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Unexpected Changes in Soil Phosphorus Dynamics Following Tropical Deforestation to Cattle Pasture

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Abstract

Phosphorus (P) is widely believed to limit plant growth and organic matter storage in a large fraction of the world's lowland tropical rainforests. We investigated how the most common land use change in such forests, conversion to cattle pasture, affects soil P fractions along forest to pasture chronosequences in the central Brazilian Amazon and in southwestern Costa Rica. Our sites represent a broad range in rainfall, soil type, management strategies, and total soil P (45.2 – 1228.0 μg P / g soil), yet we found some unexpected and at times strikingly similar changes in soil P in all sites. In the Brazilian sites, where rainfall is relatively low and pasture management is more intense than in the Costa Rican sites, significant losses in total soil P and soil organic carbon (SOC) were seen with pasture age on both fine-textured oxisol and highly sandy entisol soils. However, P losses were largely from occluded, inorganic soil P fractions, while organic forms of soil P remained constant or increased with pasture age, despite the declines in SOC. In Costa Rica, SOC remained constant across the oxisol sites and increased from forest to pasture on the mollisols, while total soil P increased with pasture age in both sequences. The increases in total soil P were largely due to changes in organic P; occluded soil P increased only slightly in the mollisols, and remained unchanged in the older oxisols. We suggest that changes in the composition and/or the primary limiting resources of the soil microbial community may drive the changes in

organic P. We also present a new conceptual model for changes in soil P following deforestation to cattle pasture.

Introduction

Ecosystems worldwide are undergoing unprecedented rates of land conversion and land use change (Meyer and Turner 1992; Ojima et al. 1994). Land-management practices such as fire, grazing, tillage, and fertilizer application, among others, affect ecosystem composition, the distribution of organic matter, and a variety of nutrient cycling processes, including losses of limiting and essential elements to atmospheric and aquatic realms (e.g. Ewel et al 1991, Reiners et al. 1994; de Moraes et al. 1996; Matson et al. 1997; Neill et al. 1997). The most dramatic recent land use changes have been centered in tropical and sub-tropical forested ecosystems (Skole and Tucker 1993, Houghton et al. 2000), where deforestation now removes roughly 2% of the remaining forest cover per year (Williams and Chartres 1991; Nepstad et al. 1999), most of which becomes cattle pasture (Fearnside 1996).

The biogeochemical consequences of land use change in the tropics are potentially quite different from those in temperate regions, in large part because tropical ecosystems frequently occur on soils that have not been rejuvenated by recent glacial activity, and are therefore often extremely old. The combination of greater soil age along with a warm, often wet climate, leads to highly weathered soils that are typically depleted in phosphorus (P) and base cations (Ca, Mg, K), rich in iron and aluminum oxides, and of variable charge (Uehara and Gilman 1981; Sollins et al. 1988; Bruijnzeel 1991); these are the oxisols and ultisols that dominate many tropical regions. Carbon uptake and storage in ecosystems on such soils are often limited by phosphorus and/or base cation supply (Vitousek and Sanford 1986; Cuevas and Medina 1988; Herbert and Fownes 1995; Vitousek and Farrington 1997). Thus, any land use driven changes in P and/or base cation availability may be central to predicting the sustainability of cleared land, as well as land-atmosphere exchanges of carbon and trace gases following forest conversion.

Phosphorus limitation, in particular, is thought to be common in tropical forests on old soils, and the constraints imposed by low P availability are a widely recognized problem in tropical agriculture (e.g. Sanchez et al. 1982). Not only are many tropical soils relatively low in total soil P, but their high iron and aluminum oxide content causes strong "fixation" of plant available inorganic P into more occluded forms that are thought to be largely unavailable to biota (Sanchez et al. 1982, Uehara and Gillman 1981). Thus, soil organic matter (SOM) and soil organic P are important to tropical soil fertility, both as a source of P at biotic time scales, and potentially as a buffer against P fixation by clay minerals (Tiessen et al. 1994, Afif et al. 1995, Guggenberger et al. 1996). Finally, because primary mineral sources of P have been depleted in many old tropical soils, and inputs of P from the atmosphere are much lower than are those for other key rock-derived elements (Graham and Duce 1979; Chadwick et al. 1999), any losses of P during and after deforestation may have long-term consequences for productivity and community composition well after cleared lands are abandoned.

Slash-and-burn clearing for pasture initially creates a pulse of available P (and other key nutrients), as the large pools held in biomass are released to the soil environment. Burning and subsequent ash deposition not only creates a nutrient pulse, but also elevates soil pH, which decreases the strength of P sorption and occlusion reactions (Anghinoni et al. 1996; Beauchemin et al. 1996). However, this initial pulse of fertility is typically short-lived, and significant P losses can occur during and just after deforestation via transport of P in particulate matter (Kauffman et al. 1995, 1998). In addition, there is evidence that P constraints already present in undisturbed tropical soils are exacerbated by prolonged use of cleared lands (Tiessen et al. 1992). It is not clear, however, whether this pattern is due to actual losses of P from the system, or to a redistribution of total soil P from more labile to more recalcitrant forms. The fact that labile forms of P are relatively immobile in soils suggests that the latter transformations may be more likely.

Recent work by our group near Santarém, Pará, in the central Amazon showed significant declines in foliar and labile inorganic soil P with pasture age, and these depressions in P cycling were tightly correlated with declines in leaf area index and grass productivity (Asner et al. 1999). As for many other pasture chronosequences (Davidson et al. 1995), we also observed significant decreases in soil organic matter with pasture age. Thus, our original hypothesis was that declines in SOM would be accompanied by increased mineralization of soil organic P, creating a pulse of inorganic P that was highly susceptible to occlusion by clay minerals (Figure 1). This net transfer of P from organic to occluded forms would feed back toward even greater P limitation, potentially driving declines in pasture productivity.

However, in the moist tropics, there is enormous variation in precipitation, soil types and management strategies, even when restricting the focus to pastures alone, and not all aging pastures show strong declines in soil organic matter or productivity. For example, Neill et al. (1997) reported stable to even increasing SOM pools with pasture age along chronosequences in Rhondonia. More recently, Garcia-Montiel et al. (2000) described a pattern of increases in soil organic P and declines in occluded soil P with pasture age in these same sites. Thus, it appears that where environmental conditions or management practices maintain or even increase SOC in soils following forest to pasture conversion, concomitant maintenance or augmentation of soil organic P may also occur.

Again, our hypothesis for the Santarém sites was that we would see very different patterns in soil P than those reported by Garcia-Montiel and colleagues. We observed decreases in SOC pools along pasture chronosequences near Santarém, and thus as outlined in figure 1, we expected to find declines in soil organic P and increases in occluded P. Essentially, our working model was that changes in soil P fractions would be related to those in SOM: where climate, soil type and/or management strategies do not create SOM losses, we did not expect losses in soil organic P and increases in occluded P, but where SOM losses do occur, we predicted a net transfer from organic to occluded pools with pasture age.

Finally, due to the wide range in climate, soils, and management across the tropics, we chose to search for a second set of pasture chronosequences where all three variables were considerably different from those in the Santarém area. Our goal here was to test for any consistent, general patterns in soil P dynamics following deforestation that transcended the wide range in potential driving variables. There is considerable variation in soils, rainfall and management schemes within the Amazon basin alone, but the range in all three variables is even greater when one considers the entire neotropics. In particular, portions of lowland Central America have higher rainfall and shorter dry seasons than in any part of the Amazon, large gradients in soil type from very young, highly fertile soils to old oxisols such as those found in Amazonia, and management practices in which burning is rarely used. Thus, we located a second set of sites with such characteristics in southwest Costa Rica.

Methods

Study Sites

Brazil: The Brazilian sites consist of two pasture chronosequences located on two ranches south of Santarém, Pará, and east of the Tapajós River (3°16'S 54°56'W; 3°8'S 54°40'W). Mean annual rainfall is 2000mm, the bulk of which occurs between January and May, and mean annual temperature is 25°C. All sites are on upland *terra firme* that has pockets of relic depositional surfaces, creating a mix of high clay oxisols and highly sandy entisols (Parrotta et al. 1995; Silver et al. 2000). We established one chronosequence of pastures on the oxisols dating 2, 7 and 15 years since conversion, and a second trio of sites (1, 7 and 15 yrs old) on the sandy entisols. Five of the six pastures were on a single ranch; the 2 year old oxisol pasture was the exception. Three of the sites (1 year entisol, 2 and 7 year oxisols) were dominated by the common pasture grass *Brachyaria brizantha*; the other three sites were characterized by a second common grass, *Pennesetum clandestinum*. Some woody invaders, notably *Solanum paniculatum*, were sparsely distributed in some of the sites, and all but the two youngest pasture sites had been burned since conversion as a means for controlling woody pioneer species. Relief in all sites is minimal, and none of the pastures have been fertilized.

Costa Rica: We established a second pair of chronosequences in southwest Costa Rica. All sites are located on a single ranch (8°43'N, 83°37'W) approximately 5 km inland of the town of Agujitas, which is located at Drake Bay on the Osa Peninsula. The entire Osa Peninsula was formed in three large seafloor volcanic events between roughly 75 and 40 million years ago, but some parts of the region were below sea level in more recent geologic eras (Berrange and Thorpe 1988). This created a wide range in parent material ages and subsequent soil types, from highly weathered 40+ million year old oxisols to highly fertile alluvial mollisols of Quaternary origin. Again, we chose sites at both ends of this soil gradient: primary forest, a 5 year old pasture, and a 20 year old pasture on oxisols, and a primary forest and 20 year old pasture on mollisols. The high fertility of the mollisols led to extensive clearing on these soils some time ago, thus recently converted pastures are rare to nonexistent. All five sites were within a few hundred meters of each other; the oxisol sites had a consistent and gentle relief (<10%) but continue to uplands with slopes of 40% or greater, while the mollisol sites occupy lowland areas of minimal relief. The two forest sites were typical of the region in their extraordinary species diversity; no species dominated the forest canopy. The three pasture sites were dominated by the common introduced grass *Panicum maximum*. All pastures were cleared by slash and burn methods, but none of the pastures had been burned since initial clearing; instead, weedy ingrowth in this region is typically controlled via cutting and the use of herbicides. None of the pastures had been fertilized.

Soil Collection and Analyses: Ten soil samples per site were collected from 0-10cm depth along random intervals within 100m transects. Soils were air dried, sieved at 2mm, and analyzed for total carbon, nitrogen, phosphorus, P fractions, texture and pH. Bulk density measurements were determined using an excavation method in which the volume of removed soil is measured by replacing it with a known volume of sand, and the soil removed is dried and weighed . Subsamples for total carbon and nitrogen were ground to a fine powder and analyzed using a combustion-reduction elemental analyzer (Carlo Erba, Inc). Total P analyses were performed by digesting 5g of sieved, air-dried soil in H_2SO_4 and H_2O_2 (Parkinson and Allen 1975); the digested solution was then analyzed for phosphate concentrations using a flow-injection autoanalyzer (Alpkem, Inc.).

Approximately 1g of soil from each sample was analyzed for soil P fractions using the modified Hedley fractionation technique described by Tiessen and Moir (1993). Briefly, the soil was subjected to a series of extractions in the following order: a resin extraction (in water), bicarbonate, 0.1M NaOH, 1M HCl, hot concentrated HCl, and a final peroxide/sulfuric acid digest (residue fraction). Digests were also done on the solution following bicarbonate, NaOH and HCl extractions, and organic P in each fraction was determined by difference. Resin and bicarbonate pools are the most labile forms of soil P, and their sum is often taken as a proxy for readily available (labile) P, as previous studies have shown that bicarbonate extractable P is well correlated with plant growth (Bowman et al. 1978; Levy and Schlesinger 1999). The 1M HCl fraction is thought to reflect primary mineral P (Ca-bound), while the remaining inorganic fractions are believed to distinguish P pools of varying recalcitrance, from weakly to strongly occluded (Tiessen and Moir 1993; Cross and Schlesinger 1995; Levy and Schlesinger 1999). In theory, the sum of all fractions at the end of the analyses should be equal to total soil P, but we chose to do separate digests for total P, as a check on the efficiency of the fractionation procedure. Phosphate concentrations in each fraction were determined using an Alpkem autoanalyzer. The protocol described by Tiessen and Moir (1993) requires that each fraction be neutralized via hand titration prior to Murphy-Riley colorimetric analysis, but we avoided this time consuming step by adjusting the normality of the sulfuric acid in the Alpkem color reagent. This adjustment is specific to each fraction, and calculated to achieve a mixture of sample and color reagent that creates the desired acidity at the detector (Lefer and Townsend submitted).

Finally, statistical analyses of differences among sites and along each chronosequence were performed using the one-way ANOVA procedure in SPSS v.10.0 (SPSS Inc., Chicago, IL). Where significant trends were found, further analyses of differences between each site were evaluated using the same software to perform a post-hoc Tukey's HSD test.

Results

Percent soil C and N were higher in all five Costa Rican sites than in any of the Brazilian sites (Table 1; Tukey HSD p<.05), but the higher soil bulk densities in Brazil indicate that total soil C and N pools were not consistently greater in Costa Rica (Table 1). Overall, total soil carbon values ranged from a maximum of 5.51 kg C / m^2 in the Costa Rican mollisol pasture, to a minimum of 2.00 kg C / m^2 in the oldest Brazilian entisol pasture. Total soil carbon was similar in all oxisols across both countries with the exception of the youngest Brazilian pasture, where soil C was significantly greater than in the other five oxisol sites (Table 1; Tukey HSD p<.05). Soil carbon pools decreased with pasture age in both Brazilian chronosequences (entisols: F=14.8, p<.001; oxisols: F=139.8, p<.001). In Costa Rica, % soil C values declined from forest to older pastures, but the total soil C pool did not differ along the oxisol chronosequence. In constrast, soil C was significantly greater in the 20 year mollisol pasture than in its forest counterpart (F=28.4, p<.001). Patterns in soil N followed those for soil C.

The range and patterns in soil P were more striking than for those in soil C and N. Total soil P varied by more than an order of magnitude across all eleven sites, from a maximum of 121.57 g/m^2 in the 20 year Costa Rican mollisol pasture, to a minimum of 6.46 g/m^2 in the 15 year Brazilian entisol (Table 1). Soil P values in the Brazilian sites were all relatively low, and those in the entisol pastures were much lower than values commonly reported in the literature (e.g. Cross and Schlesinger 1995). The effects of land use on total soil P were very different between the two countries. In Costa Rica, soil P was 47.95 g/m^2 in the 20 year oxisol pasture, an increase of 66% over the 28.97 g/m^2 measured in the adjacent oxisol forest (Table 1). A similar pattern was seen in the Costa Rican mollisols, where soil P in the 20 year old pasture was 75% greater than in its forest counterpart (Table 1). It's important to note, however, that the large increases in total soil P were due to the increases in bulk density that are typical as pasture soils are compacted (Veldkamp 1994); no significant differences in soil P concentration were found (Figure 2).

In Brazil, where soil C and N declined with pasture age, so did total soil P. Values in the two 15 year old oxisol and entisol pastures were 29% and 40% lower, respectively, than in the youngest pastures on each sequence (Table 1). The decline was particularly striking in the sandy entisols, where decreases in soil P – assumed to be a far less mobile element than C and N – were proportionately greater than those in the latter two elements (Table 1). Soil P concentrations (µg P / g soil) also declined significantly with pasture age in both Brazilian chronosequences (Figure 2).

Not surprisingly, many of the soil P fractions also changed significantly along the land use gradients, but the general patterns did not support the hypothesis presented in Figure 1. Data for each fraction from the modified Hedley procedure are presented in Table 1, but the overall patterns are more easily seen by grouping the fractions into four categories. These categories are: 1) non-occluded P, equal to the sum of resin extractable, bicarbonate inorganic and NaOH inorgnanic P fractions; 2) organic P (sum of all organic fractions); 3) occluded P, equal to the sum of the concentrated HCl and residue inorganic P fractions; and 4) primary mineral P (the 1M HCl fraction). These divisions are useful for separating "biological" vs. "geochemical" pools of soil P, as discussed by Cross and Schlesinger (1995). Some of the more surprising results from our analyses are shown in Figure 2, which depicts changes in these major P fractions along the four chronosequences. In both Brazilian sequences, despite significant declines in soil organic C and N with pasture age, soil organic P either increased (oxisols) or remained unchanged (entisols). As a percentage of total soil P, soil organic P increased markedly along both chronosequences, rising from 25% to 39% on the oxisols, and from 26% to 44% on the entisols (Figure 3). The declines in total soil P seen in each Brazilian sequence were due to large decreases in the non-occluded and occluded P fractions (Figure 2). The decline in occluded P was especially striking: this pool was 37% lower in the oxisols and 59% lower in the entisols as compared to the youngest pasture on each sequence.

In Costa Rica, organic P again increased significantly from forest to pasture in both chronosequences (Figure 2). Unlike Brazil, however, the major inorganic fractions did not decline with pasture age: both non-occluded and occluded P were not significantly different between the primary forests and oldest pastures on each soil type (Figure 2).

Discussion

Walker and Syers' (1976) model for P changes with soil development has led to a general notion that soil P in old tropical soils is mostly highly recalcitrant and immobile, a product of millions of years of intense weathering. In many respects, this general model has been proven accurate (e.g., Cross and Schlesinger 1995; Crews et al. 1995), but our data suggest that land use disturbances can cause rapid and substantial changes in soil P fractions. In particular, while there are clearly differences in soil P responses across major gradients in soil type, climate and management, forest-to-pasture conversion does seem to cause two general and surprising trends. First, organic forms of soil P increase with pasture age, or at the very least do not decline, even in sites where large declines in total soil organic matter are observed. Second, occluded soil P does not increase with pasture age, either in pool size or as a percentage of total soil P, and in sites were total soil P declines, much of that change appears to be from losses in the occluded fraction.

While not without recent precedence (Garcia-Montiel et al. 2000), this latter trend was quite unexpected, and suggests that the occluded fraction is not as recalcitrant as is typically assumed. Consider, for example, that the proportional declines in occluded P we observed in the Brazilian chronosequences were greater than those in soil carbon on both the entisols and the oxisols. The mechanisms behind these sharp declines in occluded P are still unknown, but we offer two possible explanations. First, sorption and occlusion of labile, inorganic P is stronger at lower pHs (Lopez-Hernandez and Burnham 1974, Afif et al. 1995, Guggenberger et al. 1996), and soil pH values typically increase by an order of magnitude or more following conversion of forest to pasture. This decline in acidity may cause a transfer of inorganic P from occluded to more labile forms. Second, soils under pasture are frequently subject to significant compaction, as evidenced by the increases in bulk density seen in our data and elsewhere (Veldkamp 1994, de Moraes et al. 1996). Such compaction can strongly limit oxygen availability in the soil, creating a more reducing environment (Chauvel et al. 1991, de Moraes et al. 1996), which could also lead to a net release of inorganic P from more to less occluded forms (Uehara and Gilman 1981).

Finally, physical transport of soil aggregates via erosion could also cause losses in total soil P, especially in coarser soils like the sandy entisols, and such a mechanism would produce significant declines in occluded P as it is the most abundant soil fraction. However, occluded P tends to increase with soil depth as a percentage of total P, suggesting that if erosion were a major factor in the entisol sequence, a proportional increase in occluded P across the chronosequence would be observed. This tendency could only be offset by proportional increases in new soil organic P that were even greater than those seen in the finer textured soils, which seems unlikely given the very strong declines in available nutrients, leaf area and productivity seen in the entisol sequence (Asner et al. 1999).

Thus, the declines in occluded P are most likely due to a net transfer of inorganic P out of this pool. Whatever the mechanism for such a transfer, its occurrence should create a pulse of P fertility as inorganic forms of P are liberated into plant-available forms. Yet, in the Brazilian chronosequences where the strong declines in occluded P were seen, we also observed large declines in non-occluded inorganic P (Figure 2), increases in foliar C:P ratios in the pasture grasses, and decreases in aboveground biomass and productivity (Asner et al. 1999). It therefore seems likely that the losses in productivity seen in both of the Brazilian pasture sequences were at least partly driven by a steady decline in P availability in soils that were P-poor prior to conversion. Finally, this apparent paradox in which there seems to be a source of new labile P from declines in occluded P, and yet no evidence for increases in P fertility, is deepened by the observation of increases in soil organic P with pasture age.

Organic forms of soil P are thought to be critical to tropical soil fertility, largely because labile, inorganic P is subject to occlusion by mineral surfaces of many tropical soils (e.g., Tiessen et al. 1994). Thus, one would expect an increase in soil organic P, along with a decrease in occluded P, to increase the P fertility of a given site. How then does one explain a pattern in which soil organic P increases and occluded P decreases, yet plant-available forms of P also decrease, and the plants show strong signs of increasing P limitation? Moreover, when expressed as a percentage of soil mass, we found that while soil organic C decreases in all four chronosequences, soil organic P increases in three of those four, and remains stable in the Brazilian entisols (Figure 4). Garcia-Montiel et al. (2000) also reported significant increases in soil organic P, but in their sites, SOC did not decline with pasture age and they attributed the change in organic P to new inputs of organic matter from productive, shallow rooted grasses. However, in our Brazilian sites soil organic C:P ratios decline sharply in all four chronosequences and the dynamics of soil organic P are clearly decoupled from those in total organic matter, therefore the patterns in soil organic P cannot be due only to changes in organic matter inputs.

We believe that changes in the composition and/or function of the soil microbial community may be driving many of the patterns we observed. Since all forms of inorganic P either remain constant or decline with pasture age in our sites while organic P increases, it is clear that the rate at which organic P is mineralized must decline. In other words, the increases in organic P are not simply due to new inputs because they are not matched by increases in total organic matter. Instead, the rate at which organic P is converted to inorganic forms must decrease to produce the patterns we report. P mineralization can occur via the production of extracellular phosphatases by plant roots (Speir and Cowling 1991), therefore a change from forest to pasture vegetation may be partly responsible for the decline in mineralization rates. However, P mineralization by both fungal and bacterial communities is enormously important, and several recent lines of evidence suggest that these communities may be heavily affected by forest-to-pasture conversion.

Two possibilities exist to explain how an altered soil microbial community might create the patterns seen in our data. First, just as it does for the more readily observed organisms in the ecosystem, it is quite likely that conversion from forest to pasture creates major shifts in soil microbial communities. Until quite recently, our ability to characterize microbial communities was quite limited, but the advent of modern molecular techniques now allows much more comprehensive descriptions of community structure (Pace 1997), and we now know that the conversion of primary forest to pasture can sharply alter the composition of the belowground microbial community (Nüsslein and Tiedje 1999; Borneman and Triplett 1997; Atlas et al. 1991). For example, Nüsslein and Tiedje (1999) showed that a change from forest to pasture in Hawaii led to a significant change in the dominant bacterial phyla, and resulted in a 49% shift in overall microbial composition. In addition, microbial DNA analysis has shown substantial differences in community composition between forest and pasture sites in Brazil (Borneman and Triplett 1997), with forest sites displaying greater species diversity and redundancy in physiological groups than disturbed pasture sites. A number of studies also suggest that conversion of natural vegetation to used land, as well as agricultural intensification, leads to decreases in microbial biomass, and shifts in the relative abundance of fungal and prokaryotic microorganisms (Henrot and Jacobson 1994; Luizao et al. 1992). Changes in community structure such as those described above do not necessarily equate to a change in function, but it seems unlikely that community changes of such magnitude would not alter functions such as the mineralization of organic P. In this specific case, the facts that fungal communities seem especially sensitive to land use changes (Janos 1980) and that plant-fungal associations play a major role in tropical P cycling (Parker 1994), make it all the more likely that any community shift could alter P mineralization.

Second, it is possible that the primary limiting resources for microbial activity also change along the land use sequences. Recent evidence from the Costa Rican oxisol forest site shows that microbial processing of both labile and more recalcitrant forms of soluble carbon, including dissolved organic carbon leached from forest litter, is strongly limited by P availability (Cleveland et al. submitted). However, despite the increases in organic P and relatively constant levels in non-occluded P between forest and pasture, preliminary data show that microbial biomass and phosphatase activity decline along the same sequences. In part, this pattern may be due to community shifts such as described above, but changes in the forms and quality of soil carbon, as well as in the availability of other nutrients, may also be important. One intriguing possibility concerns the effects of nitrogen availability on phosphatase production. The N requirement for producing phosphatase enzymes is surprisingly high (Treseder and Vitousek 2001), and while N frequently cycles in relative excess in many tropical forests (Vitousek 1984; Matson et al. 1999), N availability often declines with pasture age (Neill et al. 1999). Thus, it is possible that changes in carbon substrates and lowered N availability may constrain phosphatase production in older pastures, and therefore decrease P mineralization, leading to an increase in the organic P pool. In addition, Saa et al. (1993) report significant declines in phosphatase activity following forest burning. Finally, if other resources decline significantly with pasture age, the relative importance of P to the microbial community may also decline.

The fact that liberation of P from organic matter is highly dependant on specific enzymes helps explain how one could find very different trends in soil organic P and soil organic C (Figure 4). In addition, given that microbial communities in many tropical forests may be P limited (Hobbie and Vitousek 2000; Cleveland et al., submitted), it is possible that any pulse in labile P from the loss in occluded fractions is rapidly immobilized by microbial communities. If production of phosphatases is also increasingly constrained in older pastures, either by community or resource shifts, then a pattern in which organic P increases or remains stable, but P fertility still declines, becomes plausible.

Finally, we wish to stress that while we did find some surprisingly consistent patterns among our sites, the enormous variation in climate, soil types, and management strategies across the tropics must be accounted for in predicting the biogeochemical effects of land use change. This statement is clearly true for patterns in soil carbon pools following land conversion (Davidson et al. 1995). In the case of P dynamics, the combination of our data and those reported by Garcia-Montiel et al. (2000) suggests to us that there are some general responses, but that they likely vary along gradients from high to low environmental and/or management stress on the converted lands (Figure 5). At the former extreme, in which there are more pronounced dry seasons, poorer soils, frequent pasture burning and higher grazing loads, we would predict losses in total soil P, but that those losses would be from inorganic rather than organic fractions (Figure 5a). Even in these highly stressed sites, we suggest that the effects of land conversion on soil microbial communities – in all probability the strongest in such sites – can lead to increases in soil organic P even when total soil carbon pools decline. At the other end of the spectrum, conversion to pastures on more fertile soils, with greater rainfall and much lighter management, total soil P may actually increase from forest to pasture, and again, this increase will be due to an increase in organic forms of P.

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Figure Legends

Figure 1. Hypothetical model for changes in soil P fractions following conversion of moist tropical forest to cattle pasture, where declines in total soil organic matter (SOM) are seen. We predicted that P mineralized during the loss of SOM would be increasingly vulnerable to occlusion by mineral surfaces of soils, because of both decreased SOM content and periods of relatively low plant uptake immediately following burning or during the drier months. Thus, over time an artificially elevated rate of P occlusion would further exacerbate P limitation, creating declines in plant available and organic P and plant production, which in turn would feed back to even greater P impoverishment and overall pasture degradation.

Figure 2. Non-occluded (dotted line), organic (solid line), occluded (small dashed line) and total (large dashed line) soil P with pasture age along two Brazilian and two Costa Rican chronosequences. All values are sums of fractions from a modified Hedley fractionation procedure as described in the text. Non occluded P is equal to the sum of resin, bicarbonate and NaOH inorganic fractions; occluded P is the sum of the concentrated HCl and residue inorganic fractions; and organic P is the sum of bicarbonate, NaOH and concentrated HCl organic fractions. Total soil P here is the sum of all fractions from the Hedley analysis, thus there are differences between the total P

values shown here and those in Table 1, which are derived from a separate digest. The sum of the Hedley fractions is used in this figure to allow a more direct comparison to changes in the individual fractions. Significant differences (Tukey HSD, $p < .05$) along the chronosequence for a given fraction are denoted by different letters that are specific to each fraction: a-c = total P; d-f = occluded P; g-h = organic P; j-l = non-occluded P. Bars indicate standard errors; where error bars cannot be seen they are smaller than the label box.

Figure 3. Non-occluded, organic, and occluded soil P in six Brazilian and five Costa Rican sites expressed as a percentage of total soil P in each site.

Figure 4. Relative changes in soil organic C (dashed line) and P (solid line) along each of the four chronosequences. Values are relative to the youngest site in each sequence, and are taken from data that measured each variable as a concentration (% soil C. µgP/g soil).

Figure 5. Generalized predictions for changes in major soil P fractions following conversion of moist tropical forest to cattle pasture in sites with high (A) or low (B) environmental and/or management stress. The high stress end of the spectrum would include a prolonged dry season, low fertility soils, frequent pasture burning and heavy

grazing loads. A low stress site would have high rainfall and a minimal dry season, more fertile soils, no repeated burning and light grazing levels.

Table 1. Surface soil carbon, nitrogen, phosphorus, phosphorus fractions, texture, pH, and bulk density for six Brazilian and three Costa Rican pastures, and two Costa Rican primary forests. Phosphorus fractions are those defined by the modified Hedley technique as described in Tiessen and Moir (1993).

	Brazilian Sites					
	2 yr oxisol pasture	7 yr oxisol pasture	15 yr oxisol pasture	1 yr entisol pasture	7 yr entisol pasture	15 yr entisol pasture
Texture (sand/silt/clay)	37/3/60	39/2/59	40/5/55	89/4/7	92/2/5	91/4/5
pH	5.30	5.40	5.00	5.60	5.60	5.30
Soil C (%)	4.35	2.28	2.02	1.85	1.54	1.40
Soil N (%)	0.32	0.19	0.15	0.12	0.09	0.08
Soil P (ug/g)	173.80	82.20	97.40	75.30	52.30	45.20
Bulk density	1.20	1.53	1.52	1.44	1.43	1.43
Total C (kg/m2)	5.22	3.49	3.07	2.66	2.20	2.00
Total N (kg/m2)	0.38	0.29	0.23	0.17	0.13	0.11
Total P (g/m2)	20.86	12.58	14.80	10.84	7.48	6.46
P Fraction (ug/g)						
Resin Pi	13.89	7.53	7.79	6.84	3.39	1.43
Bicarb Pi	5.55	1.76	2.06	2.53	0.63	0.16
Bicarb Po	4.70	3.92	7.47	4.93	3.40	2.81
1M HCl	44.36	0.97	1.36	1.11	1.33	0.86
NaOH Pi	33.69	9.62	11.51	10.88	10.06	3.47
NaOH Po	22.33	20.31	30.95	12.3	13.5	11.39
Conc. HCl Pi	45.52	38.16	28.83	15.3	9.12	6.92
Conc. HCl Po	18.62	12.22	14.94	3.62	3.15	2.98
Residue	39.96	33.78	34.82	22.66	14.82	9.60

Table 1 continued

	Costa Rican Sites				
	oxisol forest	5 yr oxisol pasture	20 yr oxisol pasture	mollisol forest	20 yr mollisol pasture
pH	5.43	5.08	5.14	6.01	5.91
Soil C (%)	6.45	5.41	4.96	6.78	5.57
Soil N (%)	0.56	0.47	0.43	0.58	0.48
Soil P (ug/g)	557.14	566.45	639.33	1051.43	1227.99
Bulk density	0.52	0.64	0.75	0.66	0.99
Total C (kg/m2)	3.35	3.46	3.72	4.47	5.51
Total N (kg/m2)	0.29	0.30	0.32	0.38	0.48
Total P (g/m2)	28.97	36.25	47.95	69.39	121.57
P Fraction (ug/g)					
Resin Pi	4.22	4.14	2.02	8.86	9.42
Bicarb Pi	3.37	3.20 (0.07)	2.70	5.13	7.41
Bicarb Po	13.70	16.30	20.34	27.64	33.49
1M HCl	1.89	1.45	1.93	23.29	53.66
NaOH Pi	53.87	69.57	56.67	76.31	161.90
NaOH Po	77.50	102.64	106.88	167.18	217.54
Conc. HCl Pi	166.96	148.99	189.80	209.37	199.53
Conc. HCl Po	18.99	12.22	41.48	38.71 (3.67)	37.97
Residue	155.42	116.78	198.83	369.98	378.85

Figure 1

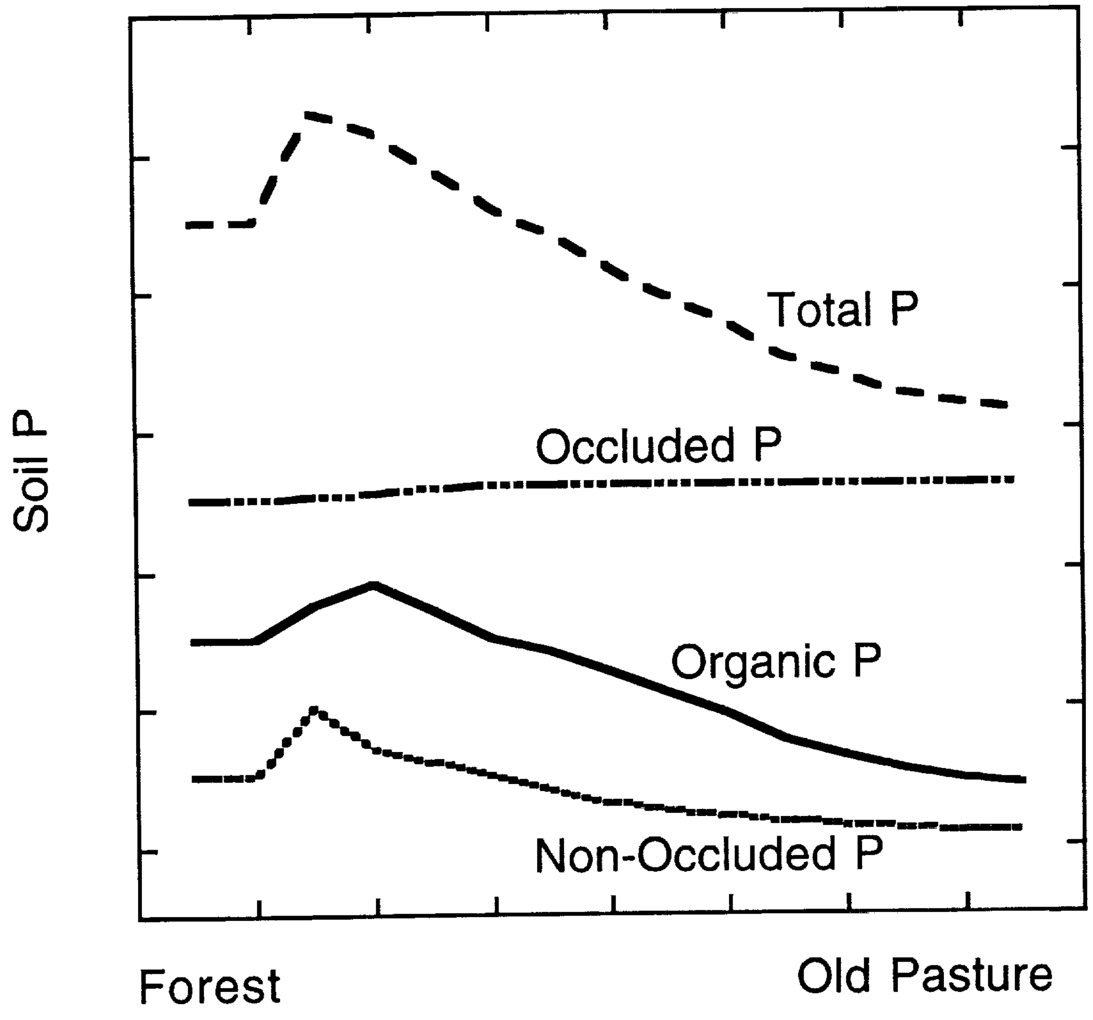

Total P
Occluded P
Organic P
Non-Occluded P
Soil P
Forest
Old Pasture

Figure 2

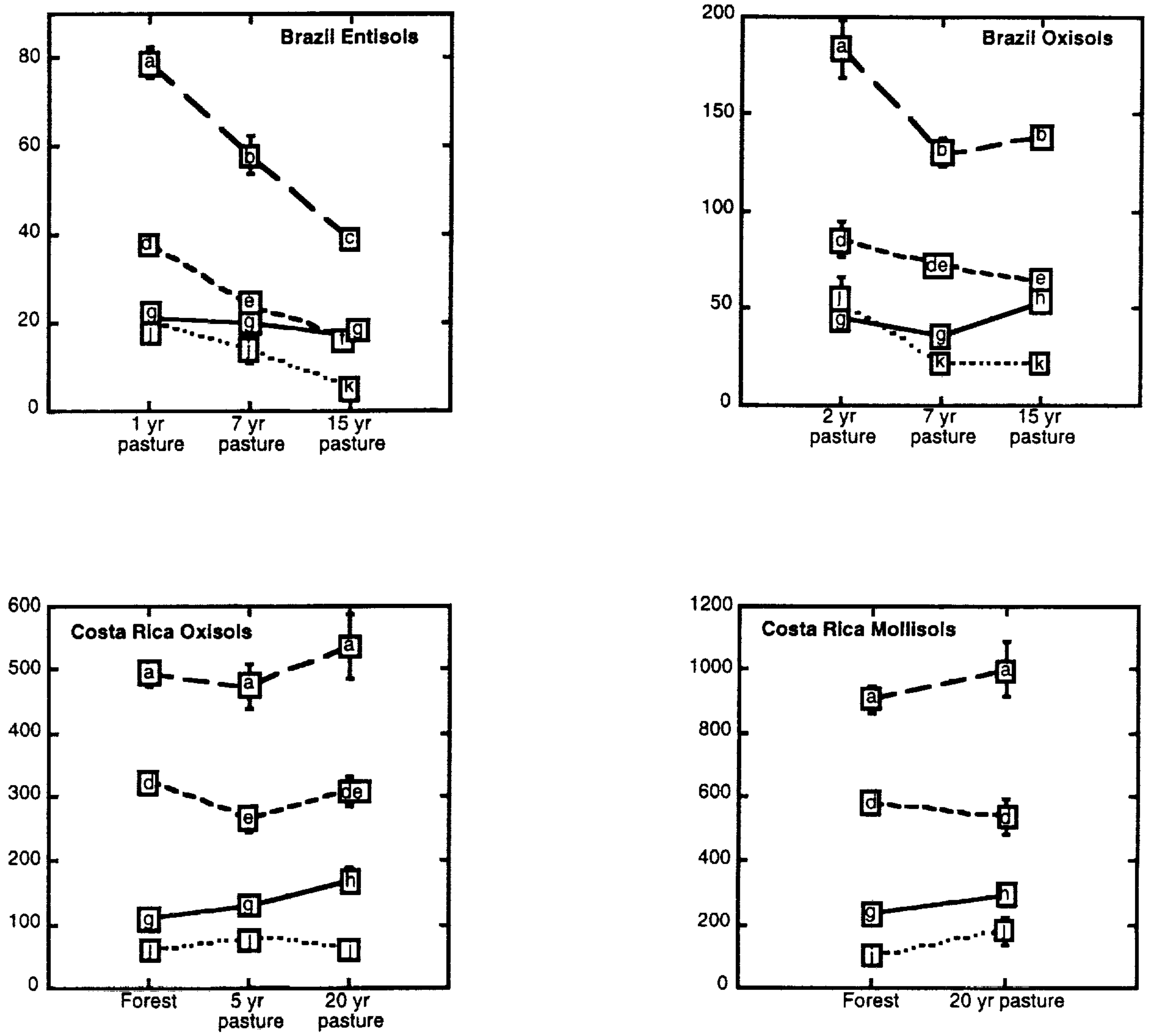

Brazil Entisols
0
20
40
60
80
1 yr pasture
7 yr pasture
15 yr pasture
a
b
c
d
e
f
g
g
g
j
j
k
Brazil Oxisols
0
50
100
150
200
2 yr pasture
7 yr pasture
15 yr pasture
a
b
b
d
de
e
j
g
g
h
k
k
Costa Rica Oxisols
0
100
200
300
400
500
600
Forest
5 yr pasture
20 yr pasture
a
a
a
d
e
de
g
g
h
i
i
i
Costa Rica Mollisols
0
200
400
600
800
1000
1200
Forest
20 yr pasture
a
a
d
d
g
h
i
j

Figure 3

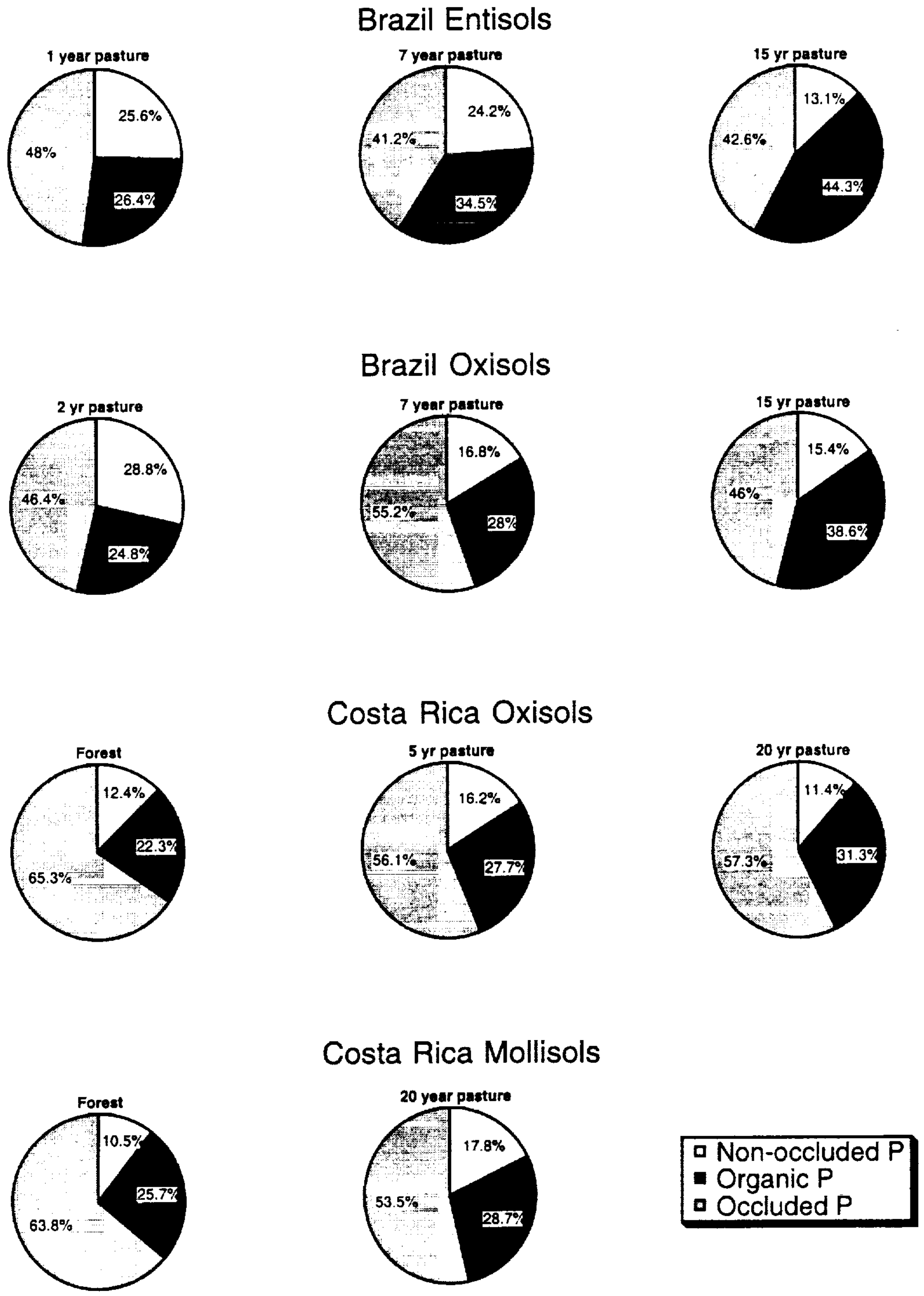

Brazil Entisols
1 year pasture
25.6%
26.4%
48%
7 year pasture
24.2%
34.5%
41.2%
15 yr pasture
13.1%
44.3%
42.6%
Brazil Oxisols
2 yr pasture
28.8%
24.8%
46.4%
7 year pasture
16.8%
28%
55.2%
15 yr pasture
15.4%
38.6%
46%
Costa Rica Oxisols
Forest
12.4%
22.3%
65.3%
5 yr pasture
16.2%
27.7%
56.1%
20 yr pasture
11.4%
31.3%
57.3%
Costa Rica Mollisols
Forest
10.5%
25.7%
63.8%
20 year pasture
17.8%
28.7%
53.5%
□ Non-occluded P
■ Organic P
▨ Occluded P

Figure 4

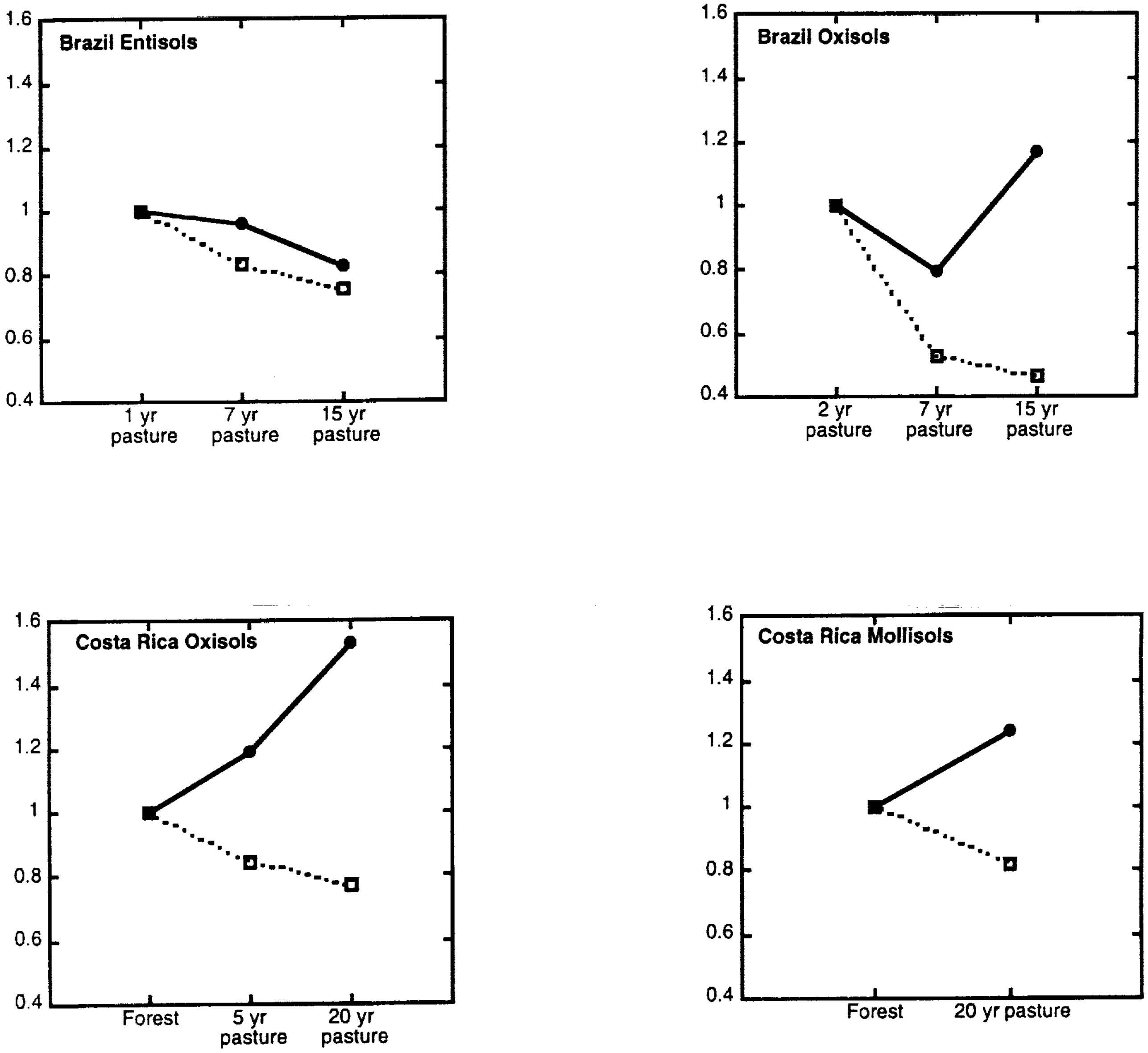
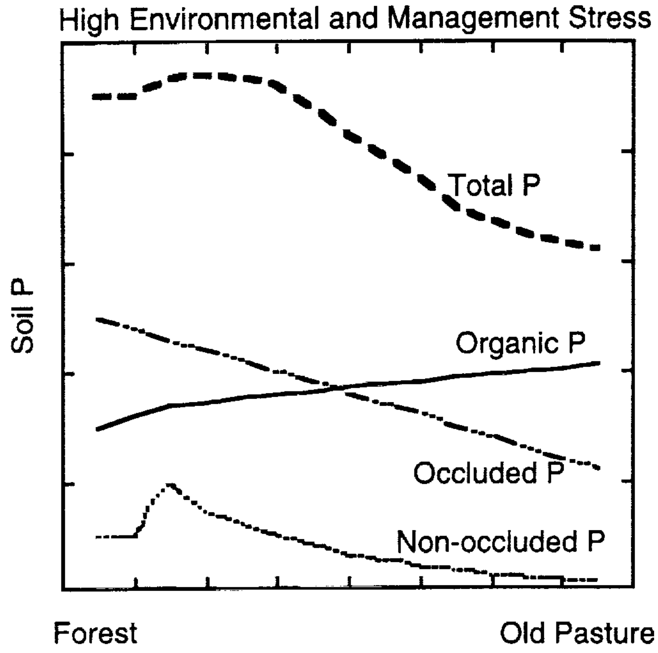
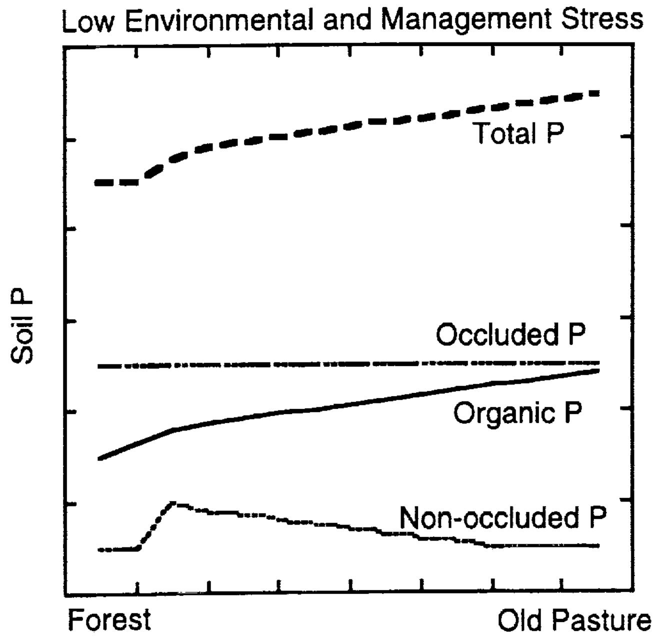

Brazil Entisols
1.6
1.4
1.2
1
0.8
0.6
0.4
1 yr pasture
7 yr pasture
15 yr pasture
Brazil Oxisols
1.6
1.4
1.2
1
0.8
0.6
0.4
2 yr pasture
7 yr pasture
15 yr pasture
Costa Rica Oxisols
1.6
1.4
1.2
1
0.8
0.6
0.4
Forest
5 yr pasture
20 yr pasture
Costa Rica Mollisols
1.6
1.4
1.2
1
0.8
0.6
0.4
Forest
20 yr pasture

Figure 5


High Environmental and Management Stress
Total P
Organic P
Occluded P
Non-occluded P
Soil P
Forest
Old Pasture


Low Environmental and Management Stress
Total P
Occluded P
Organic P
Non-occluded P
Soil P
Forest
Old Pasture