slower and less pronounced in deeper portions of the soil profile. In terms of spatial arrangement, reduced discrepancies in soil total P between groves and other landscape elements in lower soil layers results in diminished spatial heterogeneity (Figs. 4a and 6). Spatial GLS models also revealed that fine root biomass explained large proportions of the variation in soil total P throughout the soil profile (Table 2); however, the strength of this relationship decreased with depth. In deeper portions of the profile, soil pH was strongly correlated with total P (Table 2), suggesting P dynamics in topsoil and in subsoil may be controlled by different regulatory mechanisms. In this study site, CaCO₃ concentrations in subsurface soils beneath groves are higher than those beneath grasslands by up to one order of magnitude (Zhou and Boutton, *unpublished data*). This, taken together with the fact that subsurface soils of this study site have higher pH values (Zhou et al. 2017a), may lead to P accumulation by favoring its fixation into insoluble calcium phosphates (Schlesinger and Bernhardt 2013). Additional experiments are needed to explore the mechanisms leading to P accrual and storage in upper vs. lower portions of the soil profile.

CONCLUSIONS AND IMPLICATIONS

In this subtropical savanna ecosystem, soil total P in the upper 1.2 m of the soil profile increases dramatically as N₂-fixing *P. glandulosa* trees and associated woody species encroach into the grassland matrix. The accumulation of P underneath woody patches is most likely driven by translocation of deep soil P via root uptake. Substantial accrual of soil total P underneath woody patches alters patterns of spatial heterogeneity in soil P to considerable depth, albeit at reduced magnitude deeper in the profile. We speculate that the transfer of P from deeper to shallower portions of the soil profile may foster a positive feedback that enables the persistence and ongoing encroachment of woody species, which have relatively high tissue P concentrations compared to the grasses and forbs that once dominated this region.

Since P functions as a limiting nutrient and its availability can impose strong controls on plant and soil C and N cycles (Vitousek et al. 2010), it is critical to parameterize and represent the P cycle and its interactions with C and N cycles in earth system models (Reed et al. 2015, Yang et al. 2016, Sun et al. 2017). Considering the vast geographical extent of woody encroachment in arid and semiarid regions throughout the world (Eldridge et al. 2011, Stevens et al. 2017), our results suggest that further efforts to characterize spatial variability in P storage and dynamics in horizontal and

vertical soil space in response to this vegetation change would lead to improved efforts to model the interactions between vegetation change, biogeochemistry, and the climate system.

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