An investigation of the duration of phosphorus fertilization effects on phosphorus and nitrogen cycling patterns of Pinus elliottii plantations in the southern Cape

by

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ABSTRACT

The effects of phosphorus fertilization and its duration of impact on nutrient cycling patterns in Pinus elliottii plantations were investigated by examining soil phosphorus and nitrogen turnover and litterfall in a 8, 20 and 25 year old plantation age sequence. Each stand contained plots fertilized with between 30-60 kg ha^{-1} superphosphate at establishment and an equal number of control (unfertilized) plots. At the oldest stand there were additional variables, namely timing of fertilizer application (at establishment versus 10 years after establishment) and fertilization frequency (double application, at establishment and 10 years later).

Phosphate fertilization produced a significant increase in soil phosphorus availability at the 8 and 20 year old stands. At the 25 year old stand, increased phosphorus availability was only significant in the plots fertilized twice. It was only at these latter plots that a significant increase in soil annual net phosphorus turnover with fertilization was evident. Thus, only with a double application of phosphate will increased phosphorus availability and turnover be maintained up to 25 years. Phosphate fertilization significantly reduced soil nitrogen availability and soil annual nitrogen turnover at all the stands. This was ascribed to inorganic nitrogen being immobilized by the large microbial population supported by the increased phosphorus availability. This contention is supported by the investigation of the factors influencing nutrient mineralization - while fertilization was the most significant factor determining phosphorus mineralization, nitrogen mineralization was shown to be strongly controlled by environmental factors, indicating the role of micro-organisms in this process. Thus phosphorus release is mainly a physiochemical phenomenon while nitrogen turnover is biologically controlled. The reduction of nitrogen turnover rates with phosphate fertilization intensified with increasing age, presumably as the nitrogen became bound in biomass which decomposes slowly.

Annual litterfall rates were significantly higher in the fertilized plots. While the unfertilized plots showed peak litterfall rates at 20 years, litterfall increased steadily with age up to 25 years in the fertilized plots. Variability in the mass of pine litter accumulated on the plantation floor corresponded to trends of litterfall rates. Before making the conclusion that litter accumulation was controlled only by litterfall, estimated decomposition constants were examined. Contrary to predictions that phosphorus fertilization increases decomposition rates, lower decay constants were found in the fertilized plots (ascribed to the lower nitrogen concentration of the fertilized litter). At the 25 year old stand, both litterfall and decomposition were contributing to litter accumulation. The observed effects of phosphate fertilization (increased soil phosphorus and reduced soil nitrogen turnover rates, increased litterfall and litter accumulation rates and lower decomposition rates) were usually not significant at the 25 year old plots fertilized once only, 10 years after establishment. Thus, the value of this fertilization regime is not apparent from our study. The effects of phosphate fertilization were most pronounced at the plots fertilized twice and hence a double application of phosphate fertilizers is recommended to maintain long-term enhanced phosphorus availability. However, reduced nitrogen turnover rates and lowered decomposition rates will result and should be monitored. A NPK fertilizer treatment could be used in later rotations to prevent elemental imbalances.

Since nutrient mineralization processes, particularly nitrogen, are influenced directly by environmental factors, the findings of this study should not be extrapolated to pine plantations in other climatic regions. Similar studies to this one are essential, particularly in areas such as the Eastern Transvaal where large litter masses accumulate and might severly impact nutrient cycling processes.

CONTENTS

CHAPTER 1

INTRODUCTION

Natural pine stands are reported to be well adapted to achieve high growth rates on nutrient poor soils by being able to capture, retain and cycle nutrients efficiently within the ecosystem (Miller et al. 1979). The species studied in this thesis, P. elliottii var. elliottii Engelm., occurs naturally in the southeastern United States (Florida and Georgia) (Darrow 1984) in regions of low nutrient status. It shows rapid nutrient uptake, high growth rates and efficient nutrient cycling (Gholz et al. 1985a). It is thus well suited to the nutrient poor soils of the southern and south-western Cape. Since it is also easily established, it has been widely planted as a commercial plantation species in both the United States (Gholz et al. 1985b) and southern Africa (Darrow 1984).

In the southeastern United States, the conversion of natural forest stands of P. elliottii to commercially managed plantations has had an impact on processes of nutrient cycling (nutrient turnover became less efficient) (Gholz et al. 1985a). Deficiencies of two elements most limiting to tree growth (nitrogen and phosphorus) often arise when nutrients are lost from the system due to management practises (e.g. burning and harvesting) or immobilized in the dense litter layers which develop (Gholz et al. 1985a & b). Deficiencies of phosphorus are particularly severe in the Cape regions where growth rates decline as the stand ages (Payn et al. 1988). This reduced production is currently being overcome by the application of phosphate fertilizers. However, due to the increasing cost of fertilizers and the decreasing availability of land to convert to plantations, research has been undertaken to determine the optimal quantity, frequency and timing of fertilizer applications for maximal timber yields on existing plantations through more than one rotation (Herbert & Schönau 1989).

To date few studies have attempted to determine the effects of fertilizers on nutrient cycling processes in pine ecosystems in southern Africa. In the southern Cape, plant nutrient contents and soil nutrient levels relative to soil fertility have been determined by Payn & Clough (1987), Payn et al. (1988) and Payn & Clough (1989). Versfeld & Donald (1991) in the south-western Cape have examined nutrient cycling within the litter layer. However, no studies have examined the rates at which processes occur in the complete ecosystem cycle.

The extensive research programmes into fertilization and growth responses in pine plantations undertaken since the 1930's (Donald et al. 1987) by particularly the South African Forestry Research Institute (now Forest Science and Technology) have resulted in a range of different aged fertilizer trials which lend themselves to studies of the effects of fertilizers with time. This study examines the effects of phosphate fertilization on the rates of phosphorus and nitrogen cycling processes in a chronosequence of P. elliottii plantations from 8 to 25 years old. Indications of whether fertilization produces long-term effects, which may be maintained into the next rotation, or merely a short-term pulse, returning to pre-fertilization levels can thus be obtained. Both phosphorus and nitrogen cycles were examined, since there is a high level of interaction between the two cycles (Cole & Heil 1981). It

is also believed that phosphorus levels control the economy of other nutrients, including nitrogen (Groves 1983).

Besides having a chronosequence of P. elliottii plantations available for study, there were also trials of different fertilization timing and frequency. P. elliottii has been reported to have consistently good responses to phosphate fertilization, irrespective of whether application occurred at time of planting or at midrotation (Gholz et al. 1985b in USA; Donald et al. 1987, Payn & Clough 1988, Schafer 1988 and Herbert & Schönau 1989 in SA). Further discussion of the effects of different timing of fertilizer application is included in the literature review (Chapter 2).

Effects of different fertilization timing on nutrient cycling rates were investigated in 25 year old plots fertilized at planting and in those fertilized only 10 years after establishment. Comparing nutrient cycling patterns in these plots fertilized once with that of 25 year old plots fertilized twice, at plantation establishment and again 10 years later, allowed the effects of fertilization frequency to be elucidated. Details of the study sites and fertilization treatments are given in Chapter 3.

For this study, the nutrient cycle was divided into two major components where nutrient flux through the system was thought to be limiting - (i) soil mineralization processes (Chapter 4) and (ii) litter turnover (Chapter 5).

(i) Soil mineralization: Not only are the levels of soil inorganic phosphorus and nitrogen determined in Chapter 4, but their rates of mineralization were also examined. While nutrient levels indicate what is present in the soil at any given time, mineralization rates show what is ultimately becoming available (in inorganic form) to the plants over time. The "net" mineralization rates (the difference between microbial release of nutrients (gross mineralization) and incorporation into microbial biomass (immobilization)) of phosphorus and nitrogen in soils were determined by a soil incubation study described in the "methods" (Chapter 3) and discussed in the literature review (Chapter 2). The effects of phosphate fertilization on phosphorus and nitrogen mineralization rates are examined in relation to selected environmental factors .

(ii) Litter turnover: The most important input to the soil nutrient cycle comes from the decomposition of leaf/needle litter (Escudero et al. 1987). It is well documented that the slow decay rates of pine needles results in the accumulation of large masses of litter on the plantation floor (Gholz et al. 1985a in USA; Morris 1986, Herbert & Schönau 1989 in SA). This may represent the immobilization of a substantial quantity of essential nutrients and thus limit nutrient turnover and availability in the soil. Litterfall and decomposition rates are presented in Chapter 5 and their relative significance in contributing to the accumulation of litter on the plantation floor evaluated. The severity of the problem of nutrient immobilization in the accumulated litter mass is assessed for P. elliottii plantations in the southern Cape by quantifying the levels of nutrients (phosphorus and nitrogen) in the litter.

Factors controlling forest floor decomposition need to be understood in order to effectively manage plantations (Morris 1986). The influence of litter nutrient content and soil fertility on decomposition is also examined in Chapter 5. It is widely accepted that the nutrient content of the litter is an important controlling factor of decomposition. An increase in litter nutrient levels (or a decrease in litter C:P and C:N ratios) increases decomposition rates (Edmonds 1980; Yavitt & Fahey 1986). Thus if the application of phosphorus increases the nutrient content of the needle litter, it should enhance the rate of decomposition. This contention is examined in Chapter 5. (Decomposition rates were not determined directly but were estimated from the ratio of the rate of litterfall to the accumulated litter mass).

It was thought that an examination of nutrient cycling patterns in a chronosequence of stands with plots of different fertilization timing and frequency would indicate which fertilization regime showed the greatest potential for long-term productivity, perhaps into the next rotation. The productive potential of the 25 year old plots can only be inferred from soil nutrient availabilities and turnover rates determined in Chapter 4 and litterfall rates, decomposition rates and nutrient use efficiencies from Chapter 5. The findings of Chapters 4 and 5 on the relative fertility of the different fertilization treatments 25 years after establishment are confirmed by the bioassay presented in chapter 6, in which P. elliottii seedlings were grown on soils from the different treatments of the 25 year old stand. Since seedling growth response is a direct indication of a soil's potential productive capacity, it should show which of the fertilization treatments can maintain elevated growth rates for another rotation.

The information presented in Chapters 4-6 is integrated in Chapter 7 to provide a more complete account of the interrelated processes of nutrient cycling. This final chapter also presents the major conclusions and recommendations for future research.

By achieving the main objectives of this study, namely (i) identifying the effects of phosphate fertilization on rates of phosphorus and nitrogen cycling in P. elliottii plantations of the southern Cape, (ii) determining the duration of the effects in different fertilization treatments representing different timing and frequency of phosphate application and (iii) identifying the fertilization treatment capable of sustaining long-term productivity, recommendations can be made aimed at more efficient management of existing pine plantations which is essential if current productivity in southern Africa is to be maintained without expansion into areas of marginal forestry potential.

CHAPTER 2

LITERATURE REVIEW

2.1 Forestry in South Africa

2.1.1 Background

The South African forestry industry was reported as having 1 131 922 ha under plantation in 1982 (Directorate of Forestry 1983, cited by Donald et al. 1987). Assuming that afforestation increased at the recommended rate of 39 000 ha annually, the current extent of forestry plantations is about 1 443 922 ha. It has been estimated that this will have to be increased to about 2 000 000 ha by the year 2000 to meet the future demand for forest products (Schönau 1989). It is doubtful whether so much additional land can be found which is also suitable for new timber plantations. Forestry is in direct competition with other forms of landuse, particularly agriculture, for a limited resource. This competition has led to substantial increases in the price of good forestry land (Schönau 1989; Grey 1989). Nevertheless, plantation forestry has continued increasing its area of influence in a number of areas in South Africa in recent years (Musto 1991).

An alternative to increasing afforested areas is to increase and maintain productivity on existing plantations. One of the major problems affecting plantation productivity throughout most of southern Africa are the nutritionally poor soils. They are extremely leached, acidic and low in bases and phosphorus (Donald et al. 1987). Phosphate deficiency is considered as the most significant factor reducing timber yields, particularly in the southern and south-western Cape regions of South Africa. To correct this deficiency and increase yield, foresters throughout the Cape are using increasing amounts of phosphate fertilizers. However, economic returns are being reduced by increasing costs of both fertilizers and the labour involved in application (Payn & Clough 1988). Thus, research is needed not only into growth responses to fertilizing, but also into the most effective and efficient use of fertilizers for long-term benefits (Herbert & Schönau 1989).

There is an urgent need to change the attitudes of foresters from one of management for short-term gains towards a regard for long-term benefits (Grey 1989). The present emphasis on cost control per unit of product will have to be shifted to optimization of production per hectare at the lowest cost (Schönau 1989). To improve long-term productivity, site specific characteristics such as rainfall regime and effective rooting depth must be considered prior to plantation establishment (Payn & Clough 1988) together with the species most suited to the particular site conditions. Once the plantation is established and the appropriate fertilzer recommendation applied, management should aim at maintaining the improved soil fertility and relieve the need to repeatedly introduce inorganic fertilizers (Herbert & Schönau 1990). Thus, foresters who consider trees to be the primary resource will have to appreciate and understand the "real" primary resource, the land and its soil. This is where the help of the researcher is urgently required (Grey 1989; Schönau 1989).

Morris (1986) and Herbert & Schönau (1989 & 1990) have stressed the need to examine nutrient availability and cycling relative to soil fertility and time (stand age) in order to understand the prospects of maintaining long-term site productivity. This study investigates the effects of phosphate fertilization on nitrogen and phosphorus cycling processes in a chronosequence of P. elliottii plantations in the southern Cape. It seemed appropriate to carry out such a study in pine plantations, since they account for 52.6% of the total afforested area in South Africa (Directorate of Forestry 1983, cited by Donald et al. 1987) and Pinus is also the dominant genus planted in the Cape (Herbert & Schönau 1990).

2.1.2 Study species

The study species, P. elliottii, was introduced into South Africa in the 1920s and now covers 143 718 ha (24.1% of the area planted to coniferous species). It is second only to P. patula in economic importance (Darrow 1984). However, in the southern Cape it is of secondary importance to P. radiata and P. pinaster. Plantations of the all year rainfall region of the southern Cape are subject to poor drainage, which is a major factor limiting tree growth (Donald et al. 1987). However, P. elliottii tolerates poorly drained sites better than other locally grown pine species. It has been grown most successfully on the Tsitsikamma plateau where soils are deeper and usually quite wet (Schafer 1988). Thus it seems that P. elliottii has the potential to become the most important commercial pine species in the southern Cape, replacing P. radiata and P. pinaster on sites where these species are limited by poor drainage.

2.1.3 Timing of fertilizer application

P. elliottii has consistently produced good responses to phosphate fertilization, whether application occurred at time of planting or after canopy closure (Donald et al. 1987; Payn & Clough 1988; Schafer 1988; Herbert & Schönau 1989).

"Fertilizing at planting is one of the most efficient ways of increasing land productivity in forestry" (Schönau 1989). Since phosphorus is particularly important for root development, phosphate fertilization at planting allows seedlings to develop a sound and extensive rooting system, capable of exploiting the full potential of the site (Morris 1986; Herbert & Schönau 1990). As this beneficial effect is maintained throughout the rotation, fertilized trees will have a continual advantage and achieve higher growth rates as long as the site can support it. This fertilizer regime may also indirectly boost site productivity - the deeper root systems of the fertilized trees can acquire nutrients from the subsoil and deposit them in the topsoil (Herbert & Schönau 1990). By reducing nutrient stress in seedlings, fertilization increases their survival rates. Since fertilization gives each seedling an equal supply of nutrients at the start, it also improves stand uniformity (Schönau 1989).

Responses to fertilization may vary relative to soil physical characteristics. A problem of applying phosphate to heavier textured, highly acid soils common in the southern Cape, is that it may become fixed in forms unavailable to the plant. This problem is more severe when phosphate is applied at the

time of planting, since at this stage it is taken up relatively slowly by the seedlings while it is removed rapidly from the soil solution by fixation (bound to iron, aluminium and calcium ions in the soil). This effectively reduces the applied phosphate available to the seedlings (Payn & Clough 1989) and hence the importance of understanding site and soil characteristics before recommending a specific fertilizer regime is crucial.

The long-term benefits of fertilizing at planting are a potential shortening of the rotation and increased production per hectare. Earlier canopy closure is an added advantage in that it suppresses understorey weeds (Morris 1986; Herbert & Schönau 1989). An apparent negative aspect of this fertilization regime is the long period (15-20 years) before any profits are gained. However, Donald et al. 1987) showed that returns from the first thinning (at 8-10 years) will cover the fertilizer cost, while the profit earned from fertilizing (increased yield) will still be available at harvesting. An example of the profitability of fertilizing pines at establishment in the southern Cape is a P. elliottii trial at Quar where the compound interest rate of return was 21.9%, 15 years after application (Herbert & Schönau 1989).

Another fertilization regime, used routinely only in the Cape, is the fertilization of intermediate-aged trees (Herbert & Schönau 1989). Without fertilization at establishment, trees often develop nutrient deficiencies later in the rotation. This is due to the initial low soil nutrient status and nutrient immobilization in the litter. Before treatment, foliar and soil nutrient analyses are necessary to identify which nutrients are limiting (Morris 1986; Herbert & Schönau 1990). Thus, fertilizing some years after establishment aims at increasing productivity by enhancing the nutritional status of trees (Herbert & Schönau 1990).

Responses to fertilization are strongly influenced by stand age at time of application (Morris 1986). As nutrients become limiting, trees begin to rely increasingly on the internal retranslocation of nutrients to meet their growth demands. During this stage there is no response to fertilizers (Bowen & Nambiar 1984). However, as nutrient immobilization in the litter increases, the efficient internal cycle is interrupted sufficiently to reduce growth (Morris 1986). Good responses to fertilization will occur at this stage, which Morris (1986) found to be the 12th year of rotation in P. patula stands of the Usutu forest, Swaziland.

Fertilization of older stands is economically attractive as the compound interest period is shorter, the quality of additional wood better than that from earlier in the rotation and the increment is added to fewer trees, increasing the size and value of the logs and reducing harvesting costs (Donald 1987).

This study investigated the rate of nutrient cycling (soil phosphorus and nitrogen mineralization and litter dynamics) in stands fertilized at planting, 10 years after establishment as well as in stands fertilized twice (at planting and 10 years later). It was hoped that this would indicate which fertilization regime increased the nutrient turnover rate and thus showed the greatest potential for long-term productivity.

2.1.4 Litter nutrient immobilization

Morris (1986) identified excessive immobilization of nutrients in the litter layer as the greatest threat to long-term productivity of P. patula stands in the Usutu forest, Swaziland. While P. patula is the most productive pine species in South Africa, it also produces the greatest accumulations of litter - up to 320 $t.ha^{-1}$ have been reported (Schutz 1982). While de Ronde (1984) reported that similar accumulations occurred in second rotation stands of P. patula in the Tsitsikamma, generally litter accumulation does not occur to the same extent in the Cape. Litter masses of 30-70 $t\ ha^{-1}$ are common in mature pine stands in the southern Cape (de Ronde 1984) and only 6-10 $t\ ha^{-1}$ in the south-western Cape (Versfeld & Donald 1991). Nevertheless, it still represents a loss of nutrients from the soil-plant nutrient cycle.

If the litter mass of the first rotation is not burned before establishment of the second rotation, the latter rotation litter will accumulate on the residue of undecomposed first rotation litter. Thus, second rotation stands have a larger litter mass than first rotation stands. This accentuates nutrient deficiencies and may be the cause of poorer growth in second rotation stands (Morris 1986). Burning of the plantation floor prior to replanting may seem to be the solution. This is a common practice in South African forestry (Morris 1986; Schönau 1989). While slash burning may be a cheap and effective method of reducing litter loading (de Ronde 1984) it also results in substantial losses from the system by volatilization, particulate matter (smoke) emission and leaching (Morris 1986; Schönau 1989). Nitrogen losses are almost entirely by volatilization while losses of phosphorus and other nutrients occurs through both volatilization and particulate matter. Ash remaining after a fire contains highly soluble nutrients which may be lost through leaching (Morris 1986). Burning also restricts microbial activity in the soil, reducing the decomposition of the freshly fallen litter (Schönau 1989).

This review indicates that site fertility is the most important aspect of forestry in South Africa, particularly in the southern Cape where water availability is not a limiting factor. Site fertility and productivity would thus be largely controlled by the rate of nutrient turnover (mineralization) in the soil-plant (tree) cycle. Since improved productivity is sought through the application of inorganic fertilizers, it was important to investigate the effects of these applications on the rate of nutrient cycling. This was carried out by examining soil nutrient mineralization and litter input and accumulation relative to phosphorus fertilization regimes and stand age.

2.2 Soil Mineralization

2.2.1 Soil incubation techniques

The most common methods used to determine rates of nutrient mineralization in the soil component of the cycle is by in situ soil incubation studies. In situ assays are favoured over laboratory estimates as they are supposedly sensitive to site environmental factors known to influence soil mineralization processes (Hart & Firestone 1989).

The sensitivity of the in situ technique to environmental conditions depends on the method of incubation. One of the most common methods used (that used in this study) is the "buried-bag" method developed by Eno (1960) where soil is incubated inside a gas-permeable, water impermeable polyethylene bag. This method is sensitive to soil temperature changes, but soil moisture is kept constant (Hart & Firestone 1989). A similar method that also isolates the incubated soil from the moisture of the surrounding soil is that used by Maggs (1991) where sealed metal cores were used. The rates of mineralization measured by these methods may differ from actual rates in the surrounding soil (Maggs 1991) since fluctuations in soil moisture do influence mineralization (Adams et al. 1989). Therefore, alternative methods have been developed that are more sensitive to fluctuations in soil moisture.

Perforated cores, which are believed to allow moisture in contained soil to equilibrate fully with changing conditions in the surrounding soil, were used by Adams et al. (1989). This method would also reduce the large accumulations of nitrogen that are reported to occur in the "moisture tight" methods which may alter mineralization processes such as nitrification (Raison et al. 1987). However, the possibility of nutrient losses by leaching from perforated cores does exist. DiStefano & Gholz (1986) developed a method which overcame these problems - an intact core within a PVC tube was buried upright in the soil with an ion exchange resin (IER) bag closing off either end. These cores were sensitive to soil fluctuations, prevented unusually high accumulations of nitrogen and detected any losses due to leaching.

Comparisons of the buried-bag and core-IER methods have been undertaken by Hart & Firestone (1989). Differences were found, but they were not consistent with stand age or between studies. Thus more research is still needed. Hart & Firestone (1989) suggested that since the core-IER method responds to changes in soil moisture and prevents large nitrogen accumulations, incubations could be conducted for longer periods of time. In contrast, the buried-bag method should be confined to short incubation periods (30-60 days).

Incubation methods sensitive to moisture fluctuations will have to record these fluctuations constantly, throughout the incubation period, if mineralization is to be correlated with soil moisture levels. This was not possible in the study reported in this thesis due to a lack of data loggers. Thus, a method similar to the buried-bag technique was used where the contained soils were maintained at initial moisture content throughout the period of incubation.

The most critical assumption on which the validity of the in situ technique rests is that the method by which the soils are contained does not significantly alter the naturally occurring rate of mineralization (Adams et al. 1989). However, Adams et al. (1989) found that the natural rate of mineralization is affected by in situ incubation and that artifacts introduced by this method become more pronounced the longer the period of incubation. Raison et al. (1987) tested the effect on nitrogen mineralization rates of incubating cores for periods of up to 131 days. They concluded that periods of 30-90 days were most appropriate, since the period should be long enough so that changes in inorganic nitrogen concentration

can be measured relative to fluctuations in the environment. However, Adams et al. (1989) showed that the best estimates of mineralization were obtained if the period of incubation is 2 weeks or less. Smethurst & Nambiar (1989) agree that incubation periods should be short but they also note that the resulting increased coring frequency will influence the number of mineralization flushes caused by disturbance of the soil during core placement.

Therfore, it seems that there is no general ideal period of incubation. The use of longer incubation periods (>4 weeks) may be dictated by the practicality of visiting distant forests (as was the case in this study) as well as for comparative purposes (Adams et al. 1989). In this study, phosphorus and nitrogen mineralization rates were determined relative to phosphorus fertilization and not so much to know the exact amount of net mineralization. What was important was that the incubation period of 6 weeks was constant at all the study sites, throughout the period of study.

2.2.2 Phosphorus mineralization

It was essential to examine nutrient mineralization rates in this study, rather than simply determining soil nutrient concentration. An increase in phosphorus concentration with phosphate fertilization would be expected, but concentration does not indicate how and at what rate phosphorus availability is maintained. The availability of soil phosphorus to plants depends partly on the concentration of phosphorus in the soil solution and partly on the rate at which more phosphorus comes into solution when that already dissolved is taken up by plants (Tate 1984).

Inorganic phosphorus enters the soil solution as a result of weathering of parent materials. It is then taken up by plants and micro-organisms or transformed into secondary mineral forms. In acidic, clay soils, secondary phosphorus minerals will be present as aluminium and iron phosphates, adsorbed on clay-humus colloids. The strong adsorption properties of acid clays renders phosphorus immobile and often quite unavailable for plant uptake (Lajtha & Schlesinger 1988), which means that very high levels of added phosphate are required to significantly raise the phosphate supplying power of the soil (Vitousek 1984; Payn & Clough 1989).

As inorganic phosphorus is taken up by plants and micro-organisms and becomes assimilated into organic phosphorus containing compounds, the release of inorganic phosphorus from organically bound phosphorus through mineralization becomes increasingly important (Harrison 1982; Stewart & Tiessen 1987). While inorganic phosphorus fertilization increases phosphorus availability (Schwab & Kulyingyong 1989), many studies (cited by Stewart & Tiessen 1987) have shown that it also results in the build up of organic phosphorus in soils. Since inorganic phosphorus compounds are almost immobile in soil, organic phosphorus compounds which are highly mobile, appear to be important for the movement of phosphorus through soils. However, these compounds can also be rapidly leached from the soil column (Schwab & Kulyingyong 1989). Thus, as the inorganic phosphorus added by fertilization is utilized by the plants/trees and organic phosphorus accumulates, mineralization rates become fundamental to the maintenance of available phosphorus in the system (Harrison 1982). The

mineralization process of the phosphorus cycle must be highly efficient at maintaining and recycling added nutrients, since there are many reports of the longevity of phosphorus fertilization responses (Witkowski et al. 1990). This response may last several decades, and in forestry situations may be important in subsequent rotations (Hart & Binkley 1985; Turner & Lambert 1986b).

Organic phosphorus can re-enter the cycle and soil solution as inorganic phosphorus by biological and biochemical mineralization. Biological mineralization is driven by the energy requirements of soil micro-organisms. Organic (carbon-bound) phosphorus is taken up by the organisms, metabolized and carbon is lost as respired CO_2 (Tate 1984; Stewart & Tiessen 1987). Unfavourable environmental conditions for microbial survival will result in the release of labile phosphorus into the soil solution (Lajtha & Schlesinger 1988). When the soil organic matter C:P ratio is high (as in phosphorus deficient soils), less phosphorus will be taken up for a specific carbon gain and so phosphorus mineralization will be slower (Tate 1984). Also, the organisms will compensate for the low phosphorus acquired from organic matter by competing with the plants for soil inorganic phosphorus. When soil micro-organisms take up more soil inorganic phosphorus than is being mineralized, microbial immobilization of phosphorus occurs (Lajtha & Schlesinger 1988). Thus, the net mineralization rates measured in this study by the in situ incubation technique will be the balance between microbial mineralization and immobilization, and are controlled by the many factors which control soil characteristics and the population dynamics and activities of soil micro-organisms. These factors include soil pH, texture, organic matter content, temperature and moisture (Stewart & Tiessen 1984).

Biochemical phosphorus mineralization results from the actions of phosphatase enzymes which occur extracellularly, associated with soil particles and humates. They are also produced by soil microflora and plant roots (Stewart & Tiessen 1987; Rojo et al. 1990). Phosphatases are inducible enzymes and the intensity of their excretion is determined by the need for phosphorus. Therefore, they will be excreted to a greater extent in response to low inorganic phosphorus availability. Phosphatase activity is also increased in the presence of large amounts of soil organic matter (Appiah & Thomas 1982; Stewart & Tiessen 1987). Thus, the release of inorganic phosphorus from organically bound complexes by phosphatases would be important in the phosphorus deficient soils of the Cape where the bulk of the phosphorus is organically bound (Straker & Mitchell 1986).

Environmental factors influencing phosphatase activity are temperature and pH. High temperatures inactivate the enzyme. With pH, different forms of the enzyme have different optimal pHs, namely alkaline and acid phosphatases (Rojo et al. 1990). This explains the apparent contradictory responses of phosphatases to liming reported by Trasa-Cepeda et al. (1991). The effect of phosphate fertilization on phosphatase activity is a decrease in its activity, obviously due to the increase in inorganic phosphorus availability (Appiah & Thomas 1982). Thus, it seems that if phosphate fertilizers were added to a phosphorus deficient system in which biochemical mineralization was the dominant turnover process, an initial drop in the mineralization rate would be expected. However, as the microbial population increases in response to the increase in phosphorus availability, more phosphorus is immobilized by these organisms and biological release of phosphorus becomes of greater significance.

2.2.3 Nitrogen mineralization

Phosphorus and nitrogen mineralization rates are closely linked (Cole & Heil 1981), therefore nitrogen cycling in relation to phosphorus mineralization and fertilization was also investigated in this study. While the phosphorus cycle has been described as "tight" (Miller et al. 1979) since it shows minimal losses from a system and no significant external inputs other than by geochemical means (there is no gaseous component) (Lajtha & Schlesinger 1988), the nitrogen cycle has an important external component. This comprises inputs of nitrogen from microbial fixation and precipitation from the atmosphere, as well as outputs, especially by leaching (Gökçeoglu 1988).

Inorganic nitrogen in the soil is made available for plant and microbial uptake by nitrogen mineralization which is the microbial conversion of soil organic nitrogen to ammonium (ammonification) and subsequently to nitrite and nitrate (nitrification) (Jackson et al. 1989). The amount of nitrogen available for plant uptake, "net mineralization", is the difference between microbial release of nitrogen (gross mineralization) and incorporation of nitrogen into microbial biomass (immobilization) (Gökçeoglu 1988; Bell & Binkley 1989). Since the incubation technique used in this study to measure soil mineralization rates includes microbial activity while excluding plant uptake, the "net" nitrogen mineralization rates or potential plant uptake rates were determined.

Low net nitrification rates and thus low nitrate concentrations are often observed in coniferous forests (DiStefano & Gholz 1989). It has been proposed that the soil C:N ratio may be a controlling factor of nitrification (Adams & Attiwill 1986b; Edmonds & McColl 1989). Adams & Attiwill (1986b) found that in nitrogen-rich forests where the C:N ratio is low, mineralization proceeds and all nitrogen undergoes nitrification. Where C:N ratios are high, net mineralization is reduced and only ammonification occurs. The low nitrogen availability results in intense competition between plants and micro-organisms for ammonium and so it is quickly taken up by plant roots or immobilized (Adams & Attiwill 1986b). This would support the proposition of Edmonds & McColl (1989) that the rate of nitrogen immobilization is likely to increase when the C:N ratio of the soil is high. If ammonium is immobilized by micro-organisms other than Nitrosomonas and Nitrobacter (organisms responsible for nitrification; found in low numbers in soils of pine forests (Gökçeoglu 1988)) they will not be mineralized to nitrate. Thus, nitrification rates depend on the levels of ammonium and its availability to the nitrifier populations (Edmonds & McColl 1989). The advantage of reduced nitrification in nutrient poor systems is that losses by leaching are minimized (ammonium is much less mobile than nitrate) (Nadelhoffer et al. 1984; Vitousek & Matson 1984).

Environmental factors that inhibit nitrification are low soil pH, temperature and soil texture, since it determines the water-holding capacity of soils (Nadelhoffer et al. 1982; Burke 1989). While high nitrogen mineralization rates generally correspond with periods of high soil moisture (Burke 1989), denitrification can occur in poorly-drained clay loam soils if they become anaerobic (Groffman & Tiedje 1989). Denitrification is the reduction of nitrogen oxides (NO_3) by anaerobic bacteria to yield gaseous products including NO, N_2O and N_2 (Knowles 1981). Thus, nitrate is not only lost by

leaching (in well-drained soils) but may also be lost into the atmosphere (in fine-textured, poorly-drained soils). Lack of available nitrate limits denitrification (Groffman & Tiedje 1989) which would support the hypothesis of Adams & Attiwill (1986) that ammonium is the dominant inorganic nitrogen form in nutrient deficient systems where losses must be limited. Denitrification should if possible be considered when interpreting the soil mineralization results of this study, since the soils often became waterlogged.

Another factor which influences nitrification is phosphorus availability - phosphorus deficiency limits the growth rate of nitrifying bacteria and thus restricts nitrification (Purchase 1974; Pastor et al. 1984). Cole & Heil (1981) hypothesized that the overall rate of nitrogen cycling may be partly determined by the rate of phosphorus cycling. This is supported by the findings of Tate et al. (1991) where soil nitrogen and phosphorus availability appeared to be synchronized. When nitrogen (and carbon) was readily available, a large microbial population developed which depleted labile inorganic phosphorus and stimulated mineralization of organic phosphorus. This in turn would allow high nitrogen mineralization to be maintained. If organic phosphorus is not mineralized and phosphorus availability in the soils decreases, nitrogen turnover rates decrease as organic nitrogen accumulates (Cole & Heil 1981).

The effect of applied phosphorus on nitrogen mineralization in coniferous forest systems is varied. While DiStefano & Gholz (1989) found that phosphorus availability had little apparent affect on net nitrogen transformations, Turner & Lambert (1986b) showed that levels of nitrogen in the soil increased as the level of applied phosphorus increased. They attributed this to the more effective root distribution in phosphate treated plots which enhanced the uptake of nitrogen from deeper layers in the soil profile. Another process whereby nitrogen levels are increased by phosphorus supply is through nitrogen fixation by both free-living soil micro-organisms and nitrogen fixing legumes as nitrogen fixation is often phosphorus limited (Cole & Heil 1981). Carey et al. (1981) cite many studies which have found a negative effect of applied phosphorus on nitrogen mineralization. This could be due to more effective root growth in response to phosphorus addition, resulting in increased mineral nitrogen uptake from the soil. If this nitrogen becomes bound in carbon-rich compounds, mineralization will be reduced. Inorganic nitrogen may also be immobilized by the large microbial population supported by the increased phosphorus availability. Since an increase in phosphorus availability may stimulate nitrification, nitrogen may be lost as nitrate by leaching or through denitrification (Cole & Heil 1981).

Thus it is essential to know the effects of phosphate fertilization on both phosphorus and nitrogen soil mineralization processes, especially if the effects were to be negative on the nitrogen cycle. While phosphate application may correct phosphorus deficiencies it may, in the long run, lead to reduced nitrogen availability and so again limit productivity of the system. While, in plantation systems, phosphorus availability may be increased into the next rotation, nitrogen fertilization may be required to overcome inbalances in nitrogen availability induced by the initial phosphorus fertilization.

2.3 Litter dynamics

Coniferous trees are reported to be well adapted to nutrient poor soils by means of mechanisms which improve the efficiency of nutrient cycling in the ecosystem (Miller et al. 1979). However, reduced growth induced by nutrient deficiencies is a common problem that occurs late in the rotation, even where supplies were adequate during the earlier, rapidly developing stage when demands were greater (Williams 1983; Bowen & Nambiar 1984). Because of the finite nature of soil nutrient supplies (particularly in nutrient poor soils) and the long rotation usually associated with forest crops, the maintenance of satisfactory growth is dependent on the recycling of essential nutrients, mainly by means of litterfall and decomposition (Carey et al. 1981). Therefore, the rate of decomposition of litter may increasingly become the factor limiting nutrient availability and tree growth as a stand ages. The accumulation of litter and immobilization of large quantities of nutrients in the forest floor as a plantation matures (Carey et al. 1981; Gholz et al. 1985a; Turner & Lambert 1986b; Herbert & Schönau 1990) indicates that the turnover of nutrients is not very efficient in these systems. The very slow decomposition of litter, characteristic of coniferous systems (Berg & Söderström 1979), together with the corresponding immobilization of nutrients in the forest floor, causes reduced uptake rates, slowing down the entire nutrient cycle of the system (Gholz et al. 1985a). The immobilization of nutrients in the humus (partially decomposed litter) is also considered as a process that enables forests to conserve nutrients, limiting losses from the ecosystem by leaching (Williams 1983). The substantial litter layer that accumulates on coniferous forest floors, it is widely recognized as a vital link in the nutrient cycle (Mitchell et al. 1986; Escudero et al. 1987) and it therefore warrants further investigation.

In forest systems where fire (an important agent of mineralization (Mitchell et al. 1986)) is not a natural event or where it is protected from fire, decomposition of plant litter is the primary mechanism by which organic matter and nutrients are returned to forest soils (Birk & Simpson 1980; Aber & Mellilo 1980; Escudero et al. 1987; Entry et al. 1991). The mass of litter which has accumulated on the forest floor (X) at any time represents the balance between the rate of litterfall and decomposition (Birk & Simpson 1980). This mass balance model of Olson (1963) is widely used to calculate decomposition rates by the equation $k=L/Xss$ (k=decay constant, L=rate of litterfall and Xss=the mass on the forest floor). An assumption of this model is that the floor litter mass is in a "steady state" i.e. its composition and biomass is constant. If the steady state condition has not been reached, the determined k values will be overestimated by the amount $1/X.dX/dt$. This error value decreases as X approaches Xss (Birk & Simpson 1980). In this study, the rate of litterfall and the mass of pine litter on the plantation floor were determined for the different aged stands. Therefore, the rate of decomposition could be calculated using the mass balance equation given above.

2.3.1 Litter decomposition

Any examination of the dynamics of the litter layer (such as in this study) requires an understanding of the factors controlling decomposition. Decomposition is a complex process, regulated by a range of variables including climate, exogenous nutrient availability, the physical and chemical properties of the litter and macro- and microfaunal responses. These factors are closely related and may either contribute towards creating environmental conditions that enhance microbial growth and activity, or otherwise determine the susceptibility of the litter to attack by specialized decomposers (Meentemeyer 1978; McClaugherty et al. 1985).

Climatic factors reported as having the strongest influence on microbial activity include temperature and moisture (of the litter microenvironment) (Berg & Söderström 1979; Edmonds 1980; Entry et al. 1991). Vitousek (1984) found a "temperature-precipitation" interaction term to be the best single predictor of litterfall dry mass. However, the correlations for this term are substantially smaller than that obtained by Meentemeyer (1978) who showed that the actual evapotranspiration (AET) has a correlation of $r=0.98$ with average annual decomposition rate. AET is a measure of the concurrent availability of energy and moisture from soil and litter storage and thus represents the microenvironmental control of the decomposers (Meentemeyer 1978).

Studies where temperature alone gives the strongest correlation with litter decay rates are usually from very cold climates where temperature limits overall biological activity (Edmonds 1980). It would probably not be the only significant factor in the plantations of the southern Cape. Moisture may be of equal or greater importance in these regions. The ease of entry of moisture into and out of litter has been recognized as having a bearing on decomposition rates (Meentemeyer 1978). An important reason why pine needles decay more slowly than the leaf litter of other trees may be because they dry more rapidly, hold less water at saturation and have lower water potentials at low moisture contents. This would reduce the growth of non-xerophytic fungi and the activities of soil fauna and so slow the preparation of the litter for invasion by litter-decomposing agarics (Dix 1984). Specht (1981) found that the dry weight and nutrient content of the top layer of Banksia ornata litter, exposed to the desiccating influence of the atmosphere and separated from the litter-soil interface, remained relatively constant. Only when covered by the following year's leaf fall did decomposition proceed.

In order to determine the influence of environmental variables on the decomposing matter, studies of the seasonal variations in the intensity of decay are necessary. Another factor controlling decomposition is the chemical nature of the litter. However, studies of the seasonal variations of decomposition have shown that when environmental conditions are unfavourable for microbial activity (eg. the dry summer season of the mediterranean climate), these limiting conditions override the litter quality regulation of decomposition (Escudero et al. 1987).

When the environmental conditions are favourable for microbial activity and thus decomposition, the chemical composition of the litter controls the decomposition process. The initial weight loss of litter is

suggested to be due to leaching by water of water-soluble substances. Water-soluble substances in litter not physically leached may be metabolized by invading micro-organisms which thus have an easily available nutrient source for growth. When the amount of water-soluble substances decreases, it is assumed that the microflora becomes dominated by fungi with a greater potential for decomposition of the insoluble substances with a higher C:N ratio. Thus fungi appear to play a crucial role in the process of accumulation of nitrogen in the needles (Berg & Söderström 1979; Edmonds 1980). The change from loss to accumulation of needle nitrogen coincided with the time when the fungal biomass showed its most rapid increase and appeared to be correlated to fungal biomass increase thereafter (Berg & Söderström 1979). Using ^{15}N-tracer methods, Hart & Firestone (1991) estimated that fungal translocation from the soil to the forest floor may account for all of the increase in litter nitrogen.

Entry et al. (1991) compared microbial biomass, needle decomposition rates, nutrient release from needles and exchangeable soil nutrients in soils with extensive ectomycorrhizal fungus hyphal mats and in adjacent non-mat soils in a Douglas fir forest. Microbial biomass and needle decomposition rates were found to be higher in fungal mat soils since fungal hyphae provides a favourable microenvironment for other soil microbes and soil arthropods which accelerate organic matter decomposition and nutrient turnover. The fungi may also stimulate decomposition directly via saprophytic action. Ectomycorrhizal fungi produce proteases, phosphatases, cellulases and phenol oxidases which suggests that they are capable of degrading a variety of organic substrates including holocellulose, lignocellulose and lignin (Entry et al. 1991). In order to degrade the more recalcitrant compounds such as lignin, fungi require an additional source of easily degradable carbon. This may initially be taken up directly from the litter but the bulk is most likely to be obtained from the exudates of living roots (Cheng & Coleman 1990; Entry et al. 1991) and would support the findings of Cheng & Coleman (1990) that the presence of living roots stimulates the decomposition of organic matter. Since fungal hyphal development at the soil-litter interface is sensitive to moisture and temperature (Entry et al. 1991) it will probably not develop until there is a substantial litter layer covering the soil surface so as to prevent drying out and excessive temperature fluctuations of the soil-litter interface. In the oldest stand of this study where the litter layer is between 10-15cm thick, fungal mats were observed. Therefore the role of fungi will have to be considered when interpreting the decomposition and nutrient turnover rates.

Conflicting evidence exists as to whether lignin content or the C:N ratio of litter is the major aspect of litter chemical quality controlling the rate of decomposition. Litter with a high lignin concentration and large C:N ratios shows slow decomposition rates (Meentemeyer 1978). Meentemeyer (1978) states that climate is the dominant control of decomposition on a global scale but with uniform terrain and macroclimate, lignin concentration is the best predictor of decay rates of litters of different origins. Climatic factors and lignin content are related in that the greater the abundance of energy and moisture (AET) the faster the decay rate for a given lignin content but the higher the lignin content, the more energy and moisture are required to cause the breakdown in a unit time (Meentemeyer 1978). However, the significance of lignin in controlling the overall decomposition process may be overemphasized. Since lignin is the last component to decompose, it appears to be the primary control of decomposition

and tends to dominate the shape of the long-term decomposition curve once the more labile components have been removed (Berg et al. 1982).

Other workers (Edmonds 1980; Yavitt & Fahey 1986) have stressed the importance of the C:N ratio in determining the rate of litter decomposition. C:N ratios between 20:1 and 30:1 (Lutz & Chandler 1946, cited by Edmonds 1980) are frequently cited as the levels at which mineralization of nitrogen from litter occurs. Above these levels microbial immobilization of nitrogen occurs. This has been observed in many studies as an increase in nitrogen concentration in the litter, and acts to reduce the initial C:N ratio of the litter (Edmonds 1980; Yavitt & Fahey 1986). It was believed that the increased nitrogen levels came from atmospheric inputs. However, the accumulation levels are usually quite high so that translocation of nitrogen from the underlying soil by saprophytic fungi must be occurring (Yavitt & Fahey 1986). Hunt et al. (1988) found that decomposition rates of pine litter were higher when nitrogen was added to the soil. Aber & Mellilo (1980) showed that the inverse linear regression obtained by expressing the percentage of original litter biomass remaining as a function of the nitrogen concentration in the residual material was altered to give an exponential curve when no continuous extenal source of nitrogen was available. The linear slope requires an initial increase in nitrogen which represents immobilization of nitrogen from the soil (which exhibits net mineralization).

While Yavitt & Fahey (1986) were able to fit a similar inverse linear relationship to the initial stages of their litter-decay data, the slope declined during later stages and a second inverse-linear relationship with a much lower slope appeared. Even though nitrogen accumulation continued, the decay rate slowed. This suggests the formation of recalcitrant nitrogen compounds in the residue (Yavitt & Fahey 1986). This trend seems to support the decomposition model described in Berg et al. (1982) which suggests an early nutrient-regulated phase and a late phase during which the rate is regulated by lignin. During the first nutrient-regulated phase of decomposition, increased nitrogen levels resulted in faster decomposition. However, the higher nitrogen levels reduces lignin decomposition (ammonium binds with lignin to form complexes which are degraded very slowly by the soil microflora) (Berg et al. 1982). This would support Yavitt & Fahey's (1986) suggestion that recalcitrant nitrogen forms during the later stages of decomposition, if nitrogen accumulation continues.

The role of the C:P ratio in litter decomposition is less certain. As with C:N ratios, critical C:P ratios have also been proposed for phosphorus mineralizaton. Alexander (1977) suggested that phosphorus mineralization begins when the C:P ratio of the litter is between 100:1 and 300:1. However, Edmonds (1980) and Yavitt & Fahey (1986) proposed that phosphorus mineralization can proceed at much higher C:P ratios. Yavitt & Fahey (1986) observed a slow accumulation of phosphorus in the litter such that the C:P ratio changed from 1250:1 to 420:1 after nine years. Nevertheless, efficient recycling of detrital phosphorus within the litter-microbe system was apparently maintained. Vitousek (1984) also reports very little phosphorus return and high C:P ratios in litterfall of tropical forests but considers these systems as having a highly efficient phosphorus cycle (the concepts of nutrient efficiency will be discussed later).

Contrary to the results of the decomposition studies reviewed thus far where levels of nitrogen accumulation in litter were high and phosphorus accumulation was very small (if any), Gholz et al. (1985a) found phosphorus accumulated to a large degree in the decaying needles while no overall addition of nitrogen occurred (after 24 months). This increase in phosphorus, besides being directly related to stand age and indirectly related to the initial phosphorus concentration, was shown to be related to the initial N:P ratio. By examining a range of similar studies, Gholz et al. (1985a) found that where initial N:P ratios were low, phosphorus did not apparently accumulate; where N:P ratios were higher, significant phosphorus accumulation occurred. The main source of phosphorus accumulation in the litter was believed to be from lower levels of decaying litter or from the mineral soil. The lack of accumulation of nitrogen in the litter was not due to a limited source, since nitrogen availability was abundant in the soil and litter solution (Gholz et al. 1985a).

Since this study is examining the effects of phosphorus fertilization on the rate of nitrogen and phosphorus cycling processes, it seems more appropriate to calculate the initial N:P ratios of the litter than C:N/C:P. By comparing our N:P ratios with those of Gholz et al. (1985a) and other studies they document, it is possible to infer whether nitrogen or phosphorus accumulation is occurring. The way in which this ratio changes with stand age and phosphorus fertilization will also be examined.

Another aspect of the interaction between litter dynamics and nutrient levels examined in this study, is the relationship between the rate of litterfall and phosphorus and nitrogen levels in the litter. A positive interaction between phosphorus concentration and litter production is expected, since Vitousek (1984) found litter phosphorus to be the best predictor of litterfall (where environmental conditions were favourable). This relationship was strong and positive where phosphorus was low and limiting production, and absent at higher phosphorus concentrations. This study examines litter production where phosphorus is limiting, as well as at various stages after phosphorus fertilization. Witkowski (1989) found that phosphorus addition to a nutrient-poor fynbos system had no significant effect on litter production two years after fertilization and so concluded that phosphorus was not limiting litter production.

2.3.2 Nutrient retranslocation

The large degree of litter accumulation and nutrient immobilization in an already nutrient stressed system would further reduce nutrient availability and could result in nutrient deficiencies and reduced growth rates (Turner 1981; Bowen & Nambiar 1984). However, plants are able to reduce their dependence on soil nutrient uptake and avoid growth limitations by internal nutrient retranslocation. This retranslocation is accomplished by re-absorption of nutrients from senescing tissues prior to leaf abscission, followed by translocation to other sites of high demand (Jonasson 1989). The proportion of nutrient requirement fulfilled by retranslocation is calculated as the difference between plant requirement and uptake of the nutrient. At peak nutrient demand (found to be at 6-8 years for P. radiata by Turner & Lambert (1986a)), both nutrient requirement and uptake are high. However, this often rapidly depletes available soil nutrients and reduces uptake which creates potential nutritional problems

(Turner & Lambert 1986a). Evidence that the nutrient demand for growth at this stage is met by retranslocation of nutrients arises from the lack of response to fertilizer application at this stage (Bowen & Nambiar 1984). Retranslocation appears to supply an increasing proportion of the growth requirement, with increasing stand age (Turner 1981). Gholz et al. (1985b) reported that internal retranslocation increased greatly after canopy closure (10 years) - the proportion of growth requirement met by retranslocation increased at a constant rate for nitrogen and increased exponentially for phosphorus, reaching very high values in the older stands indicating that phosphorus may have become limiting in their study.

Nutrient retranslocation on a seasonal basis, especially for phosphorus, can occur even in 6 month old needles at periods of peak demand and when phases of retranslocation coincide with new flushes of shoot growth. It was estimated on a tree basis that 86% of phosphorus and 48% of nitrogen in summer shoots could have come from retranslocation of nutrients from young needles formed during the preceding spring (Turner & Lambert 1986a). This may lead to premature needle loss, with litter of low nutrient content. Thus decomposition and subsequent release will be slow (Gholz et al. 1985b).

The retranslocation mechanism provides the plant with considerable flexibility in its utilization of nutrients (Turner 1981; Turner & Lambert 1986a). The extent to which species differ in their inherent capacity to store and retranslocate nutrients is not known. Retranslocation appears to be controlled by growth patterns, nutrient availability for circulation and nutrient stress at a site (Bowen & Nambiar 1984). It has been considered as an important adaptation for success in infertile environments where the plants are said to have a high "nutrient use efficiency". In contrast, other studies have shown that species with low leaf nutrient levels re-absorb a lower fraction of their maximum nutrient pool than species with high leaf nutrient levels (Jonasson 1989). Jonasson (1989) found nothing to indicate that re-absorption is higher in evergreen species (usually associated with nutrient poor conditions (Chapin 1980)) than in species growing under favourable soil nutrient conditions.

In this study, the proportion of nutrients retranslocated from the needles prior to abscission was calculated as the difference in nutrient levels between leaves (needles) and freshly fallen litter. The effect of nutrient availability and stand age on retranslocation in P. elliottii needles was investigated. Retranslocation in phosphorus deficient and phosphorus fertilized plots were compared in three different aged stands. The oldest stand allowed retranslocation to be examined relative to the additional variables of phosphorus fertilization timing and frequency. Since applied phosphorus does affect the nitrogen mineralization process in forest floor materials (Carey et al. 1981), retranslocation was also examined at different nitrogen availability levels. This would increase our understanding of how plants respond, via retranslocation, to different soil nutrient regimes and stand age.

It seems that a plants' potential for retranslocation determines its "nutrient use efficiency". Vitousek (1984) describes efficient use as the stage when relatively large amounts of organic matter are fixed per unit nutrient taken up or when a large fraction of nutrients is reabsorbed from senescing plant parts. Thus by continued retranslocation of nutrients, the plant may accumulate large quantities of nutrients

relative to nutrient availability. Chapin (1980) realized that a high efficiency of nutrient use was an important adaptation to nutrient stress. However, by omitting the role of retranslocation and simply defining "efficiency" as the quantity of dry matter produced per gram nutrient (the inverse of tissue concentration), it seemed that plants from nutrient-poor habitats were less efficient. Thus Chapin (1980) proposed that the production rate may be a more useful measure of efficiency.

Vitousek (1984) suggests that dry mass/nutrient ratios in litter are a good index of the nutrient economy in a stand, since it incorporates the degree of retranslocation occurring. When efficient retranslocation of a nutrient is occurring, the concentration of that nutrient in the litter will be low and so the index of efficiency will be high (provided nutrient stress does not drastically reduce the litter mass). If retranslocation is a response to nutrient poor conditions, then high nutrient efficiency will be found under such conditions. As with the determination of retranslocation, nutrient efficiency indexes (for phosphorus and nitrogen) will be calculated across the phosphorus fertilization regime.

Calculating nutrient effiency indexes together with all other aspects of nutrient cycling examined in this study should increase our understanding of the processes limiting production in P. elliottii plantations.

CHAPTER 3

MATERIALS AND METHODS

3.1 Study Area

Study sites were located on state forest plantations in the Knysna - Keurboomsrivier area, southern Cape, South Africa (Fig. 3.1). The natural vegetation of this region is Knysna Forest (Von Breitenbach 1968) interspersed with "islands" of fynbos vegetation (Midgley & Bond 1990). Plantations are often established within these fynbos remnants. The mean annual rainfall for the whole region (determined from the means of the annual rainfall at Millwood, Gouna and Keurboomrivier weather stations) is 987 mm with no definite seasonal pattern.

Three study sites were selected to give an age sequence of P. elliottii stands. The stands were in the Goudveld, Keurboomsrivier and Kruisfontein State Forests and were established in 1983, 1971 and 1966 respectively (representing an age sequence of 8, 20 and 25 years old).

The youngest stand (8 years old), Goudveld (Lat. 33° 54'S, Long. 23° 02'E) (Fig. 3.1, Table 3.1), occurs on a northern slope of the foothills zone of the Outeniqua Mountains. It falls within the Farleigh forest land type (Schafer 1991). This land type consists of a very shallow topsoil overlying a fine siltstone of the Table Mountain Sandstone group, Goudini (Tchando) formation. This zone is subject to accumulation of colluvial material from higher in the landscape (the mountainous Outeniqua land type) (Schafer 1991).

Differences in soil form occur down the foothills as a result of differences in drainage. The soil of the upper, well drained, steeper slopes is of the Vilafontes form (South African Binomial Soil Classification, MacVicar et al. 1977). The Vilafontes soil form extends to the middle, less steep slopes but in a slightly wetter state than that of the upper slopes. On the flatter slopes where drainage is restricted, the soil is much wetter, resulting in a Longlands form (MacVicar et al. 1977). All the study plots in this stand were situated on the upper and middle slopes, thus being of the Vilafontes form (unpubl. FORESTEK records). The soil texture (Table 3.1) was sandy loam (Soil Classification Working Group 1991).

The Goudveld trial was laid out in 1983 to test the effects of phosphate fertilization on various Pinus species. The six plots of P. elliottii consist of three plots fertilized at establishment with 30 kg ha^{-1} superphosphate and three unfertilized plots (controls). Each plot is laid out in rows of 10 x 10 trees, 2.74 m x 2.74 m apart. This trial is a second rotation stand. After clearfelling the earlier plantation, seedings were planted within the slash (harvest residue). No burning was carried out (pers. comm. N. de Ronde). The P. elliottii trees are now about 4-5 m tall in the unfertilized plots and 5-6 m in the fertilized. Canopy closure has not yet occurred and thus there is a dense understorey of mesic fynbos.

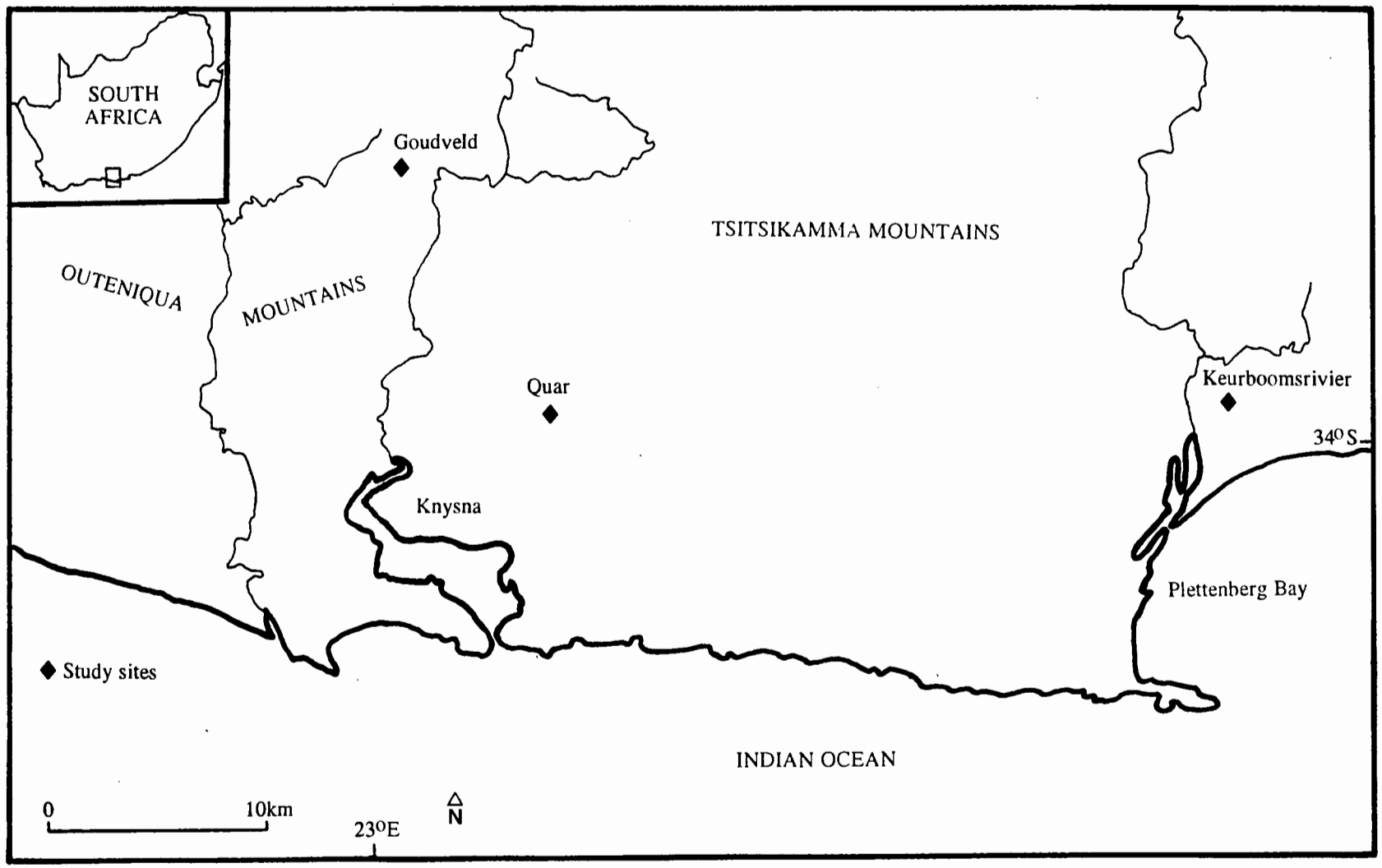


FIG.3: Map of study area. Inset shows location of study area in South Africa.

TABLE 3.1: Characteristics of the three study sites.

SITE LOCALITY	PLANTATION AGE (Years)	ASPECT	SLOPE (°)	ALTITUDE (m)	MEAN ANNUAL RAINFALL (mm pa)	SOIL FORM	SOIL TEXTURE (%)
Goudveld State Forest	8	North	10-14	450	1113 [a]	Vilafontes	24.3 silt 11.7 clay 61.6 sand
Keurboomsrivier State Forest	20	North	2	200	868 [b]	Escourt	14.7 silt 7.3 clay 78.8 sand
Kruisfontein State Forest (Quar)	25	South-west	3	250	980 [c]	Kroonstad	22.3 silt 11.7 clay 62.7 sand

Rainfall recorded at [a] Millwood weather station
[b] Keurboomsrivier weather station
[c] Gouna weather station

The dominant fynbos elements are tall grasses, sedges and restios, approximately 1.5 m in height. Leucadendron and Erica species are also prominent.

The second stand in the age sequence (20 years old) is Keurboomsrivier (Lat. 33° 59'S, Long. 23° 25'E) (Fig. 3.1; Table 3.1). This trial lies on a level to gently seaward sloping, south-westerly aspect of the southern Cape Coastal platform, within the Barrington forest land type. The thin layer of Table Mountain Sandstone derived surface soil rests on a substantial layer of marine deposited clay. This makes these soils highly prone to waterlogging. They have been classified as an Escourt form (MacVicar et al. 1977; unpubl. FORESTEK records). Soil texture (Table 3.1) was classified as loamy sand (Soil Classification Working Group 1991).

The Keurboomsrivier P. elliottii stand was established as a NPK fertilizer trial on land previously covered by 1m tall, dense fynbos vegetation (unpubl. FORESTEK records). Three plots were chosen which received only phosphate fertilization at establishment at the level of 60 kg ha^{-1} superphosphate. Three unfertilized plots (controls) were also demarcated for study. Here again each plot is laid out in rows of 10 x 10 trees, 2.74 m x 2.74 m apart. The height of the P. elliottii trees range between 15-18 m. The taller, fertilized trees show a greater degree of canopy closure and thus have very little understorey vegetation.Remnants of the pre-plantation fynbos vegetation still occur in the unfertilized plots in the form of a few Leucadendron and Erica species. However, the dominant understorey elements are monocotyledonous (grasses and geophytes). A common feature of a plantation floor is the substantial accumulation of needle litter (Gholz et al. 1985a). In this stand, a continuous needle litter layer of about 5-8 cm thick covers the ground.

The third and oldest stand (25 years old), part of the Kruisfontein State Forest, is referred to as Quar (Lat. 33° 59'S, Long. 23° 06'E) (Fig. 3.1; Table 3.1). This stand lies on the level to gently sloping upper regions of the coastal platform, within the Barrington forest land type. Generally, the surface soil consists of marine clays of the Kroonstad form (MacVicar et al. 1977). Variations in soil moisture are prominent across the stand, resulting in a range of soil series. Kroonstad series occurs in the regions with better drainage. The wetter soils are of the Bluebank and Katspruit series (MacVicar et al. 1977). Periodic flooding is common in these soils (unpubl. FORESTEK records). Soil texture was classified as sandy loam (Soil Classification Working Group).

The Quar trial was set up to determine i) the response of P. elliottii to various levels and combinations of N, P and K fertilizers on land not previously under plantation and ii) if there is an additional response to a subsequent application of phosphate. Of the 12 plots demarcated for study, 3 were fertilized with 56 kg ha^{-1} superphosphate at establishment (1966) only, 3 received 56 kg P ha^{-1} at establishment plus an additional 50 kg P ha^{-1} 10 years later (1977), 3 were fertilized with 50 kg P ha^{-1} only at the second application in 1977 and 3 were unfertilized (controls). All the plots consist of rows of 10 x 10 trees at an espacement of 2.74 m x 2.74 m. The trees are now about 20-25 m tall. The degree of canopy closure appears to be related to the level of fertilization. Plots fertilized at establishment as well as those which received a second application have a dense P. elliottii canopy and

almost no understorey vegetation. Plots fertilized only 10 years after establisment have a more open canopy and a sparse understorey, comprised mainly of grasses. The unfertilized trees form a very open canopy, allowing a 1-1.5 m high dense understorey vegetation to be maintained. The dominant understorey element is a Gleichenia fern species, interspersed with fynbos Leucadendron and Erica species. A prominent feature of this plantation floor is the large amount of accumulated needle litter, up to 15 cm thick.

3.2 Soil Nutrient Dynamics

The effects of phosphate fertilization on soil phosphorus and nitrogen mineralization patterns in the different aged P. elliottii stands were investigated by an in situ soil incubation study. By determining soil nutrient mineralization in different aged stands and plots subject to differential fertilization frequencies, the effects of fertilization as well as the duration of the effects were investigated. The incubation study not only determines the absolute amounts of phosphorus and nitrogen in the soil, but more importantly, it also indicates what is becoming available to the plants over a period of time (the nutrient turnover/mineralization rate).

Net soil phosphorus and nitrogen mineralization rates were determined using an incubated (buried) soil core procedure, similar to that described by Raison et al. (1987). At each study plot, 3 permanent sampling sites were demarcated. In order to take soil samples it was necessary to clear loose litter to expose the soil; otherwise the site was left undisturbed.

At each sampling site, 2 adjacent PVC cylinders (inner diameter of 4.3 cm, length of 10 cm) were driven into the soil to a depth of 10 cm, avoiding large surface roots. The cores were then carefully removed from the soil. One soil filled PVC tube was enclosed in a polyethylene bag (20 x 13 cm) and buried in the soil at the depth from where it was removed. The litter layer was replaced over the soil and core. This core represents the in situ incubated soil. Since the polyethylene bags are water-impermeable, the soil moisture of the incubated cores are supposedly kept constant during the incubation period. They are also gas-permeable, thus maintaining an aerobic situation and sensitivity to soil temperature changes. The other core was emptied into a plastic bag and returned to the laboratory immediately for analysis. This represents the initial or fresh soil sample from which the ambient nutrient concentrations are determined for the beginning of each incubation period.

The incubation period used in this study was 42 days. It falls within the recommended incubation period suggested by Raison et al. (1987). Adams et al. (1989) suggest that an incubation period should ideally not exceed 2 weeks. Such a short period may have been more suitable in this study since the combination of high rainfall and poor soil drainage resulted in frequent saturation of the soils and cores. However, for practical reasons, namely long distance to the study area and a large number of samples to be processed (72 fresh + 72 incubated samples) a shorter incubation period was not possible.

At the end of each incubation period, the buried cores were removed from the soil and returned to the laboratory for analyses together with a set of fresh soil samples. Another set of cores were installed for the next incubation period. This study was run from July 1989 to October 1990, namely 12 incubation periods of 6 weeks (42 days) each.

All the soils were returned to the laboratory within 24 hours where they were stored at 0°C for a maximum of 4 days. During this period all the soils were sieved through a 2 mm mesh sieve and inorganic phosphorus and nitrogen extractions were carried out as described in Section 3.9. Extracts were analysed for resin-extractable (available) phosphorus, ammonium and nitrate/nitrite.

In order to interpret soil nutrient mineralization patterns, it is important to know the soil "environmental" conditions at which mineralization is occurring. Therefore, the following soil measurements were taken - soil temperature, moisture, organic content, pH and texture.

3.3 Soil Temperature

Soil temperatures at 10 cm depth were measured at each sampling site when soil cores were taken for the incubation study. A Fluke 2175A digital thermometer with a copper/constantin thermocouple was used.

3.4 Gravimetric Soil Moisture and Organic Matter Content

Moisture content of all the soil samples was determined as the mass lost by a 10 g fresh soil sample, dried in a forced-draught oven at 105°C for 24 hours. The oven-dried soil was used to determine the organic matter content as the mass lost during 16 hours in a furnace at 450°C. Moisture and organic matter content was expressed as a percentage of the soil dry mass.

3.5 Soil pH Determination

Soil pH was determined by shaking 20 g fresh soil in 50 ml 0.01 M calcium chloride for 30 minutes. The pH values of the soil solutions were measured using a Radiometer M29 pH meter.

3.6 Soil Textural Analysis

The sand, clay and silt content of the soils was determined by the Bouyoucos method (Bouyoucos 1962). Fifty grams of soil in 50 ml 10% Calgon solution was stirred for 5 minutes, transferred to a Bouyoucos flask and made up to volume. After standing overnight, the flask was shaken for 1 minute and after standing for 7 minutes a hydrometer reading was taken. This gave the "silt and clay" reading. After standing for 7 hours, a second reading was taken with the hydrometer and entered as "clay". The flask was shaken again, allowed to stand for another 7 minutes after which the silt and clay suspension was decanted. This was repeated until the sand was free of silt and clay. The sand content was

determined by weighing the sand after ovendrying at 105°C. %Silt was calculated as ("silt and clay" reading - "clay" reading) x2, %clay as ("clay" reading - blank reading) x2 and %sand as the mass of dry sand x2.

3.7 Nutrient Dynamics in P. elliottii Foliage and Litter Components

In an attempt to understand the dynamics of the litter layer of the plantation floor and its role in the nutrient cycle, the nutrient content of the foliage and litter components of the sites were quantified. This would indicate the proportion of nutrients held in the litter layer relative to the amount in the soil and foliage.

Fresh foliage (previous 2 years' needles) was collected from the P. elliottii trees in order to quantify the needle nutrient content prior to abscission and litterfall. After ovendrying at 70°C, the needles were ground and analysed for total phosphorus and nitrogen. A comparison of the nutrient levels of fresh needles with that of the litter indicates the degree to which nutrients are withdrawn from needles prior to litterfall. Also, the effect of fertilization on this nutrient withdrawal process is examined.

The rate of litter fall was determined by setting up 2 littertraps at each study plot (i.e. 6 traps per treatment at each plantation). Each trap consisted of 2 mm mesh netting suspended from a 50 cm diameter wire hoop and held above the ground by 3 metal poles. Litter was collected at 6 week intervals, from March 1990 to March 1991. Collected litter was oven-dried at 70 °C, separated into pine needles and understorey foliage and weighed. Subsamples of pine litter from each season were kept for nutrient analyses (to quantify the litter nutrient input potential to the soil nutrient turnover cycle). Samples were ground in a Wiley Mill with a 20 mesh sieve before being analysed for total phosphorus and nitrogen.

The biomass of the accumulated standing needle litter as well as the understorey vegetation was determined for 3 1x1 m quadrats per study plot. The whole sample was weighed in the field. A subsample was returned to the laboratory, weighed, ovendried and reweighed so that the biomass could be expressed as a dry mass.

3.8 Soil Bioassay

The nutrient dynamics of the soil, foliage and litter components of the 3 different aged P. elliottii plantations were examined with respect to phosphate fertilization. At the oldest stand (Quar), the frequency of fertilization application was an additional variable. While the tree growth response to the different fertilization treatments at Quar was pronounced (unpubl. FORESTEK records), soil nutrient differences were small. In order to determine whether these soils could still produce a similar growth response (25 years after the initial applications of phosphate fertilizers), a bioassay relating growth to soil nutrient levels was set up on soils collected from the Quar study plots. A 5 cm tall P. elliottii seedling was placed in about 2 kg of soil from each study plot, replicated 3 times. After growing in the

greenhouse for 8 months, the seedlings were removed from the soil, washed, oven-dried, weighed and the performance on each soil evaluated.

3.9 Nutrient Analyses

3.9.1 Phosphorus analyses

Inorganic phosphorus

The inorganic phosphorus content of the soil samples was determined by the Anion Exchange Resin Extraction procedure described by Sibbesen (1977). Field moist, 2 mm mesh sieved soil (20 g) was tumbled in sealed jars on a mixer with 100 ml distilled water and a resin bag (300 micron mesh polyester bags containing 8 g anion exchange resins, activated by stirring in 0.5 M sodium chloride) for 16 hours. The phosphate absorbed by the resin of each bag was extracted with 75 ml 0.4 M hydrogen chloride by shaking/tumbling for 1 hour. A 10 ml aliquot of the filtered eluate was then assayed for phosphorus by adding 8 ml of Murphy & Riley's (1962) solution (prepared each time by adding 500 ml 5 M hydrogen sulphate, 5.28 g ascorbic acid dissolved in 300 ml water, 150 ml ammonium molybdate and 50 ml potassium antimony tartrate). The solution was made up to 50 ml with distilled water and after 40 minutes of colour development, read at 882 nm on the Spectronic 21 digital spectrophotometer (Baush and Lomb, New York). Resin-extractable (plant available) phosphorus concentrations were determined using a standard curve in the range 0 to 8 μg P ml^{-1} .

Inorganic phosphorus fractionation

Soil inorganic phosphorus forms insoluble in water are not detectable by the resin-extractable technique used in this study for inorganic phosphorus determination. A modified Chang and Jackson (1958) method (in Lambert 1982) was used to determine the levels of inorganic phosphorus bound to heavy metals and ions in the soil. One gram of air-dried, 2 mm mesh sieved soil was sequentially extracted with 0.5 M ammonium chloride to release the soluble phosphorus fraction, 0.5 M ammonium fluoride to release aluminium bound phosphorus, 0.1 M sodium hydroxide to release the iron bound phosphorus and 0.25 M hydrogen sulphate to release the calcium bound phosphorus. A more detailed outlay of this procedure was given by G. Brown (1982). The Murphy & Riley (1962) method was used to analyse the levels of phosphorus in the various extractions.

Soil total phosphorus

Total phosphorus levels in the soils were determined using a modified method of a triacid digestion described by Grimshaw (1985). A 0.2 g air-dried, sieved sample was weighed into a 50 ml thick-walled boiling tube and digested with 3.5 ml of a 10 nitric acid: 1 perchloric acid (60%): 1 sulphuric acid mixture. The flasks were gently boiled at 150^{o}C for about 1 hour with only a gradual loss of mainly nitric acid. As the white fume stage approached, heating was increased to 250^{o}C for about 20 minutes

(or until all the white perchloric fumes were dissipated) until mainly sulphuric acid remained. The clear digest was more viscous but drying out was not permitted. When cool, the digests were diluted to 25 ml, mixed thoroughly and allowed to settle. Three blanks (acid only) were also digested. A 10 ml sample was used for the Murphy & Riley (1962) determination of phosphorus. A set of standards in the range 0.2 to 10 μg P ml^{-1} were also run with the Murphy & Riley (1962) determinations.

Plant total phosphorus

A 0.1 g sample of ground plant material was weighed into a 50 ml thick-walled boiling tube and digested with 1 ml concentrated nitric acid at 150°C for about 20 minutes (until the sample was dry but not charred). Once cool, 1 ml triacid mixture (10 nitric acid: 1 sulphuric acid: 4 perchloric acid) was added to each tube. The samples were digested at 180°C for 30 minutes to 1 hour, until the samples were clear and all the white fumes had dissipated. When cool, the digests were diluted to 25 ml with distilled water and mixed thoroughly. A 10 ml sample was used for the Murphy & Riley (1962) determination of phosphorus. Standards in the range 2 to 30 μg P ml^{-1} were included in the Murphy & Riley (1962) determinations.

3.9.2 Nitrogen analyses

Inorganic N extraction

For each field-moist, 2 mm mesh sieved sample, 10 g soil was added to 40 ml 1 M potassium chloride and shaken for 1 hour. The filtrate (filtered through Whatman No 1 filter paper) was used for ammonium, nitrate and nitrite analysis.

Ammonium determination

Ammonium was determined by a manual Indo-phenol blue procedure described by Stock (1983). To 2 ml of sample extract or standard the following reagents were sequentially added: 1.6 ml 10% (w/v) sodium potassium tartrate solution, 0.2 ml 0.16% (w/v) sodium nitroprusside solution, 0.4 ml sodium phenate reagent and 0.2 ml sodium hypochlorite with 5% available chloride. The reagents were mixed, made up to 10 ml with distilled water and incubated for 20 minutes in a waterbath at 40°C. After cooling, the absorbance was read within 10 minutes at 625 nm with a Spectronic 21 digital spectrophotometer (Baush and Lomb, New York). Because of the 10 minute time limit for taking readings, not more than 18 samples were run simultaneously. Each run included 6 standards prepared from a 0.1 M ammonium chloride stock solution made up in 1 M potassium chloride in the range 2.5 to 30 μg N ml^{-1}, 3 1 M potassium chloride blanks and 3 Whatman No 1 filtered 1 M potassium chloride blanks (to analyse the solutions for ammonium which may be present in the filter paper) (Stock 1983; Wiltshire & Laubscher 1989). These blanks and standards were used to construct a standard curve from which ammonium concentrations were calculated.

Nitrate and nitrite determinations

These were also carried out according to Stock (1983) whereby nitrate is reduced to nitrite by the copper-cadmium method. Nitrite was determined by the Griess-Ilosvay method.

For copperized cadmium reduction, 0.1 ml 1 M magnesium chloride, 2 g prepared copper cadmium and 1.9 ml 0.4 M ammonium chloride buffer (pH 9.6) were added to 3 ml potassium chloride soil extracts. This mixture was shaken for precisely 10 minutes afterwhich a 1 ml aliquot was removed for nitrite determination by the Griess-Ilosvay method. Three 1 M potassium chloride blanks, 3 Whatman No 1 filtered potassium chloride blanks and 6 standards (0.1 M potassium nitrate prepared in the range 0.2 to 3.0 μg N ml^{-1}) were run simultaneously.

Griess-Ilosvay nitrite determinations involved adding 1 ml 1% (w/v) sulphanilamide in 1.5 M hydrogen chloride and 1 ml 0.01% (w/v) N-(1-napthyl)ethylene hydrogen chloride solution to 1 ml potassium chloride soil extracts or copper cadmium reduced solution. After 10 minutes of colour development, absorbances were read at 540 nm on the L & B Spec 21. Five nitrite standards (using sodium nitrite) were prepared in the range 0.1 to 1.0 μg N ml^{-1}.

Total nitrogen

Total nitrogen was determined by a micro-Kjeldahl digestion. One gram of 2 mm mesh sieved, air-dried soil or 0.5 g ground plant material was weighed into 50 ml Kjeldahl digestion tubes. To each tube 1 ml distilled water, 3 ml nitrogen-free concentrated hydrogen sulphate containing 34 g l^{-1} salicylic acid, a selenium-catalyst tablet and 0.2 g (spatula tip) sodium thiosulphate were added. After digestion on an aluminium block digester (carried out by initially leaving the tubes overnight at 150°C, increasing the temperature from 220 to 300°C at 1 hour intervals and after digest cleared, digested at 350°C for 2 hours) the digest was made up to 50 ml with distilled water. The ammonium content was determined by a phenol-hypochlorite method (Smith 1980).

Phenyl-hypochlorite determination was carried out by adding 25 ml 0.12% (w/v) EDTA, 2 ml reagent A (equal parts of 0.5% (w/v) sodium nitroprusside and 10% (w/v) phenol in 95% ethanol) and 5 ml (for soils) or 3.5 ml (for plant material) reagent B (4 parts alkaline phosphate buffer to 1 part 1.5% sodium hypochlorite) to 1 ml soil or 0.5 ml plant digestion solution. The solution was made up to 50 ml, left for 60 minutes and read at 635 nm. Three blanks and 6 ammonium sulphate standards in the range 0.1 to 3.0 μg N ml^{-1} for soils or 0.25 to 3.0 μg N ml^{-1} for plant material were run simultaneously.

The rate of inorganic phosphorus and nitrogen production (mineralization) was calculated as the difference between concentrations in the incubated soils and fresh samples (taken at the beginning of each incubation period) over the incubation period. Inorganic phosphorus was taken as the resin-

extractable phosphorus component. Inorganic nitrogen was taken as the sum of the concentrations of ammonium and nitrate (nitrite levels were found to be negligible).

Soil moisture content was determined for each batch of soils returned from the field. Analyses that were only carried out on selected batches of soils were organic matter content, total nitrogen, total phosphorus, phosphorus fractionation, pH and soil texture.

3.10 Statistical Analyses

A three-way analysis of variance (ANOVA) (using STATPAC) was carried out on soil inorganic phosphorus and nitrogen concentrations, phosphorus and nitrogen mineralization rates and on the litterfall rates. The factors tested for significance were plantation age, fertilization treatment and time of incubation period/collection (month). When variables were tested at each aged stand individually or when time was not a factor, a two-way ANOVA (using STATGRAPHICS) was carried out. One-way ANOVAs were used to test the effect of a single factor on a variable.

In order to determine which environmental factors and site characteristics were significant in determining the observed trends of phosphorus and nitrogen mineralization rates, a "Stepwise Multiple Linear Regression" (STATGRAPHICS) was carried out.

Simple linear regression analyses (STATGRAPHICS) were used to test the strength of litterfall and decomposition in determining litter accumulation. Simple linear regression analyses were also used to test the correlations of litter phosphorus or nitrogen versus annual litterfall rates and nutrient use efficiency.

The significance levels (p) of the F values and coefficients of determination (r^2) were obtained from the appropriate tables in Zar (1984).

CHAPTER 4

SOIL NUTRIENT DYNAMICS

INTRODUCTION

The turnover of nutrients with the soil-plant-litter system should be viewed as one continuous cycle. However, for this study, the nutrient cycle was divided into two components - soil mineralization processes and litter turnover. In this chapter, soil phosphorus and nitrogen availability and mineralization rates are examined in relation to phosphate fertilization. Since nutrient cycling processes alter with age in coniferous systems (DiStefano & Gholz 1989; Turner & Lambert 1986b), the study was carried out in a chronosequence of P. elliottii plantations.

While phosphorus mineralization rates have been shown to be strongly influenced by soil chemical and physical properties (Harrison 1982; Lajtha & Schlesinger 1988), nitrogen mineralization is biologically controlled (Edmonds & McColl 1989; Hart & Firestone 1991). This chapter investigates the relative significance of phosphorus fertilization effects, site characteristics and environmental factors on soil phosphorus and nitrogen mineralization rates.

RESULTS

4.1 Soil Inorganic Phosphorus

Levels of available (inorganic) soil phosphorus in the unfertilized plots of all the sites did not exceed 100 μg P kg^{-1} soil and showed no significant differences between the sites. At the youngest stand, Goudveld (Fig. 4.1a), phosphate fertilization produced a significant increase in soil inorganic phosphorus levels ($F=7.07, p<0.01$). However, this increase only resulted in inorganic phosphorus levels above 100 μg P kg^{-1} soil in August 1989, March and May 1990 (to 105-133 μg P kg^{-1}). The observed monthly variations in available phosphorus at this site were not significantly different ($p>0.05$).

Levels of inorganic phosphorus at the 20 year old stand, Keurboomsrivier (Fig. 4.1b), were found to be significantly greater in phosphate fertilized soils than in the unfertilized control soils ($F=79.53, p<0.0001$). Inorganic phosphorus in the fertilized soils almost always exceeded 100 μg P kg^{-1} (with the exception of only March and October 1990). The highest levels were recorded in August 1989 and June 1990 (210 and 190 μg P kg^{-1}). At this site, the recorded variation in inorganic phosphorus with month was shown to be significant ($F=4.39, p<0.0001$) with August 1989, May and June 1990 being most different to July and November 1989 and October 1990.

The oldest stand, Quar (Fig. 4.2), received three different fertilization treatments. The treatment that resulted in inorganic phosphorus levels least different to the levels of the unfertilized plots were those

which were fertilized only 10 years after establishment (15 years ago, Fig. 4.2b). Here, levels of inorganic phosphorus were less than 100 μg P kg^{-1} soil and not significantly different ($p > 0.05$) to the unfertilized levels. Inorganic phosphorus at the plots fertilized at establishment only (25 years ago, Fig. 4.2a) were slightly higher than those of the latter treatment (160-190 μg P kg^{-1} in December 1989, March and May 1990). This treatment was also not significantly different to the unfertilized. The plots that received a double application of phosphate (at establishment and again 10 years later, Fig. 4.2b) showed inorganic phosphorus levels significantly higher than that of any of the other treatments ($F = 19.01, p < 0.0001$). The highest inorganic phosphorus levels recorded for this treatment were 300-360 μg P kg^{-1} (in August and November 1989 and May 1990), higher than the levels at any of the other aged stands' fertilized plots. The monthly variation of all the treatments at this site was also significant ($F = 3.76, p < 0.001$). August 1989 to May 1990 were shown to be different to June to October 1990.

4.2 Net Phosphorus Mineralization Rates

Comparing net phosphorus mineralization rates in the unfertilized soils across all the stands showed a significant difference ($F = 9.1, p < 0.001$) with the youngest stand being most different from the 20 year old stand. However, after phosphate fertilization there was no significant difference between the stands. Net phosphorus mineralization rates from all the fertilized and unfertilized plots were used together in a "three-way ANOVA" to test how it is affected by plantation age, fertilization treatment and time of incubation (month). It was shown that overall the difference in net phosphorus mineralization between the three plantations was not significant. The effects of fertilization and time were significant ($F = 5.18, p < 0.05$; $F = 4.94, p < 0.001$). The interaction of all these factors was not significant. The only significant interaction was that of plantation age with time (month) ($F = 2.58, p < 0.01$). However, the variation between plantations may be due to many other factors other than an age effect e.g. different rainfall, soil type etc. Therefore, to eliminate these site effects, each plantation was tested individually for treatment and month effects.

At the youngest stand, Goudveld (Fig. 4.3a), it was only during December 1989 and February 1990 that there appeared to be a substantial difference in net phosphorus mineralization between the unfertilized and fertilized plots. Overall, the effect of fertilization tested non-significant for this stand. The monthly variation was significant ($F = 2.91, p < 0.05$) with December 1989 and February 1990 being most different to August 1989, June and October 1990.

At the 20 year old stand, Keurboomsrivier (Fig. 4.3b), fertilization treatment was again shown not to affect net phosphorus mineralization rates. A pattern of alternating phases of net phosphorus mineralization (positive) and immobilization (negative) was evident. This trend proved to be significant over time ($F = 3.43, p < 0.01$) with the months that produced positive net mineralization namely August and December 1989, February, May and August 1990 being significantly different from those with negative net mineralization (immobilization) namely September 1989, June and September 1990.

As with the previous two stands, phosphorus fertilization at the oldest stand, Quar (Fig. 4.3c), did not influence the net phosphorus mineralization rates significantly. Again, monthly variation was significant ($F=7.58, p<0.0001$). August 1989 and October 1990 were most different from the other months, being the only months showing positive mineralization.

4.3 Annual Soil Phosphorus Turnover

Since the soil phosphorus mineralization rates (per day) showed great differences between months and no overall significant effect with treatment (phosphate fertilization), the annual net phosphorus turnover (mineralization over a year) was calculated (which eliminated the monthly variability) (Fig. 4.4).

Annual net phosphorus turnover at the unfertilized plots of the 8 and 25 year old stands was negative (immobilization). Of the unfertilized controls only the 20 year old unfertilized plots showed a positive annual phosphorus turnover. Comparing the fertilized plots of the 8 and 20 year old stands showed a slight decrease (not significant) in annual phosphorus turnover with age increase. After 25 years (at the plots fertilized at establishment only, F(1)), this decrease was much greater. However, the overall variation with age proved non-significant. The effect of treatment was shown to be significant ($F=9.99, p<0.005$). Analysing the significance of the difference with treatment at each age indicated that treatment was significant at the youngest ($F=5.14, p<0.05$) and oldest stand ($F=5.26, p<0.005$) but not at the 20 year old. At the oldest stand, the significance of treatment was due to the plots fertilized twice (F(1,2)) having an annual net phosphorus turnover of more than double that of the other treatments. There was no difference between the plots fertilized at establishment (F(1)) and those fertilized 10 years after establishment (F(2)).

4.4 Soil Phosphorus Fractions and Total Phosphorus

The size of the calcium-, aluminium- and iron-bound fractions of inorganic phosphorus in relation to soil total phosphorus is shown in Fig. 4.5 (note that these levels are larger than the resin-extractable inorganic phosphorus measured in the incubation study (Section 4.1) by a factor of almost 1000).

Soil total phosphorus levels varied significantly between the stands ($F=56.9, p<0.0001$) - the highest total phosphorus levels were recorded at the youngest stand, the lowest at the 20 year old stand. Phosphate fertilization did not alter the soil total phosphorus levels at the younger stands. However, the plots of the oldest stand, fertilized twice, had total phosphorus levels significantly higher than the other treatments at this stand ($F=4.56, p<0.01$).

Soil inorganic phosphorus bound to ions and metals was found to constitute a large proportion of the soil total phosphorus pool. At the youngest stand, the bound fractions in the unfertilized soils made up 41.1% of the total phosphorus and 47.7% in the fertilized. At the 20 year old stand the bound fractions were 43.2% of the unfertilized and 58.9% of the fertilized. At the 25 year old stand, the bound fractions were 52.9% of the total phosphorus in the plots fertilized twice. At the other treatment plots

of this stand, the bound proportion was lower with 33.8% at the plots fertilized once at establishment, 23.6% at the plots fertilized 10 years after establishment and 24.1% at the unfertilized plots.

Of the fractions measured, the calcium-bound fraction was significantly lower ($F=15.93, p<0.0001$) than the aluminium and iron fractions. The calcium-bound phosphorus differed significantly with age ($F=5.56, P<0.05$), with the 20 year old stand having lower levels than the other two. The aluminium-bound phosphorus levels were significantly higher at the youngest stand ($F=11.92, p<0.01$). The iron-bound fraction did not vary significantly with age. None of the fractions were greatly affected by fertilization, except for the iron-bound phosphorus at the oldest stand. Here the iron fraction was significantly higher at the plots fertilized twice ($F=4.62, p<0.05$).

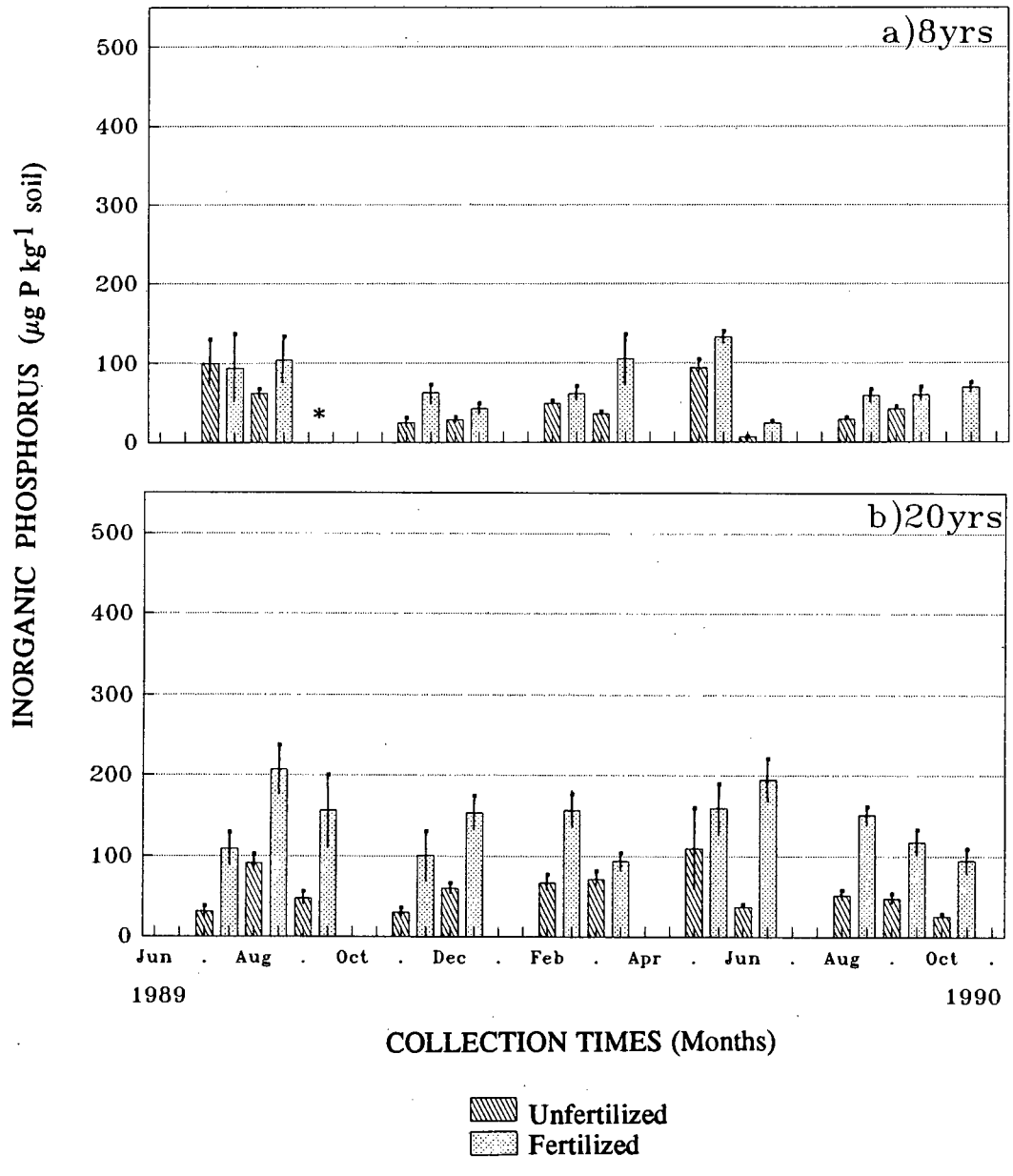


FIG.4.1: Monthly variation of inorganic (available) phosphorus levels (μg P kg^{-1} soil) in the "fresh" soil samples (collected at the start of each incubation period) from the unfertilized and phosphate fertilized plots of P. elliottii stands at a)Goudveld (8 years old) and b)Keurboomsrivier (20 years old). Periods when no sampling took place, due to site inaccessibility, are indicated with * . Vertical lines represent ± 1 S.E.M.

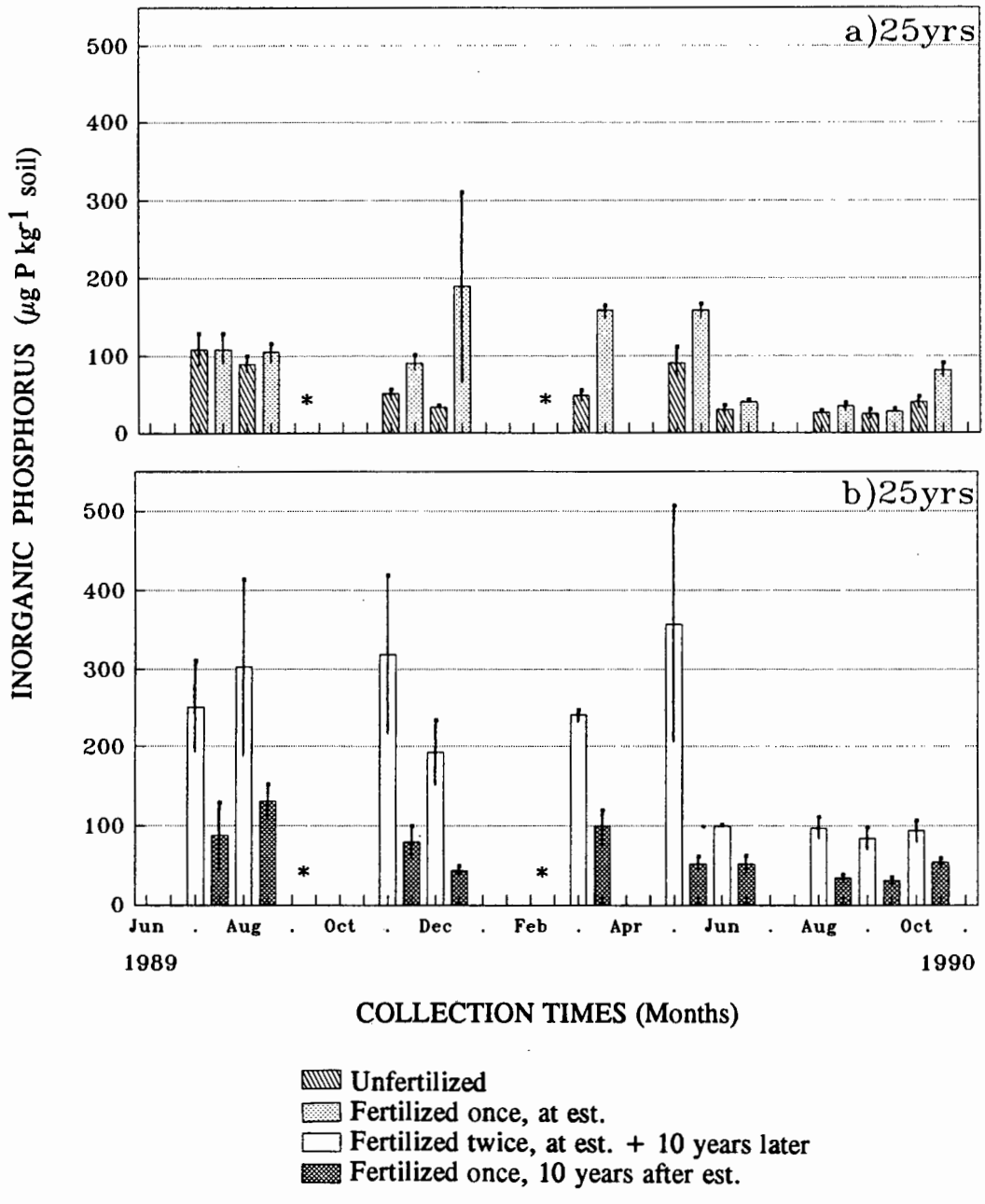


FIG.4.2: Monthly variation of inorganic (available) phosphorus levels (μg P kg^{-1} soil) in the "fresh" soil samples (collected at the start of each incubation period) from the different treatments of the P. elliottii stand at Quar (25 years old). The unfertilized controls and plots fertilized with phosphate once, at establishment, are presented in (a). Plots fertilized twice, at establishment and again 10 years later, and those fertilized once, 10 years after establishment, are presented in (b). Periods when no sampling took place, due to site inaccessibility, are indicated with * . Vertical lines represent $\pm$1 S.E.M.

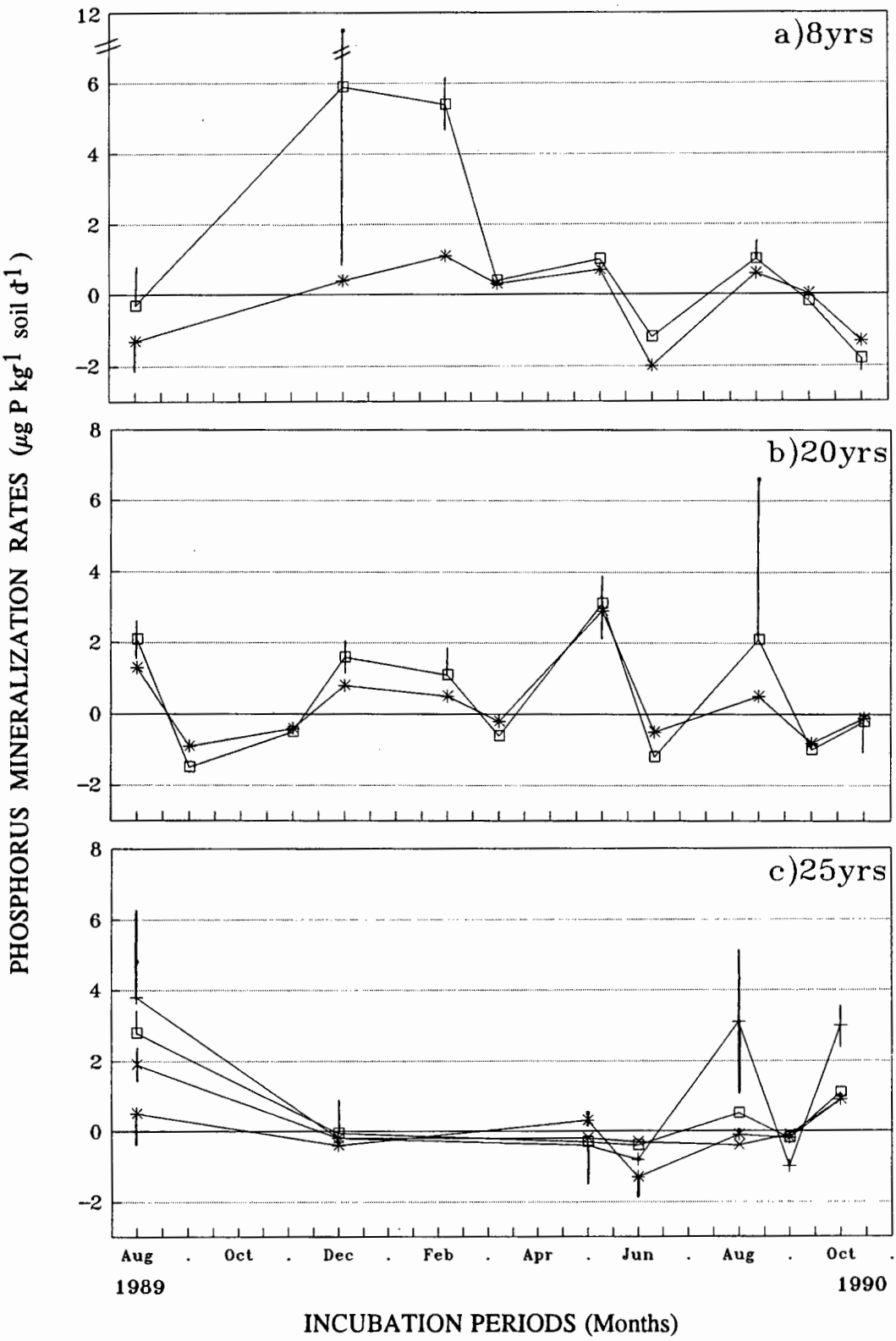


FIG.4.3: Seasonal patterns of soil phosphorus mineralization rates (μg P kg^{-1} soil day^{-1}) in the unfertilized and phosphate fertilized plots of P. elliottii stands at a)Goudveld (8 years old), b)Keurboomsrivier (20 years old) and c)Quar (25 years old). Vertical lines represent ± 1 S.E.M.; S.E.M. not represented if < 0.2.

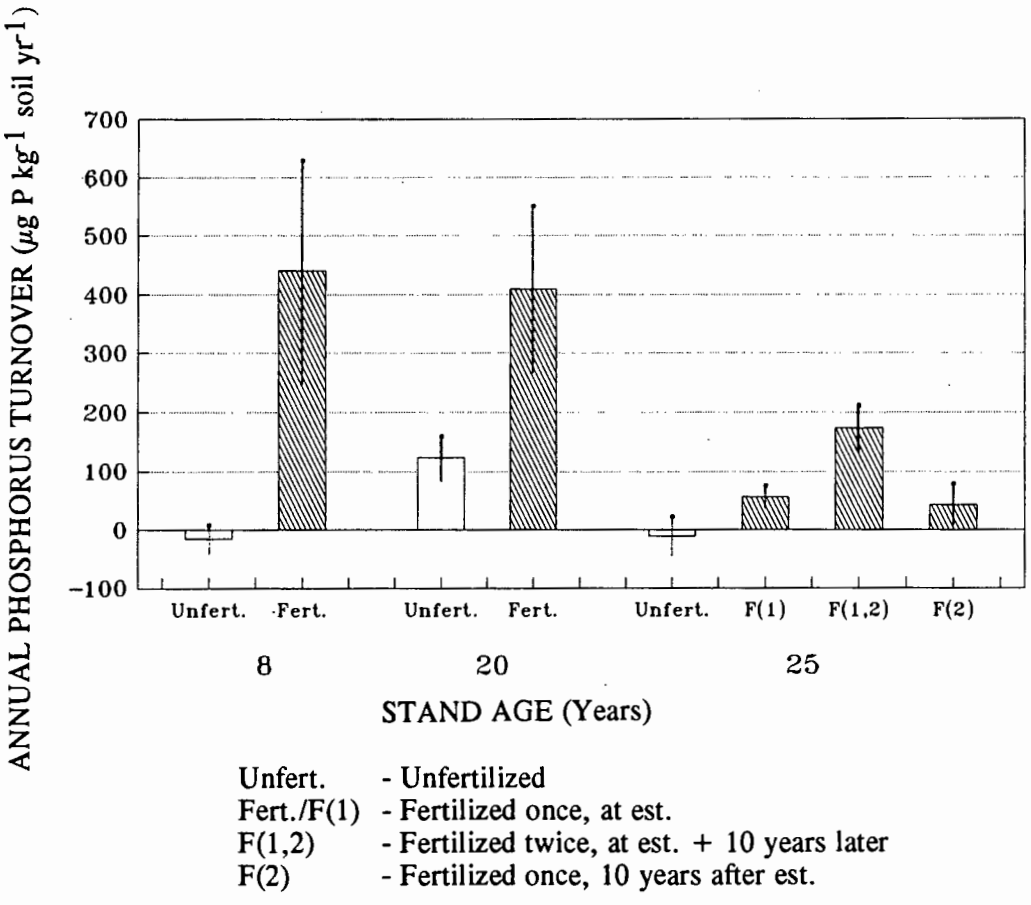


FIG.4.4: Annual soil phosphorus turnover (μg P kg^{-1} soil year^{-1}) in the unfertilized and phosphate fertilized plots of the different aged P. elliottii stands (Goudveld - 8 years, Keurboomsrivier - 20 years and Quar - 25 years old). Vertical lines represent $\pm$1 S.E.M.

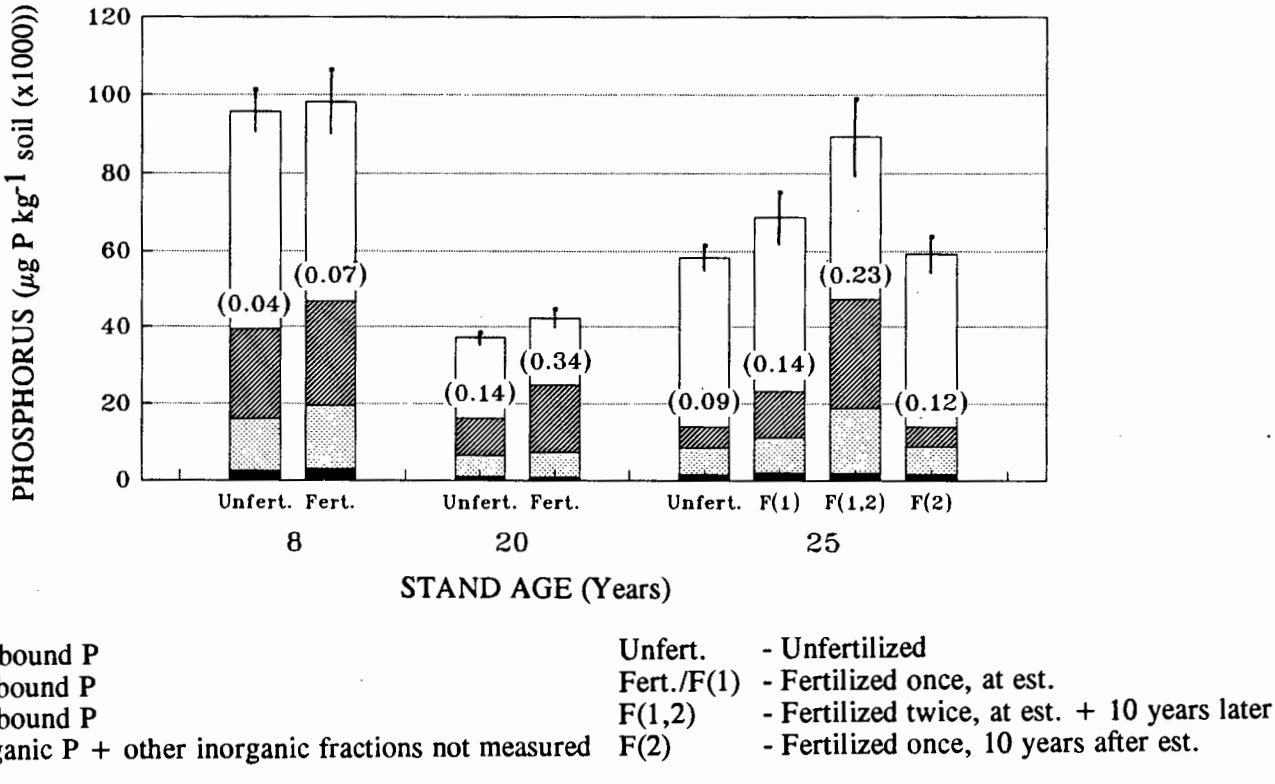


FIG.4.5: Soil total phosphorus levels (organic + calcium-, aluminium- and iron-bound fractions) (μg P kg^{-1} soil) in the unfertilized and phosphate fertilized plots of the different aged P. elliottii stands (Goudveld - 8 years, Keurboomsrivier - 20 years and Quar - 25 years old). Mean available soil phosphorus as a percentage of total phosphorus is shown in brackets for each plot. Vertical lines represent $\pm$1 S.E.M.; S.E.M.'s of the fractions were too small to represent).

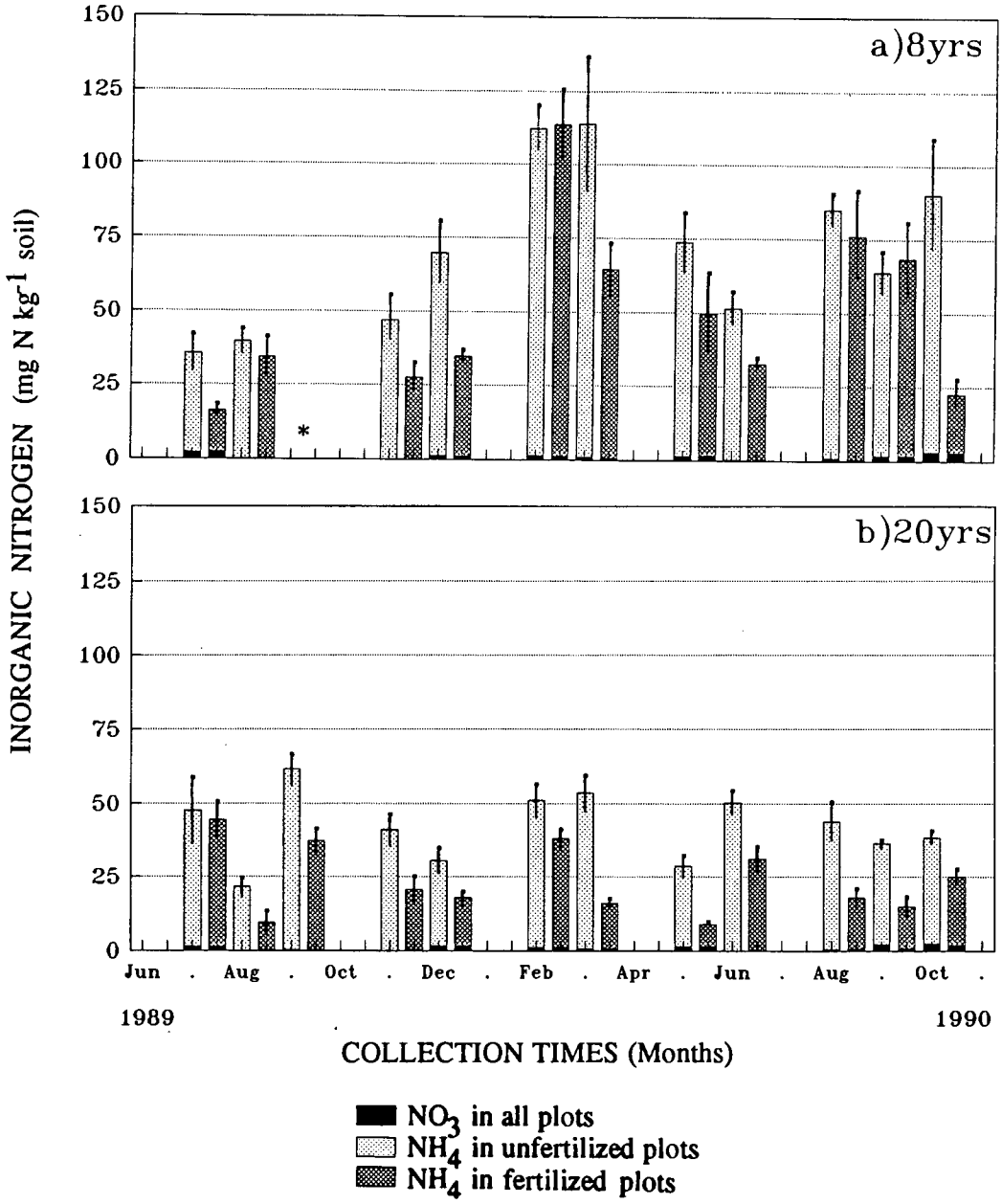


FIG.4.6: Monthly variation of inorganic nitrogen levels (ammonium + nitrate) (mg N kg^{-1} soil) in the "fresh" soil samples (collected at the start of each incubation period) from the unfertilized and phosphate fertilized plots of P. elliottii stands at a)Goudveld (8 years old) and b)Keurboomsrivier (20 years old). Periods when no sampling took place, due to site inaccessibility, are indicated with * . Vertical lines represent ± 1 S.E.M.

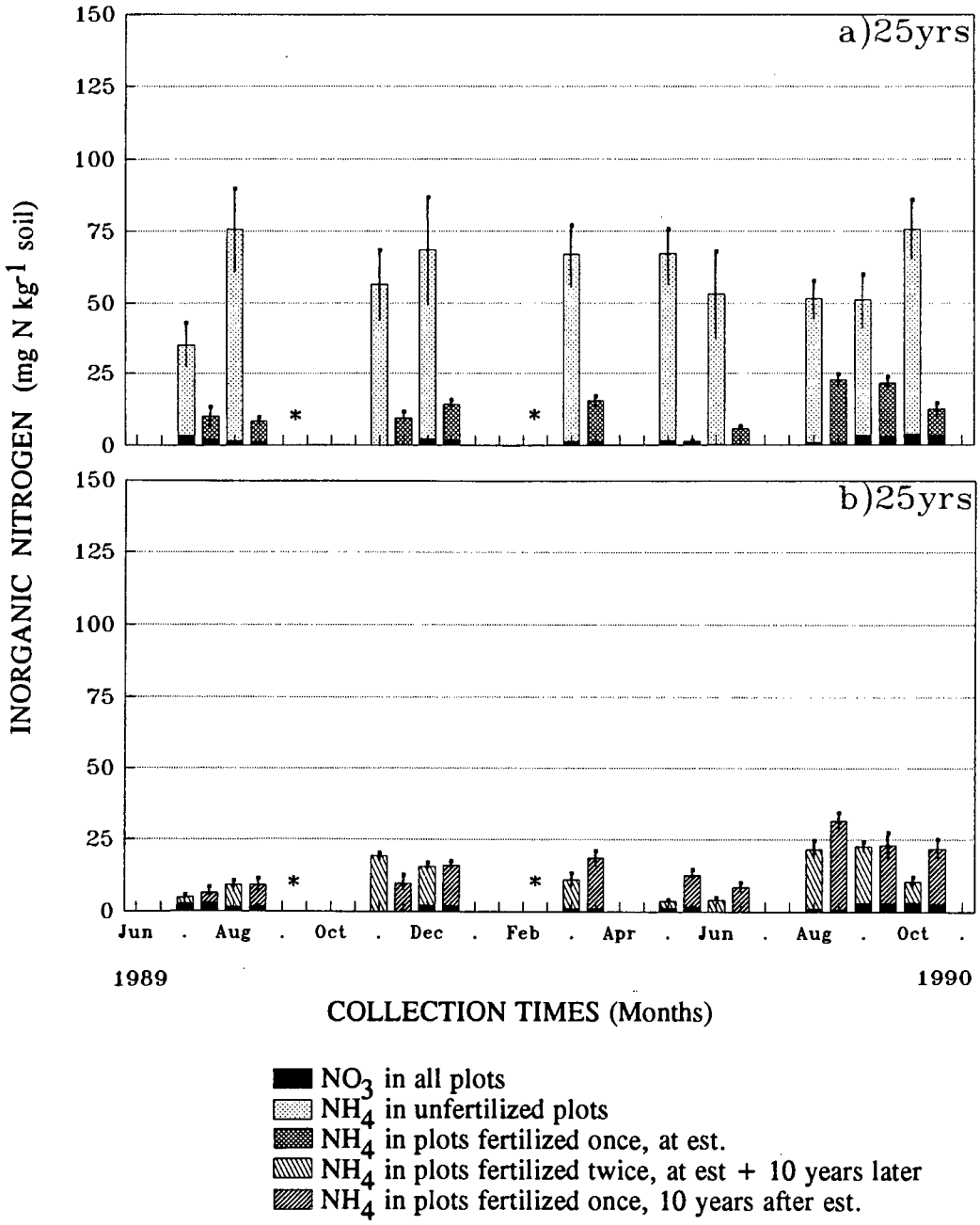


FIG.4.7: Monthly variation of inorganic nitrogen levels (ammonium + nitrate) (mg N kg^{-1} soil) in the "fresh" soil samples (collected at the start of each incubation period) from the different treatments of the P. elliottii stand at Quar (25 years old). The unfertilized controls and plots fertilized with phosphate once, at establishment, are presented in (a). Plots fertilized twice, at establishment and again 10 years later, and those fertilized once, 10 years after establishment, are presented in (b). Periods when no sampling took place, due to site inaccessibility, are indicated with * . Vertical lines represent ± 1 S.E.M.

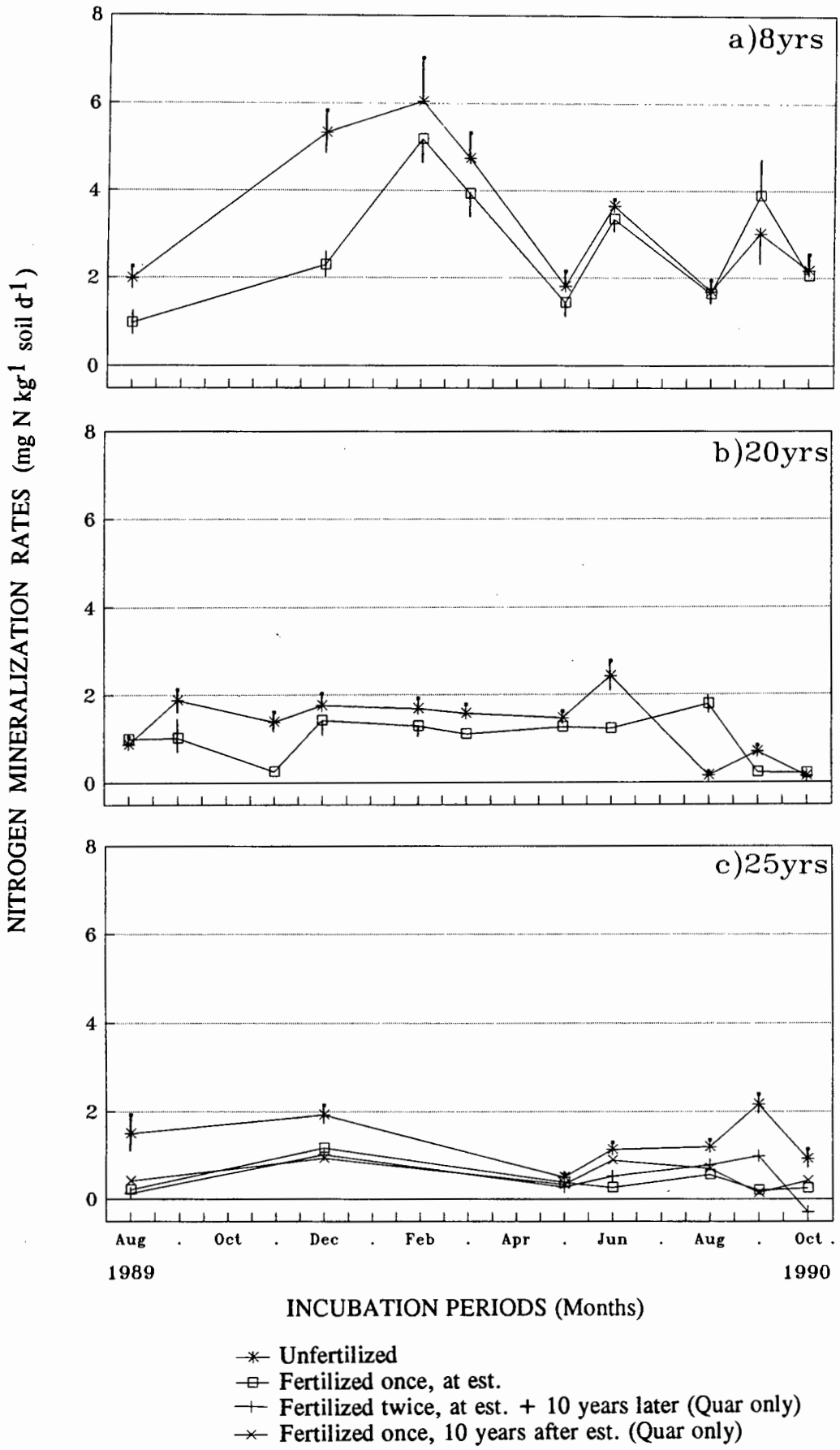


FIG.4.8: Seasonal patterns of soil nitrogen mineralization rates (mg N kg^{-1} soil day^{-1}) in the unfertilized and phosphate fertilized plots of P. elliottii stands at a)Goudveld (8 years old), b)Keurboomsrivier (20 years old) and c)Quar (25 years old). Vertical lines represent ± 1 S.E.M.

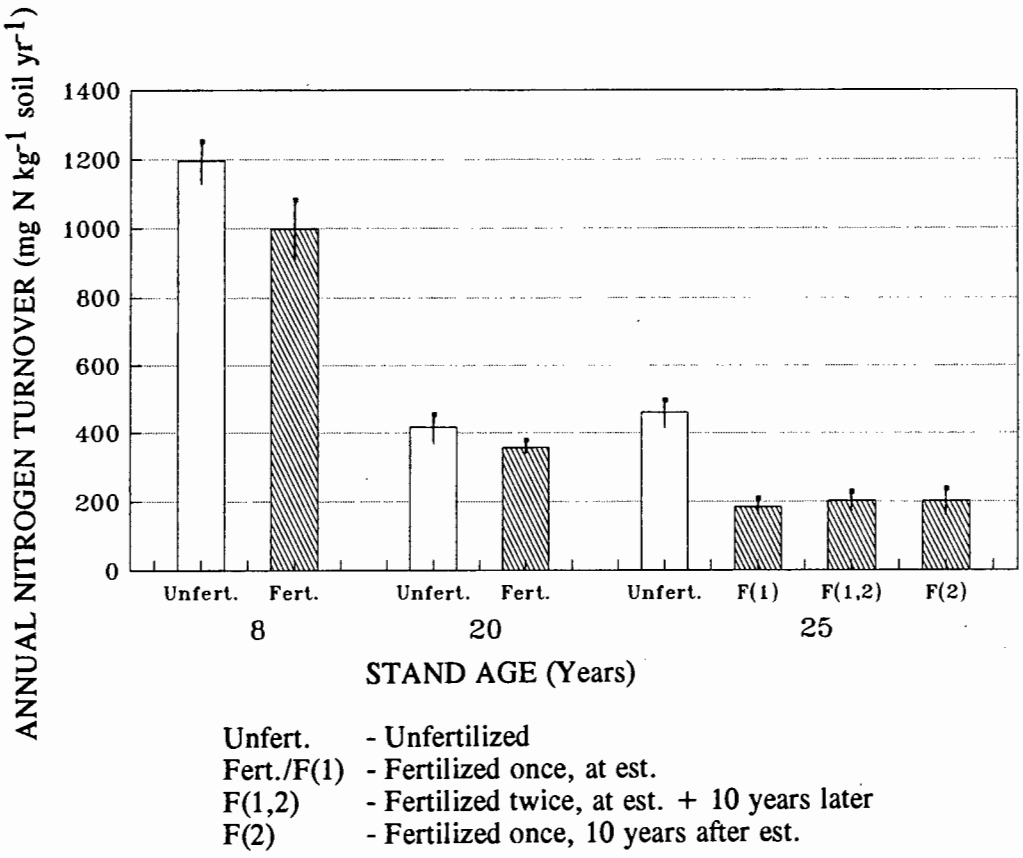


FIG.4.9: Annual soil nitrogen turnover (mg N kg^{-1} soil $year^{-1}$) in the unfertilized and phosphate fertilized plots of the different aged P. elliottii stands (Goudveld - 8 years, Keurboomsrivier - 20 years and Quar - 25 years old). Vertical lines represent ± 1 S.E.M.

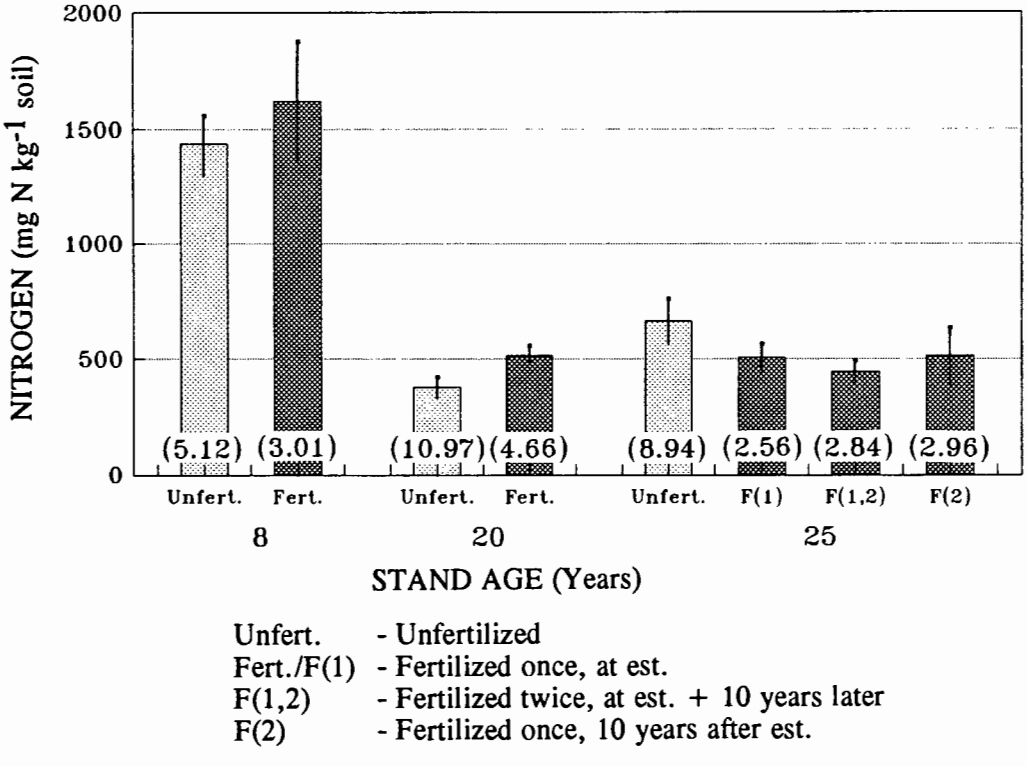


FIG.4.10: Soil total nitrogen levels (mg N kg^{-1} soil) in the unfertilized and phosphate fertilized plots of the different aged P. elliottii stands (Goudveld - 8 years, Keurboomsrivier - 20 years and Quar - 25 years old). Mean available nitrogen as a percentage of total nitrogen is shown in brackets for each plot. Vertical lines represent ± 1 S.E.M.

4.5 Soil Inorganic Nitrogen

In situ inorganic nitrogen levels at all the sites showed similar trends - ammonium was the dominant inorganic nitrogen form and levels were higher in the unfertilized soils (Figs 4.6 & 4.7).

Soil inorganic nitrogen levels at the unfertilized plots of the youngest stand, Goudveld (Fig. 4.6a), appeared to be higher than those of the two older stands (Figs 4.6b & 4.7). The highest inorganic nitrogen levels recorded in unfertilized plots were between 114-116 mg N kg^{-1} soil (in February and March 1990). Overall, the inorganic nitrogen levels in the unfertilized soils at this site were significantly higher than those recorded in fertilized soils ($F=28.91, p<0.0001$). The variation with month was also significant ($F=7.94, p<0.0001$) with July, August and November 1989 being most different from February, March, August and September 1990.

Since the effect of treatment and month on nitrate levels in a statistical analysis of total inorganic nitrogen is masked by the high ammonium levels, nitrate levels were analysed alone. At the 8 year old site, only monthly variation and not treatment was shown to have a significant effect on soil nitrate levels ($F=47.53, p<0.0001$).

Unfertilized soils from the 20 year old stand, Keurboomsrivier (Fig. 4.6b) showed the lowest inorganic nitrogen levels relative to that of unfertilized soils of the other two stands ($F=22.98, p<0.0001$), never exceeding 61 mg N kg^{-1} soil. Inorganic nitrogen levels at these unfertilized plots was still significantly higher than that at the fertilized plots ($F=92.05, p<0.0001$). The monthly variation in total inorganic nitrogen was also significant ($F=9.36, p<0.0001$). July, September 1989 and June 1990 were shown to be most different from August, December 1989, May and September 1990. Here, nitrate was affected significantly by both treatment ($F=9.08, p<0.05$) and month ($F=49.77, p<0.0001$).

At the oldest site, Quar (Fig. 4.7), where there were three different fertilization treatments, inorganic nitrogen levels at the unfertilized plots were significantly higher than that at any of the other treatment plots ($F=168.48, p<0.0001$). Inorganic nitrogen levels in the unfertilized soils were between 50-75 mg N kg^{-1} (only July 1989 was less at about 35 mg N kg^{-1}) (Fig. 4.7a), just slightly lower than the unfertilized levels at the youngest stand (Fig. 4.6a). Of the three fertilized treatments, the plots fertilized once only 10 years after establishment (Fig. 4.7b) appeared to have the least reduction in inorganic nitrogen levels. The plots fertilized at establishment only (Fig. 4.7a) and those fertilized at establishment and 10 years later (Fig. 4.7b) showed similarly low inorganic nitrogen levels. The levels at these treatments are significantly lower than the levels at the fertilized plots of all the other stands ($F=80.91, p<0.0001$). Inorganic nitrogen levels decreased significantly ($F=81.4, p<0.0001$) with age (time after fertilization) - the youngest stand showed the highest levels, followed by the 20 year old stand and the oldest stand (fertilized at establishment) with the lowest nitrogen availibility.

Monthly variation of soil inorganic nitrogen was also significant at the oldest stand ($F=3.99, p<0.001$) (Fig. 4.7c) with July 1989 and June 1990 most different to August, September and October 1990.

Nitrate levels also varied significantly with month ($F=95.12, p<0.0001$) and treatment ($F=3.88, p<0.01$) with unfertilized levels being most different from the nitrate levels of the plots fertilized at establishment only.

4.6 Net Nitrogen Mineralization Rates

Net nitrogen mineralization rates (Fig. 4.8) of the unfertilized plots were significantly higher at the youngest stand than at the other two sites ($F=51.81, p<0.0001$). Similar to the trend with inorganic nitrogen, net nitrogen mineralization rates in the fertilized plots decreased with stand age with the youngest stand having the highest mineralization, followed by the 20 year old stand and the oldest showing the lowest rates ($F=74.4, p<0.0001$).

At the youngest stand, Goudveld (Fig. 4.8a), net nitrogen mineralization rates in the unfertilized plots were found to be slightly higher than those in the fertilized, but this difference was not significant. Monthly variation was significant ($F=11.92, p<0.0001$) with August 1989, May, August and October 1990 most different from December 1989, February, March, June and September 1990.

At the 20 year old stand, Keurboomsrivier (Fig. 4.8b), nitrogen mineralization rates were higher in the unfertilized than fertilized soils (except for August 1990), but again not significantly. Monthly variation was significant ($F=13.27, p<0.0001$) with December 1989, February, March, May and June 1990 most different from September and October 1990.

Net nitrogen mineralization rates of the unfertilized plots at the oldest stand, Quar (Fig. 4.8c), were significantly higher than all the fertilized treatments ($F=37.73, p<0.0001$). Monthly variation was also significant with August 1989, May and October 1990 being most different from December and September 1990.

4.7 Annual Soil Nitrogen Turnover

As with phosphorus mineralization rates (per day), net nitrogen mineralization was found to be highly variable with month but with no distinct trends. Here again net mineralization rates were used to calculate the annual nitrogen turnover of each plot (Fig. 4.9).

The youngest stand had the highest annual nitrogen turnover rate. This resulted in age being a significant factor ($F=149.9, p<0.0001$) affecting nitrogen turnover. An ANOVA across all the sites showed that the reduction of annual nitrogen turnover due to phosphate fertilization was significant ($F=19.28, p<0.0005$). However, analyses of the effect of treatment at each stand showed that the difference with treatment was only significant at the oldest stand. Here, the unfertilized plots had an annual nitrogen turnover significantly higher ($F=18.24, p<0.0001$) than that of all the other treatment plots. All the fertilized treatments of the oldest stand showed very similar annual nitrogen turnover rates.

4.8 Soil Total Nitrogen

Soil total nitrogen levels were much higher at the youngest stand than at the other two stands (Fig. 4.10). This resulted in age being a significant factor defining soil total nitrogen ($F=56.89, p<0.0001$). The effect of fertilization treatment across all the stands was not significant. While the 8 and 20 year old stands were found to have higher total nitrogen at the fertilized than unfertilized plots (with this difference being significant at the 20 year old stand ($F=4.81, p<0.05$), the unfertilized plots of the oldest stand had higher soil total nitrogen levels than any of the fertilized treatments.

4.9 Soil Organic Matter Content

Variations in soil organic content with stand age (Appendix, Fig. 1) were similar to those of soil moisture. The youngest stand had the highest soil organic content (6-10%), followed by the oldest stand (3-4.5%). The 20 year old stand had the lowest soil organic content (2-2.8%). Soil organic matter content of all three stands were significantly different ($F=377.32, p<0.0001$).

Variations in organic content with treatment also proved significant ($F=21.46, p<0.0001$). At the 8 and 20 year old stands, organic matter content was lower in the unfertilized plots. The oldest stand was analysed alone to include the various fertilized treatments. Here, unlike the younger stands, soil organic matter content was significantly higher in the unfertilized plots than in all the other fertilized plots ($F=15.69, p<0.0001$).

4.10 Soil Temperature

Soil temperatures (measured at 10cm depth) (Appendix, Fig. 2) showed a similar distinct seasonal trend at all the stands ($F=1000, p<0.0001$). As expected the highest temperatures (25-30^{o}C) were always recorded during the summer months (December to March) and the lowest (10-15^{o}C) during winter (June to August). Temperatures at the oldest stand were always slightly lower than those at the 8 and 20 year old stands. The temperature range at the oldest stand was about 12-22^{o}C compared to 14-28^{o}C at the younger stands. Slight differences found between the unfertilized and fertilized plots were not significant.

4.11 Soil Moisture Content

Soil moisture contents, determined at the start of each incubation period, are presented in the Appendix, Fig. 3. Again, significant seasonal trends were evident across all the stands ($F=10.37, p<0.0001$). Overall, the soil moisture content was lowest between February and March 1990 and highest between November and December 1989.

While the differences in soil moisture content between the unfertilized and fertilized plots were not significant, the differences with stand age were significant ($F=83.48, p<0.0001$). Highest soil moisture contents (ranging from 10-38%) were measured at the youngest stand, followed by the oldest (6-27%). The 20 year old stand had the driest soils (3-19%).

4.12 Models of Factors determining Phosphorus and Nitrogen Mineralization Rates

In order to determine which environmental factor (soil temperature, moisture, organic matter content, time of year (month), total or inorganic phosphorus/nitrogen) and site characteristics (plantation age, fertilization treatment) were most significant in determining the observed trends of phosphorus and nitrogen mineralization rates, a "stepwise multiple linear regression" was carried out. Results are presented in Tables 4.1 and 4.2.

When only environmental factors were entered into the system with phosphorus mineralization (Table 4.1), temperature was the first factor accepted by the model and it accounted for only 1.8% of the variation in phosphorus mineralization rates. When site characteristics were included in the analysis, fertilization treatment was shown to be the most significant factor, determining 2.1% of the variation in phosphorus mineralization. The final model selected by the analysis included treatment and time (month) which together determined only 4.2% of the variance.

When the net nitrogen mineralization rates and environmental factors were analysed, soil moisture was shown to be the most significant factor, determining 59.8% of the variance in net nitrogen mineralization rates (Table 4.2). The final model included soil total nitrogen and inorganic nitrogen together with soil moisture, explaining some 65.4% of the variance. When site characteristics were included in the analysis, the final "environmental" model was still accepted. Stand age was the first factor to be incorporated into this model, increasing the coefficient of determination to 66.6%. At the next step, soil temperature was added, bringing the determination coefficient to 67.7%. The final model thus consisted of soil moisture, soil total and inorganic nitrogen, stand age, soil temperature as well as fertilization treatment. In combination, these factors accounted for 68.2% of the variance in net nitrogen mineralization rates.

TABLE 4.1: Results of the "stepwise selection multiple regression" to determine the relative significance of environmental factors and site characteristics on the phosphorus turnover rates (mineralization).

		Variables in Model	Coefficient of determination, r^2	df	p
Step	1 *	Temperature	0.018	377	<0.010
	1	Treatment	0.021	377	<0.005
	2 **	Treatment Month	0.042	376	<0.001

* indicates final model when only environmental factors were entered into system

** indicates final model when site characteristics were also entered into the system

Other factors entered into the system but not accepted for the final model were:

environmental - total phosphorus
inorganic phosphorus
moisture
soil organic content

site - stand age

TABLE 4.2: Results of the "stepwise selection multiple regression" to determine the relative significance of environmental factors and site characteristics on the nitrogen turnover rates (mineralization).

		Variables in Model	Coefficient of determination, r^2	df	p
Step	1	Moisture	0.598	377	< 0.001
	2	Moisture Total N	0.644	376	< 0.001
	3 *	Moisture Total N Inorganic N	0.654	375	< 0.001
	4	Moisture Total N Inorganic N Stand Age	0.666	374	< 0.001
	5	Moisture Total N Inorganic N Stand Age Temperature	0.677	373	< 0.001
	6 **	Moisture Total N Inorganic N Stand Age Temperature Treatment	0.682	372	< 0.001

* indicates final model when only environmental factors were entered into the system

** indicates final model when site charateristics were also entered into the system

Other factors entered into the system but not accepted for the final model were soil organic content and time of year (month).

DISCUSSION

Phosphorus availability and Mineralization rates

Mineralization is essential in nutrient cycling, since it is the process whereby organic compounds are converted by microbial activity to inorganic nutrients. Inorganic nutrients may then be taken up by plants. However, soil micro-organisms compete with plant roots for nutrients, especially in nutrient poor systems where the nutrient content of organic compounds is low (Tate 1984; Bell & Binkley 1989). In the phosphorus cycle, calcium, iron and aluminium ions in the soil act as phosphorus scavengers and may compete directly with plants for inorganic phosphorus (Stewart & Tiessen 1987). Calcium-, iron- and aluminium-bound phosphorus is unavailable for plant or microbial uptake (Payn & Clough 1989). The fraction of inorganic phosphorus accessible to plants will be referred to as "available" phosphorus. Thus, a study of soil phosphorus dynamics must take all of the following into account in relation to soil phosphorus availability - microbial immobilization, plant uptake and phosphate adsorption which are outputs of the phosphorus availability pool and organic phosphorus mineralization and phosphorus desorption which are the inputs.

Without fertilization, levels of available soil phosphorus at all the P. elliottii plantations were very low - $< 100\ \mu g\ P\ kg^{-1}$ soil. This represented only 0.04-0.14% of soil total phosphorus (Fig. 4.5). With phosphate fertilization this was increased to 0.07-0.34%. This increase was too small to result in a significant increase in total phosphorus. Only the increase produced by a double phosphate application was substantial enough to produce a significant increase in soil total phosphorus.

While there were low levels of plant available inorganic phosphorus in all the soils examined, overall inorganic phosphorus levels were quite substantial (up to 59% of soil total phosphorus). However, this latter component was calcium-, aluminium- and iron-bound. The aluminium- and iron-bound fractions being significantly higher than the calcium-bound fraction is characteristic of highly weathered, acidic soils as found in this study (Appendix, Table 1) (Stewart & Tiessen 1987; Lajtha & Schlesinger 1988).

The strong adsorption properties of southern Cape soils are regarded as a problem in relation to phosphate addition. Phosphate being removed from the soil solution by adsorption effectively reduces the applied phosphate immediately available to the tree (Payn & Clough 1988 & 1989). However, in this study it was only the iron-bound phosphorus fraction which increased significantly with phosphate fertilization and then only in the 25 year old plots fertilized twice. This finding that iron adsorption occurs is not surprising as this element is highly abundant in these acidic soils. Payn & Clough (1988) found in their study in the region that the bulk of added phosphorus was recovered in the form of aluminium phosphate, the other adsorbing fraction common in acidic soils.

The significant increase in phoshorus availability with phosphate fertilization at the 8 and 20 year old stands indicates that an application of 30-60 kg ha^{-1} superphosphate at plantation establishment was sufficient to raise phosphorus availability, despite adsorption of phosphate in these acidic soils. The

application rate was also enough to maintain significantly elevated soil phosphorus levels for up to 20 years after application. This was expected, since phosphorus fertilization of pine plantations commonly results in long-term increases of phosphorus availability in surface soils and growth responses lasting one to several decades (Hart & Binkley 1985; Turner & Lambert 1986b). Turner & Lambert (1986b) cite a study in which phosphate applied to a P. radiata stand was still detectable in the soil 18 years after application and the growth response of the trees was evident into the second rotation, 34 years after initial fertilizer application.

At the 25 year old stand of this study, phosphorus availability in the plots fertilized once, whether at establishment or 10 years later, was depleted to levels similar to those in the unfertilized plots. A double application of phosphate fertilizer (at establishment and again 10 years later) was shown to be necessary if phosphate availability is to remain significantly higher than unfertilized levels after 25 years. This is in agreement with Hart & Binkley (1985) and Turner & Lambert (1986b) who stated that the longevity of phosphorus fertilization effects was dependent on the rate of fertilizer application. Schwab & Kulyingyong (1989) found that soils fertilized more frequently maintained higher phosphorus availability than soils that were fertilized once. Thus to maintain elevated phosphorus availability, reapplication of phosphorus fertilizers later in the rotation seems more preferable than a single large application. In their study of a 30 year old P. radiata stand in eastern Australia, Turner & Lambert (1986b) found that a single application of phosphorus in excess of 75 kg ha^{-1} was not retained effectively and showed no growth response.

Phosphate availability showed no distinct seasonal peak. The only trend consistent at all the stands was that highest phosphorus availability was recorded in August 1989 (late winter) and March to May 1990 (Autumn). An examination of environmental conditions (Appendix, Figs 2 & 3) indicated that seasonal fluctuations in soil temperature and moisture content did not coincide with variations in phosphorus availability. There was no apparent explanation for the consistently high phosphorus availability of August 1989.

Phosphorus availability is also influenced by plant uptake. Plant roots in the soil system act as a phosphorus sink which lowers inorganic phosphorus concentrations in the soil solution (Stewart & Tiessen 1987). Nutrient uptake by plants varies seasonally, controlled by fluctuating environmental conditions (Turner & Lambert 1986a; Payn & Clough 1988) e.g. rainfall facilitates nutrient uptake by creating the soil solution from where nutrient acquisition occurs. Thus, at the study sites, periods of low soil moisture content during February-March (Apppendix, Fig. 3) may have restricted nutrient uptake. This could account for the higher levels of available phosphorus determined during the March to May 1990 period.

While the factors discussed so far (phosphate adsorption, environmental conditions and plant uptake) may contribute to the observed trends of phosphorus availability, "the ultimate limit on the availability of soil phosphorus to plants and micro-organisms is the rate of inorganic phosphorus release by mineralization" (Tate 1984). The higher net phosphorus mineralization rates of the 20 year old

unfertilized plots compared to those of the unfertilized plots of the other stands were probably due to site differences. With fertilization, these differences seem to be reduced, resulting in greater uniformity in net phosphorus mineralization rates between the stands - variations in net phosphorus mineralization rates between the different aged fertilized plots was not significant. However, the significant interaction of plantation age and time (month) indicates that variations between the sites does occur over time, due probably to differences in environmental conditions between the sites. From the environmental factors measured in this study, soil moisture content (Appendix, Fig. 3) seems to be the factor most likely to be influencing inter-site variations. While the variations in temperature between the sites (Appendix, Fig. 2) were not great, soil moisture varied significantly between the sites. The lower soil moisture content at the 20 year old stand was accounted for by the lower mean annual rainfall at Keurboomsrivier (868mm compared to 1113 and 980mm at Goudveld and Quar respectively (Table 3.1)). The higher sand content of the surface soil at Keurboomsrivier (Table 3.1) would result in better drainage and thus also contribute to a lower soil moisture content. Thus, variations in net phosphorus mineralization rates with plantation age will not be emphasized.

The most obvious trend at all the sites was the alternating phases of net mineralization and immobilization. Interpretation of the dynamics of phosphorus turnover is difficult, since the factors controlling mineralization are complex. Not only must microbial effects be considered, but soil physical and chemical properties are of equal importance (Stewart & Tiessen 1987).

The phosphorus cycle may be divided into three major components - (i) phosphorus in soil solution which is accessible to plants and microbes (available phosphorus), (ii) the labile phosphorus pool which undergoes transformation and replenishes available phosphorus and (iii) non-labile phosphorus. The rate of release of the non-labile component is too slow to significantly contribute to seasonal processes (Tate 1984). Thus it is assumed that the incubation technique used in this study determines only the transformations between the labile phosphorus and available phosphorus pools.

The most important component of the labile pool is organic phosphorus. At all the study sites, organic phosphorus was the largest fraction (Fig. 4.5). Its value as a source of plant available phosphorus depends on the rate at which it is transformed to a soluble form. In this study, and as is characteristic of coniferous systems (Miller et al. 1979), net phosphorus mineralization rates (rates of exchange between organic and available phosphorus) are very low (Fig. 4.3). The amount of organic phosphorus that appears to be transformed daily is about 10 000 times smaller than the total soil organic phosphorus levels (Fig. 4.5). This difference is even greater, since there are frequent periods of immobilization. The result is that organic phosphorus levels are more than 100 times greater than soil available phosphorus.

Soil micro-organisms are considered to be the main agents responsible for transformations (mineralization) of phosphorus (Tate 1984). Seasonal variations in net phosphorus mineralization (or immobilization) rates are attributed either directly to microbial activities (phosphate uptake by and

immobilization within microbial cells and phosphate release into soil solution when they die (Schaefer 1973)) or indirectly by the secretion of phosphatase enzymes by soil micro-organisms (Harrison 1982).

In spite of the low net phosphorus mineralization rates determined in this study, it is possible that it may even be an overestimation of the rate of transformation of organic phosphorus of plant origin. In phosphorus deficient soils where the C:P ratio of the plant organic matter is high, microbial uptake (immobilization) of soluble inorganic phosphorus will be great. When the microbial population dies and degrades, it is microbial organic phosphorus that is converted to available phosphorus. This could result in the accumulation of plant organic phosphorus in the soil. An increase in organic phosphorus was observed from the 20 to 25 year old stands (Fig. 4.5). The high soil organic phosphorus content of the 8 year old stand was as a result of this stand being established within the slash (harvest residue) of a previous plantation.

Another phenomenon that may have contributed to the observed patterns of mineralization and immobilization is the adsorption and release of phosphate by iron compounds. Since the largest inorganic phosphorus fraction in the study soils was iron-bound (Fig. 4.5), this process may be important. The exchange between phosphate adsorption and release is a chemical process influenced by the physical environment; it is non-biological. The most important physical factor influencing this process is soil moisture content. When soils become water saturated and anaerobic, hydration and reduction of ferric oxyhydroxide occurs. This results in the conversion of crystalline ferric oxyhydroxide to amorphous iron oxides (ferrous oxide or ferrous hydroxide). While the ferrous forms have a high reactivity with phosphate because of their high specific surface area, they do not bind phosphate as firmly as does ferric oxyhydroxide. If the concentration of soil soluble phosphates is low, iron adsorbed phosphates will be released into the soil solution. Where there are high levels of phosphate in solution, adsorption occurs (Patrick & Khalid 1974). Due to the poor soil drainage at the study sites, soils and the incubated cores were often waterlogged. This would have resulted in anaerobic conditions. It is thus possible that reduction of iron compounds occurred in the soils of the study sites. The effects of this phenomenon on mineralization patterns would have been to boost net mineralization rates in the unfertilized plots where levels of soluble phosphorus were low. Since fertilization significantly increased available phosphorus at the 8, 20 and 25 year old plots fertilized twice, increased adsorption of phosphate by the ferrous compounds is expected. This would have resulted in greater apparent phosphate immobilization than that caused by micro-organisms alone. Thus, the overall effect would be to reduce the difference in net phosphorus mineralization rates between unfertilized and fertilized soils.

Even though there were significant increases in phosphorus availability with fertilization up to 20 years after fertilization and to 25 years with a double fertilizer application, there were not correspondingly significant increases in net phosphorus mineralization rates. Besides the above described effects of iron adsorption possibly reducing the effects of phosphate fertilization on net phosphorus mineralization rates, there may be other contributing factors. From Fig. 4.3 it is evident that the standard errors of the seasonal net phosphorus mineralization rates were often quite large. Also, while mineralization rates are

almost always higher in the fertilized plots over periods of positive mineralization, immobilization is often also greater (more negative) in the fertilized plots. This would reduce the significance of fertilization increasing net phosphorus mineralization rates. Thus, to investigate the overall effect of phosphorus fertilization on phosphorus mineralization without seasonal fluctuations, net annual phosphorus turnover rates were calculated.

In the unfertilized plots of both the 8 and 25 year old stands, annual net phosphorus turnover was negative (immobilization rates were greater than mineralization) but appeared to have resulted from different conditions. The negative phosphorus mineralization at the 25 year old unfertilized plots was probably caused by phosphorus immobilization in the litter later (investigated in the next chapter) which reduces mineralization. However, at the 8 year old stand litter accumulation has not yet occurred. The soil phosphorus immobilization here was more likely due to the high soil organic matter content (6.5% compared to 2-3% and 3-4.2% at the 20 and 25 year old stands respectively) which would support a large microbial population, resulting in a high level of nutrient immobilization. The 8 year old stand had a high soil organic content since it was a second rotation stand that was established without slashburning.

Environmental factors and Phosphorus mineralization

In spite of the suggestions presented so far to explain the observed trends of phosphorus availability and net mineralization, the results of the "stepwise selection multiple regression" (Table 4.1) showed that fertilization was the most significant factor determining the variations in phosphorus mineralization. This is not unexpected, since chemical factors are important in the phosphorus cycle (Lajtha & Schlesinger 1988). However, the predictive value of fertilization as a determinant of phosphorus mineralization was very low (r^2 was only 0.021). The soil chemical properties shown by Harrison (1982) to account for over 90% of the variation in rates of phosphorus mineralization was primarily soil pH and extractable calcium. These factors are unlikely to be contributing to the observed mineralization patterns in this study since pH did not vary between sites (Appendix, Table 1) or seasonally (Brown 1982) and thus neither will the calcium-bound fraction since it is directly influenced by soil pH. The low soil pH at all the study sites (Appendix, Table 1) resulted in a small calcium-bound fraction.

The lack of environmental control of the phosphorus mineralization process (a correlation of 0.018 for temperature is too low to be of importance) indicates that biological turnover of phosphorus is of limited magnitude in the study sites. The inorganic phosphorus component undergoing mineralization was only about 0.04-0.34% of soil total phosphorus (Fig. 4.5). Even though most inorganic phosphorus was calcium-, aluminium- and iron-bound (between 22 and 53% of soil total phosphorus), it could contribute to the observed mineralization/immobilization phases of phosphorus mineralization by the release of inorganic phosphorus during periods of soil waterlogging. However, if this process was of importance, soil moisture content should have been incorporated in the "environmental" model.

Even though soil phosphorus levels and mineralization rates are much lower than that of nitrogen (even with phosphate fertilization), there is usually a significant interaction between the two cycles (Cole & Heil 1981). Thus, any change in one of the cycles is likely to affect the other. The reported effects of increased phosphorus availability (due to phosphate fertilization) on nitrogen processes are varied (Carey et al. 1981). Thus it was essential to include nitrogen cycling in this study.

Nitrogen availability and Mineralization rates

Nitrogen is not considered to be a limiting element in plantations of the Southern Cape since no growth responses were found to applications of nitrogen fertilizers (Herbert & Schönau 1989). (Inorganic nitrogen in the nitrate and ammonium forms is accessible to plants and microbes and will be referred to as available nitrogen). Since soil nitrate levels were very low, ammonium must be the predominant inorganic nitrogen form taken up by the pine trees as it was the most abundant form in the study soils (Figs 4.6 & 4.7). Nadelhoffer et al. (1984) cites a range of nitrogen nutrition experiments that show that growth responses to the form of mineral nitrogen varies among species. Pinus species grew best when fed ammonium alone (in contrast to other coniferous species). A requirement for the effective uptake of ammonium would be an extensive and dense fine root system, since ammonium is relatively immobile in soil (Nadelhoffer et al. 1984).

According to Nadelhoffer et al. (1982) it should not be assumed that the nitrogen form in abundance is favoured by plants for uptake. They stated that low nitrate levels may have resulted from rapid plant uptake (supported by Jackson et al. (1989)) and/or leaching of the highly mobile nitrate and thus the assumption of some investigators that a small soil nitrate pool indicates low nitrification rates may be incorrect. In the in situ soil incubation technique used in this study to determine net mineralization rates (the sum of nitrification and ammonification rates), plant uptake and leaching losses were excluded. Nitrate levels in the cores were also found to be very low. Low nitrate concentrations and nitrification rates (due to low numbers of Nitrosomonas and Nitrobacter (Gökçeoglu 1988)) are commonly observed in coniferous forests (DiStefano & Gholz 1989). DiStefano & Gholz (1989) showed that low nitrate levels cannot be accounted for by vegetation uptake, since low levels were also found in clearcut stands. Their incubation cores were not enclosed but had a resin-bag at either end to allow drainage. No nitrate was detected by the lower resin-bag which indicates that there was not a large amount of nitrate leaching.

The most noteworthy effect of phosphate fertilization detected in this study was the significant reduction in soil nitrogen availability at all the stands (Figs 4.6 & 4.7). The assumption is that the higher foliar biomass and more effective root distribution in the phosphate treated plots enhanced the capture of incident ions, including available nitrogen (Turner & Lambert 1986b). Since the major portion of the inorganic nitrogen pool in this study was in the ammonium form, the observed trends and statistical results of each were the same. The slight yet significant reduction of nitrate by phosphate fertilization at both the older stands does not necessarily indicate increased nitrate uptake. It could be the result of a decreased supply of ammonium to nitrifying bacteria with a consequent reduction in the

production of soil nitrate (Pastor et al. 1984; DiStefano & Gholz 1989; Edmonds & McColl 1989). Thus, if ammonium availability decreases (as it does with increasing age) so would nitrification and nitrate levels.

Another reason for the lowered ammonium levels and overall reduced inorganic nitrogen that must be investigated is the possible direct effect of phosphate on nitrification. Pastor et al. (1984) proposed that phosphate supply was an important regulator of nitrification. Low soil phosphate content was given as the reason for low nitrification. They stated that fertilization of soils with phosphate would be an appropriate experiment to test the degree to which nitrification is limited by phosphate supply. In the study described here, only total inorganic nitrogen turnover rates and not nitrification rates were calculated. However, the lower ammonium levels in the fertilized plots may indicate that more ammonium was transformed to nitrate (by nitrification; the increased phosphate levels stimulated the growth of nitrifying bacteria (Purchase 1974)). Since nitrate is rapidly leached from soils there would be an overall reduction in nitrogen levels. However, as was stated earlier, leaching was probably not an important means of nitrogen loss in the poorly drained soils of the study sites. Thus, if this process was operative in the study plantations, phosphorus fertilization would have resulted in increased nitrate levels with fertilization. Instead, nitrate levels were significantly reduced by fertilization in the two older stands. Before dismissing this process due to lack of evidence of nitrate loss by leaching, another way in which nitrate is lost from the soil nitrogen turnover cycle must be considered, namely denitrification. It is likely that denitrification occurred in the study soils, since this process results from anaerobic conditions in saturated soils (Knowles 1981), which commonly occurred at the study sites. Denitrification could have occurred undetected in the buried cores, since the plastic bags enclosing the cores were gas-permeable.

Not only was there a reduction in available nitrogen with phosphate fertilization but levels also decreased as plantation age increased. Without fertilization, the youngest stand had inorganic nitrogen levels higher than that of the two older stands (Figs 4.6b & 4.7). This was probably due to the very high soil total nitrogen content of the youngest stand (Fig. 4.10) which is as a result of it being a second rotation stand that was established within the slash of the first rotation. No slashburning was carried out and so the soil developed a high organic content (Appendix, Fig. 1). This would support a large microbial biomass. Since there would be little competition between ammonifying bacteria and other soil micro-organisms for organic compounds, the conversion of organic nitrogen to available forms would be high. The lack of a significant difference in inorganic nitrogen between the unfertilized plots of the two older stands as opposed to the significant decrease in both ammonium and nitrate levels from the 20 to 25 year old fertilized plots indicates that this reduction of inorganic nitrogen levels with age is related to phosphate fertilization.

It is uncertain which of the two proposed processes (increased uptake of ammonium by fertilized trees or stimulation of nitrification by increased phosphate availability followed by loss of nitrate by denitrification) was responsible for the decreased levels of inorganic nitrogen in the fertilized plots. The most likely of the two would be that process whose effect intensified (or accumulated) with time after

fertilization. With the increased uptake assumption, an aspect of plant nutrition that must be considered is retranslocation of nutrients. While retranslocation will be discussed further in the next chapter, it must be mentioned here that retranslocation of nitrogen occurred at all the stands and increased with fertilization. Thus, part of the extra nitrogen demand by the fertilized trees will be compensated for by retranslocation. However, if nitrogen is being withdrawn from needles prior to litterfall, then the C:N ratio of the litter will be large and decomposition slow. Return of organically bound nitrogen to the soil solution in available forms will also be slow. Since the accumulated litter mass increased with plantation age, so too will the extent of nitrogen immobilization. Thus, nitrogen availability would decrease with age.

Denitrification may also contribute to nitrogen loss from the soil cycle up to 25 years. If this process occurred regularly over the 25 years, its accumulated nitrogen loss could be great. It could intensify with age if the larger litter mass of the older stands reduced surface soil water loss by evaporation and so prolonged the periods of saturation and anaerobic conditions.

It is likely that all of the processess described here are contributing to the observed reduction of inorganic nitrogen and the effects are still evident up to 25 years.

Even though monthly variation of available nitrogen was significant at each stand, no overall seasonal trends were evident. The only monthly pattern common to all three stands was that inorganic levels in July 1989 were consistently low and September 1990 consistently high. Soil "microclimatic" factors that vary seasonally, namely soil temperature and moisture content were quite similar over July and September (Appendix, Figs 2 & 3). Thus, the significant difference in inorganic nitrogen levels cannot be explained. Monthly fluctuations in net nitrogen mineralization rates at the three stands were just as irregular as that of nitrogen availability. Even though available nitrogen is a product of mineralization, the fluctuations did not coincide.

Trends of net nitrogen mineralization rates were similar to that of inorganic nitrogen in that mineralization rates in the unfertilized plots showed a significant decrease between the youngest stand and two older stands and in the fertilized plots mineralization rates decreased with stand age. However, the most important dissimilarity is that the effect of phosphate fertilization on net nitrogen mineralization rates was not significant at the 8 and 20 year old stands. Only after 25 years was the effect of fertilization apparent on nitrogen mineralization. Net nitrogen mineralization rates of all the fertilized treatments were significantly lower than that of the unfertilized 25 year old plots. This could be due either to immobilization of nitrogen in the litter layer or by the microbial biomass. The production of nutrient poor litter (explained earlier) which leads to slow decomposition rates and low input of organic nitrogen compounds into the soil nitrogen mineralization cycle of the older fertilized plots, results in lower turnover rates of inorganic nitrogen. DiStefano & Gholz (1989) found lowest net ammonification rates at the oldest stand (29 years). They ascribed it to greater competition for soil organic nitrogen by microbes. Net mineralization rates can be reduced when organic nitrogen compounds are taken up by micro-organisms and not released in available form. This immobilization of

organic (and inorganic) nitrogen is increased with fertilization by the increased phosphorus availability which can support a large microbial population (Cole & Heil 1981).

The reduction of inorganic nitrogen levels by phosphate fertilization is related to time after fertilization application (the reduction of inorganic nitrogen levels in the plots fertilized only 10 years after establishment were not as great as that by the treatments where fertilization was applied at establishment), but not to frequency of application (inorganic nitrogen levels in the plots fertilized once, at establishment, were not significantly different to the levels in the plots fertilized twice). However, neither frequency nor time of application affected net nitrogen mineralization rates. Annual nitrogen turnover (Fig. 4.9) was similar at all the fertilized treatments of the 25 year old stand. While annual nitrogen turnover showed only a slight reduction with phosphate fertilization after 20 years when applied at plantation establishment, the 25 year old plots fertilized only 10 years after establishment (15 years ago) had significantly reduced annual nitrogen turnover. Thus phosphate fertilization of established stands appears to reduce nitrogen mineralization rates more rapidly than when it is applied at establishment. This could be due to the applied phosphate boosting an already substantial soil microbial population which would be present in the 10 year old plantation and hence microbial immobilization of nitrogen would be rapid.

Environmental factors and Nitrogen mineralization

The effects of phosphate fertilization and plantation age on inorganic nitrogen levels and net nitrogen mineralization rates have been discussed in detail. However, seasonal fluctuations of nitrogen mineralization rates and the effect of environmental variables were not easily observed from the graphs. The "stepwise selection multiple regression" (Table 4.2) showed that moisture was the most significant factor ($r^2=0.598$) determining the variance in net nitrogen mineralization rates. This correlation has been found by many nitrogen mineralization researchers. Pastor et al. (1984), Gökçeoglu (1988), Burke (1989) and Edmonds & McColl (1989) all found that highest rates of net nitrogen mineralization generally corresponded with periods of high soil moisture. However, temperature was usually shown to be of equal or only slightly lesser importance. In this study, temperature was not a strongly correlated environmental factor in the nitrogen mineralization process. After soil moisture, total and inorganic nitrogen were the next most significant factors influencing net nitrogen mineralization rates. Since total nitrogen is seasonally stable and will thus not account for the monthly variations in net nitrogen mineralization rates, it must be the most important factor controlling inter-site variability. The importance of total nitrogen is as the substrate for the nitrogen mineralization process, since over 90% of total nitrogen is in organic form (Fig. 4.10). These results are in agreement with the findings of Burke (1989) who showed that both soil moisture and substrate availability control net nitrogen minralization rates. The good correlation between nitrogen mineralization and available (inorganic) nitrogen levels is understandable, as inorganic nitrogen is the product of mineralization. This may indicate that losses of inorganic nitrogen such as by plant uptake, microbial and litter immobilization and denitrification are negligible compared to inorganic levels and mineralization. Otherwise, all these processes are in equilibrium. The significance of stand age in the mineralization process was discussed

earlier. In contrast to phosphorus mineralization where fertilization was the most significant factor determining variation, fertilization was only added to the nitrogen model in the final step, increasing the coefficient of determination (r^2) by only 0.005. This is lower than the determinant value of fertilization in phosphorus mineralization ($r^2=0.021$). The strong influence of environmental factors on nitrogen mineralization indicates the role of micro-organisms in this mineralization process.

CONCLUSIONS

The most important findings of this study were the negative effect of phosphorus fertilization on nitrogen release and that this effect intensifies with time (plantation age). This stresses the importance of understanding the effects of this fertilization practice on both phosphorus and nitrogen soil mineralization processes. While phosphate application may correct phosphorus deficiencies it will, in the long run, lead to reduced nitrogen availability and so again limit productivity of the system.

CHAPTER 5

LITTER DYNAMICS

INTRODUCTION

Nutrients removed from the soil system by plant uptake are not lost forever. Nutrients are returned to the soil for recycling by means of litterfall and decomposition. The increased productivity of pine plantations in response to phosphate fertilization (Donald et al. 1987; Herbert & Schönau 1989 & 1990) may only be maintained to the end of the rotation by the efficient recycling of essential nutrients (Carey et al. 1981). The large accumulation of litter in pine stands indicates that decomposition and recycling is not very rapid.

The proposal that phosphate fertilization increased plant growth and nutrient uptake (seen in Chapter 4 as reduced soil nitrogen levels in fertilized plots) leads to the question of how this fertilization affects the return of nutrients to the soil system. According to Miller et al. (1979) the rate of addition of litter to the forest floor is a function of tree growth rates (high growth rates results in greater rates of litterfall). Since unpublished FORESTEK records of the trials used in this project indicated that phosphate fertilization resulted in substantial increases in P. elliottii growth, litterfall rates were examined relative to fertilization treatment and plantation age. Owing to various findings such as those of Kelly & Henderson (1978) and Martikainen et al. (1989) that phosphorus fertilization of nutrient poor soils increased decomposition rates, Olson's (1963) decomposition constants were calculated to test the effects of fertilization.

RESULTS

5.1 Seasonal Rates of Litterfall

Litterfall rates ($g\ m^{-2}\ d^{-1}$) were analysed (in a "three-way ANOVA") in relation to plantation age, fertilization treatment and month (period of collection). All factors were shown to have a significant effect on litterfall. With respect to age, the rate of litterfall at the youngest stand was significantly lower than at the two older stands ($F=39.52, p<0.0001$) (Fig. 5.1). While the scale of the graphs in Fig. 5.1 is sometimes too large to clearly show the difference in litterfall with treatment, the overall effect of treatment proved to be significant ($F=39.05, p<0.0001$): fertilization increased the rate of litterfall. Over the year, all the stands showed seasonal variability with significant reductions in rates of litterfall between August and December 1990 (late winter to early summer) and peaks in March or April (Autumn) ($F=127.77, p<0.0001$). (Spring was taken as September, October, November; summer as December, January, February; autumn as March, April, May; winter as June, July, August).

Interactions of factors were also significant - age and month ($F=61.32, p<0.0001$), age and treatment ($F=9.17, p<0.001$), month and treatment ($F=15.54, p<0.0001$) and the "three-factor" interaction ($F=7.48, p<0.001$).

An examination of site characteristics (Chapter 3) and environmental conditions (Chapter 4) indicated that factors other than age, such as soil type and rainfall, also contributed to the variation between plantations. Therefore to eliminate site effects, each plantation was tested individually for treatment and month effects.

At the youngest stand, Goudveld (Fig. 5.1a), the rates of litterfall (g m^{-2} d^{-1}) were significantly higher in the fertilized plots ($F=14.77, p<0.0005$). A significant reduction in litterfall occurred from August 1990 to January 1991 (late winter to summer) with a peak in April 1990 (Autumn) ($F=18.85, p<0.0001$).

At the 20 year old stand, Keurboomsrivier (Fig. 5.1b), there was no significant difference in litterfall rate between the unfertilized and fertilized plots. There was however a significant pattern with month ($F=71.1, p<0.0001$). Litterfall was lowest during August to December 1990. However, April 1990 was similarly low. Here, the litterfall rates seems to have an earlier Autumn peak (in March) than at the younger stand. By January 1991 the rate of litterfall had already increased substantially.

At the oldest stand, Quar (Fig. 5.1c) the lowest litterfall rates were recorded at the unfertilized plots and the highest at the plots fertilized once, at establishment. The variation with treatment was significant ($F=18.24, p<0.0001$). Monthly variation was also significant ($F=378.97, p<0.0001$). Again, August to December 1990 showed very low rates of litterfall. An increase in litterfall was evident in January, but as at the youngest stand, litterfall only peaked in April.

The youngest and oldest stands both showed a peak in the rate of litterfall during April. However, these peaks were very different. At the youngest stand, the highest litterfall recorded (at the fertilized plots) was only about 2.1 g m^{-2} d^{-1}. This increased to 3.8 g m^{-2} d^{-1} at the 20 year old fertilized plots and to 4.5-7.6 g m^{-2} d^{-1} at the ferilized plots of the oldest stand. Thus, peak litterfall rate increased with age as would be expected from the greater biomass of the older stands.

5.2 Annual Litterfall Inputs

Annual rates of litterfall (Fig. 5.2) showed similar trends to the seasonal rates (Section 5.1) - litterfall rates increased with plantation age ($F=20.46, p<0.0001$) and fertilization ($F=19.88$, $p<0.0005$). As with seasonal rates, annual litterfall rates at the youngest stand were significantly lower than at the other two stands. While the overall effect of fertilization was significant with fertilization at the 20 year old stand (Fig. 5.2). Comparing annual litterfall of the unfertilized plots showed that it increased from 8 to 20 years but decreased after 25 years. However, this decrease was not significant. In the fertilized plots, litterfall increased with stand age. At the oldest stand, all the fertilization treatments produced

significantly greater annual litterfall inputs than in the unfertilized plots ($F=12.84, p<0.0005$). Litterfall in the plots fertilized once, at establishment (F(1)) was also significantly higher than that in the other fertilization treatments.

5.3 Standing Pine Litter

The mass of pine litter accumulated on the plantation floor (standing pine litter) is shown in Fig. 5.3. The youngest stand had the lowest standing litter mass. It was significantly different to the older stands ($F=173.62, p<0.0001$). Comparing the standing litter mass of the unfertilized plots of all the aged stands showed that again the lowest mass was recorded at the youngest stand. The higest mass occurred at the 20 year old stand. Comparing the fertilized plots of all the stands (the plots fertilized once, at establishment of the oldest stand) showed an increase of standing litter mass with increasing age.

Across all the stands, the effect of fertilization was shown to be significant ($F=73.16, p<0.0001$). However, analysing each stand alone indicated that fertilization was only a significant factor at the youngest ($F=19.43, p<0.005$) and oldest ($F=15.74, p<0.0001$) stands. At the oldest stand, the greatest litter mass was found at the plots fertilized only at establishment. The plots fertilized twice had the second largest litter mass followed by the plots fertilized 10 years after establishment. The unfertilized plots had the lowest standing litter mass.

These trends in standing litter mass appeared to correspond with rates of litterfall (Section 5.1). Regression analyses were applied to test the relative significance of litterfall in determining litter accumulation. At Goudveld (8 year old stand) and Quar (25 year old stand) significant correlations were found ($r^2=0.602, p<0.005$ and $r^2=0.526, p<0.0001$ respectively). At Keurboomsrivier (20 year old stand), the litterfall versus standing litter relationship was not significant ($r^2=0.018, p>0.05$).

5.4 Non-pine Understorey

The non-pine understorey (Fig. 5.4) may also contribute to variations in standing litter mass. The most noticeable result in Fig. 5.4 is that the highest non-pine understorey biomass occurred at the youngest stand. This is significantly higher than the non-pine biomass of the older stands ($F=126.11, p<0.0001$). Comparing the unfertilized plots across all the stands showed that while the highest non-pine biomass was found at the youngest stand, the lowest was found at the 20 year old stand. Considering all the fertilized plots (only the plots fertilized once, at establishment of the oldest stand), the non-pine understorey biomass decreased as stand age increased.

The difference in non-pine understorey biomass between unfertilized and fertilized plots was only significant at the oldest stand. Non-pine biomass of the unfertilized plots was significantly higher ($F=27.67, p<0.0005$) than that of all the other treatment plots(there was no significant difference in non-pine biomass between the three fertilized treatments)

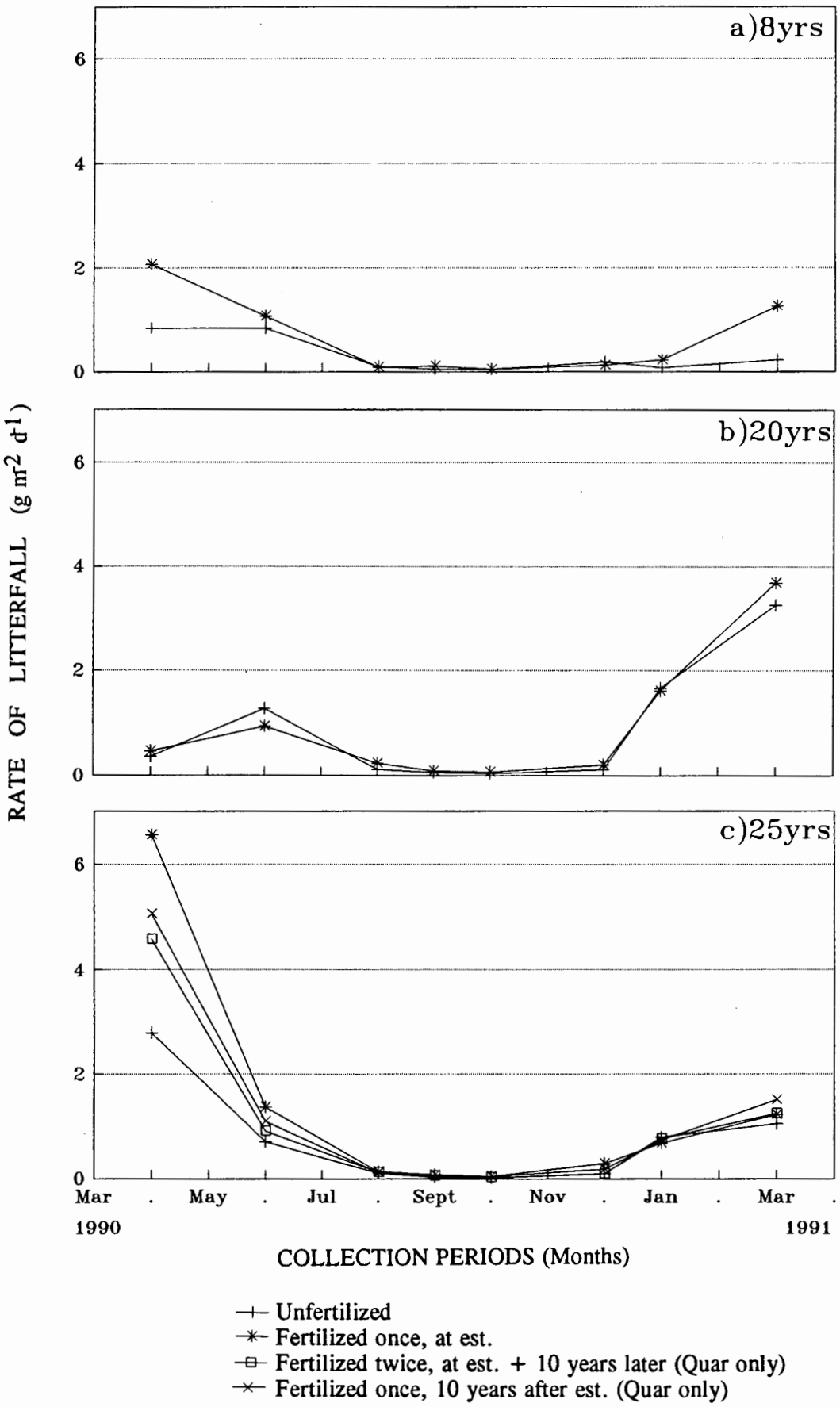
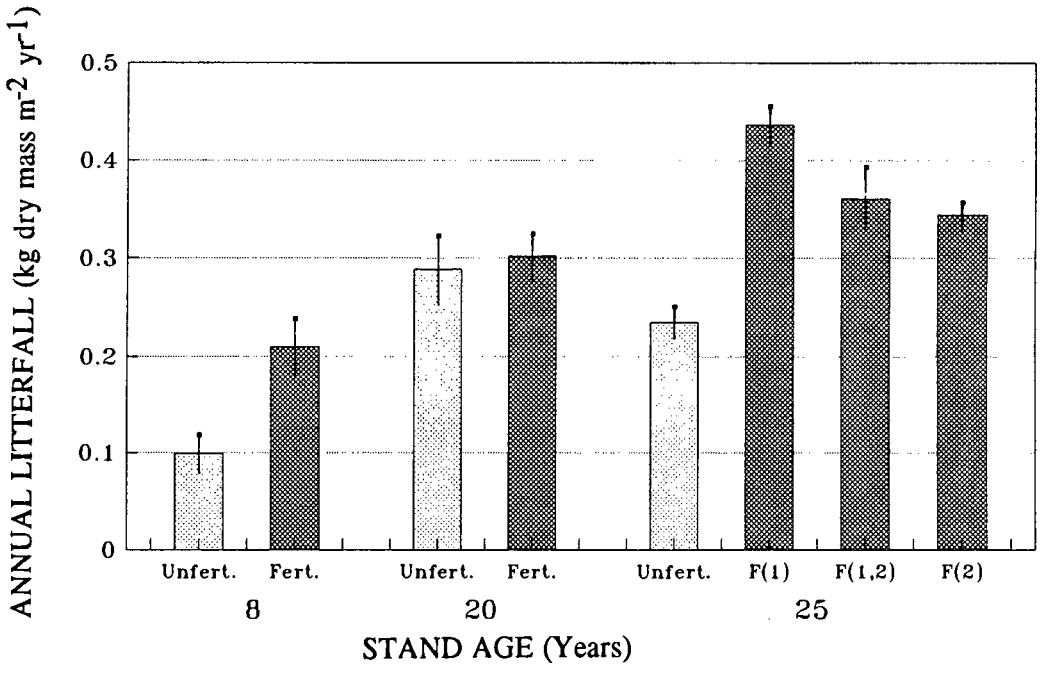
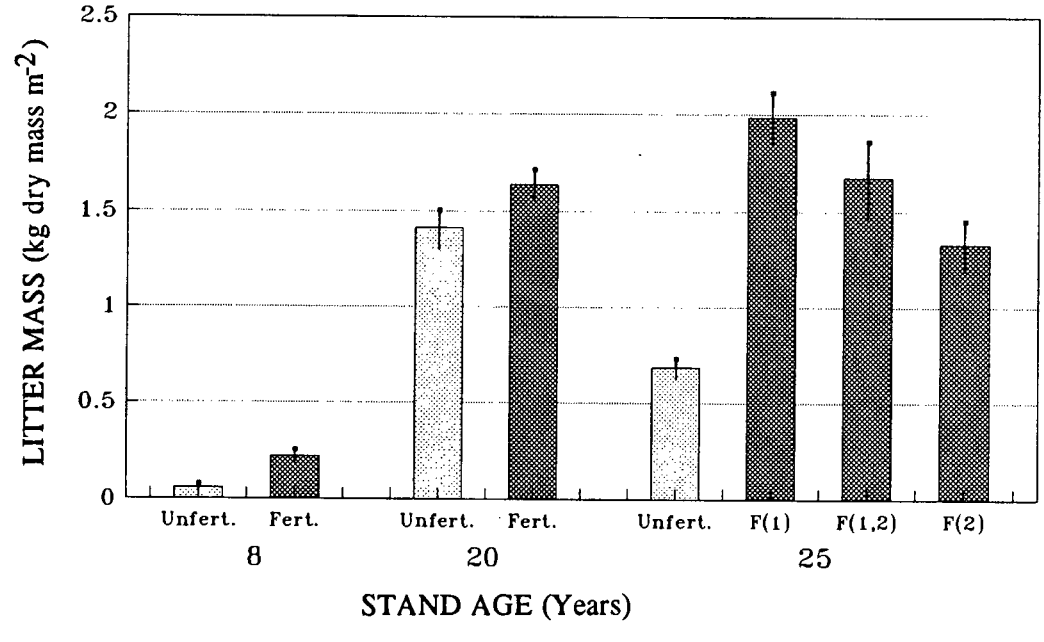


FIG.5.1: Monthly variation of litterfall rates (g m^{-2} day^{-1}) in the unfertilized and phosphate fertilized plots of P. elliottii stands at a)Goudveld (8 years old), b)Keurboomsrivier (20 years old) and c)Quar (25 years old). Error lines too small to represent.



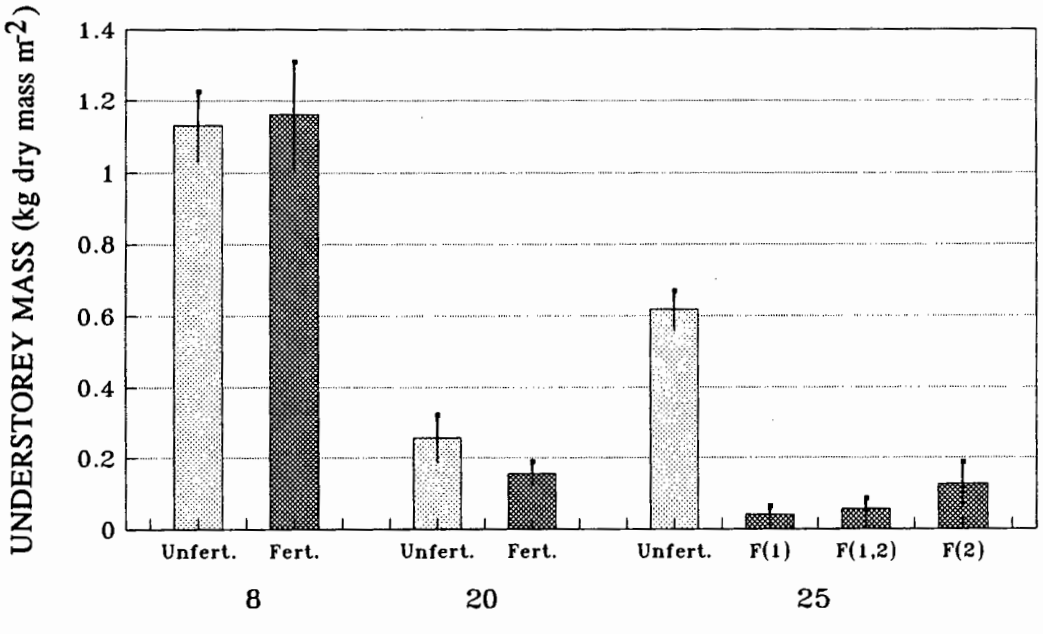
Unfert. - Unfertilized
Fert./F(1) - Fertilized once, at est.
F(1,2) - Fertilized twice, at est. + 10 years later
F(2) - Fertilized once, 10 years after est.

FIG.5.2: Annual litterfall rates (kg dry mass m^{-2} yr^{-1}) of the unfertilized and phosphate fertilized plots at the different aged P. elliottii stands (Goudveld - 8 years, Keurboomsrivier - 20 years and Quar - 25 years old). Vertical lines represent ± 1 S.E.M.



Unfert. - Unfertilized
Fert./F(1) - Fertilized once, at est.
F(1,2) - Fertilized twice, at est. + 10 years later
F(2) - Fertilized once, 10 years after est.

FIG.5.3: The mass of the pine litter accumulated on the plantation floor (kg dry mass m^{-2}) of the unfertilized and phosphate fertilized plots at the different aged P. elliottii stands (Goudveld - 8 years, Keurboomsrivier - 20 years and Quar - 25 years old). Vertical lines represent ± 1 S.E.M.



Unfert. - Unfertilized
Fert./F(1) - Fertilized once, at est.
F(1,2) - Fertilized twice, at est. + 10 years later
F(2) - Fertilized once, 10 years after est.

FIG.5.4: Non-pine understorey biomass (kg dry mass m^{-2}) of the unfertilized and phosphate fertilized plots at the different aged P. elliottii stands (Goudveld - 8 years, Keurboomsrivier - 20 years and Quar - 25 years old). Vertical lines represent ± 1 S.E.M.

TABLE 5.1: Decay constants, k=L/Xss (L was the measured annual litterfall and Xss the accumulated litter mass), mean litter concentrations of phosphorus and nitrogen and litter N:P ratios of the unfertilized and fertilized plots of the different aged P. elliottii plantations.

PLANTATION	TREATMENTS	k (yr^{-1}) (± 1 S.E.M.)	LITTER P ($\mu g\ P\ g^{-1}$) (± 1 S.E.M.)	LITTER N (mg $N\ g^{-1}$) (± 1 S.E.M.)	N:P RATIO (± 1 S.E.M.)
Goudveld (8 yrs)	Unfertilized	/	84.24 ± 14.29	0.70 ± 0.07	8.23 ± 0.65
	Fertilized	/	81.02 ± 9.17	0.31 ± 0.05	3.90 ± 0.21
Keurboomsrivier (20 yrs)	Unfertilized	0.21 ± 0.03	92.04 ± 10.26	0.60 ± 0.03	6.96 ± 0.81
	Fertilized	0.19 ± 0.02	169.55 ± 26.21	0.36 ± 0.05	2.15 ± 0.07
Quar (25 yrs)	Unfertilized	0.35 ± 0.03	53.15 ± 2.83	0.42 ± 0.03	7.90 ± 0.72
	Fertilized(1)	0.22 ± 0.01	186.07 ± 29.96	0.30 ± 0.05	1.64 ± 0.09
	Fertilized(1,2)	0.23 ± 0.03	519.29 ± 26.45	0.36 ± 0.09	0.63 ± 0.02
	Fertilized(2)	0.27 ± 0.02	124.72 ± 4.89	0.28 ± 0.06	2.28 ± 0.17

Fertilized(1)- Fertilized once, at est. only
Fertilized(1,2)- Fertilized twice, at est. and 10 years later
Fertilized(2)- Fertilized once, 10 years after est.
/ - sites where k constant not calculated

5.5 Decomposition constant, k

Annual litterfall (L, g m^{-2} yr^{-1}) and the accumulated litter mass (Xss, g m^{-2}) was used to estimate decomposition constants, k (yr^{-1}), using the equation k=L/Xss (Olson 1963) (Table 5.1). Calculation of the k value for the youngest stand was not valid, since the litter layer was not in a "steady" state (a condition for use of this equation). If the litter layers of the older stands were not in a "steady state" (i.e. at constant biomass), the calculated k values would be overestimated. Therefore, these values will only be used to demonstrate the effect of fertilization on decomposition and not to predict actual litter decomposition rates.

There was no significant difference in k values between the 20 and 25 year old stands. Also, the effect of fertilization at the 20 year old stand was not significant. At the 25 year old stand there was a significant variation in k constants with fertilization treatment ($F=4.15, p<0.05$). The plots fertilized once, at establishment and those fertilized twice had k values significantly lower than that of the unfertilized plots (since the k constant is an estimation of the proportion of litter mass lost per year, a lower k value represents less litter lost or decomposed in a year). The k values of the plots fertilized only 10 years after establishment were not sigificantly different to those of the unfertilized or other treatment plots.

Since decomposition rates may influence litter accumulation, regression analyses were applied to test the decay constant-standing litter mass relationship. At Keurboomsrivier (20 year old stand) the k constant accounted for 39.9% of standing litter mass trends ($r^2=0.399, p<0.05$). At Quar (25 year old stand) the regression relationship between k constants and standing litter was stronger with $r^2=0.613, p<0.0001$.

5.6 Seasonal Litter Phosphorus Levels

Factors investigated in relation to phosphorus levels in litter (Fig. 5.5) were age, treatment and season. Variation with age was significant ($F=22.47, p<0.0001$) with the youngest stand having the lowest levels and the 20 year old the highest. The effect of fertilization treatment was also significant ($F=126.54, p<0.0001$) with the overall trend being that litter phosphorus levels were higher at the fertilized plots than at the unfertilized. The significant effect of season ($F=27.18, p<0.0001$) was due to constantly higher phosphorus levels during spring. The interaction of factors was also significant - age and season ($F=2.44, p<0.05$), age and treatment ($F=41.44, p<0.0001$) and season and treatment ($F=4.48, p<0.01$).

An examination of each stand separately, showed that while the overall trend of higher litter phosphorus levels at fertilized plots was significant, this trend was not evident at the youngest stand (Fig. 5.5a). Only during winter and summer were the phosphorus levels higher in the fertilized litter. Litter collected during autumn and spring showed higher phosphorus levels at the unfertilized plots. The seasonal variation of litter phosphorus was significant ($F=9.54, p<0.0005$) with the highest levels

in spring and the lowest in autumn. The high levels in spring coincides with the lowest rates of litterfall (Fig. 5.1a). The low phosphorus levels of autumn coincides with the peak litterfall.

At the 20 year old stand (Fig. 5.5b) the litter phosphorus levels were always significantly higher in the fertilized plots ($F=44.94, p<0.0001$). Here again the highest litter phosphorus was recorded in spring ($F=13.16, p<0.0001$), when litterfall rates were lowest (Fig. 5.1b). Levels of phosphorus in the litter from the other seasons appear to be very similar.

At the oldest stand (Fig. 5.5c), fertilizer treatment effects seem to be consistent throughout the year. Phosphorus levels in the litter from the plots fertilized twice were always much higher than that in the other treatments. The plots fertilized at establishment only, had the next highest litter phosphorus levels, followed by the plots fertilized 10 years after establishment. The lowest phosphorus levels were found in the litter from the unfertilized plots. These treatments were all significantly different from each other ($F=362.12, p<0.0001$). The seasonal variation was also significant ($F=7.59, p<0.0005$) with spring again having the highest levels of litter phosphorus.

5.7 Seasonal Litter Nitrogen Levels

Age, treatment and season were all significant factors affecting the levels of nitrogen in the litter ($F=18.37, p<0.0001$; $F=138.67, p<0.0001$; $F=24.96, p<0.0001$). The overall pattern with age was a decrease in litter nitrogen as age increased, since the oldest stand had the lowest litter nitrogen and the youngest had the highest (Fig. 5.6). The overall effect of treatment was to lower the litter nitrogen levels. The overall seasonal pattern was higher litter nitrogen during spring and summer than autumn and winter.

Analysing the youngest stand, Goudveld (Fig. 5.6a), alone showed that nitrogen levels were always significantly higher in the unfertilized litter ($F=54.39, p<0.0001$). As with litter phosphorus, litter nitrogen levels were highest in spring and lowest in autumn ($F=7.01, p<0.001$).

At the 20 year old stand, Keurboomsrivier (Fig. 5.6b), litter nitrogen was again always significantly higher in the unfertilized plots ($F=121.08, p<0.0001$). The lowest nitrogen levels were determined for the autumn litter. Spring levels were only slightly higher than the winter and summer levels but it was shown to be significant ($F=16.3, p<0.0001$).

At the oldest stand, Quar (Fig. 5.6c), the effect of treatment on the litter nitrogen was not as clear as with litter phosphorus. Nevertheless, treatment was still shown to be a significant factor ($F=12.43, p<0.0001$) with the litter nitrogen levels of the unfertilized plots being significantly higher than that of the other treatments (which were overall not different to each other). Seasonal variation was also significant ($F=56.14, p<0.0001$) with autumn and winter having the lowest litter nitrogen levels. Spring again showed the highest litter nitrogen levels. The high spring nitrogen levels found in the litter

from the plots fertilized twice is unusual since it is inconsistent with the trend that occurred during the other seasons.

5.8 Litter N:P ratios

N:P ratios of the freshly fallen litter were significantly higher in the unfertilized plots of all the stands compared to that of the fertilized plots (Table 5.1) ($F=115.35, p<0.0001$). Variation with stand age was also significant ($F=3.91, p<0.0005$), with the youngest stand being most different to the older stands.

5.9 Fresh Foliage Phosphorus

Phosphorus levels in the fresh foliage (pine needles from the trees) from the unfertilized plots of all the stands were very similar (Fig. 5.7). Comparing foliar phosphorus levels of the fertilized plots of the 8 and 20 year old stands with that of the oldest stand plots fertilized at establishment only (F(1)) showed that the lowest levels occurred at the youngest stand, followed by the oldest. The 20 year old stand had the highest foliar phosphorus levels. This variation with age was statistically significant ($F=26.37, p<0.0001$).

Phosphate fertilization did not appear to alter the phosphorus levels of the fresh foliage at the youngest stand. At the 20 year old stand, fertilization significantly increased the foliar phosphorus levels ($F=64.06, p<0.0001$). At the oldest stand, only the plots fertilized twice had foliar phosphorus levels significantly higher than the unfertilized levels ($F=19.3, p<0.0001$). The other fertilized treatments were not significantly different from the unfertilized.

Comparing phosphorus levels in the fresh foliage with that in the litter indicated that at the 8 year old stand, foliar phosphorus levels (Fig. 5.7) were more than double the litter phosphorus (Fig. 5.5a). At the 20 year old fertilized plots, foliar phosphorus (Fig. 5.7) was again about double the levels of litter phosphorus (Fig. 5.5b) while at the unfertilized plots foliar phosphorus was almost four times greater than the litter phosphorus. At the 25 year old unfertilized plots, foliar phosphorus (Fig. 5.7) was eight times greater than that of the litter phosphorus (Fig. 5.5c), twice as great at the plots fertilized once at establishment and four times as great at the plots fertilized once 10 years after establishment. At the plots fertilized twice, the foliar phosphorus was only about 1.5 times greater than the litter phosphorus. Therefore it seems that removal of phosphorus from foliage in the production of litter is greater in the unfertilized plots. This removal (retranslocation) is lowest where foliage phosphorus is highest (i.e. in plots of the oldest stand fertilized twice).

5.10 Fresh Foliage Nitrogen

A comparison of foliar nitrogen levels at the unfertilized plots of all the stands (Fig. 5.8) indicated that the youngest stand had the highest levels. There appeared to be little variation in foliar nitrogen between the fertilized plots. Thus, as would be expected, age and treatment were non-significant factors with regard to foliar nitrogen across all the stands. However, at the youngest stand only, treatment was significant ($F=15.13, p<0.01$) with foliar nitrogen levels lower at the fertilized plots.

In the unfertilized plots of the two younger stands, foliar nitrogen levels (Fig. 5.8) were about 1.5 times greater than the litter nitrogen levels (Fig. 5.6a & b). In the fertilized plots, foliar levels were about double the litter levels. At the 25 year old unfertilized plots, foliar levels were twice as great as the litter levels (Fig. 5.6c). At the fertilized plots, this difference was more than double, being up to three times in the plots fertilized 10 years after establishment. Therefore, differences between foliar and litter nitrogen levels are more pronounced in the fertilized than the unfertilized plots.

5.11 Annual Litter Phosphorus Input

Annual levels of phosphorus input to the litter layer are shown in Fig. 5.9a. Variation with plantation age was significant ($F=16.85, p<0.0001$). Phosphorus input appeared to increase with age, but only the difference between the youngest stand and the older two was significant (there was no significant difference between the 20 and 25 year old stands ($p>0.05$).

Phosphate fertilization produced a significant effect ($F=46.32, p<0.0001$) at all the stands by increasing annual litter phosphorus. All the fertilization treatments of the oldest stand were significantly different ($F=70.3, p<0.0001$). Highest phosphorus inputs were found in litter from the plots fertilized twice followed by the plots fertilized once, at establishment.

5.12 Annual Litter Nitrogen Input

Annual levels of nitrogen input to the litter layer are shown in Fig. 5.9b. Age was a significant factor ($F=10.45, p<0.0005$) with the youngest stand having significantly lower nitrogen input than the older stands. Fertilization did not produce a significant effect at the youngest stand ($p>0.05$). At the 20 year old stand, fertilization significantly reduced annual nitrogen input. However, at the oldest stand nitrogen input was greater in all the fertilized plots. Only the plots fertilized once at establishment were significantly different from the unfertilized plots ($F=4.74, p<0.05$).

5.13 Annual litterfall rate vs litter phosphorus/nitrogen

The strong positive relationship between litterfall and litter phosphorus in phosphorus limited systems found by Vitousek (1984) was tested in this study. A similar strong, positive correlation was obtained (Fig. 5.10a) ($r^2=0.715, p<0.0001$). All the unfertilized and fertilized treatment results occurred close to the regression line, except for an outlier which represented the plots of the 25 year old stand, fertilized twice (F(1,2)).

The positive linear correlation between annual litterfall and litter nitrogen was significant but much weaker than that for phosphorus ($r^2=0.475, p<0.0001$). There was no apparent effect of phosphorus fertilization on the litterfall vs litter nitrogen relationship (Fig. 5.10b).

5.14 Nutrient Use Efficiency (NUE)

The ratio of litter dry mass : annual litter nutrient input has been used as an index for within-stand NUE (Chapin 1980; Vitousek 1982 & 1984). Plotting this ratio against the annual input of nutrient in litterfall (g m^{-2} yr^{-1}) indicated the relationship between NUE and the amount of that nutrient returned annually through litterfall (Vitousek 1982 & 1984). The resulting exponential trend for phosphorus use efficiency (Fig. 5.11a) showed that at low litter phosphorus levels, phosphorus use efficiency was high. Thus, as would be expected, all the unfertilized plots (as well as the youngest fertilized plots) had relatively high indices of phosphorus use efficiency. With phosphorus fertilization and higher phosphorus litter levels, these indices dropped. The lowest values were calculated for the 25 year old plots fertilized twice.

The only apparent trend for nitrogen use efficiency (Fig. 5.11b) was that the unfertilized plots had lower nitrogen use efficiency indices than any of the fertilized treatments.

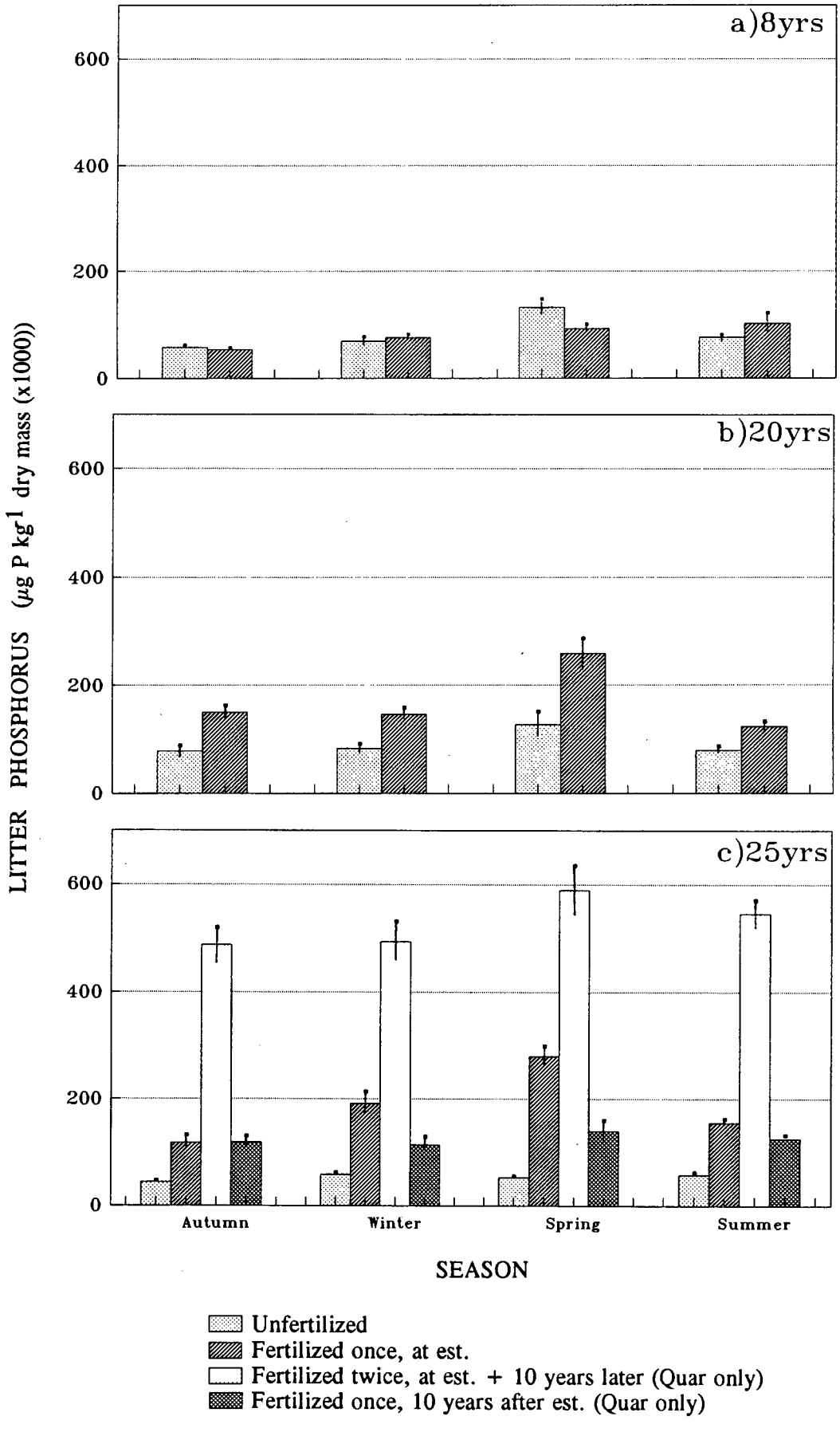


FIG.5.5: Seasonal variation of phosphorus levels (μg P kg^{-1} dry mass) in the litter collected from littertraps in the unfertilized and phosphate fertilized plots of P. elliottii stands at a)Goudveld (8 years old), b)Keurboomsrivier (20 years old) and c)Quar (25 years old). Vertical lines represent $\pm$1 S.E.M.

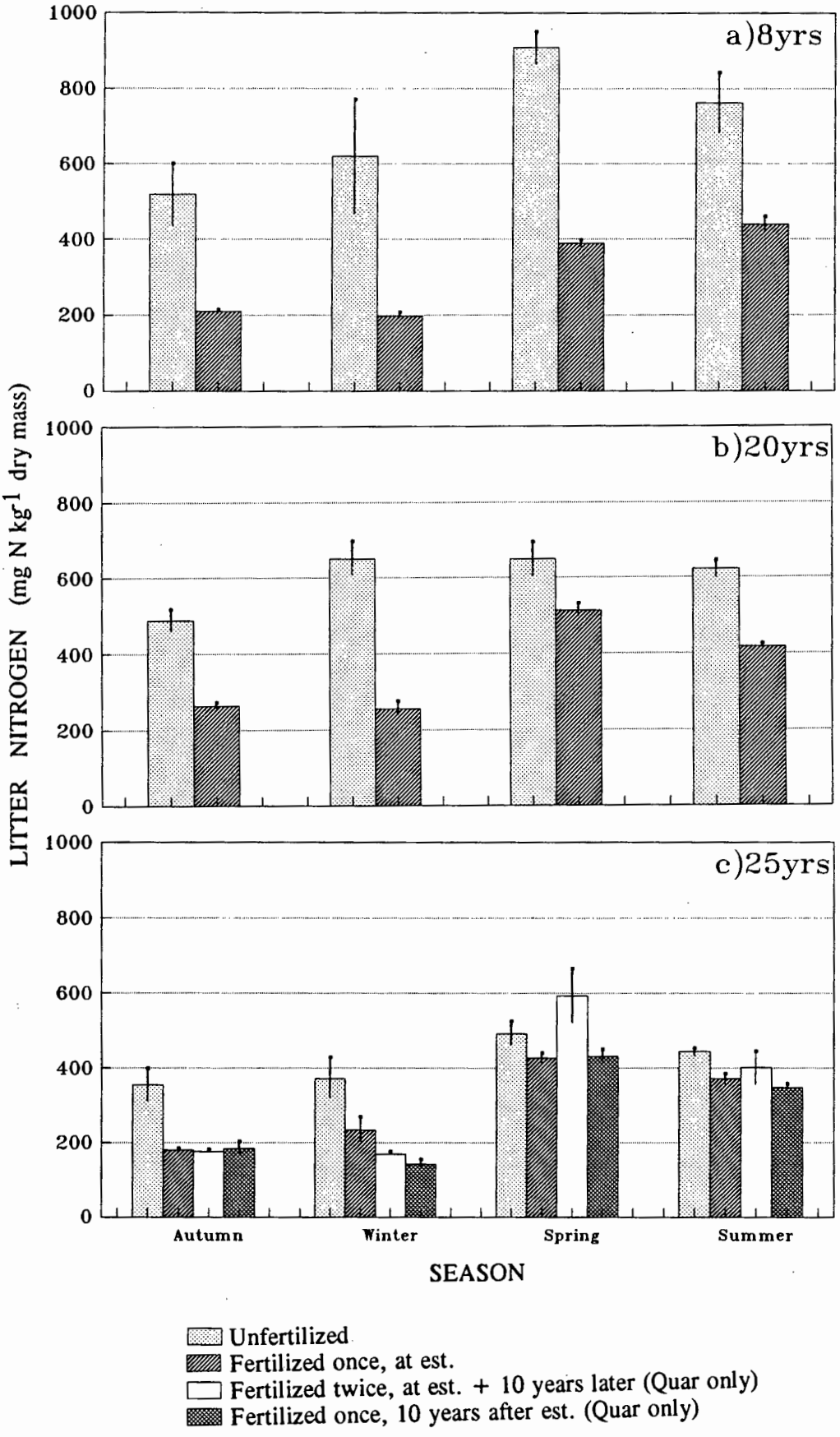
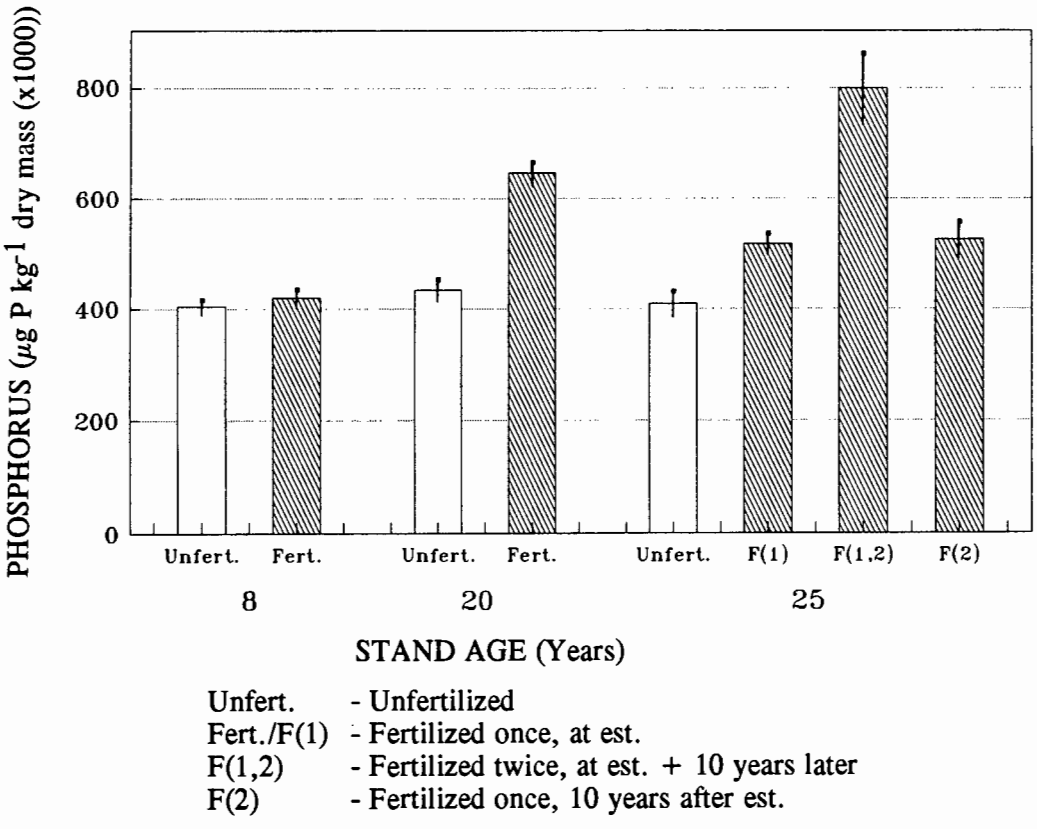
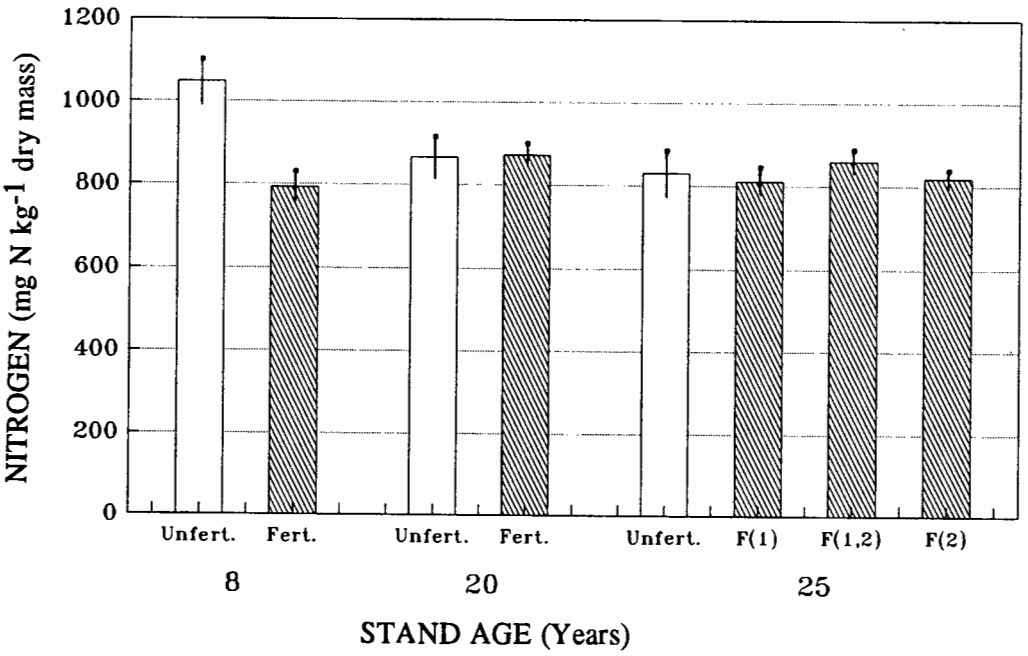


FIG.5.6: Seasonal variation of nitrogen levels (mg N kg^{-1} dry mass) in the litter collected from littertraps at the unfertilized and phosphate fertilized plots of P. elliottii stands at a)Goudveld (8 years old), b)Keurboomsrivier (20 years old) and c)Quar (25 years old). Vertical lines represent ± 1 S.E.M.



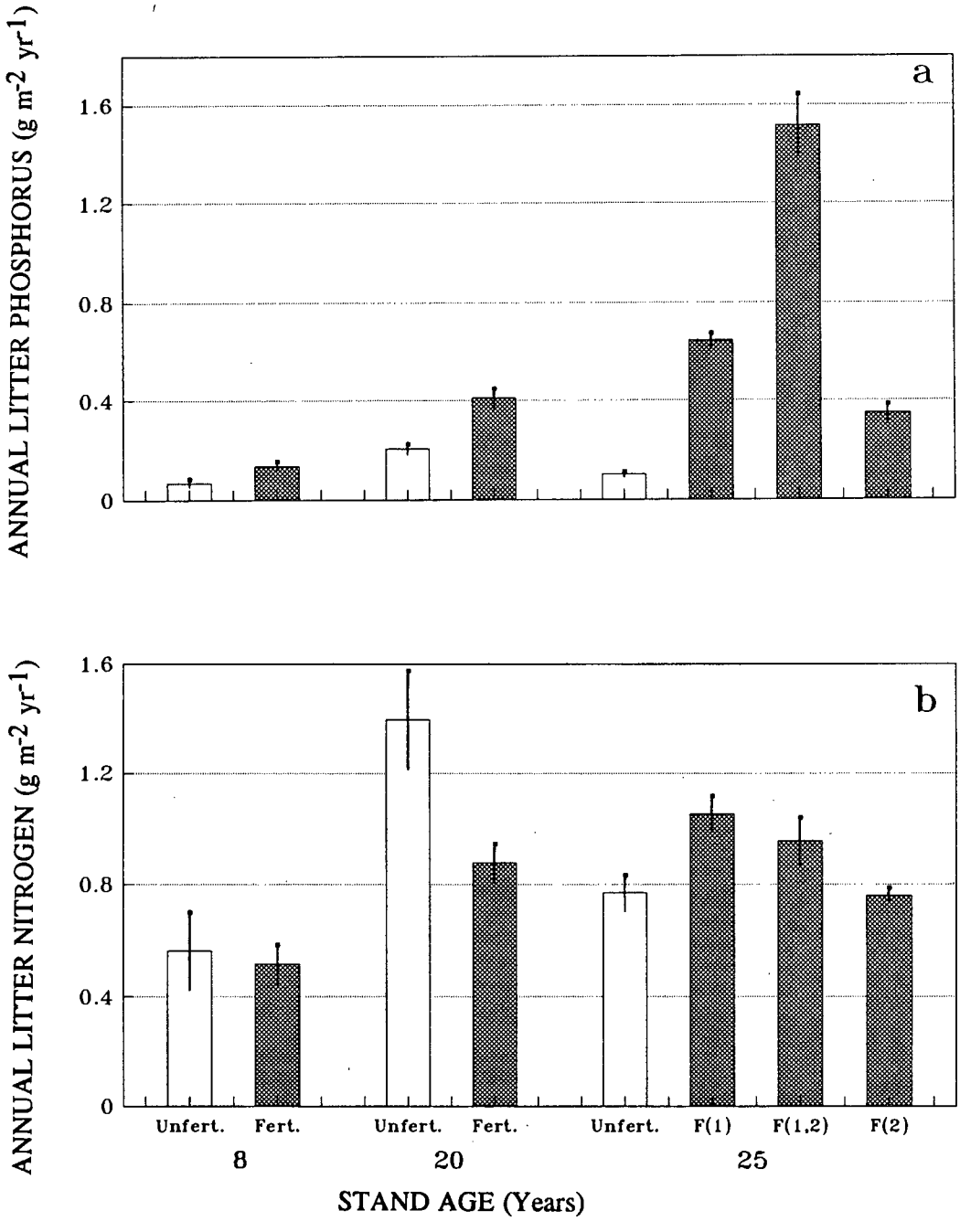
Unfert. - Unfertilized
Fert./F(1) - Fertilized once, at est.
F(1,2) - Fertilized twice, at est. + 10 years later
F(2) - Fertilized once, 10 years after est.

FIG.5.7: Phosphorus levels (μg P kg^{-1} dry mass) of the fresh pine needles from the unfertilized and phosphate fertilized plots at the different aged P. elliottii stands (Goudveld - 8 years, Keurboomsrivier - 20 years and Quar - 25 years old). Vertical lines represent $\pm$1 S.E.M.



Unfert. - Unfertilized
Fert./F(1) - Fertilized once, at est.
F(1,2) - Fertilized twice, at est. + 10 years later
F(2) - Fertilized once, 10 years after est.

FIG.5.8: Nitrogen levels (mg N kg^{-1} dry mass) of the fresh pine needles from the unfertilized and phosphate fertilized plots at the different aged P. elliottii stands (Goudveld - 8 years, Keurboomsrivier - 20 years and Quar - 25 years old). Vertical lines represent $\pm$1 S.E.M.



Unfert. - Unfertilized
Fert./F(1) - Fertilized once, at est.
F(1,2) - Fertilized twice, at est. + 10 years later
F(2) - Fertilized once, 10 years after est.

FIG.5.9: Annual litter phosphorus (a) and nitrogen (b) input (g m^{-2} yr^{-1}) to the plantation floor of the unfertilized and phosphate fertilized plots at the different aged P. elliottii stands (Goudveld - 8 years, Keurboomsrivier - 20 years and Quar - 25 years old). Vertical lines represent ± 1 S.E.M.

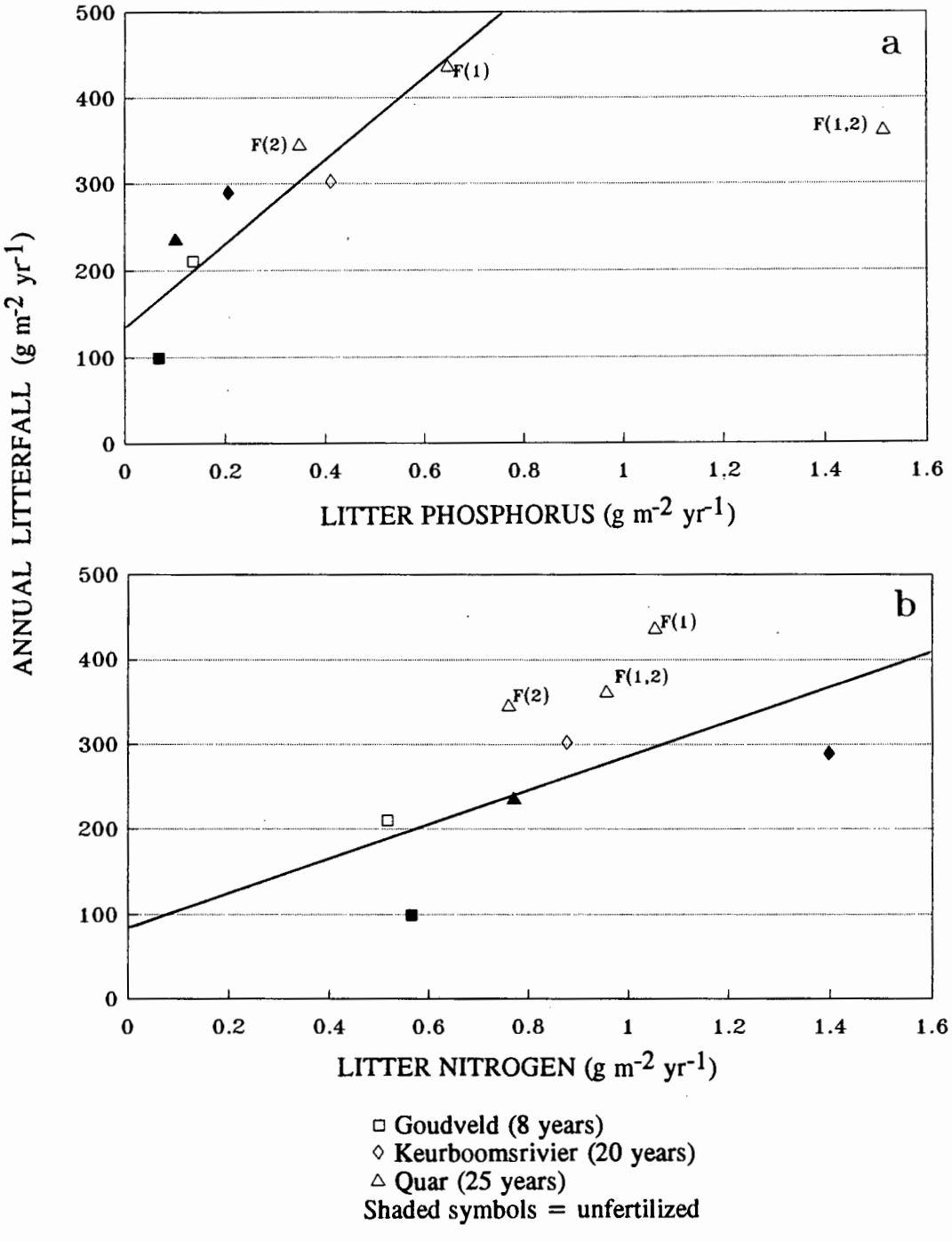
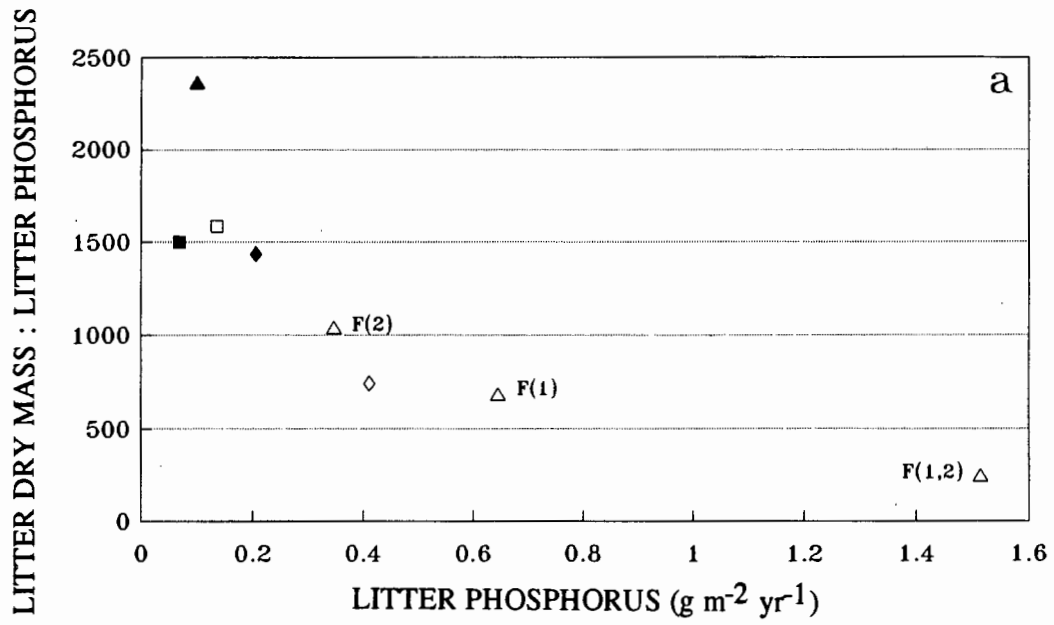
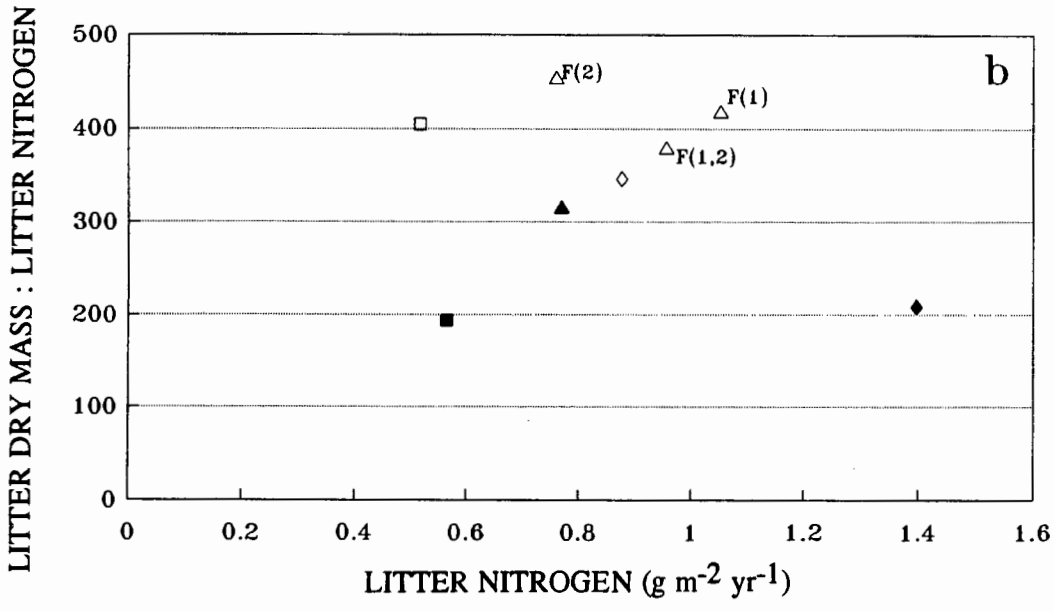


FIG.5.10: Annual litterfall (g m^{-2} yr^{-1}) vs litter phosphorus (a) and nitrogen (b) input (g m^{-2} yr^{-1}) in the unfertilized and phosphate fertilized plots of the different aged P. elliottii stands (Goudveld - 8 years, Keurboomsrivier - 20 years and Quar - 25 years old). The equation of the relationship in a was $y=467.697x + 140.026$, $r^2=0.715$ and in b was $y=204.328x + 85.545$, $r^2=0.475$.





□ Goudveld (8 years)
◊ Keurboomsrivier (20 years)
△ Quar (25 years)
Shaded symbols = unfertilized

F(1) - Fertilized once, at est.
F(1,2) - Fertilized twice, at est. + 10 years later
F(2) - Fertilized once, 10 years after est.

FIG.5.11: The litter dry mass : litter phosphorus(a)/nitrogen(b) input ratio used as an index of phosphorus(a)/nitrogen(b) use efficiency, plotted against litter phosphorus(a)/nitrogen(b) input for unfertilized and phosphate fertilized plots at different aged P. elliottii stands (Goudveld - 8 years, Keurboomsrivier - 20 years and Quar - 25 years old).

DISCUSSION

Seasonal and Annual rates of Litterfall

Seasonal litterfall rates at P. elliottii stands (Fig. 5.1) indicated that while litter fall occurred throughout the year, there was an Autumn peak (March or April) at all the different aged stands. This is in agreement with the findings of other workers. Gholz et al. (1985a) found autumn always had the greatest needlefall in a P. elliottii plantation age sequence of 9-35 years which is similar to Versfeld & Donald's (1991) recorded maximum litterfall rates for P. radiata which occurred in autumn of each year from 1976 to 1980.

According to Vitousek (1984), the interaction of temperature and precipitation has a strong control on litterfall, particularly where these factors fluctuate seasonally. At the study sites, the highest soil temperatures and lowest soil moisture contents were recorded during February and March (Appendix, Figs 2 & 3), which is just prior to the peak litterfall period (the strength of this relationship was not tested, since temperature/soil moisture and litterfall rates were not determined concurrently). An increase in litterfall during or after a dry period may be attributed to the trees reducing canopy leaf area in response to reduced water availability (Gholz et al. 1985a).

In addition to environmental factors such as temperature and soil moisture, the effects of fertilization treatment and plantation age also influenced seasonal litterfall rates. To determine the effects of fertilization treatment and plantation age on litterfall more clearly, annual litterfall rates (Fig. 5.2) were used to eliminate problems associated with seasonal effects. A significant increase in annual litterfall rates with phosphate fertilization were observed at Goudveld (8 years old) and Quar (25 years old) but not at Keurboomsrivier (20 years old). Thus it seems that the proposal of Miller et al. (1979), that an increase in tree growth rates (induced here by phosphate fertilization) results in greater rates of litterfall, does not apply in the latter plantation.

Gholz et al. (1985a) found that P. elliottii needle litterfall increased with stand age to peak at age 15-16 years, then declined in older stands. A similar trend was observed in the unfertilized plots of this study where litterfall increased from 8 to 20 years but decreased after 25 years. From the age sequence in Fig. 5.2 it seems that peak litterfall occurred at 20 years. However, the age interval between 8 and 20 years is quite large, with no corresponding stand at 15-16 years which could have had a higher litterfall rate than that at the 20 year old stand. This seems possible when considering that Gholz et al. (1985a) found the peak litterfall rate to be 0.445 kg m^{-2} yr^{-1} compared to 0.289 kg m^{-2} yr^{-1} recorded in the 20 year old unfertilized plots of this study.

Fertilization not only increased the rate of litterfall but also increased the age at which peak litterfall occurred. It is uncertain whether peak litterfall in the fertilized plots occurred at 25 years, since there is no older stand. However, it is interesting to note that the rate of litterfall at the 25 year old plots

fertilized once at establishment (F(1)) was 0.436 kg m^{-2} yr^{-1} compared to the peak litterfall of 0.445 kg m^{-2} yr^{-1} recorded by Gholz et al. (1985a).

Standing Pine Litter and Decomposition rates

Since fertilization increases the rate of litterfall, it is important to know how it in turn affects the accumulation of litter on the plantation floor (standing pine litter). It is well documented that the slow decay rates of pine needles results in the accumulation of large masses of litter (Gholz et al. 1985a in USA; Morris 1986, Herbert & Schönau 1989 in SA). Morris (1986) identified excessive litter accumulation, which may represent the immobilization of a substantial quantity of essential nutrients, as the greatest threat to long-term productivity of P. patula stands in the Usutu forest, Swaziland. The significantly higher standing litter mass observed in the fertilized plots of our study (Fig. 5.3) indicated that phosphate fertilization intensified the problem of litter accumulation. Whether this represents an increase in the immobilization of nutrients (phosphorus and nitrogen) will be discussed later in this chapter.

Even though variations in the accumulated pine litter mass appeared to correspond to trends of litterfall rates, the conclusion that litter accumulation was controlled by the rate of litterfall alone cannot be made without examining the respective decomposition constants, (k) (Table 5.1). Morris (1986) believed that variations in forest floor accumulations between P. patula stands in the Usutu forest, Swaziland was due to differences in rates of decomposition rather than litterfall.

Estimated k values at the 20 and 25 year old stands ranged from 0.188-0.350 yr^{-1} (Table 5.1). This means that 18.8-35% of the standing litter mass was lost annually. This is within the range measured for pines by other workers. Versfeld & Donald (1991) estimated a decay rate of 0.30 for P. radiata in the southwestern Cape. Gholz et al. (1985a) found a slightly lower value of 0.15 yr^{-1} for P. elliottii plantations in northern Florida (southeastern United States). These values represent slow decay rates and results in the accumulation of large masses of litter on the plantation floor (Gholz et al. 1985a; Morris 1986). From our data, comparing trends of decay constants (Table 5.1) and standing litter (Fig. 5.3) indicates that high standing litter mass coincides with low decay constants.

From the regression analyses applied to test the relative significance of litterfall and decay rates in determining litter accumulation, it was found that while the significance of decomposition increased with stand age, the effect of litterfall was variable. At the youngest stand, a litter mass was still in the process of accumulating and it is thus understandable that litterfall rates would be the most important factor determining the standing litter mass ($r^2=0.61$). Decomposition is an unlikely factor controlling litter mass here. Decomposition will only proceed once the needles at the litter-soil interface are covered by a substantial later of litter that separates it from the desiccating influence of the atmosphere (Specht 1981). Pine needles have been shown to dry more rapidly, hold less water at saturation and have lower water potentials at low moisture contents than the litter of other trees (Dix 1984). Thus, limited or no decomposition of the exposed, dry litter at the youngest stand would occur, since growth

and activities of non-xerophytic fungi, soil fauna and decomposing micro-organisms would be reduced (Dix 1984). This would also explain the increasing significance of the decay constant on standing litter with increasing stand age (the regression value of the standing litter-k constant relationship increased from $r^2=0.39$ at Keurboomsrivier to $r^2=0.61$ at Quar). Presumably as the litter layer ages so the number of decomposing organisms flourishing beneath it should increase. This would explain the higher k values at the oldest stand.

The correlation between standing litter and litterfall rates ($r^2=0.53$) was almost as strong as the standing litter-k constant relationship ($r^2=0.61$) at the 25 year old stand. This may indicate that the observed standing litter mass was the balance of two equally important processes - litterfall (input) and decomposition (output). Since decomposition only becomes of importance later in the rotation and operates at a much slower rate than litterfall, litter masses accumulate. Greater litter accumulations at the fertilized plots coupled with lower k constants than those of the unfertilized plots shows that phosphate fertilization did not increase the rate of decomposition as may have been expected.

Litter and Fresh foliage Nutrient content

An important factor controlling decomposition when environmental conditions are favourable is the chemical nature of the litter (Escudero et al. 1987). Often decomposition rates are greater in litter with a high nutrient content or low C:N and C:P ratios.

At all the stands, phosphate fertilization significantly increased litter phosphorus concentrations and reduced litter nitrogen concentrations (Table 5.1). As a result of findings such as that of Martikainen et al. (1989) and other work cited by them where phosphorus addition was found to enhance decomposition in forest systems, it was expected that the higher litter phosphorus concentrations of the fertilized plots would result in greater decay constants (k). Comparing litter phosphorus concentrations with decay constants (Table 5.1) at the 20 and 25 year old stands showed that the greater k value at each stand was from the unfertilized plots where litter phosphorus levels were lower. Even though phosphate addition may be reducing the C:P ratio of the litter it is uncertain how important this ratio is in determining litter decomposition. From the literature (Edmonds 1980; Yavitt & Fahey 1986; Vitousek 1984) it seems that decomposition proceeds at a wide range of C:P ratios.

The importance of litter nitrogen levels (or C:N ratio) in determining the rate of litter decomposition is widely accepted (Edmonds 1980; Yavitt & Fahey 1986). In contrast to the negative relationship between litter phosphorus levels and decay rates, litter nitrogen levels showed a positive correlation with k values at both the 20 and 25 year old stands (litter nitrogen levels and k values were higher in the unfertilized plots, Table 5.1). This indicates that litter nitrogen levels may be controlling decomposition rates in this system, and the effect of phosphate fertilization on the decomposition process is therefore indirect.

Most decomposition studies have considered the C:P or C:N ratio as important in determinining decomposition rates. If either ratio is too high for decomposition to proceed, phosphorus or nitrogen will accumulate in the litter until the ratio is reduced. However, Gholz et al. (1985a) proposed that nutrient accumulation in the litter (particularly phosphorus in their study) was related to the initial N:P ratio of the litter. By examining the N:P ratios of a range of other decomposition studies they found that where the N:P ratio was <6, phosphorus did not accumulate. Thus, in all our fertilized plots which had N:P ratios <6 (Table 5.1) and significantly different from those of the unfertilized plots, decomposition would not be delayed by accumulation of phosphorus in the litter. In the unfertilized litter, a small degree of phosphorus accumulation should occur. Therefore, the significantly higher decay constants calculated for the unfertilized plots (Table 3) which was deduced as being due to the higher litter nitrogen concentration of these plots, occurred in spite of the requirement for phosphorus accumulation prior to decomposition.

Phosphorus and nitrogen concentrations in pine litterfall were determined seasonally so that it could be compared to the seasonal trends in litterfall rates. At all the stands, litter phosphorus and nitrogen concentrations were highest during spring (Figs 5.5 & 5.6) which is when litterfall rates were lowest (Fig. 5.1). This apparent inverse relationship was extended at the youngest stand (Goudveld) for phosphorus and at all the stands for litter nitrogen in that the lowest litter nutrient concentrations were found in autumn when highest litterfall occurred. Gholz et al. (1985a) found similar trends in their chronosequence of P. elliottii plantations. Thus potential excessive losses of nutrients from P. elliottii trees when litterfall rates are high, are restricted by reduced litter nutrient concentrations during periods of peak litterfall.

To obtain the actual litter nutrient input to the plantation floor, the product of phosphorus/nitrogen litter nutrient concentrations and litterfall rates were calculated for the study period April 1990 to March 1991, i.e. 1 year ($g\ m^{-2}\ yr^{-1}$). While trends of annual nitrogen input to the litter layer were variable (Fig. 5.9b) and unlike that of either annual litterfall or litter nitrogen concentrations, annual phosphorus input (Fig. 5.9a) corresponded with trends of litterfall rates and litter phosphorus concentrations. Annual phosphorus input was highest where both litter phosphorus concentrations and litterfall rates were high, namely in the fertilized plots. In these plots phosphorus availability was higher (Chapter 4) and the extent of retranslocation lower (later in this section) so that more phosphorus was returned in litterfall than at the corresponding unfertilized plots. The higher litterfall rates would be due to the greater foliage biomass of the fertilized trees. The increasing annual litter phosphorus input with increasing plantation age in the fertilized plots was similar to the trends of annual litterfall (Fig. 5.2) and could also be attributed to increasing litterfall as tree biomass increased with plantation age. However, within the fertilized plots of the 25 year old stand (Quar), litter phosphorus trends did not coincide with that of litterfall. As might have been expected, annual litter phosphorus input in the plots fertilized twice (F(1,2)) was much greater than that at any of the other plots (Fig. 5.9a). This was not due to a similarly high annual litterfall. Here, a very high litter phosphorus concentration (Table 5.1) accounted for this high annual litter phosphorus input.

Annual litterfall vs Litter Phosphorus/Nitrogen

The difference in litter phosphorus dynamics between the 25 year old plots fertilized twice (F(1,2)) and the rest of the study plots is clear in Fig. 5.10a, which illustrates the relationship between annual litterfall and litter phosphorus input. Litterfall rates appear to reach a maximum and thus only litter phosphorus input increases where phosphorus availability is high, as in the F(1,2) plots.

Vitousek (1984) found the litterfall versus litter phosphorus relationship to be strongly positive only where phosphorus was low and limiting production. Therefore, since all the study plots with the exception of only F(1,2) plots formed a strong positive correlation ($r=0.715$), phosphorus was still the element limiting production. Thus even though a single application of phosphate fertilization was shown to improve growth rates in these plantations (unpubl. FORESTEK records) it was not sufficient to break the control of phosphorus availability over biomass production (represented by litter phosphorus input and annual litterfall respectively (Fig. 5.10a)). Since F(1,2) did not fall on the regression line it may be assumed that a double phosphate application increases phosphorus availability to levels that are not limiting.

Earlier in this chapter it was questioned whether the increase in litter accumulation with phosphate fertilization also represented an increase in the immobilization of nutrients. While there was no clear increase in litter nitrogen input with fertilization, the increase in litter phosphorus input at all the fertilized plots, especially at the plots where phosphate was applied twice, showed that there was an increase in phosphorus immobilization. This greater input of phosphorus to the litter layer in the fertilized plots together with their lower rates of decomposition suggests that phosphate fertilization intensified the problem of phosphorus accumulation in the litter layer.

Retranslocation and Nutrient Use Efficiency

Litter nutrient concentrations appear to be ultimately controlled by the process of nutrient retranslocation. When root uptake of nutrients from the soil does not meet plant nutrient requirements, the "outstanding" amount is fulfilled by retranslocation of nutrients from senescing tissues prior to leaf abscission (Turner & Lambert 1986a; Jonasson 1989). The overall lower phosphorus concentrations in the litter compared with that of the fresh P. elliottii needles indicated that retranslocation of phosphorus occurred at all the stands. As early as 8 years (Goudveld), tree phosphorus demand is already partially met by retranslocation (here litter phosphorus concentration was half that of fresh foliage). At this age the effect of fertilization on retranslocation was not yet evident. With phosphate fertilization, this rate of retranslocation was maintained for 25 years, which indicated that the extent to which plant phosphorus requirements are fulfilled by uptake from the soil did not decrease with stand age when phosphate was applied. Without fertilization the extent of phosphorus retranslocation increased greatly with age - from 50% of phosphorus removed prior to litterfall at Goudveld (8 years old) to 75% and 87.5% at Keurboomsrivier (20 years old) and Quar (25 years old) respectively. This trend of increasing reliance on internal redistribution with increasing plantation age was similar to that found by Gholz

et al. (1985b) where it was taken to indicate that the supply of phosphorus had become increasingly limiting.

While trends of foliage phosphorus and soil phosphorus availability across different aged stands and fertilization treatments were similar, trends of foliage nitrogen were quite different to those of soil nitrogen availability. Even though soil nitrogen availability was significantly reduced by phosphate fertilization (Chapter 4) levels of foliage nitrogen were similar across the different aged stands and fertilization treatments (Fig. 5.8). This, together with litter nitrogen levels being lower than foliage nitrogen at all the study sites, indicated that retranslocation of nitrogen was occurring. As with phosphorus, nitrogen retranslocation was evident early in the rotation, after only 8 years (Goudveld) which would be close to the time of peak nutrient demand in pines (Turner & Lambert 1986a). The expected increase in nitrogen retranslocation with increasing stand maturity (Turner 1981) was recorded, but the increase was not as great as that of phosphorus retranslocation. After 25 years (Quar) nitrogen retranslocation in the unfertilized plots had reached 50% of foliage nitrogen levels. This will probably not increase substantially in the future, as Versfeld & Donald (1991) determined about 50% nitrogen retranslocation prior to needle abscission in 40 year old P. radiata stands.

Fertilization induced increases in the extent of nitrogen retranslocation was evident at all the aged stands, even at the youngest stand at Goudveld. In spite of the greater extent of nitrogen retranslocation in the needles of the 8 year old fertilized trees, it was not sufficient to compensate for reduced nitrogen uptake and thus foliage nitrogen levels in the fertilized plots were significantly lower than that in the unfertilized plots (Fig. 5.8). If the foliage nitrogen concentration of the unfertilized 8 year old trees, which was significantly greater than that of any of the other aged trees, is the optimal level for growth conditions at this age, then this confirms the assumption of Turner & Lambert (1986a) that peak growth and thus greatest nutrient requirement occurs at 6-8 years. Tree growth rates were greater in the 8 year old fertilized plots (unpubl. FORESTEK records) and thus the foliage nitrogen concentration was lower than that of the unfertilized trees as the nutrients are distributed in a greater and more rapidly increasing foliage biomass. Stands at later stages in the rotation (Keurboomsrivier, 20 years old and Quar, 25 years old) have the same foliage nitrogen levels between stands and fertilization treatment (Fig. 5.8). A nitrogen concentration of 800-900 mg N kg^{-1} dry mass appears to be the optimal foliage nitrogen levels for growth conditions in stands 20 years and over. The "optimal" foliage nitrogen level is maintained in the fertilized plots by a slightly greater retranslocation rate which compensates for the lower soil nitrogen availability of these plots. This again shows the flexible nature of the retranslocation mechanism.

Plants in which a high degree of retranslocation occurs would assimilate relatively large amounts of organic matter per unit nutrient taken up and are thus described as having high nutrient use efficiency (Vitousek 1984; Jonasson 1989). Since this is usually considered as an adaptation for success in infertile environments (Chapin 1980), the high phosphorus use efficiencies of our unfertilized plots (Fig. 5.11a) where the extent of retranslocation was also high, was expected.

The substantially lower phosphorus use efficiency in the fertilized plots indicates that phosphate fertilization improved the phosphorus fertility of the soils. The 25 year old plots fertilized twice (F(1,2)) appeared to use phosphorus most inefficiently but this probably indicates that the system was relatively phosphorus rich. Also using Vitousek's (1982) index of nutrient use efficiency, Gholz et al. (1985b) found that the efficiency of nitrogen and phosphorus use increased with age at their P. elliottii stands. Similarly, the oldest unfertilized plots (Quar, 25 years old) had the greatest phosphorus use efficiency, presumably due to a long period of exposure to phosphorus deficient conditions.

Unlike the findings of Gholz et al. (1985b), nitrogen use efficiency (Fig. 5.11b) did not increase with plantation age. While Vitousek (1984) found similar exponential relationships for phosphorus and nitrogen use efficiency, no such trend was evident for nitrogen use efficiency in this study. The higher nitrogen efficiencies of all the phosphate fertilized plots would be in response to their lower nitrogen availability. These nitrogen use efficiency indexes were only very slightly higher than that of phosphorus use efficiency at the F(1,2) plots (Fig. 5.11a) which were considered to be relatively inefficient due to an abundance of available phosphorus. Thus it is possible that all the low nitrogen use efficiencies are indicative of adequate availability of nitrogen in these systems.

Phosphorus use efficiency is often found to be higher than nitrogen use efficiency in forest systems (Vitousek 1984), which would agree with Miller et al.'s (1979) assessment of the phosphorus cycle as being "tight and efficient".

CONCLUSIONS

In spite of the findings of the previous chapter that phosphorus fertilization had reduced soil nitrogen turnover and availability, this negative effect was not evident in foliage nitrogen levels or total nitrogen input to the litter layer. However, by reducing litter nitrogen concentrations, fertilization slowed the litter decomposition rate. This together with a higher rate of litterfall, resulted in greater accumulations of litter on the floor of fertilized plots. While the accumulation of large litter masses is not a serious problem in most of the Southern Cape, excessive accumulations occur in some areas of the country such as the Eastern Transvaal (de Ronde 1984). In these areas, it is essential that the negative effects of phosphate fertilization on litter dynamics, which could in turn severly impact nutrient cycling, should be considered when recommending a fertilization regime.

CHAPTER 6

P. ELLIOTTII SOIL BIOASSAY

INTRODUCTION

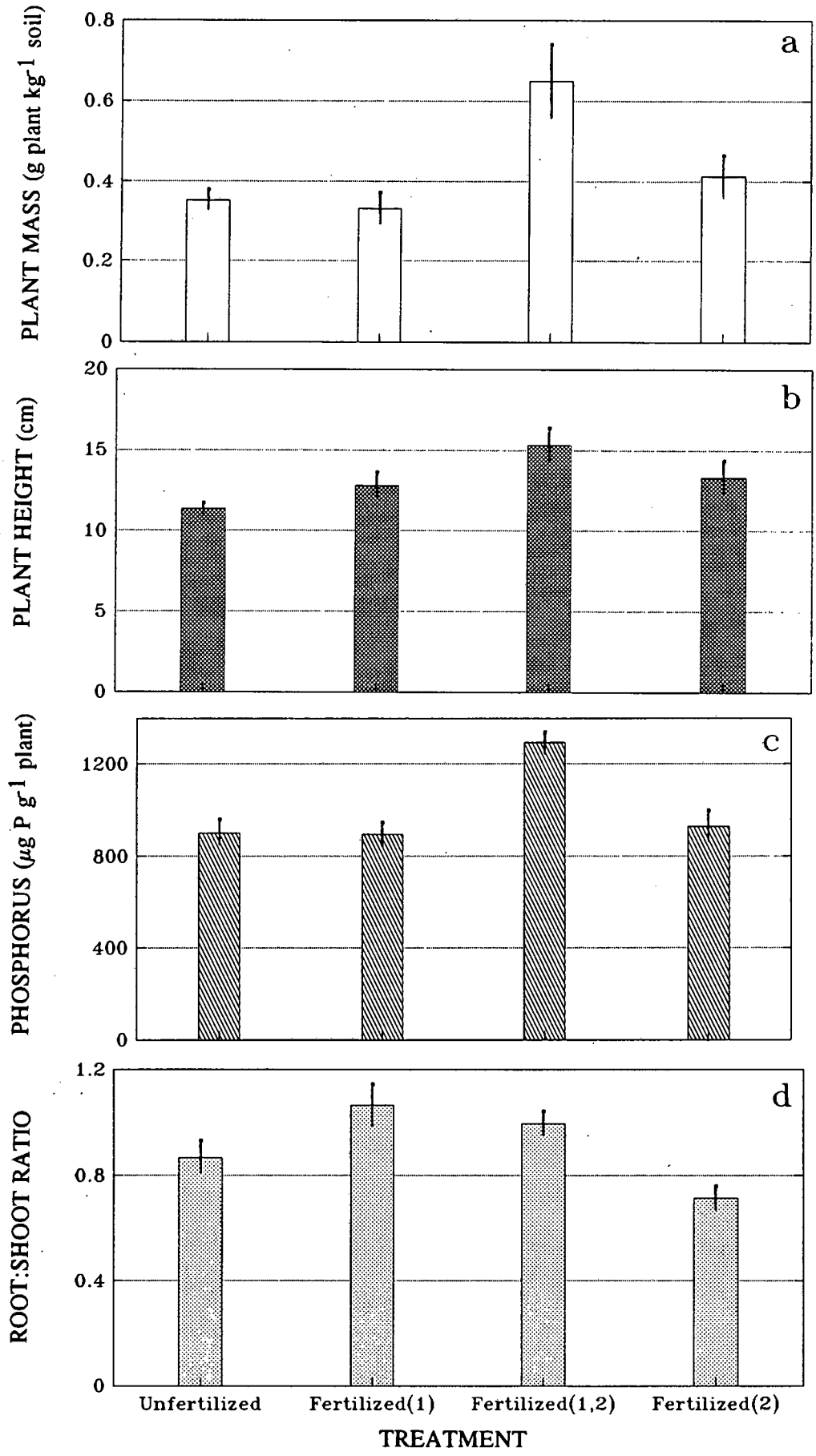
In Chapter 4 it was found that a significant increase in soil phosphorus availability after phosphate fertilization was no longer evident after 25 years in plots fertilized once. Only 25 year old plots fertilized twice, at establishment and again 10 years later showed significantly elevated levels of soil available phosphorus. However, the latter fertilization treatment together with the treatment of fertilization at establishment only, also resulted in the greatest reduction of soil inorganic nitrogen levels. Thus, the different fertilization treatments of the 25 year old stand (representing different timing and frequency of application) have resulted in plots with a range of soil phosphorus levels as well as different soil nitrogen availabilities.

In previous chapters, relative soil fertility was only inferred from soil nutrient availability, mineralization rates and nutrient use efficiencies. To obtain a realistic picture of responses to these fertilization induced changes in nutrient availabilities, a bioassay was conducted where P. elliottii seedlings were grown on soils from the different treatment plots of the 25 year old plots at Quar (refer to Chapter 3, Section 3.8 for a detailed account of the methods used in this experiment). Seedling growth response is a direct indication of the growth potential or productive capacity of these soils and should show whether the fertilized soils could maintain elevated growth rates for another rotation.

RESULTS

Seedling growth as an index of relative soil fertility was examined as seedling dry mass (shoot + root) and height (above soil level) at the end of an eight month growth period. Mass and height were greatest in the soils from the plots fertilized twice (Figs 6.1a & b). A one-way ANOVA showed that seedling mass in these soils fertilized twice was significantly different from the unfertilized soils and the soils fertilized only at establishment ($F=5.67, p<0.005$). Seedling height in the soils fertilized twice was only significantly greater than the unfertilized treatment ($F=3.45, p<0.05$).

Seedling phosphorus levels (Fig. 6.1c) were predictably highest in seedlings grown on the soils fertilized twice ($F=11.93, p<0.0001$). However, the levels of the other two fertilization treatments were no different to the unfertilized. The lowest root:shoot (R:S) ratios (Fig. 6.1d) occurred in the soils fertilized once, 10 years after establishment and this ratio was significantly different to those of the other fertilized treatments ($F=5.049, p<0.01$). Highest R:S ratios were found in the soils fertilized only at establishment, but these were not significantly different from the ratios of the "fertilized twice" treatment.



Fertilized(1)- Fertilized once, at est.
Fertilized(1,2)- Fertilized twice, at est. + 10 years later
Fertilized(2)- Fertilized once, 10 years after est.

FIG.6.1: Dry mass (shoot + root, g plant kg^{-1} soil) (a), height above soil (cm) (b), phosphorus levels (μg P g^{-1} plant) (c) and root:shoot ratios (d) of P. elliottii seedlings grown on soils from the different fertilization treatment plots of the 25 year old plantation (Quar). Vertical lines represent ± 1 S.E.M.

DISCUSSION

It was only in the soils from the plots fertilized twice that seedling mass, height and phosphorus levels were all significantly higher than those of the unfertilized soils (Fig. 6.1). Thus only with a double phosphate application can this plantation (Quar) maintain improved production for 25 years. The seedlings' positive growth response to the higher soil phosphorus availability of the soils from the plots fertilized twice was greater than any negative response to the reduced nitrogen levels at these plots. This indicates that either nitrogen availability was not reduced to levels limiting growth (as proposed by nitrogen use efficiencies in Chapter 5) or that the observed growth was an artefact of pot experiments. In pots, nitrogen becomes available more readily than in the field (A.C. Baker unpubl.). It is also possible that phosphorus was of greater importance in the early stage of seedling growth.

In support of the latter proposal, Herbert & Shönau (1990) found that fertilizing, particularly with phosphorus, has its main effect on root development and structure. Fertilizing allows the seedling to develop a sound root system capable of exploiting the full potential of the soil. The more effective rooting system of the seedlings in the soils fertilized twice was evident in that seedling phosphorus levels were significantly higher (Fig. 6.1c), where soil phosphorus availability was also high. This higher seedling phosphorus levels would support a greater growth rate evident as significantly higher plant height and mass at the plots fertilized twice (Figs 6.1a & b).

Where soil nutrient availability is low, reserves are allocated to root growth at the expense of the shoot. This results in plants with high root:shoot ratios. Shoot growth is more severely affected by nitrogen deficiencies than phosphorus (nitrogen is an essential component of plant tissue protein, photosynthetic enzymes and chlorophyll) (Chapin 1980). Thus, if the significant reduction in soil nitrogen availability observed in the plots fertilized once, at establishment and in those fertilized twice (Chapter 4) were severe, then high root:shoot ratios would be expected in seedlings grown in these soils. The root:shoot ratios of seedlings grown on soils from these plots were very close to 1 (Fig. 6.1d) i.e. there was an equal allocation to root and shoot mass. However, this was higher than the root:shoot ratios of the unfertilized soils and those fertilized only 10 years after establishment where soil nitrogen availability was significantly higher than at the plots fertilized once, at establishment and those fertilized twice. Thus at this stage of the rotation (i.e. 25 years after plantation establishment) the reduction in soil nitrogen availability, which accompanied phosphate fertilization, has had a slight affect only on seedling growth patterns, namely a slight increase in the root:shoot ratios.

Taking plant growth response as an index of soil productive capacity, this bioassay has confirmed that only a double phosphate application will maintain productivity above unfertilized levels for more than 25 years. With a single phosphate application, the potential productivity capacity returns to pre-fertilization levels in less than 25 years with only the negative side-effects of fertilization remaining, namely reduced nitrogen levels.

CHAPTER 7

SUMMARY AND CONCLUSIONS

Introduction

Extensive research programmes already undertaken in the pine plantations of southern Africa were aimed at developing fertilizer recommendations for increasing timber yields on the phosphorus deficient soils (Donald et al. 1987). Studies of the effects of fertilization on rates of nutrient turnover and interactions have, to date, been neglected. It has however, recently been acknowledged that in order to maintain fertilization effects into successive rotations (i.e. maintain long-term improved productivity) it is necessary to understand nutrient cycling patterns relative to soil fertility and time (Morris 1986; Herbert & Schönau 1989 & 1990).

The objectives of this study were to identify the effects of phosphate fertilization on rates of phosphorus cycling and the closely interactive nitrogen cycle in pine plantations of southern Africa. Determination of the long-term effects of phosphate fertilization was achieved by studying a chronosequence of P. elliottii plantations (8, 20 and 25 years old). At the 25 year old stand, treatments representing different timing and frequency of phosphate application were included so that the fertilization regime most effective at maintaining long-term productivity could be elucidated.

This chapter integrates information presented in Chapters 4-6 to provide a more complete account of the interrelated processes of nutrient turnover. Soil nutrient mineralization patterns, litterfall and decomposition in commercial pine plantations in the southern Cape are all discussed with particular reference to the interactions between phosphorus and nitrogen cycling.

Phosphorus cycling

Increased soil phosphorus availability induced by the application of phosphate fertilizers was expected and desirable, since it increases the amount of phosphorus directly accessible to plant roots (in competition with soil micro-organisms). However, it was phosphorus turnover rates that were considered of greater importance in this study (Chapter 4) since they indicate the net rate at which phosphorus becomes available in the soil solution through the process of mineralization (i.e. phosphorus in excess of that immobilized by soil micro-organisms). In unfertilized stands little phosphorus is released annually, as most is immobilized by soil micro-organisms (indicated by negative net mineralization rates). Immobilization of phosphorus reduces soil phosphorus availability which results in shortages in the unfertilized trees and hence reduced growth (unpubl. FORESTEK records) and sparser canopies (pers. obs.). The dense canopies of the 20 and 25 year old fertilized trees limit the extent of understorey vegetation while the unfertilized plots support a substantial weed understorey. These plants also compete for nutrients (de Ronde 1984) further reducing nutrients available to the pine trees of the unfertilized plots.

With phosphate fertilization a positive phosphorus mineralization rate was maintained in all the different aged stands, even though mineralization rates decreased in magnitude from 8 to 25 years. Twenty five years after establishment, only the plots fertilized twice had higher phosphorus availability and turnover rates than the unfertilized, which indicates that long-term productivity can only be maintained with a double phosphate application. This was confirmed by the bioassay in Chapter 6 where only the soils from the 25 year old plots fertilized twice produced a growth response significantly greater than that of the unfertilized soils (seedling growth response was taken as an index of soil productive potential). Therefore, frequency of fertilization application appears to be a more critical factor than actual timing of fertilizer application in maintaining long-term productivity. The advantages of fertilizing either at plantation establishment or at mid-rotation (discussed in Chapter 2) are likely to be combined when fertilizing at both times. The better root system gained from fertilizing at establishment increases uptake of fertilizers applied at midrotation, which improves wood quality. Fertilizer must be applied twice rather than a larger amount applied at planting, as there are optimal levels of fertilizing above which there is no additional response or sometimes even a negative effect (Turner & Lambert 1986b; Payn et al. 1988).

The effects of phosphate fertilization on above-ground processes such as retranslocation and litterfall were investigated in Chapter 5. Retranslocation (re-adsorption of nutrients from senescing tissues prior to leaf abscission, followed by translocation to other sites of high demand (Jonasson 1989)) compensates for low nutrient availability. Increased retranslocation of phosphorus with plantation age maintained foliage phosphorus of the unfertilized plots at similar levels from 8 to 25 years. This indicated that soil phosphorus limitation increased with plantation age (Gholz et al. 1985b). Phosphate fertilization prevented soil phosphorus from becoming increasingly limiting, as retranslocation remained the same from 8 to 25 years in the fertilized plots. The degree of retranslocation was also much lower than that of the unfertilized treatments. Twenty five years after a single phosphate application, the effect of fertilization was not evident on foliage phosphorus levels but a substantial effect on retranslocation was still detected. Phosphorus retranslocation occurred in both the unfertilized and fertilized plots suggesting that plant requirements were not being satisfied by root uptake of phosphorus alone (Bowen & Nambiar 1984). Retranslocation occurred even in the plots fertilized twice, where soil phosphorus availability and foliage phosphorus levels were significantly higher than in any of the other treatments, albeit at a much reduced level.

The fraction of foliage phosphorus that is not retranslocated is returned to the soil by means of litterfall and decomposition. Phosphate fertilization was shown to increase both the rate of litterfall and to elevate the phosphorus concentration of the litter. Contrary to the findings of Martikainen et al. (1989) the higher phosphorus concentration of "fertilized" litter did not result in increased decomposition rates. Fertilization enhanced the accumulation of litter on the plantation floor with a corresponding increase in phosphorus content of the litter layer. Thus the well documented problem in pine systems of slow decay rates resulting in excessive litter accumulation and immobilization of substantial quantities of nutrients (Gholz et al. 1985a; Morris 1986; Herbert & Schönau 1989) was intensified by phosphate fertilization.

As the accumulated litter mass of the fertilized plots increased with age, so too did the extent of phosphorus immobilization. This would explain the return of phosphorus availability to non-fertilized levels after only 25 years and substantiates Morris's (1986) proposal that excessive litter accumulation was the greatest threat to long-term productivity. Phosphate fertilization is not the solution to the problem of decreasing fertility over time. The solution lies in the management of the accumulated litter mass.

Nitrogen Cycling

A further negative result of phosphate fertilization was the effect on patterns of nitrogen cycling. Soil nitrogen availability and the rate of nitrogen turnover were reduced by phosphorus fertilization as early as 8 years after establishment, and these effects intensified with increasing plantation age. From the literature it is apparent that the effect of applied phosphorus on nitrogen mineralization in coniferous forest systems is varied. While Distefano & Gholz (1989) found that phosphorus availability had little influence on net nitrogen transformations, Turner & Lambert (1986a & b) showed that levels of nitrogen in the soil increased as the level of applied phosphorus increased. In agreement with the results of the study reported here, Carey et al. (1981) cite many studies which have found a negative effect of phosphorus application on nitrogen mineralization. They ascribed this to more effective root growth in response to phosphorus addition, resulting in increased mineral nitrogen uptake from the soil. If this nitrogen is returned to the soil bound in carbon-rich compounds, mineralization will be reduced (high C:N ratios reduces net mineralization (Adams & Attiwill 1986b)). Inorganic nitrogen may also be immobilized by the large microbial population supported by the increased phosphorus availability (Cole & Heil 1981).

No evidence of greater nitrogen uptake by the fertilized trees was evident, since foliage nitrogen values in Chapter 5 were similar across all fertilization treatments. The effect of increased nitrogen uptake may not have been detectable due to the "extra" nitrogen being distributed within a greater biomass in the fertilized trees. The uniformity of foliage nitrogen levels at all the sites suggests that a highly flexible and sensitive process such as retranslocation was involved in controlling foliage nitrogen levels. Retranslocation occurred at all the stands, but to a greater degree in the fertilized plots, which indicates that any extra uptake of nitrogen in these plots was still not sufficient to supply tree requirements.

Retranslocation of nitrogen prevented fertilized trees from experiencing the influence of reduced soil nitrogen avialability, up to 25 years after fertilization. However, the bioassay in Chapter 6 suggests that seedlings of the next rotation may be negatively affected. P. elliottii seedlings of the bioassay had higher root:shoot ratios when grown on soils where nitrogen availability was reduced.

The greater degree of retranslocation in the fertilized trees results in litter with lower nitrogen levels than that from the unfertilized trees. Comparing calculated decomposition rates with litter nutrient concentrations in Chapter 5 showed that the lower decomposition rates of the fertilized plots was most likely due to lower litter nitrogen levels (the importance of litter nitrogen levels in determing the rate of

litter decomposition is widely accepted (Edmonds 1980; Yavitt & Fahey 1986)). Reduced decomposition rates together with higher litterfall rates in the fertilized plots resulted in greater accumulations of litter. Thus it seems that not only does phosphate fertilization contribute directly to increasing the accumulated litter mass by increasing the rate of litterfall, but it indirectly decreased decomposition rates by reducing litter nitrogen levels.

The negative effect of phosphorus fertilization on nitrogen release stresses the importance of understanding the effects the phosphorus fertilization practice on both phosphorus and nitrogen cycling. While phosphate application may alleviate short-term phosphorus deficiencies, it may also lead to reduced nitrogen availability and thus limit productivity of the system.

Litter Layer Management

From the results of this study it is clear that any management plan aimed at improving long-term plantation productivity must consider manipulation of the litter layer, since it represents a store of essential nutrients. If these immobilized nutrients could be returned to the soil then the need for re-application of fertilizers would be reduced.

Disagreement exists over which methods are appropriate for the reduction of accumulated litter. De Ronde (1984) suggested a litter management programme where burning could be used as a means of reducing litter loads greater than 70 t ha^{-1}. However, burning is not recommended for areas infested with weeds such as Acacia spp. whose regeneration is stimulated by fire (de Ronde 1984). While burning is a commonly used and effective method of reducing litter loads (de Ronde 1984) it may remove substantial quantities of nutrients from the system either by volatilization or leaching (Schönau 1989). Nitrogen losses can be particularly severe, since it is easily volatilized and 90-100% losses are common (Morris 1986). Soil nitrogen availability has also been shown to decrease due to increased immobilization after burning (Bell & Binkley 1989). Phosphorus is sometimes lost as particulate matter (smoke) emission. Losses can be restricted by controlling fire intensity. Particulate losses are lowest for low intensity fires (Morris 1986).

High intensity fires not only restrict nutrient turnover processes in the soil by destroying soil micro-organisms (Schönau 1989) but also by reducing the soil organic matter content which limits the energy-rich microbial activities (Musto 1991). Further reductions in soil nutrient availability may occur when soil organic matter is reduced, as the soil exchange capacity is coupled to soil organic matter (Gholz & Fisher 1982). Incorporating the litter mass into the soil will improve soil organic matter content and so increase the exchange capacity (Musto 1991). This would be advantageous for the study sites where there is a strong tendency for phosphorus to become bound irreversibly to iron and aluminium fractions. The greater exchange capacity of organic phosphorus compounds (Stewart & Tiessen 1987) will result in phosphorus becoming available more rapidly. However, phosphorus immobilization may also increase due to the large microbial population supported by the incorporated organic matter (Gholz et al. 1985b). Evidence of this occurred at the 8 year old stand (Goudveld). Soil organic matter content

was significantly higher here than at the older stands but soil phosphorus availability was very low and the phosphorus turnover rate was negative (phosphorus immobilization exceeded mineralization). Thus, the positive and negative aspects of litter incorporation must be considered before deciding to apply this method of litter reduction. More research is needed into the consequences of litter incorporation before it is recommended as an alternative to burning.

Litter burning may not be necessary in the study area since the highest standing litter masses recorded were only about 15-20 t ha^{-1}. De Ronde (1984) suggests that litter loads of less than 70 t ha^{-1} are manageable without being reduced before the next rotation. However, in areas such as the eastern Transvaal and Swaziland where litter accumulations of up to 320 t ha^{-1} have been reported (Schutz 1982) burning is essential and the most effective option. If burning is not carried out before establishment of second rotation stands, new litter will accumulate on top of the residual undecomposed first rotation forest floor litter. This results in the early formation of a large litter mass in the second rotation stands which accentuates nutrient deficiencies and has been suggested to be the cause of the poorer productivity of second rotation stands (Morris 1986).

Since burning appears to be the most effective means of reducing large litter loads, it should be used but such that nutrient losses are limited. It could even be used at the study areas if low intensity burning is shown to be more advantageous for nutrient turnover than litter incorporation. In its natural environment (southern United States), P. elliottii occurs on infertile soil but frequent, low-intensity fires apparently kept nutrient availability relatively high and tree growth sustained (DiStefano & Gholz 1989).

Conclusions

Single applications of phosphate at 30-60 kg ha^{-1} will not sustain improved productivity into subsequent rotations, unless the phosphorus retained in the litter layer is effectively returned in turnover processes. Fertilizing twice with phosphate was the only treatment that maintained improved soil phosphorus availability up to 25 years. The advantages of fertilizing once, 10 years after establishment was not evident in the parameters measured in this study.

Problems associated with pine plantation management such as reduced yields and weed control are eliminated by phosphorus fertilization, and litter accumulation is not a severe problem in the southern Cape. However, the pronounced reduction of soil nitrogen turnover rates, litter nitrogen levels and decomposition rates in response to phophorus fertilization warrants some concern. Reduced nitrogen turnover rates induced by phosphorus fertilization may not be severe enough to cause nitrogen deficiencies in the first rotation. However, in the second or later rotations phosphorus fertilization could cause nitrogen levels to be reduced further. Thus it is important to monitor soil nitrogen turnover and perhaps apply nitrogen fertilizers to maintain productivity to the end of the second or later rotations.

Recommendations for Future Research

While this study has confirmed the expectation that phosphate fertilization would increase the rate of phosphorus turnover in the system and so improve long-term phosphorus availability, it has raised the problem of reduced rates of nitrogen cycling in the fertilized plots. Since decreased nitrogen availability could eventually reduce productivity, this problem needs attention. The application of nitrogen fertilizers may appear to be the solution but studies from different parts of the country have shown depressed growth rates associated with nitrogen fertilization. This is probably due to a N:P inbalance created by increased nitrogen levels. Positive responses to nitrogen were only obtained when this element was applied after, or with, phosphorus fertilizers (Donald et al. 1987; Herbert & Schönau 1989). Thus, more research is needed before any definite fertilizer recommendations can be made. We recommend that this study be followed up in the southern Cape with an examination of phosphorus and nitrogen cycling patterns in existing NPK factorial trials (at Quar).

This study also highlights factors that should be considered when investigating patterns of nutrient cycling in plantations. Stand age should always be taken into account, since processes vary substantially at different stages of stand development.

The value of extending the results of this study to different species is uncertain, since this investigation was restricted to stands of a single species on similar sites. According to Herbert & Schönau (1990), nutrient requirements of species within a genus do not vary greatly and so extrapolation of results within a genus and even across a range of sites is possible. However, since mineralization processes are influenced by climatic conditions as well as soil characteristics, it is not recommended that the results of this study be applied to plantations in different climatic regions.

From Herbert & Schönau's (1989 & 1990) reports, it appears that NPK factorial trials of different ages for a range of Pinus species already exists in most parts of the country where pines are grown. Thus, it should be possible to undertake nutrient turnover studies in existing fertilizer trials which would improve our understanding of the problems encountered in improving plantation production and management.

Plantation management problems such as litter accumulation and weed infestation appear be most severe in the eastern Transvaal and Swaziland areas. The positive effects of phosphorus fertilization are reduced by both the excessive immobilization of nutrients in the litter layer (up to 320 t ha^{-1}) and by the uptake of available nutrients by weeds (non-pine species) (Morris 1986; Donald et al. 1987). The results of this study are not directly applicable to the eastern Transvaal situation since conditions (climate, soil) are quite different. However, it can be used as a guide for similar studies that should be undertaken in this area, as well as in other fertilized systems throughout southern Africa.

By achieving its objectives of identifying the major effects of phosphorus fertilization on nutrient cycling processes, this study highlights effects that were adversely affecting the system, namely that phosphate fertilization reduced soil nitrogen availability and turnover rates and increased litter accumulation and nutrient immobilization. While these effects may not be affecting yields of this rotation as yet, it could reduce productivity of the next rotation. This stresses the importance of nutrient cycling studies as they provied an early warning of potential reduced productivity. The forestry industry cannot afford any reductions in current plantation yields as it is striving to meet the increasing demand for timber without necessarily increasing the extent of afforestation in southern Africa. This may seem contradictory but it is possible with highly efficient management of existing plantations. This will only be achieved with extensive research. It is hoped that this study contributes towards this goal, not only for the results presented, but by highlighting areas that require future research.

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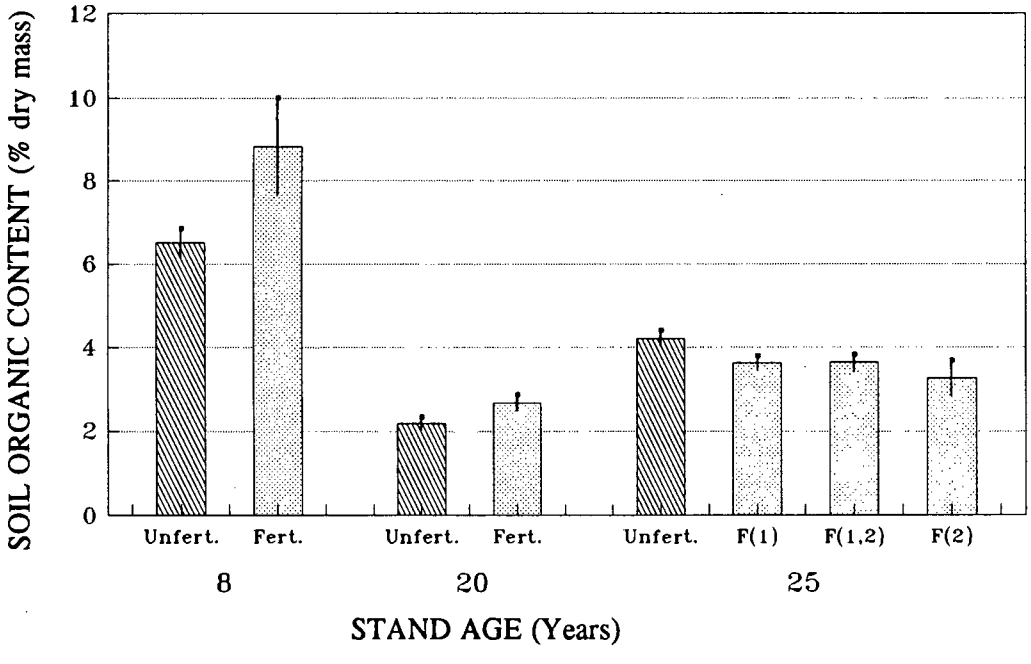
APPENDIX

TABLE 1: pH values of the top 10cm soil from the three study sites.

STUDY SITES	TREATMENTS	pH VALUES (± 1 S.E.M.)
Goudveld (8 yrs)	Unfertilized	4.06 ± 0.037
	Fertilized	4.00 ± 0.023
Keurboomsrivier (20 yrs)	Unfertilized	3.66 ± 0.027
	Fertilized	3.65 ± 0.077
Quar (25 yrs)	Unfertilized	3.78 ± 0.050
	Fertilized(1)	3.77 ± 0.040
	Fertilized(1,2)	3.85 ± 0.083
	Fertilized(2)	3.80 ± 0.057

Fertilized(1) - Fertilized once, at est. only
Fertilized(1,2) - Fertilized twice, at est. and 10 years later
Fertilized(2) - Fertilized once, 10 years after est.



Unfert. - Unfertilized
Fert./F(1) - Fertilized once, at est.
F(1,2) - Fertilized twice, at est. + 10 years later
F(2) - Fertilized once, 10 years after est.

FIG.1: Soil organic content (% dry mass) of the surface soil (0-10cm) of the unfertilized and phosphate fertilized plots of the different aged P. elliottii stands (Goudveld - 8 years, Keurboomsrivier - 20 years and Quar - 25 years old). Vertical lines represent ± 1 S.E.M.

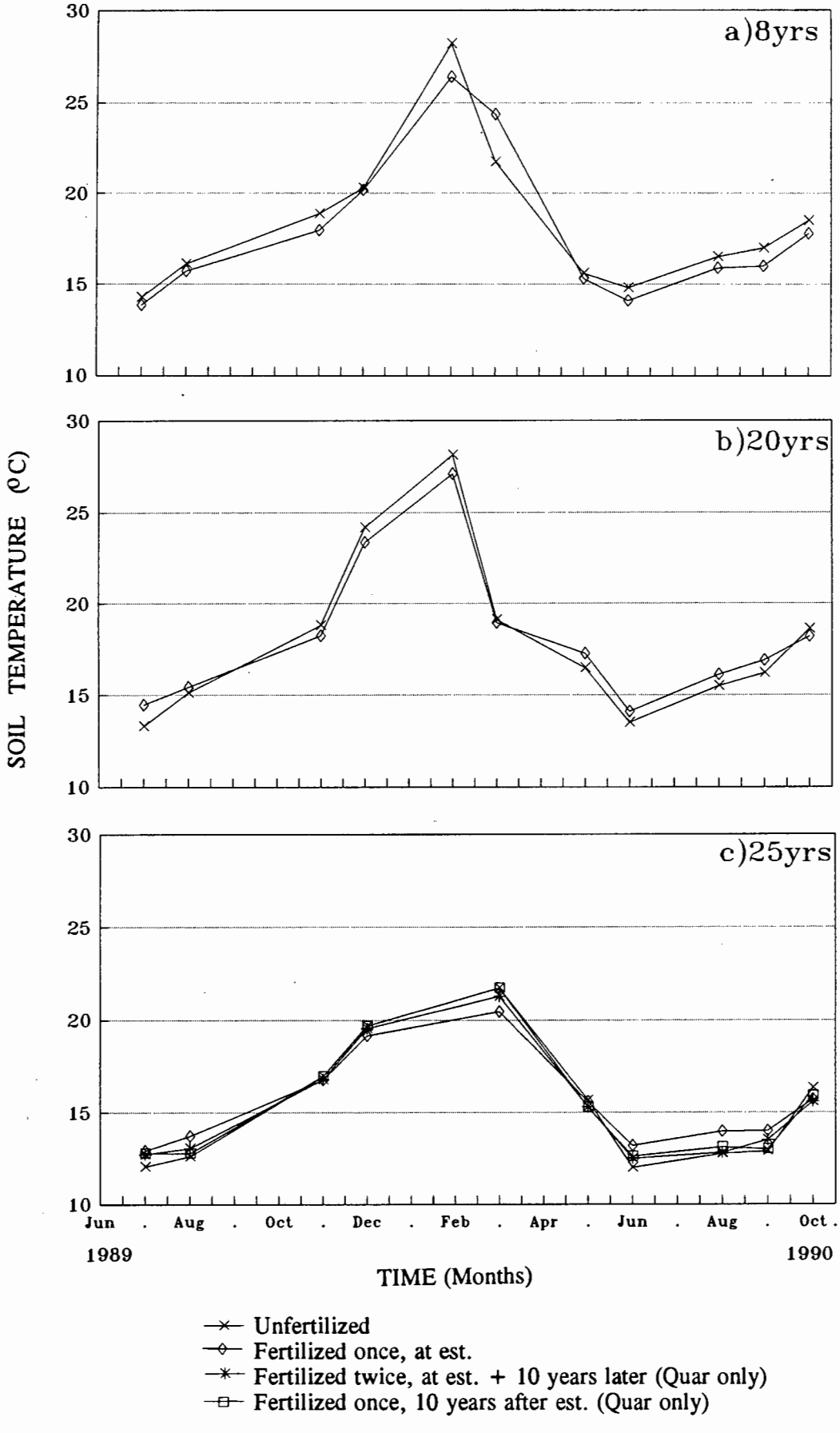


FIG.2: Monthly variations in the temperature (°C) of the surface soil (10cm depth) of the unfertilized and phosphate fertilized plots of the different aged P. elliottii stands at a)Goudveld (8 years old), b)Keurboomsrivier (20 years old) and c)Quar (25 years old). Error lines too small to represent.

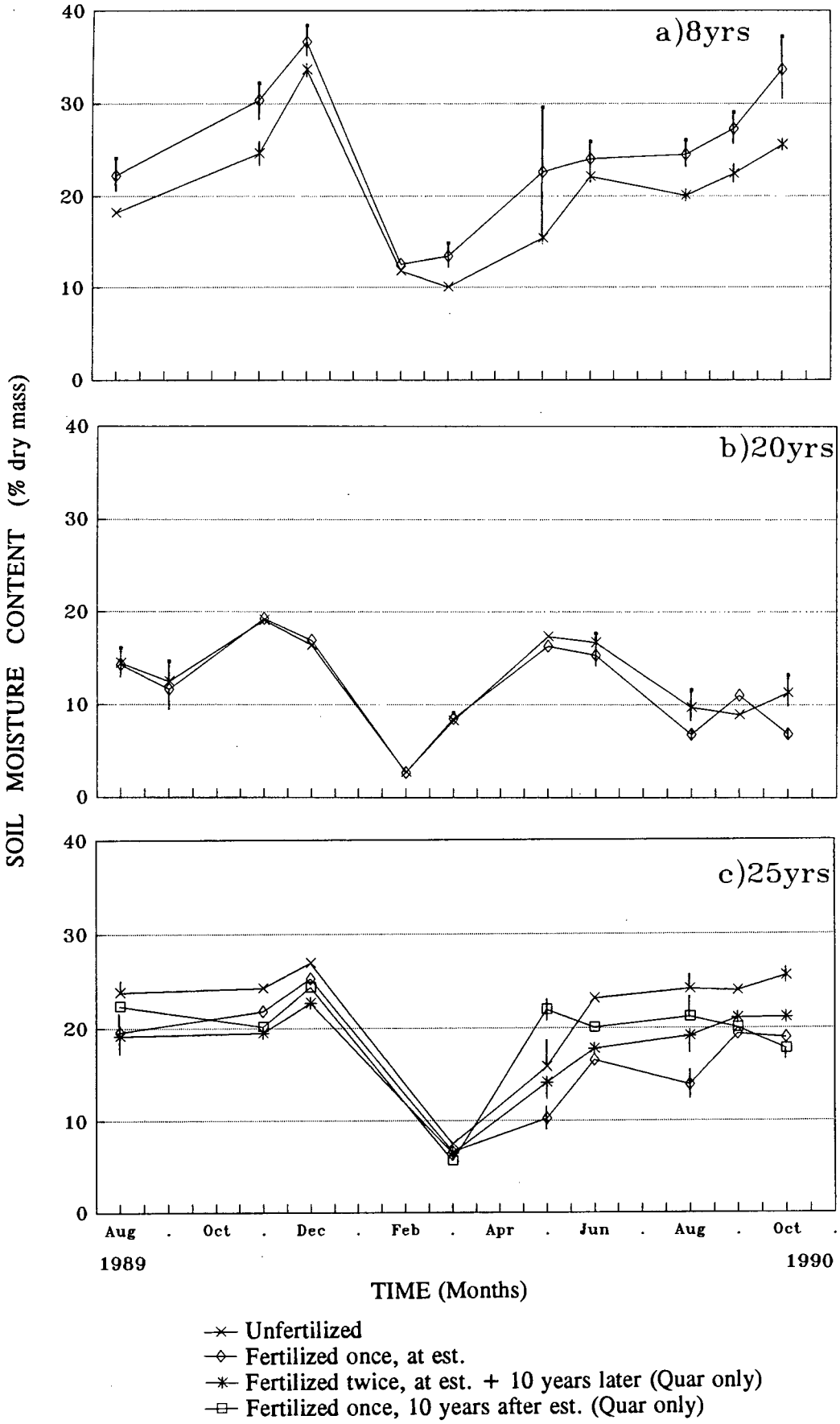


FIG.3: Monthly variations in the moisture content (% dry mass) of the surface soil (0-10cm; determined at the start of each incubation period) of the unfertilized and phosphate fertilized plots of P. elliottii stands at a)Goudveld (8 years old), b)Keurboomsrivier (20 years old) and c)Quar (25 years old). Vertical lines represent ± 1 S.E.M.