Soil phosphorus pools and supply under the influence of *Eucalyptus saligna* and nitrogen-fixing *Albizia facaltaria*

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Abstract

Replicated plantations of *Eucalyptus saligna* (Sm.) and *Albizia falcataria* (L.) Fosberg were examined for patterns in soil phosphorus (P) fractions and soil P availability. The supply of P was assessed in the field with anion exchange resin bags, which indicated that P supply was about twice as high under *Eucalyptus* as under *Albizia*. In the laboratory, solution P extracted with iron oxide-impregnated paper strips was also 45% higher under *Eucalyptus*. The effects of mixtures of the two species were intermediate between the pure-species effects. Overall, P supply either increased with *Eucalyptus* or decreased under *Albizia*. Despite significantly lower soil P availability, the *Albizia* plots appeared to take up and cycle as much P as the *Eucalyptus* plots, indicating that P supply was not independent of P demand. High rates of P uptake by *Albizia* may depend on higher allocations of carbohydrate to belowground production. © 2000 Elsevier Science B.V. All rights reserved.

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1. Introduction

Productivity of tree plantations depends strongly on soil nutrient supply, and soil nutrient supply may be malleable under the influence of management practices and species (reviewed by Sanchez et al., 1985; Binkley, 1996). Under tropical conditions, changes in soil chemistry and fertility may occur over periods of just a few years, with feedback effects on stand productivity (Fisher, 1995). Nitrogen (N)-fixing trees may increase the supply of available N in the soil, benefiting both N-fixing and non-N-fixing trees. High rates of N-fixation may require relatively high supply rates of soil phosphorus (P); high P supplies support greater nodule formation, greater N-fixation rates per g of nodule, and more rapid tree growth (Binkley, 1986; MacDicken, 1994; Binkley and Giardina, 1997).

N-fixing trees can have variable feedback effects on soil P supplies; increases in P supply could enhance long-term growth of the N-fixer, but decreases could partially offset any gains from the increase in N availability. N-fixing red alder (*Alnus rubra* Bong.)

uniformly shows greater rates of P cycling than the adjacent stands of Douglas-fir (*Psuedotsuga menziesii* (Mirb.) Franco), although the effects of alder on labile soil P pools are more variable (Giardina et al., 1996; Compton and Cole, 1998). In one unreplicated case study, a mixture of red alder and Douglas-fir showed higher availability of P than the monocultures of either species (Zou et al., 1995). Almost no information is available on the effects of N-fixing trees on soil P in tropical forests.

In the present study, we examined the relative influence of pure and mixed plantations of *Eucalyptus saligna* and *Albizia facaltaria* on soil P pools and P supply. The pattern of effects on P pools in this single case study may or may not represent the general trends for similar situations in other tropical plantations, but so few studies have examined the influence of tropical plantation trees on soil P that any information from single geographic regions should be useful.

2. Methods

Three study sites are located on the northeast coast of Hawaii, about 20 km north of Hilo (19°30′ N, 155°15′ W) at 480 m elevation with a mean annual temperature of 21°C and an average rainfall of >4 m per year (DeBell et al., 1989). The slopes are moderate (<15%), with deep (>2 m), acidic (pH 5.0 in water for *Eucalyptus*, pH 4.8 in water for *Albizia* (Garcia-Montiel and Binkley, 1998)) soils of the Kaiwiki series of thixotropic isomesic Typic Hydrudands. The three sites have been cropped with sugarcane for more than 50 years, with the last harvest in 1980 (Site 1) and 1960 (Sites 2 and 3). At each of the three sites, BioEnergy Development Corporation planted both species in pure plots with a completely randomized block design, with four blocks per site (a total of 12 plots for *Eucalyptus* and 12 plots for *Albizia*). Site 1 also had mixed plantations.

At Site 1, a mixed-species trial was established in 1982. The soil was ploughed and new vegetation sprayed with a herbicide prior to the planting of pure and mixed stands of *Eucalyptus* and *Albizia* (DeBell et al., 1989). The pure *Eucalyptus* plots received 370 kg N/ha (as ammonium nitrate) and 108 kg P/ha (as triple superphosphate), whereas the mixed-species plots (we sampled the 1 : 1 mixture only) and the pure *Albizia*

plots received a total of 80 kg N/ha and 36 kg P/ha. Tree spacing was 2 m × 2 m in 30 m × 30 m plots (pure *Eucalyptus* and 50 : 50 mixed-species plots) or 15 m × 30 m plots (pure *Albizia*). The greater P fertilization of the *Eucalyptus* plots than the *Albizia* plots at Site 1 could be problematic in our examination of soil P patterns, but we anticipate that any residual effect of this fertilizer difference is small. The consistency of the soil P patterns with the other two sites (where both species received the same quantities of P fertilizer) supports this assumption.

Sites 2 and 3 are 1 km north of Site 1. In 1981, the vegetation that developed during the fallow period was cleared, the soil ploughed, and the sprouting vegetation sprayed with a herbicide. In 1982, pure stands were planted as a species trial (tree spacing 1.5 m × 1.5 m, plot size 12 m × 18 m). Both *Albizia* and *Eucalyptus* plots received a total of 110 kg N/ha, and 50 kg P/ha.

Previous studies at these sites showed greater aboveground net primary production in the *Eucalyptus* than in the *Albizia* plots, with maximum productivity occurring in one of the mixed-species treatments (DeBell et al., 1989, 1997). Soil N accretion (0–20 cm depth) under *Albizia* was about 85 kg N/ha per year (Garcia-Montiel and Binkley, 1998).

In the present study, we used a variety of methods to examine the effects of species (at the plantation age of 12 years) on the supply of soil P and on the pool fractions of soil P. On-site P supply in the pure-species plots was assessed with anion exchange resin bags placed in the soil from October 1994 though January 1995 (4 months). The resin bags were prepared by placing 14 ml of anion-exchange resin (ASB-1POH from Sybron Chemicals, Inc.) in a nylon stocking, sealing with a glue gun to produce a resin bag that was 6 cm × 6 cm. Eight resin bags were placed in each plot at 2 m intervals along a single transect, 5 cm below the forest floor (which remained intact). Resin bags were shipped to Colorado State University and extracted with 100 ml of KCl, diluted, and analyzed colorimetrically for phosphate with a Lachat AE autoanalyzer (Lachat Instruments, Inc; Milwaukee, WI) according to the Lachat Instruments QuikChem Method 10-115-01-1-B (1992). Two of the resin bags had P values that were more than an order of magnitude beyond all others, and these were omitted as outliers.

In April 1994, we collected a 15 kg composite sample of 0–20 cm depth soil from each of the 24 plots; soils were sampled with a shovel from five points in the interior of each plot. The soils were sieved though an 8 mm mesh to remove roots and worms, and then mixed thoroughly by hand. Subsamples from each composite were shipped overnight in a cooler to Colorado State University, where they were refrigerated at 4°C until fractionation analysis 4 weeks later. A modified Hedley soil P fractionation method (Hedley et al., 1982; Cross and Schlesinger, 1995) was used to separate soil P into fractions that represent plant-available and non-plant-available forms in the soil. We used a fractionation scheme that involved the sequential extraction of 1.5 g field moist soil with: (a) an iron oxide-impregnated filter paper strip (Menon et al., 1989) removing the most readily available pool of inorganic P in the soil (solution-P); (b) 0.5 M sodium bicarbonate (adjusted to a pH of 8.5) removing the inorganic P adsorbed to iron and aluminum surfaces in the soil and organic P, such as nucleic acids, phospholipids and released organic molecules from lysed microbial cells; (c) 0.2 M sodium hydroxide removing the inorganic P sorbed to iron and aluminum surfaces, the organic P stabilized partially as soil organic matter, and the inorganic P and organic P immobilized by micro-organisms; and (d) 1 M hydrochloric acid (HCl) removing the inorganic P bound to calcium and the inorganic P occluded within sesquioxides (Crews et al., 1995). Expectations about the nature of soil P in each fraction may or may not apply to a specific soil.

For each soil sample, 1.5 g of field-moist soil, 30 ml of deionized water and a 10 mm × 60 mm iron oxide-impregnated filter paper strip were placed in a 50 ml centrifuge tube. Following 16 h of shaking, the paper strips were rinsed with water to remove soil particles, and extracted by shaking for 1 h in 30 ml of 1.0 M HCl. The soil and solution for all extraction steps were centrifuged at 10,000 rpm for 10 min, decanted and the pellet resuspended and extracted with the next solution during subsequent 16 h shakes. Total (organic + inorganic) P in the $NaHCO_3^-$ and NaOH extracts were determined by acidified ammonium persulfate digestion. Inorganic P in these extracts was measured directly after acidification with concentrated sulfuric acid to precipitate organic matter. Extractable organic P was calculated as the difference between the total P and inorganic P of these extracts. The HCl fraction rarely contains measurable quantities of Po, and was not digested. All extract solutions were appropriately diluted, neutralized and analyzed colorimetrically, as above, with a Lachat AE autoanalyzer, according to the Lachat Instruments QuikChem Method 10-115-01-1-B (1992).

We examined the effects of mixtures of the two species in two ways. First, we sampled and analyzed soils from the mixed-species plots (1 : 1 mixture) at Site I in October 1994 for solution-P (extracted with iron oxide-impregnated filter paper). Second, at Site 2, three of the blocks had randomly assigned *Eucalyptus* and *Albizia* to adjacent plots, and we used on-site resin bags placed along transects across the stand boundaries to examine the mixture effects of the species. For each of the three pairs of adjacent plots, two 18 m parallel transects were located 4 m apart, running from the center of the *Eucalyptus* plot to the center of the *Albizia* plot (Ewers et al., 1996). In June 1996, resin bags (as described above) were placed in the soil, then retrieved in September 1996, extracted, and the extract analyzed for P as before.

The original plantations were completely randomized within four blocks at each site. Combining all three sites into one analysis no longer provides a completely randomized design, so 'site' was used as the main effect, 'blocks' were used as plot effects, and species-within-blocks were a split-plot effect. The error term for the main effect was a plot-within-site sum of squares. The error for the species (equal to split-plot) effect and the site X species interaction were the sums of squares for the species X plot-within-site. We also examined the importance of replication by comparing simple ANOVAs for each site with the overall ANOVA for all three sites. To examine the effects of the mixed-species plots at Site 1, we performed an ANOVA of the pure and mixed stands, with solution-P as a function of the proportion of *Eucalyptus* in the plot (0, 0.5, or 1.0). Transect data across the plot boundaries at Site 2 were analyzed using orthogonal contrasts (Ewers et al., 1996). The 10 sampling points along each transect were grouped in the first three points (central *Eucalyptus* influence), the middle four points (mixed-species influence), and the last three points (central *Albizia* influence). We tested for linear and quadratic relationships for the pure-species groups of three points, and for linear,

Table 1
Species effects on soil P availability (in-field resin bags (µg P per bag)) and P pools (µg P/g dry soil) (standard deviations in parentheses)

Species	Site	Resin bag	Solution inorganic	Bicarbonate inorganic	Hydroxide inorganic	Hydrochloric acid inorganic	Bicarbonate organic	Hydroxide organic
Albizia	1	25 (10)[a]	4.5 (1.0)	4.4 (1.1)	50 (35)	2.0 (2.0)[b]	41 (18)	828 (259)
Eucalyptus	1	40 (11)[a]	6.1 (2.3)	5.3 (2.4)	63 (14)	6.4 (0.4)[b]	40 (20)	897 (330)
Albizia	2	20 (4)[a]	3.2 (1.3)	3.8 (1.8)	41 (32)	2.8 (1.7)	74 (53)	698 (277)
Eucalyptus	2	61 (35)[a]	5.4 (3.7)	5.7 (2.8)	52 (22)	6.8 (4.4)	28 (12)	916 (342)
Albizia	3	23 (5)	2.9 (1.2)	4.6 (2.4)	60 (28)	3.1 (1.7)	46 (7)	616 (55)
Eucalyptus	3	23 (7)	3.1 (0.6)	2.5 (0.4)	50 (24)	3.1 (1.4)	30 (15)	524 (228)
Overall *Albizia*		23 (7)[b]	3.5 (1.2)[c]	4.3 (1.6)	51 (29)	2.6 (1.7)[b]	54 (32)[a]	714 (211)
Overall *Eucalyptus*		41 (25)[b]	5.1 (2.6)[c]	4.5 (2.3)	55 (19)	5.4 (2.9)[b]	33 (15)[a]	779 (320)[a]

[a] Species effect within site, or overall species effect, significant at $p < 0.1$.
[b] Species effect within site, or overall species effect, significant at $p < 0.05$.
[c] Species effect within site, or overall species effect, significant at $p < 0.01$.

quadratic, and cubic contrasts in the mixed-influence set of four points astride the boundary. Statistical analyses were computed with SYSTAT version 7.0 (SYSTAT, 1996), with a *p* value of 0.1.

3. Results and discussion

Soil P supply was lower in the soils collected from under *Albizia* than those from under *Eucalyptus*. The on-site resin bags showed almost twice as much available P under *Eucalyptus*, which was consistent with the 45% greater solution-P extracted from *Eucalyptus* soils by the iron oxide strips (Table 1). This greater solution-P 'pool' under *Eucalyptus* may have been influenced by the significantly higher pH under *Eucalyptus* (Garcia-Montiel and Binkley, 1998); solution-P correlated weakly with soil pH in water ($r^2 = 0.2$, $p < 0.03$).

The effect of species was more pronounced at Site 1 and Site 2 than at Site 3, although no interactions between species and sites were significant. The higher rate of P fertilization of the pure *Eucalyptus* plots at Site 1 could have resulted in long-term increases in P supply relative to the *Albizia* plots. However, the species effect at Site 1 was similar to the effect at Site 2 where fertilization rates did not differ between species. The proportion of *Eucalyptus* in the plots at Site 1 had a linear effect on solution-P ($p = 0.06$), which also supports an overall effect of species rather than residual effects of higher fertilizer rates in the pure *Eucalyptus* plots. The resin bag transects across the plots at Site 2 also showed a strong linear effect of the influence of *Eucalyptus* on the availability of P. In-field resin bag P was greater for the three points near the center of the *Eucalyptus* plots than for the three points near the center of the *Albizia* plots ($p = 0.034$ linear contrast), with intermediate values for the transition points (Fig. 1). The overall linear correlation coefficient between the distance from the center of the *Eucalyptus* plots and resin bag P was 0.79 ($p < 0.01$). Both these lines of evidence (pure and mixed plots at Site 1, transects across pure-plot boundaries at Site 2)
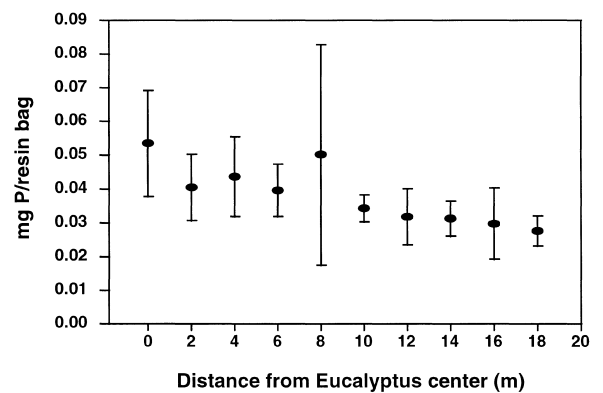

Fig. 1. Pattern of P accumulation on in-field resin bags along transects from the center of the *Eucalyptus* plots to the center of the *Albizia* plots. Distance 0 is the center of the *Eucalyptus* plots, distance 9 the plot boundary, and distance 18 the center of the *Albizia* plots. Error bars are standard errors of the means.

indicate a linear effect of the mixture of species effects, with no evidence of synergistic interaction between species in relation to P supply in the soil.

Bicarbonate extracted similar amounts of inorganic P from the two soil types, but significantly more organic P from the *Albizia* soil. We do not know how labile the bicarbonate-extractable pool of organic P may be. A rapid turnover rate would lead us to expect that mineralization of this pool would lead to higher levels of P in the more labile, inorganic pools (solution-P and bicarbonate-extractable inorganic P), but these were lower under *Albizia*. In a bioassay, *Albizia* seedlings obtained 22% less P from *Albizia* soils than from *Eucalyptus* soils (Binkley, 1997), which also indicates that the large pool of bicarbonate-extractable organic P in *Albizia* plots is not readily available to plants.

Hydroxide extracted large quantities of both inorganic and organic P, with no significant differences between species. Levels of HCl-extractable P were substantially lower in *Albizia* soils. This decrease may be related to the lower soil pH under *Albizia*, and greater solubilization of primary mineral P in the rhizosphere of *Albizia*.

The resin bag P values may best represent soil P availability as they integrate P supply over time. Resin bags compete with uptake by plants and microbes, so the lower resin bag P values under *Albizia* may have resulted from a lower P supply, or greater competition for uptake. Although it is not possible to judge the supply of a nutrient from pool size alone, the smaller pools of labile inorganic P under *Albizia* would be consistent with a lower P supply.

Over the course of stand development, did *Albizia* deplete the supply of available soil P, or did *Eucalyptus* increase the supply? With only a single comparison over time, we cannot distinguish between these two possibilities, and we hope that future studies will track the development of species' impacts over time. Future work should also examine the mechanisms behind the different effects of the species. For example, the pH_{water} of the soil under *Eucalyptus* was about 0.3 units higher than under *Albizia* (Garcia-Montiel and Binkley, 1998), but we don't know the pH of the rhizosphere soils where P solubilization would occur (Gillespie and Pope, 1989; Gahoonia and Nielsen, 1992; Illmer and Schinner, 1992). The supply of P from organic pools may be driven by differences in the

activities of phosphatase exoenzymes, either produced by the trees or by microbes in association with the trees (Fox and Comerford, 1992; Jayachandran et al., 1992). At 8 years of age, the phosphatase activity at Site 1 under *Eucalyptus* was only half of that under *Albizia* (Zou et al., 1995), but this is difficult to interpret without knowing the size of the phosphatase-labile pool under each species. Some plants have been shown to produce low-molecular weight organic acids that can chelate iron or aluminum, releasing phosphate (Ae et al., 1990), but we have no information for our sites.

Bioassays of these soil samples with *Albizia* and *Eucalyptus* seedlings indicated that the supplies of P from both types of soil were limiting to seedling growth; seedlings of both species responded to P fertilization by increasing growth by at least 40% (Binkley, 1997). At 8 years of age, labile organic P pools appeared to be lower under *Albizia* (Zou et al., 1995), consistent with the patterns found in the bioassay and reported here for the age of 12 years. At 15 years of age, the uptake of P to supply aboveground growth in the plantations was similar for both species (between 6.5 and 7.2 kg/ha per year, Binkley and Ryan, 1998), which indicates that *Albizia* obtained as much P as *Eucalyptus* even though the soil supply of P was lower under *Albizia*. The high rate of cycling of P (matching or exceeding that of the *Eucalyptus* plots at both 6 years and 15 years of age) despite lower availability of P in soil prompts us to suggest that *Albizia* may be more effective in 'mining' soils for P. Given the low diffusivity of P in soils (typically between 10^{-8} and 10^{-11} cm^2/sec, Barbour, 1995), *Albizia* may be able to obtain more P from a low-P soil by increasing the absorbing area of roots and mycorrhizae. Binkley and Ryan (1998) found that at the age of 15 years, belowground C allocation was about 30% greater for the *Albizia* plots than the *Eucalyptus* plots, consistent with the idea that the continued supply of P to *Albizia* depends, in part, on the greater investment belowground to obtain P. This idea warrants direct testing as a major mechanism of differences between species in the supply rates of nutrients; supplies of nutrients with low diffusivities should be recipient-controlled in part (Barbour, 1995), rather than a passive property of the soil. *Albizia* may also be better able to access some non-plant-available P pools than *Eucalyptus*, as indicated by the apparent

depletion of (or lack of input to?) the HCl-extractable P pool by *Albizia*.

The importance of the high degree of replication in our study is apparent from the analysis of the data on an individual site basis. The effect of species on solution-P was not significant within any one of the three sites, but was highly significant across all sites. When only the data from Site 1 were analyzed, the only significant ($p < 0.1$) effect of species were resin bag P and HCl-extractable P. For Site 2, only resin bag P differed between species. No species effects were significant for soils from Site 3. These single-site comparisons (with four replicates in each case) contrast strongly with the significance found from the full ANOVA that used all three sites (and 12 replicates). We stress that studies designed to examine the effects of tree species on soils may need to have more thorough replication than the three or four replicates (at a single site) per treatment that are common in forest nutrient cycling studies.

Many first-rotation studies have now demonstrated large differences in the effects of tree species on soils (Binkley, 1996; Binkley and Giardina, 1998), and we suggest two areas warranting substantial research. The mechanisms behind these effects remain poorly known, including the importance of differences in belowground carbon allocation and the effects of tree species on soil organisms that mediate biogeochemical cycles. The second area is simply the 'legacy' of these effects; how long will the effects of a species persist into the next rotation? These two features may have substantial importance for the long-term, multi-rotation sustainability of tropical forest plantations, especially those that seek to increase soil fertility though the use of N-fixing trees.

Acknowledgements

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