# **Chapter 13 Phosphorus Nutrition of Forest Plantations: The Role of Inorganic and Organic Phosphorus**

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## 13.1 Introduction

Forests are an important land use throughout the world. Forests covered 3,952,925,000 ha in the world in 2005, which is approximately 30% of the earth's total land surface area (FAO 2009). Forests are vital to the world's ecological, social, and economic health. Forests produce a large portion of the earth's oxygen and sequester a substantial portion of its carbon, and thus play a major role in regulating climate change. Forests preserve biodiversity and provide habitats for much of the world's plants, animals, and microorganisms. Today, wood from forests is a major economic commodity, serving as the raw material for building materials, paper, packaging, and fuelwood. Fuelwood remains the single largest use

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of wood in the world today (FAO 2009). In the near future, wood from forests will provide much of the raw material for a wide range of novel bio-based fuels and materials (Kimbrel et al. 2009).

Because of the continued increase in the worlds' population and the expanding use of wood for both traditional and novel products, the demand for wood will increase rapidly in the future (FAO 2009). However, in both temperate and tropical regions large amounts of forest land continue to be lost as they are converted to other land uses such as agricultural crops, pasture, and urban development (Brown et al. 2006; Jauregui 2007; Weir and Gries 2002). Total forest area in the world declined by 7,317,000 ha between 2000 and 2005 (FAO 2009). In addition, because of increased emphasis on noncommodity values of forests such as biodiversity, recreation, watershed protection, and wildlife habitat, the timber harvests from native forests are increasingly being restricted in many parts of the world (Sedjo and Botkin 1997).

In response to the increasing demand for wood from a shrinking forested landbase, the paradigm for forest management in many regions of the world has been shifting from a hunt and gather approach, whereby mature timber is harvested from extensive areas with little management, to an agronomic model whereby limited areas of forests best suited to production are planted and managed intensively for commodity production (Binkley 1997; Fox 2000; Fox et al. 2007c; Sedjo and Botkin 1997). Biodiversity, wildlife habitat, and other nontimber management goals can be integrated into plantation management systems, particularly when a landscape perspective is employed (Brown et al. 2006).

The use of intensive management in forest plantations to increase wood production and decrease rotation lengths can help meet the increasing demand for wood and fiber in the world, while still preserving large areas of native forests for other uses because more wood can be grown on less land (Sedjo and Botkin 1997). As an example, productivity of pine plantations in the southern USA more than doubled and the rotation length was cut in half between 1950 and 2000 as a result of improved silvicultural practices (Fox et al. 2007c). Planted forests currently produce approximately 1.4 million m<sup>3</sup> per year, which is approximately one-third of the world's industrial wood. This could increase to more than 2.1 million m<sup>3</sup> per year, which would be about one-half of the worlds' industrial timber by 2030 if more intensive management regimes were implemented (FAO 2009). Theoretical models (Battaglia et al. 2004; Landsberg et al. 2001; Stape et al. 2004b) and empirical field trials (Allen et al. 2005; Birk and Turner 1992; Borders and Bailey 2001; Ferreira and Stape 2009; Jokela et al. 2000; Gonçalves et al. 2008; Rubilar et al. 2008b; Stape et al. 2008; Trichet et al. 2009) show that these growth increases are possible in plantation forests in many regions of the world. Most forests occur on soils that are less fertile than soils used for agronomic crops and, consequently, deficiencies of P, either alone or in combination with N, limit growth of most forests. Therefore, fertilization with phosphorus alone or in combination with other nutrients is needed in many forests to achieve high levels of productivity (Fox et al. 2007a; Gonçalves et al. 2008; Rubilar et al. 2008a; Stape et al. 2004a, 2006; Trichet et al. 2009).

The objective of this chapter is to review the impact of phosphorus fertilization on growth of forest plantations and to discuss phosphorus dynamics in forest ecosystems. This review highlights the importance of both inorganic P ( $P_i$ ) and organic P ( $P_o$ ) in tree nutrition, and the transfer of P between these two pools. We discuss how trees and their associated mycorrhizas can modify the soil and increase the solubility of both  $P_i$  and  $P_o$ , increase phosphatase activity and mineralization of  $P_o$ , and increase uptake of both  $P_i$  and  $P_o$ . There are several reviews that also discuss aspects of P nutrition and fertilization in forest trees (Ballard 1984; Comerford and de Barros 2005; Fox et al. 2007a; Gonçalves and Benedetti 2004; May et al. 2009; Trichet et al. 2009) and organic P in soils (Condron et al. 2005; Chen et al. 2008).

#### **13.2** Phosphorus Fertilization of Forest Plantations

Chronically low levels of available soil nutrients, principally phosphorus and nitrogen, are the most important factors limiting forest growth in many areas of the world (Fox et al. 2007a; Gonçalves and Benedetti 2004; May et al. 2009; Rubilar et al. 2008b; Trichet et al. 2009). On an annual basis, over 100 kg ha<sup>-1</sup> of N and 10 kg ha<sup>-1</sup> of P must be available for fully stocked *Pinus* stands to maintain the high leaf area index levels necessary for maximum volume production (Battaglia et al. 2004; Ducey and Allen 2001). Greater amounts of nutrients are needed in faster growing species such as eucalyptus (Barros et al. 2004). However, most forest soils are unable to provide the levels of available nutrients required to maintain rapid growth of plantations (Comerford and de Barros 2005; Fox et al. 2007a; Miller 1981). Reduced leaf area and decreased growth efficiency occur in many forest plantations because of low soil nutrient availability, which results in poor growth and productivity (Albaugh et al. 1998; Vose and Allen 1988). In addition, nutrient limitations may develop in intensively managed forest plantations that might not develop in natural stands when other silvicultural treatments (e.g., tree breeding, vegetation control, and tillage) are used to increase crop tree growth, which also subsequently increases nutrient demand (Fox et al. 2007a).

Remarkably, little fertilization is conducted in naturally regenerated forests, even on soils where nutrient availability severely limits tree growth (FAO 2006). In contrast, forest fertilization is a widespread silvicultural practice in forest plantations in many regions of the world (Fox et al. 2007a; Gonçalves and Benedetti 2004; May et al. 2009). In the southern USA over 486,000 ha of pine plantations were fertilized with P or N+P in 2004 (Albaugh et al. 2007). In the Pacific Northwest of the USA, operational fertilization is also a common treatment with about 40,000 ha of forest land fertilized annually (Fox et al. 2007b). The main tree species fertilized in the southern USA are *Pinus taeda* and *P. elliottii*, and in the Pacific Northwest the main species is *Pseudotsuga menziesii*. Extensive plantations of *Pinus pinaster* occur in the Landes de Gascogne region of southwest France and P fertilization is a common practice in this region (Trichet et al. 2009). In Australia, approximately 173,000 ha of eucalyptus plantations including *Eucalyptus globulus*,

*E. nitens, E. dunni* and 84,000 ha of pine plantations including *Pinus radiata, P. pinaster, P. caribaeae*  $\times$  *P.elliottii* are fertilized annually (May et al. 2009). In South America, P fertilization of eucalyptus plantations is also widely used (Gonçalves and Benedetti 2004; Rubilar et al. 2008b). In the USA, P is most commonly applied as diammonium phosphate (DAP), although in the past triple superphosphate and ground-rock phosphate were commonly used P sources in forestry (Albaugh et al. 2007). In other regions of the world, other sources of P such as ground rock phosphate or blends of nitrogen, P, and potassium (NPK) such as 6:30:6 are more commonly used. For example, in Australia and South America, blends of NPKS (NPK plus sulfur) are more widely used than DAP (Rubilar et al. 2008b; May et al. 2009). In several reports, the source of the P applied seems to be less important than the rate applied (Trichet et al. 2009).

The benefits of P fertilization on forest soils that have severe P deficiencies have long been recognized (Pritchett et al. 1961). Volume growth gains in plantations of Pinus radiata (Ballard 1978a), eucalyptus (Barros et al. 2004), Pinus taeda (Gent et al. 1986), Pinus elliottii (Pritchett and Comerford 1982), and Pinus pinaster (Trichet et al. 2009) ranging from 20% to more than 100% are common on severely P-deficient soils following P fertilization near the time of planting. The magnitude of the growth response can vary widely depending on the species, soil type, understory competition, and climate (Comerford and de Barros 2005). More remarkable than the magnitude of the response is the longevity of the response to P fertilization in many forest plantations on P-deficient soils. The response to a single application of 56 kg  $ha^{-1}$  of P may last for 20 or more years (Pritchett and Comerford 1982; Comerford and de Barros 2005). There are several reports where a single application of P in one rotation continued to increase growth in subsequent rotations (Ballard 1978a; Comerford et al. 2002; Crous et al. 2007; Everett and Palm-Leis 2009; Gentle et al. 1986). Turner et al. (2002) have found that the response to P fertilization in Pinus radiata in Australia may last more than 50 years. The efficient cycling of nutrients in forest ecosystems contributes to these long-term P fertilization responses (Attiwill and Leeper 1987; Binkley 1986; Jordan 1985).

In intermediate-aged stands of both pine and eucalyptus, little response is typically observed to additions of P alone, except on the P-deficient sites described above where P was not added at the time of planting (Barros and Novais 1996; Fox et al. 2007a; Rubilar et al. 2008b). However, in many pine plantations in the southern USA, by the time of crown closure, the tree's potential to use both P and N is typically greater than the available soil supply, resulting in restricted leaf area development and growth (Allen et al. 1990; Fox et al. 2007a). These stands are generally very responsive to additions of P and N at this time in the rotation. In the majority of stands, both P and N are deficient, and the growth response following fertilization is much greater when both P and N are applied (Fox et al. 2007a). Results from an extensive series of intermediate-aged fertilizer trials in *Pinus taeda* stands established throughout the southern USA indicate that growth gains averaging  $3.5 \text{ m}^3 \text{ ha}^{-1}$  per year over an 8-year period occur following a one-time application of 224 kg ha<sup>-1</sup> N and 28 kg ha<sup>-1</sup> P (Fox et al. 2007a). The growth

response was less than half of this when either N or P were added alone. Over 85% of the stands fertilized were responsive to additions of N+P during this stage of stand development. The need for balanced fertilization with both P and N has also been shown in *Pinus radiata* in Chile (Rubilar et al. 2008b) and Australia (May et al. 2009).

Identification of forest plantations in need of P fertilization can be based on soil parent material, soil type, soil analysis, and foliage analysis (Comerford and de Barros 2005; May et al. 2009). In the Lower Coastal Plain of the Atlantic and Gulf Coasts of the USA, poorly drained, clavey Ultisols tend to be severely P deficient (Fox et al. 2007a). Along the Gulf Coast, well-drained clayey to loamy soils on the Citronelle and associated geologic formations have also been found to be P deficient (Allen and Lein 1998). The likelihood of response to P fertilization in New South Wales, Australia, can be determined on the basis of parent material (Turner et al. 1996). In some regions, P deficiencies are so widespread that all soils are considered P deficient, and P fertilization is a routine practice in all plantations. This is the case for eucalyptus plantations in South America and pine plantations in South Africa, where almost all upland soils tend to be P deficient (Attiwill and Adams 1996; Donald et al. 1987). Where soil P deficiencies are less widespread, soil analysis for P has been found to be a reliable tool for diagnosis of nutrient deficiencies in plantation forests (Ballard 1974; Wells et al. 1986). However, the critical concentration of available P varies between soils, extracting solutions, and plant age (Barros and Novais 1996). The critical value for extractable soil P in the A horizon, below which a fertilizer response is expected in *Pinus taeda* in the southern USA, is 4–6  $\mu$ g g<sup>-1</sup> based on the Mehlich-3 extraction procedure (Wells et al. 1986). The critical concentration of Bray-1-extractable P in the A horizon for *Eucalyptus grandis* in Brazil varies from 17 to 89  $\mu$ g g<sup>-1</sup>, depending on the clay content and P sorption maximum (Barros and Novais 1996). CaCl<sub>2</sub>-extractable P has been used to identify sites supporting *Eucalyptus globulus* and *E. nitens* in Australia that require P fertilization (Mendham et al. 2002). Foliage analysis is also widely used to evaluate the need for P fertilization in forests (Colbert and Allen 1996; Lambert and Turner 1998). Critical values for foliar P concentrations vary by species and range from 0.09 mg  $g^{-1}$  for *Pinus elliottii*, 0.11 mg  $g^{-1}$  for *Pinus taeda* (Allen 1987; Everett and Palm-Leis 2009; Wells et al. 1986), and 0.14 mg  $g^{-1}$  in Pinus radiata (Will 1985). Critical values of foliar P in more demanding species such as eucalyptus are generally much higher, ranging up to 0.4 or 0.5 mg  $g^{-1}$ (Attiwill and Adams 1996; Dell et al. 2001). Total P concentrations in litter have also been used to diagnose P deficiencies in *Pinus radiata* stands in southeast South Australia (May et al. 2009).

Stand attributes such as basal area and site index have also been used to determine whether nutrient deficiencies exist in forests (Duzan et al. 1982). Linkages among nutrient availability, leaf area, and forest productivity (Albaugh et al. 1998) also permit the use of leaf area as a diagnostic tool (Fox et al. 2007a; May et al. 2009). Differences between a stand's current leaf area and its potential leaf area can be used to estimate responsiveness to nutrient additions. For example, the leaf area index of a fully stocked *Pinus taeda* stand in the southern USA should be 3.5 or greater. If the leaf area index is less than this, the stand is probably in need of N+P fertilization unless other obvious problems have altered leaf area (e.g., fire, ice damage, insect attack, disease). The probability and magnitude of response will be greater in stands with lower leaf area. Remote sensing techniques using Landsat satellite imagery have been developed that can accurately determine leaf area in southern pine stands (Flores et al. 2006). Leaf area is used in a similar manner to diagnose stands of both pine and eucalyptus in Australia that are nutrient deficient (May et al. 2009).

#### **13.3** Phosphorus Dynamics in Forest Ecosystems

It is somewhat ironic that tree growth is commonly limited by P because the absolute quantities of P in forests soils are usually large and appear sufficient to support robust tree growth. However, the pools of labile P in the soil solution are small and typically growth-limiting. The concepts of soil quantity, intensity, and buffer capacity help to elucidate the processes in forest soils that determine plant-available P present in soil solution (Fig. 13.1). In forest soils, both chemical reactions and biological processes determine the buffer capacity for P and include dissolution/precipitation, mineralization/immobilization, and ligand exchange reactions (Fox 1995; Pierzynski et al. 2005).

Trees have evolved a variety of mechanisms to increase P availability and uptake in low-P soil environments, including changes in root morphology and architecture, mycorrhizal symbiosis, preferential root growth into more fertile zones in the soil, higher phosphatase activity in the rhizosphere, and the secretion of low molecular weight organic acids (Vance et al. 2003). The ability of trees to increase P availability in soils was well documented in a series of studies in which *Pinus radiata* was planted on pastures in New Zealand (Chen et al. 2008). Afforestation of grassland with *Pinus radiata* improved P availability in the topsoil due to enhanced



mineralization of organic P, improved solubility of P caused by root and microbial exudates, effects of mycorrhizas, and changes in soil moisture and temperature regimes (Chen et al. 2008).

#### 13.3.1 Phosphorus Pools and Cycling in the Forest Floor

Forest soils differ from agricultural soils in several significant ways that affect P availability and cycling in forest ecosystems (Comerford and de Barros 2005). However, the most obvious and important difference is the presence of a welldeveloped forest floor (O horizon) in forests that is typically absent in agricultural soils (Pritchett and Fisher 1987). The forest floor is a major pool of nutrients, including P, in forest ecosystems. Phosphorus content in the forest floor varies from less than 10 kg ha<sup>-1</sup> to more than 300 kg ha<sup>-1</sup> depending on the climate, soil type, species, and age of the forest (Pritchett and Fisher 1987). The importance of the forest floor to tree nutrition in forest ecosystems is well documented (Berg and Laskowski 2006). For example, repeated removal of litter from the forest floor to use as animal bedding in Germany during the 1800s led to well-documented site degradation in many forests (Evers 1991). There are examples in several parts of the world where windrowing or piling during site preparation, which removed the forest floor, along with slash and logging debris to facilitate planting caused severe deficiencies of N, P and possibly other nutrients, which decreased forest growth (Ballard 1978b; Fox et al. 1989; Jonard et al. 2009; Merino et al. 2003). The importance of the forest floor is highlighted by the fact that it has been shown that whole-tree harvesting that removes all the aboveground tree biomass, but leaves the forest floor intact, will have little impact of growth of the subsequent stand (Johnson and Todd 1998; Fox 2000).

The mass and nutrient content of the forest floor is determined by the competing process of litterfall input and decomposition (Berg and Laskowski 2006). In most forests, decomposition rates are less than litterfall and consequently the forest floor builds up over time (Richter et al. 2006). In general, hardwood litter decomposes and releases P faster than pine litter (Fisher and Binkley 2000). Well-drained soils in tropical regions supporting hardwood forests tend to have smaller forest floors with less P accumulation, whereas coniferous forest in temperate regions with poorly drained soils tend to accumulate large forest floors with more P. Forest management practices such as fertilization that increase the growth rate of the forest often increases the mass of the forest floor because of increased litterfall from stands with higher leaf area. Harding and Jokela (1994) reported that P fertilization significantly increased the size of the forest floor and the nutrient pools in *Pinus elliottii* stands. Similar results were observed in a study with *Pinus taeda* in North Carolina (Sanchez 2001).

There are substantial temporal variations in the mass and P content of the forest floor due to disturbances in the forest. Fire can consume the forest floor and oxidize the organic matter (Flinn et al. 1979). However, even in intense fires, much of the P remains in the ecosystem and its release during the fire can increase P availability, whereas N can be lost even in relatively low intensity fires (Fisher and Binkley 2000; Flinn et al. 1979). Harvesting also affects P dynamics in the forest floor. Increased temperature and moisture in the forest floor following tree harvest accelerate decomposition and mineralization of organic P. The higher decomposition rate coupled with the lack of litterfall inputs generally results in a significant decrease in the mass of the forest floor within a few years of harvest. This accelerated decomposition of the forest floor and mineralization of organically bound nutrients causes a substantial flush of nutrients into the soil known as the Assart Effect (Fisher and Binkley 2000). This results in a substantial increase in growth of vegetation for the first few years after a major disturbance such as harvest or fire. After the readily decomposed and mineralized portion of the forest floor is gone, available nutrients decline and growth rates drop. Over time, the forest floor increases again as the stand develops and the reserves of nutrients are built up again (Richter et al. 2006). This temporal variation in forest floor dynamics and associated pools of labile nutrients in the soil is an important aspect of nutrient cycling in forest ecosystems that is different from most agricultural systems.

#### 13.3.2 Organic P in Forest Soils

A large portion of the P present in forest soils is an organic form (Condron et al. 2005). Labile P in forest soil is incorporated into microbial and plant biomass (Achat et al. 2009; Walbridge 1991), which will gradually shift soil P into organic forms in forests. Organic P pools can represent 20–90% of the total P present in soils (Achat et al. 2009; Condron et al. 2005; Turner and Lambert 1985). Organic P pools in the soil generally increase over time, which suggests that biological cycling becomes more important as forest stands develop (Richter et al. 2006; Wells and Jorgensen 1975). Understanding the P<sub>o</sub> species present and how soil biota influence P<sub>o</sub> pools may be an important tool for predicting the quantity of labile P pools, especially in forest soils with a high P fixation capacity.

Several fractionation schemes have been developed that use sequential chemical extractions to partition soil P into inorganic and organic P pools that may be related to bioavailability (Chang and Jackson 1957; Hedley et al. 1982; Tiessen and Moir 1993). Each of these fractionation procedures uses a variety of extractions of increasing strength to divide soil P into pools of decreasing biological availability. For example, in the Tiessen and Moir (1993) modifications of the Hedley sequential fractionation procedure, the P<sub>i</sub> held in soil solution is first removed by anion exchange membranes. The second P fraction is extracted with 0.5 M NaHCO<sub>3</sub>. These two fractions represent labile P that is thought to cycle over a short time period, such as a single growing season (Bowman and Cole 1978; Cross and Schlesinger 1995; Johnson et al. 2003). The remaining P fractions are extracted with 0.1 M NaOH before and after sonification to break up soil aggregates, followed by an extraction with 1 M HCl, hot concentrated HCl, and a final extraction with  $H_2O_2$  and concentrated  $H_2SO_4$ . The P pools extracted by these solutions represent P that is moderately labile to highly recalcitrant (Tiessen and Moir 1993).

The rationale behind these fractionation procedures is that they represent various forms of P that vary in their availability to plants. Unfortunately, these various fractions have not been well correlated with P availability to forest trees or the growth response of trees following P fertilization (Miller 2008). The Po pools collected from the soil fractionation systems do not provide useful information on the species of  $P_0$  present and are not able to reliably quantify labile  $P_0$  pools (Condron et al. 2005; Richter et al. 2006). For example, the  $P_0$  extracted in the NaOH fraction of the Hedley fractionation is considered to be only moderately labile and only contributes to long-term P cycling. However, Liu et al. (2004) found that the NaOH-extractable Po pool decreased in the rhizosphere of Pinus radiata planted on an allophanic soil, which was accompanied by an increase in the NaOHextractable  $P_i$  pool. There were no effects on the resin-extracted  $P_i$  content of the bulk soil or rhizosphere, which suggests that biological activity in the rhizosphere caused these short-term changes in the NaOH pools, indicating that these fractions are more labile than the fractionation scheme would indicate. Similar conclusions were reached by Richter et al. (2006) in their study of long-term changes in soil P in an aggrading *Pinus taeda* plantation established on an abandoned agricultural field. Likewise, other research has show that the residual P pools can be influenced by the soil biota (Chen et al. 2002).

Liquid state <sup>31</sup>P nuclear magnetic resonance (NMR) of soil extracts can identify and quantify the P<sub>o</sub> in soils (Condron et al. 2005; Newman and Tate 1980; Turner et al. 2003; Turner and Richardson 2004). Using NMR it is possible to separate soil P into various forms such as inorganic P, orthophosphate monoester and diester phosphates, phosphonates, polyphosphates, and pyrophosphates, which vary in availability to plants (Condron et al. 1997). Although it is difficult to make comparisons of P<sub>o</sub> pools between different sites because of site specific conditions, Cade-Menun et al. (2000) found that the P<sub>o</sub> spectra from the forest floor (O<sub>e</sub> and O<sub>a</sub> horizons) of a 10-year-old burned clear-cut and an old growth forest were very similar. Although total P concentrations remained unchanged between sites, there was a decrease in the P<sub>o</sub> concentration of the spodic (Bhf2) horizon of the clear cut and burned site (Cade-Menun et al. 2000). The change in the Bhf2 was attributed to a decrease in the illuviation of P<sub>o</sub> through the soil profile.

Monoester and diester phosphates are among the most common forms of  $P_o$  in soils. Chen et al. (2004) measured  $P_o$  in a variety of soils planted with *Pinus radiata* pine in a greenhouse study and found that orthophosphate monoesters were the most common forms of  $P_o$  in a variety of soils. Orthophosphate esters may be monoesters with one C moiety per P, or diesters with two C moieties per P. The most abundant monoester in soils are inositol phosphates, which occur in various stereoisomeric forms, *myo*, *scyllo*, *D-chiro*, and *neo* (Turner et al. 2002, 2005). The monoesters also include sugar phosphates, phosphoproteins, and mononucleotides (Condron et al. 2005). Although most of the monoesters can be readily hydrolyzed

by phosphatases present in the soil (Alvarez et al. 2004; He et al. 2004), monoesters adsorb tightly to soil colloids and consequently often become resistant to enzyme hydrolysis (Chen et al. 2004).

The diester phosphates, including nucleic acids and phospholipids, are frequently found in larger quantities in acid forest soils than in agricultural soils (Cade-Menun et al. 2000; Cade-Menun 2005). Although diesters only constituted approximately 10% of the  $P_o$  in agricultural soils, Cade-Menun et al. (2000) found that they accounted for more than 50% of the extractable  $P_o$  in the acid forest soils of British Columbia. Turner et al. (2007) measured  $P_o$  in a glacial chronosequence and found that diester P continued to accumulate as the age of the soil increased and made up a significant proportion of total soil P in the older soils. Diester phosphates are generally less tightly sorbed to soil colloids than are monoesters and therefore may be more susceptible to hydrolysis by phosphatases present in the soil (Condron et al. 2005; Magid et al. 1996).

Phosphonates are organic orthophosphate compounds with C–P bonds and were first reported in soils by Newman and Tate (1980). The C–P bond is more resistant to hydrolysis and oxidation than C–O–P bonds, making their functions as a P storage compound in biotic systems less likely (Quin and Quin 2001). The phosphonates accumulate in soils that are wet (Tate and Newman 1982), cold, and acidic (Cade-Menun et al. 2000; Dai et al. 1996; Gil-Sotres et al. 1990). These conditions exist in many forest soils (Fisher and Binkley 2000), which suggest that phosphonates may be present in greater quantities in forest soils than in well-drained agricultural soils.

## 13.3.3 Availability of Organic P in Forest Ecosystems

Conventional views of nutrient cycling and tree nutrition hold that organic P must be converted to inorganic P before it can be utilized by plants (Adams and Pate 1992; Hayes et al. 2000; Tate 1984). The mineralization of organic P is mediated by phosphatases that hydrolyze C–O–P ester bonds (Condron et al. 2005). For example, phytase activity is needed to hydrolyze inositol phosphate, which often comprises a large portion of the organic P in soil (Richardson 2001; Tang et al. 2006). Acid phosphatases dominate in most acid forest soils (Tabatabai 1982). Tree roots, fungi, and bacteria produce phosphatases in soil (Chen et al. 2008; Fox and Comerford 1992b; Speir and Ross 1978). Fox and Comerford (1992b) found higher acid phosphatase activity in the rhizosphere of *Pinus elliotti* roots.

In spite of the fact that P limits productivity in many forest ecosystems and that the forest floor contains large pools of organic P that seem to influence ecosystem productivity, much less attention has been paid to P mineralization in the forest floor compared to N mineralization (Comerford and de Barros 2005). In many forest ecosystems, it appears that forest floors immobilize N in undisturbed forests and thus are a sink for N during most of the rotation (Miller 1981; Piatek and Allen 2001). Berg and Laskowski (2006) compared the results from a large number of forest ecosystems in northern temperate climates and found that in the majority of them, N accumulated in the forest floor through the rotation. It is less certain whether the forest floor is a sink or source of P in forests. Piatek and Allen (2001) found that the forest floor was a sink for P in *Pinus taeda*, whereas Polglase et al. (1992b), using both laboratory and field studies with *Pinus taeda*, concluded that P was mineralized from the forest floor. Studies with other species including several species of pine also found that P was also released from the forest floor (Comerford and de Barros 2005).

Fertilization with P may accelerate cycling of P in forest ecosystems by increasing P mineralization from the forest floor (Comerford and de Barros 2005; Polglase et al. 1992b). The P content in litterfall from fertilized forest is greater than in unfertilized forests. (Harding and Jokela 1994). Fertilization can increase total P returns in litterfall from 150 to 400% (Dalla-Tea and Jokela 1991; Piatek and Allen 2001). Release of P from decomposing needles is strongly and positively related to the needle concentration of inorganic P (Polglase et al. 1992a), which increases with fertilization (Polglase et al. 1992c). The net mineralization of organic P is probably much greater following fertilization. The importance of P fertilization on the mineralization of P was clearly documented in the 6-year-old Pinus taeda plantations growing on Spodosols in Florida studied by Polglase et al. (1992c). Higher P mineralization in laboratory incubations showed that P fertilization increased organic matter quality. In the field, mineralization in the surface 5 cm of soil supplied 0 and 25% of the annual P requirements in unfertilized and fertilized plots, respectively. Higher laboratory and field mineralization rates with fertilization were attributed to rapid recycling of P in readily mineralizable compounds. In contrast, slow growth in nutrient-deficient control plots was attributed to slower biological cycling of phosphorus.

Unfortunately, the relationship between measured amounts of phosphatase in the soil and the mineralization of organic P is not well understood (Condron and Tiessen 2005). Increased mineralization of organic P in the rhizosphere of *Pinus radiata* was attributed to higher concentrations of acid and alkaline phosphatases and phosphodiesterase (Liu et al. 2004, 2005). However, in other studies soil phosphatase activity was not related to organic P mineralization (Adams 1992; Chen et al. 2008).

Mycorrhizae associated with tree roots may have the ability to produce phosphomonoesterase that can hydrolyze  $P_o$  (Alexander and Hardy 1981; Read and Perez-Moreno 2003; Smith and Read 1997; Williamson and Alexander 1975). Dinkelaker and Marschner (1992) found that phosphomonoesterase activity was greater in the mycorrhizal roots of *Picea* and rhizomorphs of *Thelephora terrestris* than in nonmycorrhizal roots. Bartlett and Lewis (1973) measured phosphatase activity on ectomycorrhizae of *Fagus spp*. and found that more than one phosphatase was present. They suggest that the activity of phosphatases on the surface of ectomycorrhizae may lead to the immediate recycling of the organic P present in the forest floor back into the mycorrhizal root systems of trees. Although ecotmycorrhizaea can obtain P from the enzymatic breakdown of complex organic compounds (Read and Perez-Moreno 2003), recent work suggests that mineralization of organic P may be less important that previously thought in coniferous forests (Achat et al. 2009; Johnson and Gehring 2007). Lindahl et al. (2002) proposed that ectomycorrhizal fungi can directly acquire organic forms of nutrients in the forest floor and transport them to the host trees. In this hypothesis, ectomycorrhizae can acquire  $P_o$  directly from the soil and litter and may also capture organic nutrients from other soil organisms such as saprotrophic fungi (Johnson and Gehring 2007). Because mycorrhizal fungi are common in both the forest floor and the surface mineral soil, this may be an important mechanism of uptake of  $P_o$  in forest ecosystems.

## 13.3.4 Impact of Organic Acids on Phosphorus Dynamics in Forest Soils

Because tree growth is typically limited by the quantity of labile P present in the soil environment, the simple and economically viable solution in plantation forestry has been to apply inorganic P fertilizers to meet plant growth requirements (Fox et al. 2007a). Applied inorganic P is rapidly converted from labile to nonlabile P in the soil. These transformations are regulated by plants, soil microbes, and the P sorption capacity of the soil. Phosphorus sorption is rapid and there is a large sink for P in most forest soils (Beauchemin et al. 1996; Kelly and Kelly 2001; Comerford and de Barros 2005). In acid forest soils, P sorption occurs primarily at surfaces of Fe- and Al-oxide and hydrous oxide (Delgado and Torrent 2000; Pierzynski et al. 2005; Sample et al. 1980). Phosphate anions act as a Lewis base and form inner-sphere complexes with hydroxyl groups on the oxide surface, which acts as a Lewis acid. The strong sorption of P in soils is responsible for the substantial decrease in inorganic P in soil solution over time. With age and weathering, the importance of Al- and Fe-sorbed P increases (Parfitt et al. 1975).

Classical concepts involving dissolution of P minerals based on the thermodynamics of mineral equilibrium provide a theoretical basis for long-term trends soil nutrient availability in forest soils (Lindsay 1979). However, this approach has limited utility in most forest soils because P is sorbed to Fe and Al oxide surfaces and is often occluded within amorphous Fe and Al oxides that are not in thermodynamic equilibrium with soil solution. Most of these amorphous coatings are complex mixtures of Fe, Al, and organic matter rather than distinct minerals such as variscite. The heterogeneity of the soil environment affecting P sorption reactions adds to the complexity of P cycling in forest soils (Huang and Schnitzer 1986).

The desorption of surface complexed P and the dissolution of amorphous coatings containing occluded P can be greatly accelerated in forest soils by the presence of organic acids such as malate, citrate, and oxalate (Fox 1995; Jones and Darrah 1994). Solution P concentrations can be 10–1,000 times higher following the addition of organic acids to the soil (Jones 1998). The organic acids function as organic ligands that increase P release into soil solution by (1) ligand exchange with P held at metal oxide surfaces, (2) complexation of Al, Fe, and other metals in soil solution, and (3) dissolution of amorphous metal–organic matter coatings that contain occluded P (Fox 1995). Based on the kinetics of P and Al release, ligand exchange reactions can be separated from dissolution reactions (Fox et al. 1990b). Sato and Comerford (2006) suggested that P released by desorption can be separated from P released by dissolution of amorphous organic matter–metal oxide surfaces by using anion exchange membranes and soil extractions with various concentrations of oxalate to estimate disequilibria-desorbable and ligand-desorbable P.

A wide variety of naturally occurring organic acids have been identified in forest soils (Fox and Comerford 1990; Jones 1998; Pohlman and McColl 1988; Stevenson 1967). However, not all organic acids can exchange P from oxide surfaces or increase dissolution of these surfaces (Fox et al. 1990b). In acid forest soils with large amounts of Al and Fe, P desorption and dissolution reactions are mediated by organic ligands that form stable complexes with Al and Fe (Fox 1995; Jones 1998). For example, in forest soils with large amounts of Al such as Spodosols of the southern USA, those organic acids with an Al stability constant  $(\log K_{Al})$  greater than 3.5-4.0 had a much greater impact on P release than those that have a lower stability constant (Fox et al. 1990a; Lan et al. 1995). The Al stability constant is determined by the type and arrangement of functional groups on the organic acid. Those with multiple carboxylic acid groups have higher stability constants because they can form stable five- and six-membered ring structures with Al and Fe (Fox 1995). Consequently, organic acids such as oxalate, citrate and malate, which have  $\log K_{A1}$  values greater than 4, increase P release from soils whereas organic acids such as formate, acetate, lactate with  $\log K_{AI}$  values less than 4 have little impact on P release (Fox et al. 1990a; Lan et al. 1995; Jones 1998).

P release from soils generally increases as concentrations of organic ligands increase (Fox and Comerford 1992a; Gerke 1992). The concentration of low molecular weight organic acids is generally quite low in forest soils, typically less than 0.01–0.1 mM (Fox and Comerford 1990; Pohlman and McColl 1988). However, even at very low concentrations of <1.0  $\mu$ mol g<sup>-1</sup> soil continuous release of low molecular weight organic acids may promote desorption of P and dissolution of amorphous mineral coatings containing P over the course of weeks to months. Fox and Comerford (1992a) showed that, over time, the cumulative amount of P released from forest soils was similar when oxalate was added sequentially over time at very low concentrations compared to a single addition of oxalate at higher concentrations.

Tree roots and their associated mycorrhizae can modify the rhizosphere and, through the release of organic acids, can increase P availability (Fox 1995; Fox and Comerford 1990; Grierson 1992; Hinsinger 2001; Jones 1998; Raghothama 1999, 2005; Smith and Read 1997). It is well documented that ectomycorrhizal roots can exude enough oxalate to dissolve amorphous minerals (Cromack et al. 1979; Sato

and Comerford 2006). Phosphorus desorption and dissolution reactions in the rhizosphere are often greater than in the bulk soil because of higher concentrations of organic acids (Cardon and Whitbeck 2007; Jones 1998; Smith and Read 1997). The close proximity to the source of exudation and reduced volume of solution in contact with the surrounding soil can lead to increased concentrations in the rhizosphere (Jones 1998; Cardon and Whitbeck 2007). Most low molecular weight organic acids are rapidly degraded in forest soils (van Hees et al. 2002). Consequently, organic acids must constantly be replenished in the soil solution through root exudation or other means to maintain the observed concentrations (Fox 1995; Jones 1998). Large quantities of organic acids such as citrate are released by proteoid roots of shrubs such as Banksia integrifiolia (Grierson 1992). Ectomycorrhizal production of oxalate in the soil can be significant. For example, very high oxalate concentrations have been observed in forest soils associated with fungal maps in Pseudotsuga menziesii forests (Cromack et al. 1979). Fungi and soil microbes such as *Penicillium* and *Pseudomonas spp.* have been proven to be a source of oxalate in both laboratory and field experiments (Arvieu et al. 2003; Casarin et al. 2003; van Hees et al. 2000, 2003; Illmer and Schinner 1992).

The majority of organic P in soils is not soluble and thus is not susceptible to mineralization or uptake as Po by mycorrhizas (Chen et al. 2008). As discussed above, low molecular weight organic acids have a significant impact on the release of inorganic P in many soils. However, little is known about the impact of low molecular weight organic acids on release of organic P (Bar-Yosef 1996; Jones 1998; Ström et al. 2002). Previous work has shown that low molecular weight organic acids such as oxalate can significantly increase the release of Po in at least some soils (Fox and Comerford 1992a). For example, in forested Spodosols in the southern USA the release of organic P in the presence of low molecular weight organic acids was equal to or greater than the release of inorganic P in surface and spodic horizons (Fox and Comerford 1992a; Fox et al. 1990a, b). Through time, the release of organic P increased more than the release of inorganic P in these soils following addition of organic acids such as oxalate (Fox et al. 1990a, b). The release of organic P may be associated with the dissolution of the amorphous Al- and Fe-organic matter coatings that contain organic P (Fox et al. 1990b). Once released into solution, the organic P may be subject to enzyme hydrolysis by phosphatases in the soil (Adams and Pate 1992; Hayes et al. 2000). Fox and Comerford (1992b) found higher acid phosphatase activity in the rhizosphere of *Pinus elliotti* roots. It thus seems that the presence of organic acids in the rhizosphere of trees will increase the release of both inorganic and organic P. Because the solubility of organic P and not soil phosphatase activity may limit mineralization of organic P in soils (Adams and Pate 1992; Chen et al. 2008), the increased release of organic P mediated by organic acids may significantly impact P dynamics and long-term productivity in forest ecosystems (Turner and Lambert 1985; Condron et al. 2005). This effect would be even more important if the Po released by the elevated concentrations of organic acids in the rhizosphere was also directly taken up by the ectomycorrhizas and transported to the trees, as proposed by Lindahl et al. (2002).

#### **13.4** Summary and Implications to Tree P Nutrition

This review highlights the complexity of P dynamics in forest soils. Large amounts of both  $P_i$  and  $P_o$  are found in forest soils, including the forest floor and mineral horizons. However, most of this P may not be in a form that is readily available to trees. Trees and their associated mycorrhizas have evolved a number of mechanisms to modify the soil to increase P availability and uptake. Many of these mechanisms appear to operate on several levels and influence availability and uptake of both P<sub>i</sub> and P<sub>o</sub>. Concentrations of low molecular weight organic acids and phosphatases are greater in the rhizosphere of trees, which increases the solubility of both P<sub>i</sub> and P<sub>o</sub> and mineralization of P<sub>o</sub>. Ectomycorrhizas of trees present in the forest floor and the mineral soil may be able to acquire  $P_0$  directly. The ability of mycorrhizas to directly utilize P<sub>o</sub> may be a significant aspect of tree nutrition and dramatically alter our view of nutrient cycling in forest ecosystems. A comprehensive understanding of tree nutrition and forest productivity is not possible without a better understanding of both P<sub>i</sub> and P<sub>o</sub> in forest ecosystems. Additional research is clearly needed to elucidate the complex dynamics and transformations of P in forest ecosystems.

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