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The nutrient status of grasslands and adjacent Pinus patula and Eucalyptus grandis plantations on the eastern escarpment of South Africa

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1. INTRODUCTION

Pinus and *Eucalyptus* are the two most important commercial forestry genera grown in South Africa and thus have significant economic value. Both genera are fast growing exotic species. The softwood *Pinus patula* Schlechtend. & Cham. was introduced to South Africa, from Mexico (Grut 1965). The hardwood *Eucalyptus grandis* W.Hill ex Maiden. is indigenous to Australia (Grut 1965). *Pinus* is a source of timber, pulp, nuts, resin and other by-products. It is the core of exotic forestry enterprises throughout the world because of its adaptability to and successful colonisation of various habitats ranging from the arctic to the tropics (Richardson & Rundel 1998). A key aspect about *Pinus*, which has largely contributed to its success in various habitats, is its ability to alter soil chemical properties and processes, rendering the soil less suitable to other vegetation types (Richardson & Rundel 1998). *E. grandis* is widely planted in South America, Southern Africa and India to provide timber and pulpwood (Burgess 1988). It is the dominant genus grown for the commercial production of hardwoods in South Africa (Herbert 1991). Its adaptability to climatic and edaphic conditions, fast growth, resprouting ability and the wide utility range of the wood, makes *Eucalyptus* highly valued in the forestry industry (Ericsson *et al.* 1993). The South African forestry industry comprises 1.37 million hectares of pines, eucalypts and wattle plantations. It contributes approximately 9.7% to the gross domestic product of the South African economy and occupies 1.1% of the total land area in South Africa, of which *Pinus* and *Eucalyptus* occupy 51.7 and 39.5% of the land area, respectively (Godsmark 2003). Approximately 40.3% of the commercial plantations occur in Mpumalanga, with 39.6% in KwaZulu Natal, 11% in the Eastern Cape, 4.7% in Limpopo and 4.4% in the Western Cape (Godsmark 2003). In Mpumalanga, 6.8% of the land area is afforested (Godsmark 2003).

The eastern escarpment of South Africa is characterised by mountainous terrain with relatively high rainfall, highly leached and naturally acidic soils, which were previously covered by montane grasslands (White 1978). The replacement of indigenous grasslands by commercial forestry plantations, has inevitably led to the alteration of nutrient cycling. Nutrient cycling within these plantations is important

because nutrients ultimately drive production, affecting numerous related activities such as the choice of silvicultural practises, harvesting schedules, production forecasts, plantation valuation, land-use planning, long-term site productivity and estimates of future timber values (Cannell *et al.* 1998). Literature from the 1960s suggests that soils under pine plantations, less than 20 years old, showed similar or decreased nutrient stocks compared with stocks possessed at the time of tree planting, which resulted in decreased site productivity (Hamilton 1965). Older sites show enhanced acidity and loss of base status, but can also show increased soil organic matter content (Wilde 1964), usually as a result of slow decomposing litter, which forms dense mats on the forest floor (Scholes & Nowicki 1998). Richter *et al*. (1994) documented significant decreases in exchangeable Ca^{2+} and Mg^{2+} (down to depths of 60 cm) after only three decades under *Pinus taeda* L. Morris (1984) found significant reductions in N, P, K^{+}, Ca^{2+} and Mg^{2+} levels in mineral soil under 13 to 14 year old *P. patula* stands at Usutu (Swaziland) compared with adjacent grassland sites. There is general consensus that the establishment or afforestation of pines in the southern hemisphere, tends to enhance soil acidification and reduce nutrient availability (Ogden & Stewart 1995). Most commercial plantations are managed on a rotational basis. When the growth rate begins to decline, the trees are clearfelled and another crop is planted (Christie & Scholes 1995). On the eastern escarpment of southern Africa, growth rates are high, allowing for 20-25 years of *Pinus* and 7-15 years of *Eucalyptus* rotations (Scholes & Scholes 1999) depending on the market and nature of the desired end product. The successive removal of biomass through harvesting creates ecosystem imbalances, as part of the nutrient cycle is altered when basic cations are exported (Fey *et al.* 1990) instead of returned to the soil. In stable ecosystems, biomass uptake and nitrogen transformations are balanced by acid-consuming or neutralising processes such as the return of dead biomass with accompanying base cations to the soil, denitrification and nitrogen uptake by plants (Ulrich 1991).

Plantations consist of high biomass and large canopy volumes compared to that of grasslands, which render plantations more susceptible to the interception of atmospheric pollutants. Atmospheric pollutants, once deposited onto the landscape, have the potential to negatively and positively impact ecosystems, through its composition of both acidic and basic components. The basic components may buffer

soil acidification while the acidic components can enhance soil acidification and the nutritional imbalances associated with afforestation. Other factors possibly contributing to soil acidification are microbial respiration, the uptake of ammonium by both *Pinus* and *Eucalyptus*, the deposition of litter containing acidic compounds onto soil surfaces and natural processes associated with rainfall, leaching and erosion. The interplay of the above-mentioned factors, render the South African forestry industry on the eastern escarpment increasingly susceptible to soil acidification and the subsequent leaching of basic cations. The overall objective of this study was to determine the nutrient status of three different vegetation systems or land use types. Soil, litter and foliar nutrients were used to highlight differences in nutritional status i) of grasslands and commercial plantations of *P. patula* and *E. grandis* ii) and across three ages of *P. patula* and *E. grandis* plantations. The following key questions were proposed:

1.1. Key questions

1. How do selected nutrients in grasslands and *P. patula* and *E. grandis* plantations differ?
2. How do the soil, litter and lower and upper canopy foliar nutrients differ with plantation age and season?
3. What are the relationships between soil, litter and foliar variables?

2. LITERATURE REVIEW

2.1. Introduction

General concepts of nutrient transformations and more specifically, the cycling of nitrogen, phosphorus and basic and acidic cation concentrations will be discussed. Thereafter, the implications of the conversion of montane grasslands into plantations and the associated impacts on nutrient transformations and nutrient transformations within *Pinus* and *Eucalypts* plantations will be addressed. Research on high altitudinal tropical grasslands is sparse, whereas plantations have been widely researched and thus the following literature review focuses primarily on plantations. Nutrient variations with age and between the lower and upper canopies of plantations and the potential seasonal and management practises of the grasslands and plantations will be discussed.

2.2. Nutrient transformations

Nutrient transformations in the soil and plant components of an ecosystem involve the uptake of nutrients by plant roots, from mineral nutrient sources, the utilisation of these nutrients in plant biomass and its return to the soil in organic or inorganic forms with litterfall, as seeds or as dead plant remains at the end of the plant life cycle. The decomposition of plant residues provide the largest source of organic matter in soils (Ross 1994a). Generally, soil organic matter is dominated by large molecular weight humic acids and low molecular weight fulvic acids (Ross 1994a). Humic acids are regarded as the metal immobilising fraction of the soil organic matter, whereas fulvic acids have the capacity to bind and transport potentially toxic metals. Decomposition of organic inputs into the soil ecosystem return nutrients to the inorganic (mineral) form. Nutrients dissolved in soil solution and solutes of low molecular weight are transported to the roots by diffusion or mass flow.

The productivity of plantations in South Africa is determined by site factors controlling nutrient and water availabilty (Louw 1997). Physical and chemical weathering are the main sources of biologically available phosphorus and cations,

with biological turnover contributing a smaller fraction. A combination of warmth and moisture result in a high rate of annual weathering. Rates of decomposition in the low altitude sites are enhanced by higher temperatures, while rates of decomposition in the high altitude sites are enhanced by higher rainfall but are also subjected to higher rates of leaching and erosion. Water is the main agent of chemical weathering where the acidity of the water governs the rate of leaching and weathering (Jordan 1985). Protons react with minerals in the soil or the bedrock, resulting in the extraction of nutrient elements. Soluble nutrients can be absorbed by soil colloids, taken up by plants or leached (Jordan 1985).

2.3.Nitrogen transformations in soils

2.3.1. The Nitrogen (N) cycle

The N cycle is characterised by the conversion of unreactive atmospheric N_2 into reactive, biologically available forms of N. In soils, microbial organisms reduce nitrogen, present in organic matter derived from dead plants, animals and soil organisms, into mineral forms. Along this pathway, N is used up by soil microbes, converted into various forms, thereafter, reabsorbed by plants to form proteins, nucleic acids and nitrogenous compounds of living material (Lewis 1986). During the N cycle, N can be lost to the atmosphere as well as gained from the atmosphere through natural and anthropogenic processes. Figure 1 provides a diagrammatic explanation of the N cycle.

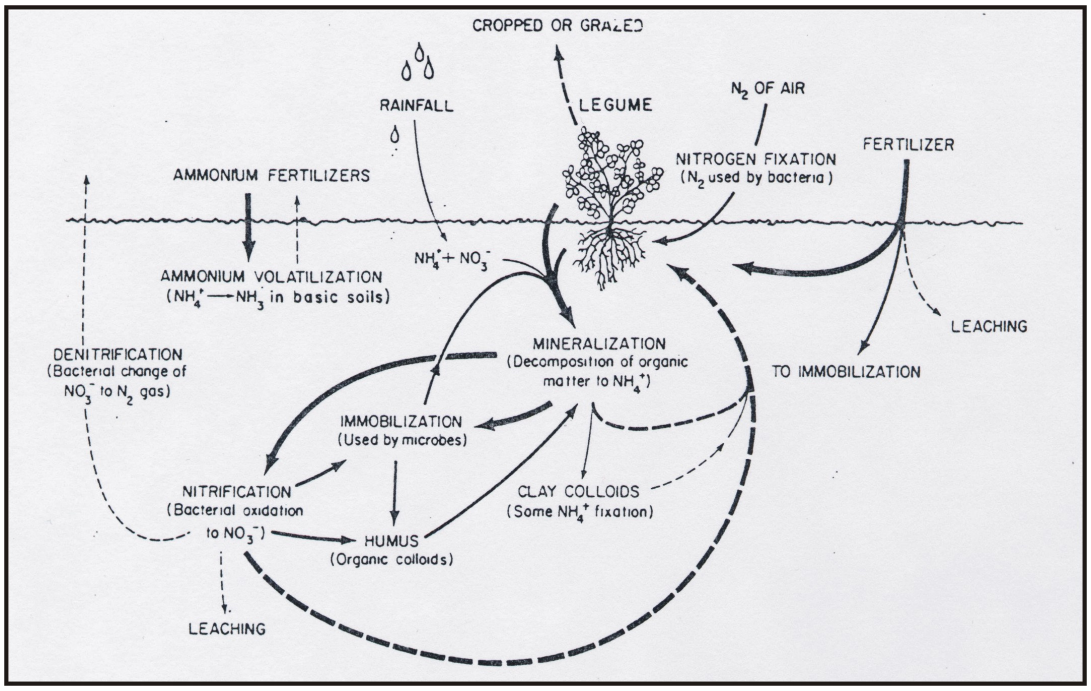


Figure 1. Diagrammtic representation of the N cycle showing soil nitrogen changes, additions and losses. Losses are represented by dashed lines; amounts of change are indicated by relative line widths (Miller & Donahue 1990).

Most plants derive their N from the soil. N in the soil is generated by biological activities associated with the N cycle. Soil microbial transformations render N available for plant uptake. Soil factors such as temperature, moisture and pH affect the rates and species compositions of microbial organisms. In South Africa, soil moisture and temperature are the driving forces behind seasonal variation. Summers are characterised by high temperatures and soil moisture, resulting in relatively higher rates of N cycling compared with that of the cool, dry winters.

The soil N status is a result of biological processes such as nitrogen fixation, microbial decomposition, nitrification and denitrification. However, some plants are able to convert atmospheric N_2 into organic forms by means of free living and symbiotic micro organisms. These plants are commonly referred to as N_2-fixers because they are able to break the strong bond between two gaseous nitrogen atoms, allowing for their combinations with other elements to form soluble compounds whereby ammonia (NH_3) is the final product (Blackstock 1989). Other non-fixing plants derive ammonia from the soil whereby organic N forms in decomposing plant and animal material are converted into mineral forms of ammonium (NH_4^+). Thus, the

soil organic matter is directly related to the nitrogen mineralisation capacity of the soil. Ammonium can either be directly taken up by the plants or nitrified, which involves the conversion of NH_4^+ into NO_3^- (nitrate), by soil micro organisms. Nitrate can be taken up by the plants or leached into drainage systems because it does not become chemically fixed in an unavailable form in the soil matrix and thus it is extremely mobile and is readily leached from the rooting zone into deeper horizons (Tainton 1984).

2.3.2. Mineralisation, ammonification, decomposition

Mineralisation is the process of decomposition or breakdown of organic forms of N in dead animal, plant and soil micro organisms into mineral, inorganic forms of N, such as NH_4^+. Heterotrophic organisms such as bacteria, fungi and actinomycetes are responsible for the decomposition of organic material, which serves as a source of carbon and nitrogen (Lewis 1986). N additions increase the rate of decay processes, thereby increasing the amount of N immobilised in microbial biomass, but if there is excess N in the organic substrate, the organisms will excrete NH_4^+ as a waste product, resulting in ammonification. The N mineralisation index is a measure of the difference between the total mineralisation and the immobilisation activities of the soil microflora (Lewis 1986). It is therefore a direct measure of N available for plant uptake and an indirect measure of the potential for nitrate leaching. The higher the N mineralisation index, the greater the amount of N available for plant uptake.

2.3.3. Factors controlling rates of N mineralisation

Temperature, rainfall and soil properties are some factors controlling mineralisation rates. For every 10ºC increase in temperature in the 0-35ºC range, there is an expected two-fold increase in N mineralisation rates (Rice & Havlin 1994). Dames (1996) found lower litter decomposition rates on higher altitudinal and colder sites. Louw & Scholes (2002) found a positive relationship between rates of N mineralisation and the mean annual temperature. However, soil properties and the quality of the organic material such as soil organic C levels (Barnes *et al.* 1997) also contribute to the rates of N mineralisation. Louw & Scholes (2002) found that high levels of organic C, subjected to low mean annual temperatures, showed low N mineralisation rates,

indicative of slow turnover. However, high levels of organic C in a warmer environment led to the highest rates of N mineralisation and highest levels of forest productivity. Sub-tropical environments may have less organic C available because of higher rates of decomposition and thus faster rates of turnover. Thus organic material in the soil varies in terms of pool sizes and rates of cycling where there are labile pools with rapid turnover and more stable pools with slower turnover, which are normally associated with organic material adsorbed on mineral surfaces or contained within soil micro-aggregates (Boone 1994). Parent material determines forest productivity through its influence on microbiological properties and biogeochemical processes. It is a major contributor to the process of soil formation through its influences on soil texture and mineralogy (Motavalli *et al.* 1995). Louw & Scholes (2002) found that soils underlain by dolomite had higher rates of N mineralisation compared with soils underlain by granite.

Mineralisation is also affected by soil pH (Harris 1988). The decomposition of plant residue and the breakdown of soil organic matter are more rapid in the soil pH range of 5.5 to 6.5 compared with more acidic environments (Noble & Herbert 1991) because of optimal soil pH ranges required for optimal levels of microbial activity. Louw & Scholes (2002) found that dolomitic soils were more alkaline compared with granitic soils, where the topsoil pH was 4.25 and 3.96, respectively. The soil water content, aeration (Goncalves & Carlyle 1994) and soil P levels (Carlyle *et al.* 1990) also influence N mineralisation rates. Dames (1996) found that soils in *P. patula* plantations, under optimum conditions, mineralised 4.66 ± 0.94 $\mu gNg^{-1}d^{-1}$.

2.3.4. Plant and microbial immobilisation

Ammonium ions can either be taken up by plants, adsorbed onto negatively charged soil colloids (cation exchange), leached from the soil or oxidised to nitrate (Binkley & Johnson 1992). The degree to which N is retained in an ecosystem is determined by competition for available N between plants, heterotrophic microbes, and nitrifiers, along with the non-biological N incorporation into soil organic matter and ammonium fixation on clay minerals. Thus, there is intense competition for the available pool of ammonium (Aber 1992). The strength of the alternative sinks for N, along with the gross N mineralisation rate, determines the degree of N limitation on biological

function, and the residual inorganic N concentrations in the soil solution and leachate (Aber 1992).

The degree to which N is utilised by the soil microflora is determined by the C:N ratio of the decomposing material (Lewis 1986). Decomposing material with a high C:N ratio provides sufficient carbohydrate supply for soil microbe C skeletons, resulting in the depletion of soil mineral N required for cells and other living activities. Relatively large quantities of carbon promotes intense competition for N compounds thereby limiting the inorganic N quantities available for other soil organisms, such as nitrifying bacteria and plant immobilisation. However, low C:N ratios of decomposing material allow for a sufficient fraction of the inorganic N to be taken up by plants and nitrified by bacteria. According to Gundersen *et al.* (1998) when the C:N ratio in the forest floor in a coniferous forest is less than 25, there is a higher potential for nitrification and therefore a higher risk of N saturation and potential for nitrate leaching. A C:N ratio greater than 30 indicates a N limited system, with low potential nitrification and thus low potential for N leaching. The relationship between the soil C:N ratios, nitrification and leaching in broadleaf forests is relatively uncertain.

Negative N mineralisation values imply that soil microfloral immobilisation is dominating, which means that N is primarily utilised by soil microflora for their sustenance. Scholes & Louw (2002) found that net N mineralisation was higher during the dormant season while immobilisation was higher during the growing season. Net N immobilisation may be highest in summer because climatic conditions are more favourable for microbial activity, resulting in lower net N mineralisation values in summer. Sites with a positive balance in N mineralisation are unlikely to produce any significant reaction to additional N inputs whereas sites experiencing N immobilisation are more likely to produce significant responses in tree growth (Louw & Scholes 2002). Thus atmospheric N deposition, which is higher in summer (Lowman 2003), is bound to have a positive effect on tree growth because N is most limiting in summer, during times of most active microbial and plant immobilisation. N deposition will also have the most significant effects during the stages of canopy closure, when nutrients are in highest demand.

2.3.5. Nitrification

The *Nitrosomonas* bacteria rapidly oxidises NH_4^+, thereby converting NH_4^+ into nitrite (NO_2^-). Thereafter, *Nitrobacter* oxidises nitrite to nitrate (NO_3^-). Nitrifying bacteria are chemotrophs and are entirely dependent upon this process for their energy supply (Lewis 1986). Thus, plants and microbes play a significant role in utilising and thereby retaining nitrate and ammonium in soil. Nitrate can be absorbed by plants for their nutritional requirements, leached or denitrified to N_2O or N_2 and released into the atmosphere. Nitrification is reported to increase significantly when the C:N ratio of the soil is below 24 (Wilson & Emmet 1998). Aber *et al.* (1989) found that low soil pH and limited ammonium reduced net N nitrification in forest ecosystems while in undisturbed forests, nitrification is limited because there is a constant demand for NH_4^+. When forests are harvested, the uptake of NH_4^+ ceases and thus NH_4^+ is nitrified, rendering nitrate available, which becomes important in the leaching process. Nitrate leaching can induce in a major flush or loss of cations after clearfelling (Jordan 1985).

2.3.6. Nitrogen supply & plant growth

The nitrogen content required for optimal growth varies between 2 and 5% of the plant dry weight. Will (1985) reported that 0.8% foliar N indicates a severe deficiency, while 1.2 to 1.5% is still restrictive to tree growth. An optimum foliar N concentration for *E. grandis* is 2.9% (Herbert 1988). When nitrogen is limiting or suboptimal, growth is retarded and nitrogen is mobilised in mature leaves and retranslocated to areas of new growth. Ammonia assimilation increases the protein content, the leaf growth and corresponding leaf area index (LAI). Provided the LAI is correlated with an increase in net photosynthesis, the requirement for carbon skeletons for ammonia assimilation does not substantially depress other biosynthetic pathways related to carbohydrates such as sugars, starch, cellulose, storage lipids and oils. Generally, the maximum nitrogen concentration in plant tissue increases with the available nitrogen content of the soil (Gordon & Burton 1956). Increases in foliar N concentration results in increased foliar biomass, which results in increased tree growth (Aber *et al.* 1989). However, as the nitrogen supply is increased, exceeding

optimal levels through chronic N additions, foliar N concentrations are elevated and a higher proportion of the assimilated nitrogen is sequestered in storage pools such as amides and amino acids for example, arginine (Aber *et al.* 1989). Pines utilise arginine in foliage as a storage compound whereas *Eucalyptus* utilise bark and stems as N stores instead of foliage (Birk & Turner 1992). Excessive N levels result in N storage because further increases in LAI would not have any effect on photosynthetic rates because of self induced shading effects associated with increased foliar biomass.

Once N levels become excessive, severe imbalances in foliage element concentrations particularly N:Mg ratios, result in chlorosis (yellowing) of foliage, premature needle drop, declining tree vigour and mortality, loss of frost hardiness and winter desiccation (Aber *et al.* 1992). Furthermore, lowered phosphorus and lignin contents may also be found in foliage (Aber *et al.* 1989). With elevated N compounds, it is expected that the C:N ratio of foliar material will decrease, thereby decreasing carbon based structural materials relative to N compounds. Excess N content in foliage can also increase pathogen and insect attacks (Aber *et al.* 1989). However, N enrichment can occur as a result of mineral nutrient deficiencies, thus signs of N enrichment may not always be indicative of high N supply (Ericsson *et al.* 1995).

2.3.6.1. Amino acids

Amino acids, peptides, amides, ureides and amines are all low molecular weight organic nitrogen compounds, which serve as intermediates between the assimilation of inorganic nitrogen and the synthesis of high molecular weight compounds such as proteins, nucleic acids and other coenzymes and secondary products such as phenolic acids (Ireland 1990). Higher plants are incapable of excreting organically bound nitrogen such as urea. Thus the formation of amino acids, amides and related compounds serve as the main pathway of detoxification of ammonium ions either taken up by the roots or ammonia derived from nitrate reduction or N_2 fixation (Marschner 1986). Amino acids are also involved in the transporting of nitrogen between roots, leaves and fruits (Näsholm 1998). Martin (1970) and Raven & Smith (1976), cited in Marschner (1986), found that nearly all assimilated ammonia is translocated to the shoots as amino acids, amides and related compounds for further utilisation. Amino acids and amides are composed of carbon skeletons, which means

that the demand for carbohydrate is high during amino acid and amide synthesis (Marschner 1986). Carbon losses are minimised by transporting N, with nitrogen rich compounds. Thus amino acids with relatively high ratios of nitrogen to carbon such as glutamine (2N/5C), asparagine (2N/4C) and arginine (4N/6C) and the ureide allantoin (4N/4C) are utililsed to transport nitrogen. Amino acids may also serve as storage compounds for N, when protein synthesis is inhibited through stress.

2.3.6.2. N storage in the form of amino acids

Påhlsson (1992) found that nitrogen fertilisation decreased foliar concentrations of P and copper, which led to nutrient imbalances relative to N and that glutamic acid, aspartic acid, glutamine and asparagine were significantly increased by N fertilisation. According to Aber (1989), arginine is a sensitive indicator of luxury consumption of N and can therefore be used as an indicator of N status. Arginine is the most common amino acid for N storage in conifer needles (Binkley & Högberg 1997). Näsholm & Ericson (1990) and Näsholm (1994) have shown that repeated additions of high amounts of N, added to conifer trees, causes changes in the soluble N fractions of needles where elevated free arginine concentrations was the most significant effect. However, van Dijk & Roelofs (1998), Edfast *et al.* (1990) and many other researchers have found elevated arginine concentrations not only increased in response to elevated N inputs but also to a low supply of mineral nutrients relative to nitrogen (Näsholm *et al.* 1997). Nevertheless, elevated arginine concentrations indicate an excess of N, which cannot be utilised for growth as a result of either relatively low mineral nutrient concentrations or N uptake in excess of biological requirement.

2.3.6.3. Protein

Organically bound nitrogen of glutamate and glutamine can be utilised for the synthesis of other amides, ureides, amino acids and high molecular weight compounds such as proteins. Gordon & Burton (1956) found that an increased concentration of soil nitrogen results in an increase in the protein content in grasses. Bi *et al.* (2004)

found that the proportion of N stored as amino acids increased as the N supply increased, but protein was the main form used for N storage.

2.4. Phosphorus

The main source of P, in terrestrial ecosystems, originates from the weathering of primary minerals, which releases P into the soil solution. Soil humus holds organic P in labile, resistant and aggregated forms (Coleman *et al.* 1983). Litterfall, root decay and death of organisms returns biologically held P forms (Gressel & McColl 1997) into forms available for plant uptake. Phosphorus is mineralised by enzymatic reactions mediated by microbial and plant activities such as the production of phosphatase enzymes by the plant roots. It is taken up by plants and microorganisms, sorbed onto solid surfaces or lost through the process of leaching (Gressel & McColl 1997) and volatilisation. However, P has low solubility and therefore low mobility in soils and therefore losses through leaching, runoff and erosion are generally low (Tainton 1984). Phosphorus fixing in soils refers to a process whereby available P in highly leached acid soils containing free aluminium and iron oxides and hydroxides, are transformed into relatively insoluble aluminium and iron phosphates, thereby reducing the amount of P available for plant uptake (Sanchez 1976). The soluble ion $H_2PO_4^-$ (orthophosphate) rapidly reacts in soil to form insoluble phosphate (Miller & Donahue 1990). Phosphate ions adsorb to insoluble iron and aluminium hydrous oxide surfaces (Miller and Donahue 1990). Thus soluble P is readily fixed into an unavailable pool, whilst the release into the available pool is slow, resulting in a low degree of P availabilty in the P cycle (Tainton 1984).

Soil pH governs the transformation of soluble P into insoluble hydroxy phosphates (Jordan 1985). In mineral soils, P is most available at pH 6.5. Increased aluminium activity occurs at low soil pH, which increases P-fixation and reduces P availability. The iron and aluminium oxides occur mainly in the clay fraction, thus phosphorus fixation increases with increasing clay contents (Tainton 1984). Louw & Scholes (2002) found that granitic soils had higher levels of plant available P while dolomitic soils had higher levels of total P. Ectomycorrhizae were shown to produce oxalic acid, which chelates aluminium, manganese and iron, thereby releasing P from iron,

calcium or aluminium compounds, rendering P more available for uptake (Gianinazzi-Pearson & Gianinazzi 1989). Ectomycorrhizal fungi are symbiotically involved with plants and play a role in phosphorus transfer and carbohydrate storage (Vogt *et al.* 1997). They penetrate the outer cell layers of roots and increase the extent of root exploration, thereby aiding plants with direct P acquisition from litter to roots.

The P requirement for optimal growth in vegetative tissues ranges between 0.3–0.5% of the plant dry weight. Foliar P levels greater than 0.14% are considered adequate for *P. radiata* D.Don (Will 1985). When P is deficient, there is a general reduction of most metabolic processes such as photosynthesis and carbohydrate metabolism of leaves as well as cell division and expansion, respiration and photosynthesis (Terry & Ulrich 1973). Excess P is stored as inorganic P in vacuolated tissues (Marschner 1986).

2.5. Cations

According to Linder (1995), nutritional imbalances can be detected without correcting for carbohydrate content, through calculating ratios between elements and N. An 'optimal' nutritional status in the foliage of trees was defined in terms of target needle concentrations for each nutrient element. Target values were obtained by laboratory and field experiments of various researchers. Another widely used chemical index is the base cation to acidity ratio which is indicative of soil nutrient status and possibly plant growth stress (Barkman & Sverdrup 1996). It conveys the effects of soil acidification on processes affecting plant growth. Ulrich & Matzner (1986), proposed the usage of the Ca:Al ratio of the soil solution as a measure of the growth response of trees to soil acidification. The base cation to aluminium ratio relates soil chemistry with tree physiology by reflecting the relationship between ions required for plant growth with non-essential toxic ions (Sverdrup & Warfvinge 1993).

Cronan & Gringal (1995) proposed a general rule for base cation to acidity ratio of $\geq$ 1 as a useful and critical value indicating forest health in European forests. They found that when the Ca:Al ratio is 0.5, the associated risk level for adverse effects on

plant growth is 75%. When this ratio reaches 0.2, the risk increases to almost 100%. They found that it is effective in evaluating changes associated with forest vitality over time. However, Binkley & Högberg (1997) showed no evidence that Ca:Al or the sum of base cation to aluminium ratios have any relevance for forest vitality in Sweden. Recent studies in Swaziland, KwaZulu Natal and Sabie, on the eastern escarpment of South Africa, have indicated that some compartments of *Pinus*, may have Ca:Al molar ratios, which have dropped since afforestation (Sugarman 1999). Sugarman (1999) found a general decrease in Ca:Al ratios associated with afforestation of grassland soils in Sabie, Mpumalanga. According to Louw (1997) the granite derived soils on the escarpment are relatively low in basic cations. Low soil pH results in P fixation into forms unavailable for plant uptake and is also associated with low soil exchangeable K^+, Mg^{2+} and Ca^{2+}.

2.5.1. Potassium

Potassium (K^+) occurs in soil plant systems as a monovalent cation of which virgin soils in South Africa are well supplied (Tainton 1984). Potassium is generally freely available in the soil. In the soil, K^+ occurs in a non-exchangeable form in the soil solution and in an exchangeable form on the colloidal system. Potassium in the dissolved form is removed from the soil solution by plant uptake and leaching, it is readily replaced from the exchangeable component of the available pool (Tainton 1984). Potassium is taken up in proportion to its availability, which means that luxury consumption can easily occur. Losses by leaching can be significant, particularly when there is a strong gradient between K^+ in solution and on the exchange complex. This occurs when Ca^{2+} and Mg^{2+} replace K^+ and dominate the exchange complex (Tainton 1984).

Potassium remains primarily in ionic form in plant tissue, playing a role in osmoregulation of stomatal opening and closing (Johnson 1992). Potassium is characterised by high mobility within cells, tissues and the whole plant system. Potassium acts mainly as a charge carrier of high mobility that forms only weak complexes in which it is readily exchangeable (Wyn Jones *et al.* 1979). High concentrations of K^+ in the cytoplasm and the chloroplasts are required to neutralise

the pH between 7 and 8 in order to optimise enzymatic reactions. In K^+ deficient plants, protein synthesis is inhibited and thus there is an accumulation of soluble nitrogen compounds such as amino acids, amides and nitrate. The K^+ requirement for optimal plant growth is ~2-5% of the dry weight of the vegetative parts. Potassium deficient plants have a lower tolerance for drought because K^+ plays a role in stomatal regulation and it maintains a high water level in tissues even under drought conditions. Low levels of K^+ may therefore be correlated with high levels of proline. Abundant K^+ may result in luxury consumption, which may interfere with the uptake and physiological availability of Mg^{2+} and Ca^{2+}.

2.5.2. Magnesium

Magnesium occurs as non-exchangeable magnesium in the soil solution and as an exchangeable and freely diffusable divalent cation on the exchange complex. Its rate of uptake can be strongly inhibited by the presence of K^+ and NH_4^+ (Kurvits & Kirby 1980), Ca^{2+} and Mn^{2+} (Heenan & Campell 1981) as well as H^+. A high proportion of the total Mg^{2+} is involved in the regulation of cellular pH and the cation-anion balance (Marschner 1986), and it plays a major role in photosynthesis within the chloroplast (Johnson 1992). The enzyme glutamate synthetase has a high Mg^{2+} requirement (O'Neal & Joy 1974), thus a Mg^{2+} deficiency may inhibit the activity of the enzyme, which will reduce ammonia assimilation within the chloroplasts. A majority of the Mg^{2+} cations act as counterions for organic acid anions, inorganic anions stored in the vacuoles and for pectates in the middle lamella of cell walls. On average, the Mg^{2+} requirement for optimal growth is ~0.5% of the dry weight of the vegetative parts (Marschner 1986). Trees may accumulate Mg^{2+} in excess of their needs and in the process, restrict the uptake of K^+ (Foster 1985). When Mg^{2+} is available beyond the growth limiting level, it is stored mostly in vacuoles as inorganic salts.

2.5.3. Calcium

Calcium occurs as non-exchangeable calcium, and as exchangeable and as freely-diffusable divalent calcium cations (Wilkinson & Lowry 1973). South African soils

are well supplied with Ca^{2+} in both forms. Calcium is usually the dominant cation on the colloidal system of most soils and together with Mg^{2+}, usually makes up 60-80% of the exchangeable cations in the soil (Tainton 1984). In highly weathered soils of high rainfall areas, the exchangeable calcium and other basic components have been leached from the soil and are replaced with H^+ and Al^{3+} ions, which increase soil acidity. Most of the highly leached acid soils of South Africa are dominated by exchangeable Al^{3+} on the cation exchange complex. High levels of soluble aluminium in the soil limit plant growth by causing direct injury to root systems and by impeding the uptake of calcium and phosphorus by the plant (Sanchez 1976). However, Ca^{2+} additions can neutralise and replace the H^+ ions on the cation exchange complex. The continued removal of H^+ ions from the soil solution, results in the precipitation of Al^{3+} ions as aluminium hydroxide and its replacement on the cation exchange complex by calcium cations. Thus calcium is a determinant of soil acidity and a combatant of Al^{3+} toxicity.

Calcium is a major component of permanent plant tissues, such as pectates in cell walls and therefore accumulates in foliage until senescence and thus, litterfall return of Ca^{2+} usually exceeds foliar Ca^{2+} content at maximum leaf biomass (Cole & Rapp 1981). Most nutrient cycling data have revealed that Ca^{2+} rather than N and P are most likely to be significantly depleted by leaching and harvesting (Federer *et al.* 1989). It is effective in detoxifying high concentrations of other mineral elements in plants (Marshner 1986). The calcium content of plants vary between 0.1->5.0% of dry weight depending on the growing conditions, plant species and plant organ. Its uptake is mainly passive and depends to a large extent on the availability of soil water and the intensity of transpiration (Ericsson *et al.* 1993). Calcium is readily replaced by other cations from its binding sites at the exterior surface of the plasma membrane. Thus, its requirement increases with the increased external concentrations of heavy metals (Wallace *et al.* 1966), sodium chloride (LaHaye & Epstein 1971) or protons. At low pH, the Ca^{2+} concentration in the external solution has to be several times higher in order to counteract the adverse effect of H^+ concentrations on root elongation.

2.5.4. Sodium

Sodium is a mineral element, which stimulates growth but may or may not be beneficial depending on the plant species or conditions. Sodium improves the water balance of plants when the water supply is limited. It improves water use efficiency of leaves under conditions of moderate water stress during the growing season (Durrant *et al.* 1978).

2.5.5. Aluminium

Aluminium concentrations in mineral soil solutions are below 1 mg kg^{-1} at soil pH values higher than 5.5, but increase at lower soil pH. Studies have shown that low Al^{3+} concentrations in soil stimulate growth (Bollard 1983). This is possibly because low Al^{3+} concentrations prevent copper, manganese or phosphorus toxicity. However, soils with low pH and higher concentrations of Al^{3+}, can also have negative effects on plant growth (Marschner 1986).

2.5.6. Manganese

Manganese is a micronutrient transition metal but is absorbed mainly as Mn^{2+} and is translocated predominantly as a free divalent cation in the xylem from the roots to the shoot (Graham 1979). Manganese can replace Mg^{2+} in many reactions (Marschner 1986). In cells, the magnesium concentrations are 50-100 times higher than that of manganese (Marschner 1986). Marschner (1986) found that there may be elevated levels of soluble nitrogen (nitrate and amino acids) in manganese deficient plants. Foliar protein content is negatively correlated with the manganese content of the leaves (Marschner 1986). Excess levels of Mn^{2+} can inhibit the uptake of Mg^{2+} and Ca^{2+} because high manganese concentrations decrease the cation exchange capacity of the leaf tissue (Horst & Marschner 1978). The range of soil total Mn^{2+} concentration considered normal is between 200 and 2000 mg kg^{-1} (Swaine 1955), whilst between 1500 and 3000 mg kg^{-1} is considered toxic (Kabata-Pendias & Pendias 1984). The normal concentration of Mn^{2+} in a plant is 15-1000 mg kg^{-1} (Bowen 1979).

2.6. Some implications associated with the conversion of grasslands to plantations

2.6.1. Soil moisture

Afforestation can have significant impacts on the amount of rainfall intercepted and ultimately on groundwater recharge (Le Maitre *et al.* 1999). The vegetation canopy allows for redirection of water, which is either evaporated or channelled to the ground by dripping as part of throughfall (Le Maitre *et al.* 1999) and stem flow. Coniferous forests and plantations have dense canopies with high leaf areas and rough bark where measured interception losses range between 15 and 24% (Calder 1992) but even 60% (Lunt 1934) water losses have been recorded where rainfall intensities are low and conditions are misty. Litter on the ground surface tends to retain more water than bare soil and improves conditions for infiltration into the soil (Le Maitre *et al.* 1999). Belsky *et al.* (1993) found that water infiltration rates were significantly higher under tree canopies compared with lightly grazed grasslands. *Eucalyptus* plantations extract more water at higher rates compared with *Pinus* (Louw 1997). *Pinus* are relatively dormant during the winter whilst *Eucalyptus* continue to be physiologically active throughout the dry season (Dye *et al.* 1995).

2.6.2. Carbon and Nitrogen

Many studies have documented the potential for C accumulation, induced by afforested vegetation in global C budgets, but soil C has been less extensively researched. Soil C is the major reservoir of terrestrial C (Schlesinger 1990). Changes in land use can have a marked effect on soil C contents (Tate 1987) because of interactions between detrital inputs and subsequent immobilisation mediated by soil microorganisms (Ross *et al.* 1990). In pastures, most C inputs are below-ground (Hart *et al.* 1990), primarily as a result of root exudation and fine root turnover (Scott *et al.* 1999). Carbon inputs in pastures are readily decomposable, resulting in high microbial activity in the rhizosphere (Tate *et al.* 1991). In plantations, the detrital matter

originates from above-ground sources, which means that the detrital material contains more recalcitrant components such as lignin compared with both the above and below ground inputs in pasture ecosystems (Heal *et al.* 1997). However, plantation litter is exposed to intermittent periods of drying, which slows rates of litter decomposition (Scott *et al.* 1999) and thereby periodically limits microbial activity, while pastures are exposed to drying on a more frequent basis.

Scott *et al.* (1999) quantified differences in soil C content between paired pasture and exotic pine forest plantations dominated by *P. radiata* in New Zealand. The mineral soil C content, to a depth of 0.30 m, was 20-40% lower under pine for all soil types, except soil with high clay activity where there was no difference. Scott *et al.* (1999) attributed the differences in soil carbon to the accumulation of forest floor material in forest ecosystems, but the litter accumulation was lowest in the site with the highest clay activity. Giddens *et al.* (1997) found small or no significant changes in mineral soil C to 0.10 m depth with afforestation at 10 paired sites located primarily on high clay activity soils in the south-central part of North Island, New Zealand. Similar soil carbon contents under pastures and plantations, on soil with high clay activity, was possibly a result of strong interactions between clay minerals and organic matter (Scott *et al.* 1999). Clay minerals including mica, smectites and vermiculite stabilise organic matter (Tate 1987) and may prevent soil organic matter losses associated with land use change (Scott *et al.* 1999). Ndala (2001) found that in Mpumalanga on the eastern of South Africa, forests underlain by dolomitic bedrock had higher levels of soil organic carbon, total N, total P and C:N ratios when compared with adjacent grasslands, whereas forest soils underlain by mixed dolomitic and quartzitic bedrock had lower levels of the same parameters when compared with adjacent grasslands.

Scott, N.A (unpublished data) found a generally lower rate of N mineralisation both in the laboratory and field in plantation forest mineral soils when compared with grasslands. Lower N mineralisation in forests may be because of rapid plant immobilisation of nitrate and ammonium N (Hart *et al.* 1994) but studies show that conifers prefer ammonium, thus it is more likely a result of lower soil pH, cation exchange capacity (Giddens *et al.* 1997) and lower temperatures in plantation soil. Soil temperatures are lower under plantations because of shading created by the forest canopy, which means that the rate of nutrient cycling in plantations may be lower

compared with that of grasslands. In addition, nitrogen mineralisation and nitrification are reduced under pines owing to poor substrate quality and possibly raised polyphenol concentrations (Scholes & Nowicki 1998). Thus plantation soils undergo low rates of decomposition and N mineralisation, rendering low N availability for the uptake by roots and consequently low N content of trees (Jordan 1985). It is expected that the introduction of pines causes a shift in dominant available nitrogen from nitrate to ammonium and from mineral N to predominantly organic N (Scholes & Nowicki 1998). However, Ndala (2001) found that forest soils showed more rapid rates of N mineralisation, on average 0.9 μgN g^{-1}soil.day^{-1}, whereas soils under grasslands had on average 0.3 μgNg^{-1}soil.day^{-1} on the clayey, dolomitic derived soils during the month of September. As the wet season progressed, the rates of N mineralisation in grassland soils increased and were equal to those found in soils under forests. Morris (1986) suggested that the accumulation of pine litter may in the long term lead to increased N mineralisation rates after the initial peak of immobilisation had passed.

2.6.3. Ammonium vs nitrate nutrition

Generally, the uptake of cationic ammonium results in net soil acidification whereas the uptake of anionic nitrate results in net soil alkalinisation (Beevers 1976). In many soils, nitrate is more abundant than ammonia but in some grasslands, hardwoods and coniferous forests, ammonia is the primary form of available inorganic nitrogen (Adams & Attiwill 1986). Nitrate is thought to be the predominant N form in well aerated soils with neutral or close to neutral pH but ammonium is thought to dominate acid soils typical of most coniferous forests (Näsholm *et al.* 1998). In many *Eucalyptus* forests, ammonium is the dominant inorganic form of nitrogen (Adams & Attiwill 1986). Most data indicate that conifers favour NH_4^+ uptake and are weak competitors of NO_3^- (Kronzucker *et al.* 1997). Louw & Scholes (2002) and Carlyle *et al.* (1990) found no correlation between the process of nitrification and pine tree growth, while significant correlations were found between tree growth and NH_4^+ mineralisation. Plants grown with ammonium have greater concentrations of free amino acids in foliage compared with nitrate fed plants (Geiger *et al.* 1999) probably as a consequence of differences in sites, patterns and rates of N assimilation (Martin *et al.* 1998).

2.6.4. Plantation canopies

2.6.4.1. Interception of atmospheric pollutants

Tree canopies intercept and collect additional nutrients from the atmosphere. The surface area of the receptor sites plays an important role in determining the extent to which an ecosystem intercepts and collects, and is therefore influenced by, atmospheric deposition. The amount of interception and collection is controlled by a number of factors, one of which is the leaf area index (Liu *et al.* 1992). Forests are efficient sinks for atmospheric pollutants and the potential for large rates of deposition are provided by the turbulent structure of air above and within forest canopies (Fowler *et al.* 1989). Conifer canopies are better aerosol trapping structures compared with open pastures, because their fine needles, dense canopy cover, branching and year round foliage provide a large surface area (Ross 1994b).

2.6.4.2. Atmospheric deposition

The main body of commercial plantations in South Africa are located downwind of major industrial regions and are therefore subjected to atmospheric deposition of N, S and acidic cations, which contribute to soil acidification processes. Scholes & Scholes (1998) found through theoretical studies that the nitrogen balance is negative in the timber growing regions of South Africa and that plantation forestry may be unsustainable without N inputs. Olbrich (1995) estimated that 0.62-24.9 NO_3^-, 1.22-17.0 Ca^{2+}, 0.1-0.8 Mg^{2+} and 0.5-1.3 K^+ kg $ha^{-1}yr^{-1}$ were dry deposited in afforested parts of Mpumalanga. Van Wyk (1990), Turner & De Beer (1993), Olbrich & Du Toit (1993) and Turner (1993) estimated that 0.37 ± 0.25 H^+, 7.4 ± 3.4 NO_3^-, 2.1 ± 0.9 NH_4^+, 3.6 ± 1.6 Ca^{2+}, 0.7 ± 0.3 Mg^{2+} and 2.1 ± 0.9 K^+ kg $ha^{-1}yr^{-1}$ were wet deposited in or close to afforested regions in Mpumalanga. A more recent study, conducted by Lowman (2003) showed that forested areas in Mpumalanga, receive 21.4 kg N ha^{-1} yr^{-1} dry and 7.8 kg N ha^{-1} yr^{-1} wet deposition while grasslands receive 7 kg N ha^{-1} yr^{-1} dry and 7.8 kg N ha^{-1} yr^{-1} wet deposition. Isotopic analyses of air borne dust for a site located 50 km east and 1000 m lower on the escarpment compared with Sabie, has

shown that the cations were composed of 5% wind borne soil particles, mainly from ploughlands, 2% from the Indian ocean, 46% from biomass burning and 47% from the coal burning regions (Piketh & Annegarn 1994).

The filtering action of forest canopies enhances atmospheric nutrient inputs onto forest canopies. Dry deposition estimates in a spruce stand in southwest Sweden measured over a five year period, using surrogate surfaces resembling needles, showed that the dry deposition of base cations represented a large fraction of the total atmospheric input (Ferm & Hultberg 1999). Plants can absorb nutrients from the atmosphere via leaf surfaces and from the soil via roots. Ions present in solution on leaf surfaces can diffuse into leaf cells or may bind to the cuticle or cell wall (Ross 1994b). Thus *E. grandis* and *P. patula* should be increasingly affected by atmospheric inputs relative to grasslands and therefore the conversion of low-biomass, herbaceous grasslands to relatively high biomass woody vegetation enhances the impacts of atmospheric inputs on ecosystems through increased efficiency at capturing pollutants.

2.6.4.3. Foliar leaching

In addition to the transfer of nutrients from the canopy to the forest floor through litterfall, foliar leaching can also make a significant contribution to the nutrient status of the forest floor. Foliar leaching is defined as the removal of solution material, that is physically or chemically bound to plant surfaces or interiors, which can account for 10-80% of nutrient return to the forest floor, whereby the remainder returns by litterfall. Foliar leaching excludes the wash off of dry deposited material, unbound to the surface (Lovett & Schaefer 1992). Foliar leaching, when leaf surfaces are wet, comprise base cations, sugars and amino acids (Schaefer & Reiners 1990). Foliar leaching is determined by climatic variables, such as the amount and type of rainfall as well as mist. Lovett & Hubbell (1991) found that mist acidity doubled the leaching of Ca^{2+} and Mg^{2+}, but had no effect on K^{+}.

Throughfall and canopy leaching results in secondary deposition and contributes to soil nutrient pools. Canopy leaching can account for 10 to 80% of the total annual return of Ca^{2+}, Mg^{2+} and K^{+} from the canopy to the forest floor, whereby the remainder occurs as litterfall (Waring & Schlesinger 1985). Olbrich *et al.* (1993) found enhanced nutrient concentrations in throughfall sampled in afforested regions of Mpumalanga relative to rainfall samples taken in open areas. The throughfall was particularly enhanced with NO_3^-, K^{+}, Ca^{2+} and Mg^{2+} ions. Zamierowski (1975) showed that high concentrations of K^{+}, Ca^{2+}, Mg^{2+} ions can be extracted from *P. patula* needles with distilled water, thereby demonstrating the leachable nature of these cations. Tamm (1951) and Madgwick & Ovington (1959) found a ten-fold increase in the Ca^{2+} content of precipitation collected beneath the forest canopy while Voigt (1960) found a five-fold increase. Ragsdale *et al.* (1992) found that K^{+} and Ca^{2+} were the dominant cations found in throughfall and stemflow, which accounted for 65-90% of the cations. Capellato *et al.* (1993) proposed that foliar base cation leaching was induced by H^{+} exchange and was one of the most important processes contributing K^{+}, Ca^{2+}, Mg^{2+} ions reaching forest floors. Leaching of basic cations from plant tissue can react with acidic substances to neutralise their acidity. The depletion of foliar base cations and the deposition and resultant increase of base cation concentrations in the soil solution, tends to increase the plants uptake of base cations. If plant uptake does not keep pace with the rate of foliar leaching, foliar cation concentrations would decrease, possibly to deficiency levels (Johnson 1992).

2.6.5. Soil acidification

Soil pH reflects the concentration of H^{+} ions in aqueous solutions that are in equilibrium with the soil solid phase. Capacity factors reflect the extent to which the soil can accommodate added acids or bases without associated changes in soil pH ie. it reflects the soils buffering capacity. A high cation exchange capacity results in a high nutrient storage capacity and resistance to pH shifts (McFee *et al.* 1976). Commonly measured capacity factors include acid neutralising capacity, exchangeable acidity, and base saturation (the ratio of base cations to the cation exchange capacity of the soil). Capacity factors represent stored acidity or alkalinity, which is controlled by the nature and composition of the solid-phase mineral and

organic acids (Binkley & Högberg 1997). It is therefore a property of decayed organic matter and silicate clays (McFee *et al.* 1976). Nutrients are stored on surfaces of clays and negatively charged colloidal organic matter (humus). Positively charged ions, such as K^+, Ca^{2+}, NH_4^+, are attracted to the negatively charged soil particles. The ability of a soil to retain cations on the surface of clay and humus is determined by the cation exchange complex. Generally, soils with a high clay content and high organic matter have high cation exchange capacities (Jordan 1985).

The composition of the cations attracted to the humus and clay particles determines the soil pH as well as the availability of many plant nutrients (McFee *et al.* 1976). Well buffered soils such as those with moderate amounts of clay or humus, will respond relatively slowly to pH shifts because of high quantities of exchangeable basic cations. If the soil has a high percentage of basic cations such as Ca^{2+}, Mg^{2+}, K^+ and Na^+, then the soil pH and the composition of the soil solution is controlled by the degree of base saturation on the exchange sites (McFee *et al.* 1976). Lathwell & Peech (1964) studied soils in the north eastern United States and found that when the soil pH in aqueous solution is between 4.0 and 5.5, the percentage base saturation can range between 0-45%. Similar relationships were found in most regions, whereby the base saturation decreases with decreasing pH, but not in a linear manner (McFee *et al.* 1976).

2.6.5.1. Soil protons

The main soil acidification process is the addition of protons, which displace basic cations from the soil exchange complex (Scholes & Nowicki 1998). Carbon dioxide (CO_2) liberated from soil respiration combines with soil water to form carbonic acid (H_2CO_3), which dissociates into bicarbonate HCO_3^- and H^+ (Jordan 1985). Carbonic acid, which is also derived from wet deposition, buffers around pH 5.6 and contributes to soil acidity. Soil respiration is high in tropical regions because of year round respiration, which results in a high CO_2 partial pressure (Jordan 1985). Protons are also derived from natural organic acid dissociation, however, organic acids decompose rapidly in tropical regions and therefore play a limited role in the leaching of basic cations from soil (Jordan 1985). Soil nitrogen transformations through the

conversion of organically bound N in decaying litter to NH_4^+ or NO_3^-, excess cation uptake by biomass (Bredemeier *et al.* 1990), and the preference for ammonium over nitrate nutrition contribute to soil acidification. Ammonium ions supplied to the roots are taken up and incorporated into amino acids and amides with a simultaneous release of protons for charge compensation (Marschner 1986). Thus, during plant NH_4^+ metabolism, NH_4^+ is biochemically converted to ammonia (NH_3^+), resulting in the release of positively charged H^+ into the soil (Arnold 1992)**.** Nitrification also releases two moles of H^+ per mole of nitrate (Wiklander 1976). Protons can displace nutrient cations on the soil colloids and the cations released into the soil solution are leached down through the soil profile (Jordan 1985). The elevated concentration of H^+ results in reduced soil pH. Ndala (2001), whose studies sites were located near Sabie, Mpumalanga, found that grassland soils had a soil pH of 5.45, whereas forest soils had a soil pH of 4.77. When the soil pH is below 5, H^+ ions react with silicate clays thereby releasing exchangeable aluminium into the soil solution (Jordan 1985).

2.6.5.2. Aluminium mobilisation

At a soil pH below 5, H^+ reacts with silicate clays, increases the solubility of organically bound aluminium resulting in the hydrolytic release and resultant mobility of aluminium in the soil solution (Jordan 1985). When aluminium is dissociated from organic complexes, it is highly toxic to plants and soil organisms because of its acidifying effects. However, Johnson (1992) found that both acid soils as well as the presence of strong organic or mineral acid anions are necessary for the mobilisation of aluminium from the exchange sites into solution. Aluminium liberated by mineral (eg. gibbsite and kaolinite) dissolution and dissociation of Al-organic matter complexes (Mulder & Stein 1994) results in enhanced exchangeable aluminium concentrations. Base cations are liberated by hydrolytic exchange and dissolution reactions and replaced with the acidic cations of H^+ and aluminium and to a lesser extent iron and manganese (Fey *et al.* 1990). Aluminium is the dominant cation associated with soil acidity in tropical regions (Jordan 1985). Nitrates and sulphates derived from dry and wet atmospheric deposition, gaseous sulphur compounds released as byproducts of microbiological activity act as mobile anions accompanying the leaching of basic cations and also contributing to soil acidity. The degree of dissociation of H^+ ions and

aluminium acid cations and replacement with base cations such as Mg^{2+}, Ca^{2+} and K^{+} is the sole focus of acid deposition research (Binkley & Högberg 1997).

Clay minerals can also adsorb nutrient anions such as phosphates and nitrates (Jordan 1985), which can be replaced by bicarbonate anions. Fine roots of plants and mycorrhizae are adversely affected by high levels of inorganic forms of aluminium (Ross 1994b). Other potentially phytotoxic elements such as manganese and boron may also be solubilised under acidic conditions and may therefore contribute to plant stress (Sumner *et al.* 1991). However, Schaedle *et al.* (1989) reviewed the effect of aluminium on tree seedlings, including coniferous and broad leaved trees, and found that aluminium stress resistance is a common phenomenon in trees.

2.6.5.3. Base cation leaching

Aluminium and H^{+} in the soil are favoured by cation exchange complexes thereby replacing base cations such as Mg^{2+}, Ca^{2+} and K^{+}. Ammonium nutrition generally inhibits cation uptake, by increasing H^{+} concentrations in the soil, and can therefore depress growth by inducing a deficiency of magnesium (Manolakis & Ludders 1977) and calcium (Pill *et al.* 1978). Dissociated base cations are water soluble and are therefore leached into drainage systems along with negatively charged nitrate. Van Miegroet *et al.* (1989) found that in alder forests, approximately 14% of the exchangeable Ca^{2+}, Mg^{2+} and K^{+} are exported annually below the 40 cm soil depth, through NO_3^{-} mediated leaching. Scholes & Scholes (1999) found an average decrease of 1.6 $cmol(+)kg^{-1}$ of exchangeable base cations and a 0.3-1.0 unit decrease in soil pH under first rotation 20 year old plantations relative to grasslands. Iron and aluminium inhibit root growth in the soil (Madji & Persson 1995) and high H^{+} availability allows for soluble phosphorus to react with Fe^{3+}, Al^{3+} and Mn^{2+} to form insoluble compounds, which result in P deficiencies in many tropical systems (Jordan 1985). Within the plant, aluminium displaces cations from adsorption sites such as cell walls and membranes and therefore influences the nutrient supply to the plant (Kuhn *et al.* 1995).

2.6.5.4. Harvesting of commercial forestry plantations

Commercial forestry processes result in a net export of biomass, thereby preventing the acid neutralising process of base cation return to the soil. After several rotations, the exportation of nutrient cations, through harvesting and rapid oxidation of litter through clearfelling, significantly intensifies soil acidification processes (Scholes & Nowicki 1998). Approximately 69% of the K^+ and 45% of the Ca^{2+} in the tree and litter pool were removed per harvest (Scholes & Scholes 1999). The relative effects of plantation species on soil pH, depends on tree growth rates, relative accumulation of base cations and the spatial distribution of roots (Scholes & Nowicki 1998). Morris (1992) calculated the average concentrations of nutrients in *P. patula* stemwood, removed through harvesting. He found 1100 ± 270 mg kg^{-1} of N, 220 ± 70 mg kg^{-1} of P, 790 ± 540 mg kg^{-1} of K^+, 540 ± 210 mg kg^{-1} of Ca^{2+} and 110 ± 40 mg kg^{-1} of Mg^{2+} in *P. patula* stemwood. Noble & Herbert (1989) calculated the average concentrations of nutrients in *E. grandis* stemwood, removed through harvesting. They found 2300 mg kg^{-1} of N, 70 mg kg^{-1} of P, 725 mg kg^{-1} of K^+, 700 mg kg^{-1} of Ca^{2+} and 215 mg kg^{-1} of Mg^{2+} in *E. grandis* stemwood. Thus, more N, Ca^{2+} and Mg^{2+} were removed through the harvesting of *E. grandis* relative to *P. patula*. *E. grandis* plantations generally have shorter rotation times, which results in frequent harvesting and thus higher quantities of nutrients exported more frequently, compared with the harvesting of *P. patula* plantations. Furthermore, *E. grandis* sequesters higher quantities of Ca^{2+} than *P. patula*, which leads to rapid soil depletion (Scholes & Scholes 1999). However, Scholes & Scholes (1999) calculated an approximate input and output analysis for granitic landscapes affortested with *P. patula* and *E. grandis* plantations in Mpumalanga. They found that the *P. patula* plantations were losing a 42.9 N, 3.68 P, 2.52 K^+, 1.87 Ca^{2+}, 11.23 Mg^{2+} kg ha^{-1} yr^{-1} whereas *E. grandis* plantations were losing 15.3 N, 0.68 P, 1.12 K^+, 1.57 Ca^{2+} and 4.13 Mg^{2+} kg ha^{-1} yr^{-1}. The mineral soil under *P. patula* plantations was losing more nutrients as a result of the formation of litter layers and the accumulation of nutrients contained therein.

After harvesting, the uptake of ammonium is reduced, rendering the potential for nitrification high (Jordan 1985). However, Jordan (1985) found that leaching losses were significant for only the first two years after the harvest. Nutrient depletion and

soil acidification processes mainly impact the upper 10 to 60 cm depths of mineral soil horizons. This effect is particularly important when afforestation of pines occurs on naturally acidic soils, which previously supported low biomass ecosystems such as grasslands (Scholes & Nowicki 1998). Thus, the naturally acidic, poorly buffered soils that occur under pine forests, combined with the pine induced soil alterations, render the soil particularly sensitive to further acidic inputs (Scholes & Nowicki 1998).

2.7.Nutrient cycling in grasslands

Annual grasses may live for as long as 15 months. The tillers of perennial grasses may also live for 15 months, but through the succession of lateral tillers, the plants develop the perennial habit. More than 85% of the mass of the root system of grasses is found in the top 15 cm of soil (Tainton 1984). Leaf removal results in either a slowing down or complete halt of root growth. However, some grasses have rhizomes, which serve as underground stems and storage organs and are effective in providing carbohydrates for root growth. The rhizomes contain non-structural carbohydrates, which are alternately accumulated and utilised by the plant in its growth cycle or when disturbed by changes in its environment, for example fire. Non-structural carbohydrates includes monosaccharides, glucose and fructose and the more complex oligosaccharides, sucrose and fructosan. Starch is a major reserve in some perennial species and nitrogen containing compounds such as protein, forms an important reserve (Tainton 1984).

In summer growing species, storage reserves may be relatively high. A small proportion of these reserves are utilised during the winter period to sustain biological processes within the plant. In spring, the reserve levels will decline rapidly as heavy demands are made by the leaf system. The reserve levels will remain low unless an adequate leaf system is allowed to develop. The reserve levels recover through the summer until flowering time, when heavy demands are made by the rapidly developing stem. On completion of flowering, reserves accumulate again, particularly in autumn, when growth rates are slow but conditions remain suitable for continued photosynthesis (Tainton 1984). Litter accumulation under natural grassland is

minimal, with most of the litter decomposing within a year (Scholes & Scholes 1999). The climax grasslands in the Mpumalanga region are assumed to have equal nutrient inputs and outputs, although long-term studies have not been undertaken (Scholes & Scholes 1999). However, grasses are burnt at regular intervals and lose N through volatilisation, but N is approximately balanced through biological N fixation by leguminous forbs (Scholes & Scholes 1999) and atmospheric deposition.

2.8.Nutrient cycling in *P. patula* and *E. grandis* plantations

In both natural and plantation forests, biogeochemical nutrient cycling is dominated by litter production and decomposition (Louw & Scholes 2002), which is a function of species specificity and climatic variables. *Pinus* have most of their roots near the soil surface, while *Eucalyptus* have roots systems which can exploit shallow and very deep soils (Schönau & Fitzpatrick 1981). Deeper-rooting plants can extract nutrients from mineralisation zones at depth, translocate it through the plant to the leaves, and deposit it via litterfall to the soil surface, thereby enriching the surface horizon (Martin & Coughtrey 1987). Studies in South Africa have shown that the accumulation of nutrients within *Pinus* litter layers and the distribution of roots within the litter layers, indicated that nutrients are taken up primarily from litter layers, suggesting that nutrients are cycled through a plant-litter-plant cycle instead of a plant-litter-soil cycle (Dames 1996). The production of a relatively large root biomass and its concentration near the soil surface, is an adaptation to a nutrient poor soil or potential aluminium toxicity in the sub soil. Dames (1996) found that the litter, roots, decomposers and other micro organisms, which are usually concentrated near the soil surface, were intimately mixed in the litter layer, thereby increasing nutrient uptake directly from the litter layer in *Pinus* plantations. In contrast, nutrients are cycled in a litter, soil, plant cycle in *Eucalyptus* plantations.

Mycorrhizas are common in Eucalypts and mycorrhizal associations are required for normal growth of *Pinus* (Wormald 1975). In *Eucalyptus* forests N and P are elements which most often limit growth and mycorrhizas play a crucial role in their acquisition (Grove *et al.* 1996). Ectomycorrhizae (ECM) increase nutrient uptake in higher plants by increasing the surface area of ion absorption (Coleman *et al.* 1983). ECM absorb

inorganic phosphates and ammonium compounds from soils of high phenolic content, where nitrates are deficient (Dames 1996). Turnbull *et al.* (1995) found that *Eucalyptus* seedlings with mycorrhizal associations grew well on a range of organic N sources, indicating that mycorrhiza associations enabled *Eucalyptus* to broaden their resource base with respect to nitrogen. ECM dominate in environments where nutrient supplies are seasonal and nutrient storage within mycorrhizal structures decreases leaching losses (Dames 1996). ECM are prevalent in *Pinus* (Dames 1996) and dominate in older *E. grandis* trees, while arbuscular mycorrhizal associations can develop in *E. grandis* seedlings (Grove *et al.* 1996). Arbuscular mycorrhizae are produced within the root tissue and play a role in phosphorus transfer and carbohydrate storage (Vogt *et al.* 1997). Mycorrhizae also play a role in the avoidance or exclusion of metals in the soil, alteration of membrane permeability, proliferation of roots in uncontaminated horizons, changes in metal binding capacities of cell walls or increase the exudation of metal-chelating substances (Verkleij & Schat 1990). Many researchers have found that ECM and ericoidal mycorrhizae have an ameliorating effect on the growth of host plants cultivated at high metal concentrations (Colpaert & Van Assche 1992).

The accumulation of litter on soil surfaces minimises nutrient movement into the mineral soil where nutrients are stored only by exchange on clay surfaces. Nutrients held by exchange are more susceptible to loss compared with nutrients incorporated into living organisms (Jordan 1985). However, competition between root uptake and microbial activity within the litter layer, can suppress the decomposer population, thereby adversely impacting on decomposition and nutrient availability for plant uptake. There is evidence to suggest that pines take up nutrients directly via their mycorrhizal fungi, which takes up nutrients directly from the soil organic matter (Näsholm *et al.* 1998). Thus, nutrient acquisition can occur without the intermediate mineralisation by independent soil microbes (Scholes & Nowicki 1998).

The productivity of forest stands increase as the leaf area index increases, reaches a maximum at a young age and thereafter declines (Binkley & Johnson 1992). Both *P. patula* and *E. grandis* plantations species have evolved mechanisms to effectively conserve nutrients through internally retranslocating nutrients. During the development of the green crown, prior to canopy closure, trees rely mostly on the site for its nutritional requirements. Upon canopy closure, up to two thirds of the total

nutrients can be obtained by retranslocation from older or dying tissues and thus the relationship between tree nutrient health and site characteristics become less conspicuous (Fisher & Binkley 1999). Before senescence of needles, nutrients are withdrawn and internally redistributed to support new growth (Proe & Millard 1995). The process of retranslocation is beneficial for the nutrient economy of the tree (Berg *et al.* 1980) and especially useful for plants growing under nutrient limiting conditions. Rates of accumulation of foliar nitrogen and phosphorus in *Eucalyptus diversicolor* F. Muell compared with those of a Corsican pine (Miller 1984), showed that foliar N and P were lower in the *Eucalypt* stand, except at an early stage.

Pinus foliage represents a small proportion of the biomass of older trees but contains a major proportion of the total nutrients, whereas *Eucalyptus* foliage is a relatively less significant nutrient storage supply (Richardson & Rundel 1998). *Pinus* foliage has greater longevity than *Eucalyptus* foliage and is therefore a sink for nutrients and a major source of nutrients for new shoot growth (Nambiar & Fife 1991). There are data to suggest that the wood and bark of the bole and branches are a commensurately more important store of nutrients in *Eucalyptus* and may therefore have a more significant role in biochemical cycling of nutrients in *Eucalyptus* than in conifers (Grove 1988).

2.8.1. Pines

Pinus species have a competitive advantage over other species because they deprive other vegetation of mineral N forms while increasing the availability and utilisation of organic N forms (Scholes & Nowicki 1998). The nutrient amounts and needle masses in *P. patula* (Morris 1992) reach a plateau between ages six to eight years, and then decline with increased age (Morris 1992; 1986). *Pinus* leaf area increases up to age ten, thereafter it remains constant until age 25 and decreases by 25% by age 35, while nutrient concentrations rapidly decline earlier in the rotation (Morris 1986). Schoettle (1994) found that large old trees of *Pinus aristata* Engelm. had lower foliar nitrogen and phosphorus concentrations relative to young trees. Thus, as the trees age, nutrients are probably removed from the woody components and nutrients are retranslocated from older to newer foliage because older needles tend to have lower tissue nitrogen concentrations (Runder & Yoder 1998). Nutrients such as N and P are mobile in the

xylem and K^+ is highly mobile within the xylem and phloem and can therefore be retranslocated within the plant. The mobility of Ca^{2+} is restricted within the plants and between cells (Marschner 1995). However, mobile elements such as magnesium accumulated in the older trees (Morris 1986). Gholz (1986) found that fertilisation of a 26 year old stand, showed a 10% increase in leaf area, which demonstrated that part of the decline in leaf area and productivity after age 25, was imposed by nutrient limitations.

Pinus effectively conserves nutrients by investing low amounts of nutrients per unit of leaf and bolewood production, and by returning low amounts of nutrients in litterfall relative to above-ground tissue (Bockheim & Leide 1991). Translocation may occur under N limiting conditions but under N saturated conditions, or where soil N availability is excessive, older needles may retain their N compounds, whilst utilising N from soil pools for new growth requirements. This would be especially useful for *Pinus* because needles are retained for many years where the clustered arrangement of foliage allows for high irradiance of both the upper and lower canopy.

2.8.2. Eucalypts

Species within *Eucalyptus* produce juvenile, intermediate or adult leaves, where the latter are characterised by a much lower specific leaf area (Ericsson *et al.* 1993). The different types of *E. grandis* leaves vary in terms of morphology, thickness and in dry matter content (Ericsson *et al.* 1993). *E. grandis* has a high requirement for nitrogen during the early establishment phase of the rotation (Noble & Herbert 1991) as leaves and twigs contain relatively high nutrient concentrations. Noble & Herbert (1991) found a highly significant relationship between soil organic C contents and the N levels in the leaves of 12 month old *E. grandis* and with increased organic C content of the soil, there was a corresponding increase in the N content of the leaves. Large proportions of nutrients are taken up and retained within the tree. This stage of growth is characterised by increasing rates of nutrient accumulation, which peaks at the time of canopy closure (Grove 1987). Following canopy closure, the rate of nutrient accumulation decreases and net primary productivity is maintained.

Eucalyptus is particularly efficient at remobilising phosphorus and potassium accumulated in the wood (Grove *et al.* 1996). Eighty percent of magnesium was incorporated in the aerial biomass during the first two years of growth whereas 50% of N and 65% of K^+ accumulated in the aerial biomass from the age of two years onwards. Nearly 50% of Ca^{2+} and Mg^{2+} were stored in the bark whereas N and K^+ accumulate mainly in the foliage and branches (Grove *et al.* 1996).

Foliage of a 4-11 year old *E. diversicolor* made up 16% of the above-ground biomass and contained 60% or more of the nitrogen and sulphur and 52% of the phosphorus (Grove & Malajczuk 1985), whereas the foliage in a 36 year old stand represented only 5% of the biomass and held 28% of the nitrogen and sulphur, and 16% of the phosphorus (Hingston *et al.* 1979). Birk & Turner (1992) found relatively small proportions of dry matter and nutrient concentrations in foliage, which suggested that the sapwood and bark of stems and branches were the major sinks for the increased amounts of nitrogen and phosphorus taken up following fertilisation. When external nutrient supplies do not limit growth, retranslocation of nutrients from older tissues still contributes a large proportion to growth (Grundon 1972). Nutrient retranslocation from senescent leaves and wood, during the transition from sapwood to heartwood, comprise major components of biochemical cycling of nitrogen, phosphorus and other mobile nutrients.

2.9. Plantation litter

Litter is composed of hydro soluble substances, organic compounds and energy substrates, which can be transferred into simple compounds by microbial activity (Jordan 1985). Phenolics are used by plants as a chemical defence to protect against nutrient loss through herbivory, which later inhibits bacterial activity and decomposition of the litter (Jordan 1985). Thick leaf litter layers absorb incoming rainfall and throughfall, slowing down water percolating into the soil and providing time for the absorption of ions, which may be absorbed by decaying litter and organic matter. Infiltration rates are positively related to litter and grass basal cover, being up to 9 times faster with 100% litter cover than for bare soil (O'Connor 1985). Moisture is required to sustain microbiological activites (Vanlauwe *et al.* 1995) but prolonged

leaching could deplete the C content of the litter because leaching alters the chemical composition of litter by lowering the sugar concentration (Ibrahima *et al.* 1995). Depleted C contents of the litter inhibits C dependent decomposing microbial activity and growth (Berg & Ekbohm 1991).

2.9.1. Pine litter

Coniferous litter is characterised by low concentrations of nutrients and proteins and high levels of polyphenolic substances, which render pine litter relatively resistant to decomposition (Berg & Staaf 1980). However, Scholes & Scholes (1999) suggested that the main reason for the accumulation of litter under *P. patula* plantations, was that the varieties of decomposing fungi, present in South Africa, do not effectively decompose pine needles under South African climatic conditions. Pine polyphenolic-rich litter combined with the lack of faunal activity in the upper soil layers leads to the formation of mor humus. Mor humus is characterised by a distinct undisturbed upper layer, a partly decomposed fermentation layer and a lower humus layer (Fenwick & Knapp 1982). Several studies have demonstrated the podzolising effect of pines (Wardenaar & Sevink 1992). Podzolisation occurs when the downward percolation of dissolved humic and fulvics acids result in characteristic layering of the soil (Scholes & Nowicki 1998), whereby the upper layer is depleted of its contents and the lower layers accumulate the contents leached from above. Humic substances form mobile complexes with iron, aluminium, base cations and natural carbonic acid, which facilitate the dissolution and removal of clay minerals (Ugolini *et al.* 1977). The metals and humic substances are then mobilised and leached out of the upper mineral soil and deposited lower down in the soil profile, thereby creating the ferrihumic B horizon. Podzolic soils are therefore characterised by an organic upper soil horizon. Below it is a bleached quartz-rich E horizon, which is depleted of clay minerals and the oxides and hydroxides of iron and aluminium (sesquioxides). Beneath the bleached E horizon is a dark, blackish-brown B horizon where the accumulation of sesquioxides associated with humic substances occur (Fitzpatrick 1980). Over time, these processes result in significant acidification and base cation deficiency in upper soil horizons.

Dames (1996) found that in the upper litter layers the nutrients were distributed N > K^+ > Mg^{2+} > P and that litter generally had higher nutrient contents than the soil. Dames (1996) found that litter quality increased with stand age, where the C:N ratios of the younger stands ranged from 40, whereas older stands ranged from 18. The uniformity of senescent needles in terms of age, shape and size, means that the structural compounds would show little variability as the tree aged (Berg & Wessén 1984). Morris (1986, 1992) found that litter production increased with stand age until canopy closure, after which the amount of litterfall remained the same. Mature stands shed dead branches from the lower stems. The shedding of branches contributed to litterfall at a time when needle fall possibly declined (Morris 1992). Thus, total annual litterfall may be less influenced by stand age after canopy closure owing to the increased contribution of branches, as observed in other pine stands (Das & Ramakrishnan 1985).

2.9.2. Eucalypts

Decomposition and mineralisation of eucalypt leaves occur rapidly, where 30 to 50% of the weight loss occurs during the first year, despite the sclerophyllous nature of the leaves (Wood & Raison 1983), provided that the soil moisture content is favourable for microbial activity (Ericsson *et al.* 1993). Thus, N mineralisation should not be a limiting factor in *Eucalypt* plantations (Ericsson *et al.* 1993) unless abiotic factors impede biotic processes. Estimates reveal that one to two thirds of the annual nutrient demand can be met from litter mineralisation in well established *Eucalyptus* plantations (Ericsson *et al.* 1993).

2.10. Nutrient variation within the canopies of *Pinus* and *Eucalyptus*

Evidence from field and laboratory studies showed that N concentrations were lowest in shade-adapted leaves and highest in leaves exposed to high levels of sunlight, thereby distributing N so as to maximise canopy assimilation (Leuning *et al.* 1991). Field (1983) found small differences in calculated assimilation rates for canopies with uniform, optimal or observed N distributions. In contrast, Hirose & Werger's (1987) calculations suggested that significant enhancement of canopy assimilation could be

obtained by optimal distribution of leaf N, relative to uniform distribution. Significant light limitations may, however, only occur after canopy closure and thus will affect older stands more than it would younger stands.

Differences in nutrient concentrations in the canopy of *Eucalyptus* were attributed to an increase in sclerophylly (lignin and cellulose contents) with leaf age, and by differences in nutrient function and mobility within the tree. Concentrations of nitrogen and phosphorus were generally greater in the outer crown and increased from lower to upper crown. Leuning *et al.* (1991) found similar N and P concentrations in the lower and upper canopies of 6 month old *E. grandis* trees but found the highest concentrations of N and P in the upper crown of 16 month old trees. However, in *Eucalyptus deglupta* Blume, a tropical eucalypt, there was little variation in nitrogen concentration between the upper and lower crown in the wet season but greater variation in the dry season (Lamb 1975). Leuning *et al.* (1991) found a marked decline in the average specific leaf area of *E. grandis* with age and Grove (1990) noted decreases in concentrations of nitrogen and phosphorus in mid-canopy leaves of *Eucalyptus diversicolor* F. Muell over a 3-year period associated with a 67% increase in specific leaf mass.

2.11. General seasonally induced nutrient variation

Seasonal variations in temperature, light and moisture induce changes in functioning of the plant and soil system. In summer, temperature and soil moisture increase the rates of chemical reactions involved in soil N transformations. Soil pH and rates of N turnover in soil systems are directly affected and related to soil climatic variables. Plant growth and function, driven by uptake rates and utilisation pathways of N, are directly controlled by soil and climatic processes. In natural systems, N-availability is high during the growing season and low during winter (Runge 1983).

On the eastern escarpment of South Africa, rainfall is highly concentrated in summer, while winter is dry and cool. The climatic combination naturally supports a grassland cover (Ellery *et al*. 1991) while the length and intensity of the dry season is the most limiting climatic factor to the growth of both *Pinus* and *Eucalyptus* (Scholes &

Scholes 1999). In plantations, more than 50% of the above ground requirement of N and 30% of P are derived from resources retranslocated during the previous autumn (Bernier 1984). Nutrient storage pools render the plant independent of soil nutrients early in the season, at a time when soil temperature results in low root activity. Nitrogen allocation among plant pools can vary, but generally, evergreen genera such as *Pinus* and *Eucalyptus*, show strong seasonal shifts in nitrogen distribution among N pools. *Pinus* are relatively dormant during the dry season whilst *Eucalyptus* continue to be physiologically active throughout the dry season (Dye *et al.* 1995).

Linder (1995) found that fertilised plots of *Picea abies* (L.) Karst showed a clear decrease in mineral nutrient concentrations during the growing season in needles older than the current season. Part of the decrease was explained by the resorption of nutrients and their transport to the developing needles and shoots (Helmissaari 1992). Most of the seasonal variation could be explained by variations in the amount of starch stored in needles, where 40% of the needles dry weight may consist of non-structural carbohydrates during the early summer. As the summer progresses, starch is broken down (Linder 1995). Nutrients expressed on a percentage basis were influenced by the accumulation and depletion of starch and can therefore obscure the interpretation of the nutritional status of the trees (Linder 1995). Aronsson & Elowson (1980) found pronounced seasonal variation in *Pinus sylvestris* (L.) for all nutrient elements analysed, independent of age-class of foliage or treatment. However, the magnitude and pattern of seasonal variation varied between elements and age-class of foliage.

Significant seasonal variation in nutrient concentrations in *Eucalyptus* foliage was observed (Knight 1988). Increased concentrations of nitrogen in foliage of 6 year old *Eucalyptus saligna* Sm. and *Eucalyptus wandoo* Blakely were observed in spring (Bell & Ward 1984). Concentrations of nitrogen and phosphorus in mature leaves in jarrah (*Eucalyptus marginata* Sm.) increased from mid-winter, peaked in mid-late summer at the time of maximum leaf-fall and thereafter decreased. The life-span of leaves in the above-mentioned forests were about 2-3 years and seasonal fluctuations in foliar concentrations probably resulted from the combined effects of high rates of nutrient uptake in spring, the onset of senescence and maximum production of new leaves in summer and ageing of leaves (Grove 1988).

2.12. Burning of the grasslands

Burning of grasslands render the soil exposed to wind, rainfall and sunlight, resulting in greater diurnal fluctuations of soil temperatures and often more rapid drying out of the surface layers of the soil (Tainton 1984). In South Africa, revegetated grasslands, after burning, are more nutritious in spring compared with unburned grasslands. Calcium, Mg^{2+} and K^{+} in the form of ash deposited onto the soil surface, are immediately available for plant uptake and thus increases the pH of the soil surface. Increased soil pH results in the precipitation and decreased concentrations of aluminium and manganese, which then increases the availabilty of phosphorus (Jordan 1985). Burning mobilises substantial amounts of nutrients locked up in above-ground biomass as well as in resistant organic pools in the soil, thereby passing the slow decomposition process which occurs in the absence of fire. Fire favours the establishment of perennial grasses because it does not destroy the underground rhizomes, which survive and resprout at the start of the next rainy season. Burning also eliminates woody vegetation, depletes soil organic matter and nitrogen stocks (Jordan 1985).

2.13. Silvicultural practices in South Africa

The clearfelling system is the main silvicultural system followed in southern African commercial plantations (Theron 2000a), which entails the choice of species, stems per hectare, genetic material, site amelioration and mechanisation allowing for uniform tree sizes and more predictable yields (Theron 2000a). Pruning, thinning and fertilising are some of the commonly used methods.

Thinning entails the routine removal of a proportion of individual living trees from a stand before clearfelling (Theron 2000b). Thinning is aimed at reducing the total stand density and maximising the volume growth per tree (Malan 2000), by providing the remaining trees with more space for root and crown development, to encourage stem diameter increment and thus reach the desired size sooner (Theron 2000b).

Pines grown for saw timber and veneer are pruned to maximise the proportion of clear wood in the stem (Malan 2000) thereby improving timber quality. Branches form knots, which are the most common defects of timber resulting in decreased pulp yield. Eucalypts undergo natural or self-pruning processes, whereas this process is slower in pines (Theron 2000c). The height of pruning varies between 1.5-9.0 m in height, depending on the tree height, where pruning should not exceed 50% of the crown height (Zwolinski & Hinze 2000). The pruned material is either removed from the site or broadcasted over the soil surface.

Fertilisation at planting or shortly after planting is a routine silvilcultural practise in the forestry industry in the production of *E. grandis* (Noble & Herbert 1991). Fertilising aims to stimulate initial root development thereby ensuring rapid colonisation of the soil by the roots. It results in better survival and growth of seedlings after transplant, which leads to rapid canopy closure, weed suppression, uniform stands and ultimately greater yields at harvesting (Norris 2000). The response of fertiliser applications with *E. grandis* in South Africa has been studied intensively since 1976 and relationships between growth and the nutrient status of the leaves have been obtained (Schönau 1982). Generally, the responses have been to P, especially on virgin soils enriched with mineralised N through cultivation (Schönau & Herbert 1983). The response to N depends on the organic matter in the topsoil and also the rate of N mineralisation (Herbert & Schönau 1989).

3. METHODS AND MATERIALS

3.1.Study area

The study areas are located on the eastern escarpment of South Africa (Fig. 2). The study areas are characterised by strong relief with variable slopes and aspects (Fig. 3). A montane grassland (Driekop) (Fig. 4) and adjacent *P. patula* plantations (Fig. 5-7) and a lower lying grassland (Brooklands) (Fig. 8) and adjacent *E. grandis* plantations (Fig. 9-11) were selected for this study.

3.2.Introduction to experimental design

It was assumed that the soil nutrient status of the Driekop grassland and the adjacent *P. patula* plantations were similar prior to afforestation while the soil nutrient status of the Brooklands grassland and the adjacent *E. grandis* plantations were similar prior to afforestation. The assumptions were fair, especially for the upper 20 cm of soil, because the Driekop grassland and the adjacent *P. patula* plantations, located on the upper escarpment are underlain by dolomitic bedrock, and therefore had a common soil origin. The Brooklands grassland and the adjacent *E. grandis* plantations, located on the lower reaches of the escarpment are underlain by granitic bedrock, and therefore had a common soil origin. Any changes prior to a change in land use, may have been associated with the lateral movement of soil materials on the catchment slopes (Ross *et al.* 1990). However, it was possible that variations in soil depth existed between the grasslands and plantations. Furthermore, three different aged *P. patula* plantations and three different aged *E. grandis* plantations were selected to assess the nutrient status across the age groups within the plantations. The comparative focus of this study lies between the i) Driekop grassland and adjacent *P. patula* plantations ii) Brooklands grassland and adjacent *E. grandis* plantations and within i) *P. patula* age-classes and ii) *E. grandis* age-classes. The sampling was conducted during late winter, August of 2002 and mid summer, January of 2003.

Insert figs 2 & 3

insert figs 4 and 5

Insert figs 6 and 7

insert figs 8 and 9

insert figs 10 & 11

The higher lying areas are characterised by extensive *Pinus* plantations on mountainous terrain while the *Eucalyptus* plantations are found on the lower escarpment regions. The altitudinal gradients have associated climatic gradients. Cooler temperate conditions occur on the higher lying areas whilst warmer temperate and sub tropical conditions occur on the lower lying regions. The mean annual precipitation (MAP) on the escarpment ranges from 2 000 mm on the higher lying areas to 600 mm per annum in the lower lying areas. Eighty three percent of the annual rainfall occurs between November and March (Louw 1997). Fog is common in summer, generally at an altitude above 1100 m, and it can make a substantial contribution to soil moisture (Louw 1997). Figures 12 & 13 represent the cumulative rainfall (mm) and monthly maximum and minimum temperatures, respectively, measured at the Graskop weather monitoring station, from February 2002 to January 2003. Graskop is located 15 km east of Driekop and the recorded weather data was most representative of the weather conditions prevalent at Driekop. Figures 14 & 15 represent the cumulative rainfall (mm) and monthly maximum and minimum temperatures, respectively, measured at the Brooklands weather monitoring station. Table 1 summarises the site characteristics of both sites on the escarpment.

Weather graphs fig 12, 13, 14 and 15.

Table 1. Site characteristics for a) Driekop grassland and adjacent *P. patula* plantations and b) Brooklands grassland and adjacent *E. grandis* plantations.

a) Driekop grassland and adjacent *P. patula* plantations				
Land Use	Driekop Grassland	*P. patula* plantation	*P. patula* plantation	*P. patula* plantation
Compartment		C25A	D07A	D06B
Age at 08/2002	15 months*	2 yrs	13 yrs	30 yrs
Longtitude **Latitude** **Altitude (m)**	30º45E 24º50S 1487-1495	30º45E 24º50S 1504-1549	30º45E 24º50S 965-1610	30º45E 24º50S 956-1607
Geology	Dolomite	Dolomite	Dolomite	Dolomite
Soil texture	Silty clay loam	Silty clay loam	Clay	Silty clay
Rainfall (mm year^{-1})	1400-1600	1400-1600	1400-1600	1400-1600
Aspect	West	West	East	East
Previous rotations		2 *Eucalyptus* 1 *P. patula*	1 *Eucalyptus* 1 *Pinus*	1 *P. patula*
Rotation of *P. patula*		2nd	2nd	2nd
Known Cumulative rotation		4th	3rd	2nd
Total area (ha)		46.0	11.6	21.4
Stems (stems ha^{-1})		1053	500	324
MAI (m^3 ha^{-1}yr^{-1})		Not available	Not available	12
b) Brooklands grassland and adjacent *E. grandis* plantations				
Land Use	Brooklands Grassland	*E. grandis* plantation	*E. grandis* plantation	*E. grandis* plantation
Compartment		R32a	R24	R35
Age at 08/2002	3 months*	2 yrs	8 yrs	13 yrs
Longtitude **Latitude** **Altitude (m)**	30º50E 25º20S 980-1000	30º50E 25º20S 899-905	30º50E 25º20S 1102-1018	30º50E 25º20S 897-961
Geology	Granite	Granite	Granite	Granite
Soil texture	Silty clay loam	Silty clay	Silty clay	Clay loam
Rainfall (mm year^{-1})	856-1000	856-1000	1059-1200	856-1000
Aspect	West	West	West	West/S/W
Previous rotations		2 *Eucalyptus*	2 *Eucalyptus*	2 *Eucalyptus*
Rotation of *E. grandis*		3rd	3rd	3rd
Known Cumulative rotation		Unknown	Unknown	Unknown
Total area (ha)		25.6	35.0	8.0
Stems (stems ha^{-1})		1736	1736	1372
MAI (m^3 ha^{-1}yr^{-1})		30	40	19

* Time after burning

3.3.Site histories

The Driekop grassland, occuring adjacent to the *P. patula* plantations, was burnt every alternate year. It was burnt in May of 2001 and 2003, which means it was sampled 15 and 20 months after it was burnt. The Brooklands grassland, occuring adjacent to the *E. grandis* plantations, was also burnt every alternate year. The last burn was in May 2002, which means that it was sampled about 3 and 8 months after it was burnt. The grasslands are classified as fire climax grasslands of potential forest areas (Acocks 1953). Both grasslands were relatively treeless, but the Brooklands grassland was interspersed with woody bush clumps, which comprised approximately 10 to 15% of the area. The dominant grass species were *Themeda triandra* (Redgrass), *Trachypogon spicatus* (Giant Speargrass), *Heteropogon contortus* and many less dominant grasses and forbs.

The history of the selected plantations is not entirely certain. It is thought that the sites were afforested to *P. patula* around the 1920s but an exact date and species is uncertain. However, the history of the sites from around 1950 was traced (pers. comm. McNamara 2004). The '2 year old' *P. patula* compartment was planted to either *E. grandis* or *E. saligna* in 1951. The *Eucalyptus* was harvested and the site was planted to *P. patula* in 1971 and a second rotation of *P. patula* was planted in 2000, which was the *P. patula* plantation used for this study. The '13 year old' *P. patula* plantation was initially planted to *E. saligna* and it was thought that a genus of *Pinus* was planted thereafter. In 1989 the site was planted to *P. patula*, which was the *P. patula* plantation used for this study. The '30 year old' *P. patula* plantation was initially planted to *P. patula* in 1948. It was harvested and a second rotation of *P. patula* was planted in 1973, which was the *P. patula* plantation used for this study.

It is thought that the sites were afforested in 1937 and the planting of *E. grandis* began around the 1970s (pers. comm. Reynecke 2003). It was assumed that two rotations of *Eucalyptus* were planted prior to the plantations used in this study, based on an average *E. grandis* rotation time of 15 years. As a result of the variability and uncertainty pertaining to the site histories, the data were interpreted with caution. Comparisons between *P. patula* and *E. grandis* plantations were further confounded

by various silvicultural practices. Tables 2 and 3 show the silvicultural practises of the current stands of *P. patula* and *E. grandis* plantations used for this study.

Table 2. Silviculture of the selected *P. patula* plantations (pers. comm. McNamara 2004).

***P. patula* plantations**			
Age (yrs)	**Date Planted**	**Pruned Date & level* (m)**	**Thinned Date & no. of stems remaining**
2	2000/03	2003/07 - 1.0	
13	1989/01	1993/10 - 1.0 1994/07 - 2.5 1996/03 - 5.0	2000/07 - 500 2003/05 - 300
30	1973/11	1976 - 1.0 1978 - 5.0 1994 - 5.0 1994 - 7.0	650 1987 - 387 1992 - 324

* The distance from the soil surface to the lowermost part of the canopy

Table 3. Silviculture of the selected *E. grandis* plantations (pers. comm. Reynecke 2003).

***E. grandis* plantations**			
Age (yrs)	**Date Planted**	**Date of Managed Burn**	**Date of Fertilisation**
2	2000/01		2000/03**
8	1994/10	1994	1994/12**
13	1989		

** Fertilised with 120g MAP (mono ammonium phosphate) per seedling, approximately 2 months after planting.

3.4.Sampling strategy

Ideally, one should measure the variations in nutrient status for a single site over a prolonged time period, using standardised methodology for sampling and analyses. However, given the time constraints of the study and the required silviculture (for example, felling), I used three different age groups of the same species, located on different sites, which introduced a degree of variability into the data, if interpreted as a linear time series. For the purpose of statistical validity, at least three plots per age-class of similar site, physical and biological characteristics should have been utilised for comparisons. However, actual sites of similar physical and climatic characteristics, of the same species, age and rotation, did not exist. Thus, replicated samples were achieved through 'pseudoreplication' whereby each compartment of various aged plantations were subdivided into three plots. Two trees or quadrats per plot were sampled for soil, litter and foliar (lower and upper canopy) material. Thus, each compartment of similar aged trees comprised of six 'pseudoreplicated' samples. Figure 16 diagrammatically represents the sampling strategy.

3.4.1. Grasslands and Plantations

3.4.1.1. Soil material

Six soil samples per site were collected to a depth of 20 cm (Anderson & Ingram 1996) using a soil auger. The soil samples were placed in plastic bags and stored in cooler boxes until returned to the laboratory, where the soil was placed in the freezer until the subsamples were weighed for the anaerobic nitrogen mineralisation index and the water correction factor (Anderson & Ingram 1996). Thereafter, the soil was oven dried at 40ºC for fourteen days and sieved through a 2 mm sieve (Anderson & Ingram 1996).

3.4.1.2. Litter material

For the purposes of this study, litter material was defined as the dead leaf material found on the soil surface (Woods & Raison 1983). Samples in this study did not include the decomposing mor layers found above the mineral soil horizon under the *P. patula* plantations. Litter material was collected within the circumference of the lower canopy, directly beneath the canopy and directly above the sampled soil. The litter material was removed with a spade to a maximum depth of 20 cm within a 0.25 m^2 quadrat. It was then placed in paper bags and stored in cooler boxes, until returned to the laboratory. All litter material was oven dried at 40ºC for fourteen days. Thereafter, it was sieved through a 0.5 mm mesh (Anderson & Ingram 1996). The dried and ground samples were stored in air tight containers for laboratory analyses.

3.4.1.3. Foliar material

Six trees per plantation were selected based on similar height. The tree heights were representative of the mean tree height of the plantations. The sampling level of the lower canopy was above the pruning level (*P. patula*), which varied with stand age. Lower canopy foliar samples were collected within the lowermost metre of the canopies whilst upper canopy foliar samples were collected within the uppermost

metre of the canopies. Where the canopy was beyond 7 metres, tree climbers were hired to sample the upper and lower canopy foliar material. A single branch was selected and sawn off from the tree. The leaves were collected and formed a composite sample. The total amount of foliage collected as a composite sample was determined by the amounts required for laboratory purposes. The foliage was placed in paper bags and stored in cooler boxes until returned to the laboratory. The foliage was oven dried at 40˚C for fourteen days. Thereafter, the samples were ground and sieved through a 0.5 mm mesh (Anderson & Ingram 1996). The samples were stored in air tight containers for laboratory analyses.

3.4.2. Grasslands

Composite 'grassland' samples constituting the foliar and litter samples were taken within a 2 m^2 quadrat. The litter material constituted the dry, dead material on the soil surface. The quadrats were randomly located within the grasslands. All aboveground foliar and litter material within the quadrat were collected. Two quadrats were sampled per area in each grassland. The number of samples collected were halved for laboratory analyses, in order to investigate initial trends (Table 4). The quantities, storage and transportation specifications were the same for grasslands as for the plantation material.

Table 4. The number of samples collected from the canopy, litter and soil from the tree to the compartment level of *P. patula, E. grandis* and the adjacent grasslands.

	Components sampled	No. of trees or quadrats of samples per plot	No. of plots per site	No. of sites	Total no. of samples per component	Samples used for laboratory analyses per component
P. patula, E. grandis	Upper canopy, lower canopy, litter & soil	2	3	3	18	9
Driekop & Brooklands Grasslands	Above-ground foliar material, Litter & Soil	2	3	2	12	6

3.5.Laboratory analyses

Table 5 provides information relating to the laboratory methodology used for the analyses and the laboratories at which, the analyses were performed. Table 5 also indicates the season in which the sampling occurred and the laboratory analyses which were performed. Samples analysed for both seasons were those which were expected to show seasonal trends. A sub sample of the lower and upper canopy foliar material was analysed for amino acid and protein contents. No significant differences were found between the lower and upper canopy amino acid and protein values. Therefore, for the purposes of the amino acid and protein analyses only, the remainder of the lower and upper canopy foliar samples were combined. Thus, the foliage was sampled in both seasons but the amino acid and protein analyses were only analysed using the winter samples as a result of the cost of analyses.

Table 5. The variable, method, season, reference of the laboratory analyses and the institution at which the laboratory analyses occurred.

Components of ecosystem	Variable	Method	Season of analyses	Reference	Institution
FOLIAGE	Total N	Kjeldahl oxidation	Winter & Summer	Anderson & Ingram (1996)	Phytotron, University of the Witwatersrand
	Total P	Kjeldahl oxidation	Winter & Summer	Anderson & Ingram (1996)	Phytotron, University of the Witwatersrand
	Total C	Acid dichromate oxidation	Winter & Summer	Anderson & Ingram (1996)	Phytotron, University of the Witwatersrand
	Total Base and Acid cations (Mg^{2+}, Ca^{2+}, Na^{+}, K^{+}) and (Fe^{2+}, Mn^{2+}, Al^{3+})	Inductively coupled plasma analyses (ICP)	Winter & Summer	Skoog *et al.* (1998)	Chemistry department, University of the Witwatersrand
	Amino acids	High performance liquid chromatography – fluorescence detection of chloroformates	Winter	Einarsson *et al.* (1983)	Irene analytical services - Pretoria
	Protein	Dumas combustion	Winter		Irene analytical services - Pretoria
LITTER	Total N	Kjeldahl oxidation	Winter & Summer	Anderson & Ingram (1996)	Phytotron, University of the Witwatersrand
	Total P	Kjeldahl oxidation	Winter & Summer	Anderson & Ingram (1996)	Phytotron, University of the Witwatersrand
	Total C	Acid dichromate oxidation	Winter & Summer	Anderson & Ingram (1996)	Phytotron, University of the Witwatersrand
	Total Base and Acid cations (Mg^{2+}, Ca^{2+}, Na^{+}, K^{+}) and (Fe^{2+}, Mn^{2+}, Al^{3+})	Inductively coupled plasma analyses	Winter & Summer	Skoog *et al.* (1998)	Chemistry department, University of the Witwatersrand
SOIL	Total N	Kjeldahl oxidation	Winter & Summer	Anderson & Ingram (1996)	Phytotron, University of the Witwatersrand
	Total P	Kjeldahl oxidation	Winter & Summer	Anderson & Ingram (1996)	Phytotron, University of the Witwatersrand
	Total C	Acid dichromate oxidation	Winter & Summer	Anderson & Ingram (1996)	Phytotron, University of the Witwatersrand
	Anaerobic N mineralisation index	Anaerobic N min index	Winter & Summer	Anderson & Ingram (1996)	Phytotron University of the Witwatersrand
	Total Bases (Mg^{2+}, Ca^{2+}, Na^{+}, K^{+}) & Acids (Al^{3+}, Mn^{2+}, Fe^{3+})	Inductively coupled plasma analyses	Winter & Summer	Skoog *et al.* (1998)	Chemistry department, University of the Witwatersrand
	Exch. (Mg^{2+}, Ca^{2+}, Na^{+}, K^{+}) & Acids (Al^{3+}, Mn^{2+}, Fe^{3+})	Ammonium acetate	Winter & Summer	Thomas (1982)	Agricultural Research Council - Pretoria
	Exchangeable acidity	Ammonium acetate (pH 7)	Winter & Summer	Thomas (1982)	Agricultural Research Council - Pretoria
	pH	H_2O	Winter & Summer	Anderson & Ingram (1996)	Phytotron, University of the Witwatersrand
	H_20 correction factor (volumetric)		Winter & Summer	Anderson & Ingram (1996)	Phytotron, University of the Witwatersrand
	Texture		Winter	Anderson & Ingram (1996)	Phytotron, University of the Witwatersrand

3.6.Statistical analyses

The data were tested for normality using the Kolmogorov-Smirnov Lilliefors and the Shapiro-Wilk's W tests for normality. The data were analysed using the repeat (within subject) measure Analysis of Variance (ANOVA), which allowed for comparisons within and between the grassland and each age class of the adjacent plantations. Furthermore, the data were used to compare the differences within the different aged plantations. The repeat measures ANOVA also allowed for the comparison of a variable taken at different time intervals. For example, the grasslands soil pH in winter, was compared with the 2 year old *P. patula* plantation's soil pH in winter. The same applied to summer and the data was used to compared the differences found between seasons. The Driekop grassland and adjacent *P. patula* plantations were compared by means of ANOVAs and the Brooklands grassland and adjacent *E. grandis* plantations were also compared using separate ANOVAs. Where the ANOVAs indicated significant differences, Tukey's Post Hoc tests were used to identify the significant differences amongst all combinations of vegetation types and seasons for each variable analysed within the soil, litter and foliage. Thus, it highlighted whether the significant difference occurred (i) within the grasslands (ii) within the age-classes of the plantations and / or (iii) between the grasslands and plantations. Significance was determined at the one and five percent levels. The differences between foliar nutrient concentrations in the lower and upper canopies of the *P. patula* and *E. grandis* plantations were analysed using t-tests for dependent samples, which measured the differences between the two means within a group. All statistical analyses were performed using Statistica 6.0.

4. RESULTS

The results were depicted primarily in table and graph format. The graphs were used to highlight the key findings, except for the amino acid data, which were presented in the form of a table only. In cases where the cations showed similarities, when comparing grasslands and plantations, a graph of a single cation was used to depict the common or interesting trend. Similarly, the seasonal and inter canopy variations, were only emphasised when an interesting pattern or statistically different pattern emerged. Statistical p values, for the post hoc Tukey tests, were indicated in the text, only where the data compared were significantly different and where it was directly applicable to the comparison made. Appendix A shows all p values, where significance at the 5% and 1% levels were highlighted in yellow and red, respectively. The tables were divided into soil (Appendix A1 & A2), litter (Appendix A3 & A4) and foliage (Appendix A5 & A6) for the comparisons made between grasslands and plantations, within the different age-classes of plantations and between seasons. Thus, Appendix A depicts, for example, the p values for comparisons made between the soil pH of the grassland, in winter, and the soil pH of the 2 year old *P. patula* plantation, in winter.

4.1.Soil

4.1.1. Texture, water content and pH

The soil texture (Table 6) of the Driekop grassland and adjacent *P. patula* plantations were dominated by approximately 50% silt, followed by 40% clay and 10% sand. However, the clay content of the 13 year old *P. patula* plantation was 63.8%, which was significantly higher ($p<0.01$) when compared with the adjacent Driekop grassland and the 2 and 30 year old *P. patula* plantations. The soil texture (Table 7) of the Brooklands grassland and adjacent *E. grandis* plantations were dominated by approximately 40% silt, 40% clay and 20% sand. The 2 and 8 year old *E. grandis* plantations had 40.8 and 47.2% clay respectively, which was significantly higher

($p<0.01$) when compared with the adjacent Brooklands grassland and 13 year old *E. grandis* plantation.

The soil water contents (Tables 6 & 7), at the time of sampling, ranged between 16 and 24% in the Driekop grassland while the *P. patula* plantations soil water contents ranged between 29 and 39%. The soil water content in the Driekop grassland was significantly lower ($p<0.05$) when compared with that of the 13 and 30 year old *P. patula* plantations. In contrast, the soil water content in the Brooklands grassland, during the summer sampling was 28%, while it ranged between 5 and 13% in the *E. grandis* plantations.

The soil pH (Tables 6 & 7) was significantly higher ($p<0.05$) in the grasslands when compared with the plantations. The soil pH in the grasslands ranged between 5.3 and 5.6, while it ranged between 4.8 and 5.2 in the *P. patula* plantations and between 4.6 and 5.3 in the *E. grandis* plantations. The older *P. patula* plantations had higher soil pH values when compared with the older *E. grandis* plantations. The *E. grandis* plantations showed a trend of decreasing soil pH with increased plantation age, where the soil pH in the 2 year old *E. grandis* plantation was significantly higher ($p<0.01$) than that of the 8 and 13 year old *E. grandis* plantations.

Insert table 6 – pine soil

insert	table	7	euc	soil

4.1.2. Total and exchangeable basic cations

The soil total and exchangeable Mg^{2+} (Fig. 17), K^{+} and Ca^{2+} (Table 6) were higher in the Driekop grassland when compared with the adjacent *P. patula* plantations. Generally, the Driekop grassland had significantly higher soil basic cations concentrations, when compared to the *P. patula* plantations. Soil exchangeable Ca^{2+} and Mg^{2+} decreased with increased *P. patula* plantation age.

Generally, the soil total and exchangeable basic cation concentrations were similar when comparing the Brooklands grassland and adjacent *E. grandis* plantations (Table 7). However, the 8 year old *E. grandis* plantation had higher soil total Mg^{2+} (Fig. 18) and Na^{+} concentrations in winter, and lower soil exchangeable Mg^{2+} and soil total Ca^{2+} concentrations when compared with the Brooklands grassland, the 2 and 13 year old *E. grandis* plantations. Soil total K^{+} concentrations in the Brooklands grassland and the *E. grandis* plantations were similar, but the soil exchangeable K^{+} concentrations were higher in the Brooklands grassland and the 2 year old *E. grandis* plantation when compared to the 8 and 13 year old *E. grandis* plantations. In summer, soil total K^{+} concentrations decreased with increased *E. grandis* plantation age.

Soil total and exchangeable Mg^{2+}, soil total K^{+} and soil total Ca^{2+} concentrations were higher in the Driekop grassland when compared with the Brooklands grassland, while soil exchangeable K^{+} and Ca^{2+} concentrations were similar. Soil total and exchangeable Mg^{2+}, K^{+} and Ca^{2+} concentrations were lower in the *P. patula* plantations when compared with the *E. grandis* plantations, except for the soil exchangeable Ca^{2+} concentration in the 8 year old *E. grandis* plantation, which was lower when compared with that of the other *E. grandis* plantations as well as the *P. patula* plantations.

Figure 17. Soil total and exchangeable Mg^{2+} (mg kg^{-1}) in the a) the Driekop grassland and the adjacent 2, 13 and 30 year old *P. patula* plantations and b) the Brooklands grassland and the 2, 8 and 13 year old *E. grandis* plantations.

fig 18 mg total and exch eucs

4.1.3. The sum of soil exchangeable basic cations

The sum of soil exchangeable basic cations (Fig. 19a) in the Driekop grassland ranged between 452 and 645 mg kg^{-1} , which was significantly higher ($p<0.05$) when compared with the range of 204 and 300 mg kg^{-1} found in the soil under the adjacent *P. patula* plantations. The sum of soil exchangeable basic cation concentrations decreased with increasing *P. patula* plantation age. The sum of soil exchangeable basic cations (Fig. 19b) in the Brooklands grassland and the 2 and 13 year old *E. grandis* plantations ranged between 397 and 653 mg kg^{-1}, while it ranged between 267 and 291 mg kg^{-1} in the 8 year old *E. grandis* plantation. The sum of soil exchangeable basic cations in the two grasslands were similar, while it was lower in the *P. patula* plantations when compared with the *E. grandis* plantations, except for the 8 year old *E. grandis* plantation, which had values in a range similar to that of the *P. patula* plantations.

Insert graphs.

Figure 19. Sum of soil exchangeable Mg^{2+}, Ca^{2+} and K^{+} (mg kg^{-1}) in the a) the Driekop grassland and the adjacent 2, 13 and 30 year old *P. patula* plantations and b) the Brooklands grassland and the 2, 8 and 13 year old *E. grandis* plantations.

4.1.4. Total and exchangeable acidic cations

Soil total Al^{3+} and Fe^{3+} (Table 6) concentrations were lower in the Driekop grassland when compared with the adjacent *P. patula* plantations. In winter, the soil exchangeable Al^{3+} in the Driekop grassland, was 130 mg kg^{-1}, which was lower when compared with the range of 180 and 301 mg kg^{-1} found in the adjacent *P. patula* plantations. However, in summer, the 2 year old *P. patula* plantation had the highest soil exchangeable Al^{3+} concentration of 400 mg kg^{-1}, whilst the soil exchangeable Al^{3+} concentrations in the *P. patula* plantations and the Driekop grassland ranged between 239 and 244 mg kg^{-1}.

Soil total Al^{3+}, Fe^{3+} and Mn^{2+} (Table 7) concentrations were lower in the Brooklands grassland when compared with the adjacent *E. grandis* plantations. Soil exchangeable Mn^{2+} concentrations were lower in the Brooklands grassland when compared with the *E. grandis* plantations. A soil exchangeable Al^{3+} concentration of 513 mg kg^{-1} found in the 8 year old *E. grandis* plantation was significantly higher ($p<0.05$), when compared with the Brooklands grassland and the 2 year old *E. grandis* plantation, which ranged between 89 and 178 mg kg^{-1}.

Soil total Al^{3+}, Fe^{3+} and Mn^{2+} concentrations were higher in the Driekop grassland and adjacent *P. patula* plantations, when compared with the Brooklands grassland and adjacent *E. grandis* plantations, except for the soil total Mn^{2+} concentration in the 30 year old *P. patula* plantation, which was similar to that of the *E. grandis* plantations. Soil exchangeable Al^{3+} and Mn^{2+} concentrations were higher in the Driekop grassland when compared with the Brooklands grassland, while soil exchangeable Fe^{3+} concentrations were similar in the two grasslands. Soil exchangeable Fe^{3+} and Mn^{2+} concentrations were similar between the *P. patula* and *E. grandis* plantations while the soil exchangeable Al^{3+} concentration was highest in the 8 year old *E. grandis* plantation.

4.1.5. Exchangeable Acidity

The soil exchangeable acidity (Fig. 20a) in the Driekop grassland and the adjacent *P. patula* plantations ranged between 0.7 and 1.6 cmol(+)kg^{-1}, with no clear trends. The soil exchangeable acidity (Fig. 20b) in the 8 year old *E. grandis* plantation was approximately 2.0 cmol(+)kg^{-1}, which was significantly higher ($p<0.05$) when compared with the Brooklands grassland and the 2 year old *E. grandis* plantation, which ranged between 0.4 and 0.9 cmol(+)kg^{-1}. The soil exchangeble acidity in the 13 year old *E. grandis* plantation ranged between 1.3 and 1.6 cmol(+)kg^{-1}.

Both grasslands had higher soil exchangeable acidities in summer, but the seasonal trend varied in the plantations. The 2 year old *P. patula* plantation had a higher soil exchangeable acidity compared with the 2 year old *E. grandis* plantation, but the older *P. patula* plantations had lower soil exchangeable acidities compared with the older *E. grandis* plantations.

Figure 20. Soil exchangeable acidity (cmol(+)kg^{-1}) in a) the Driekop grassland and the adjacent 2, 13 and 30 year old *P. patula* plantations and b) the Brooklands grassland and the 2, 8 and 13 year old *E. grandis* plantations.

4.1.6. Aluminium saturation

The soil aluminium saturation (Fig. 21a) in the Driekop grassland ranged between 17.7 and 35.7%, which was lower when compared with the range of 39.7 and 63.3% found in the adjacent *P. patula* plantations. The soil aluminium saturation (Fig. 21b) in the 8 year old *E. grandis* plantation ranged between 66.7 and 75.7%, which was significantly higher ($p<0.05$) when compared with the Brooklands grassland and the 2 year old *E. grandis* plantation, which ranged between 17.5 and 39.0%. The aluminium saturation ranged between 40.2 and 55.2% in the 13 year old *E. grandis* plantation.

The soil aluminium saturation was highest in summer in both grasslands and plantations, except for the 2 year old *E. grandis* plantation, which had similar values in both seasons. The two grasslands had similar soil aluminium saturation percentages. However, the *P. patula* plantations and the 13 year old *E. grandis* plantation had similar values while the 8 year old *E. grandis* plantation had the highest values.

Figure 21. Percentage soil Al^{3+} saturation in a) the Driekop grassland and the adjacent 2, 13 and 30 year old *P. patula* plantations and b) the Brooklands grassland and the 2, 8 and 13 year old *E. grandis* plantations.

4.1.7. Ca:Al ratios

The soil Ca:Al ratios (Table 6) ranged between 1.0 and 2.5 in the Driekop grassland while it ranged between 0.5 and 0.9 in the *P. patula* plantations. The soil Ca:Al ratios were higher in winter in the Driekop grassland and the *P. patula* plantations, except for the 30 year old *P. patula* plantation, which had similar soil Ca:Al ratios in both seasons.

The soil Ca:Al ratios (Table 7) ranged between 1.4 and 3.4 in the Brooklands grassland and the 2 year old *E. grandis* plantation, while the 8 year old *E. grandis* plantation had a Ca:Al ratio of 0.3 and the 13 year old *E. grandis* plantation, had Ca:Al ratios, which ranged between 1.1 and 0.7.

In winter, both grasslands had Ca:Al ratios over the value of 2, but in summer it was approximately 1. The seasonal trends of soil Ca:Al ratios in both plantations varied but the differences between winter and summer were smaller in the plantations compared with the seasonal variation found in the grasslands. The *P. patula* plantations and the 2 year old *E. grandis* plantation had similar soil Ca:Al ratios, but the 8 and 13 year old *E. grandis* plantations had the lowest soil Ca:Al ratios.

4.1.8. Total N, P and C

There were no significant differences in soil total N, P and C (Tables 6 & 7) when comparing the grasslands with the plantations. However, soil total N, P and C were higher in the Driekop grassland and adjacent *P. patula* plantations when compared with the Brooklands grassland and adjacent *E. grandis* plantations.

Soil total N (Fig. 22a) ranged between 0.2 and 0.4% in the Driekop grassland and adjacent *P. patula* plantations. However, soil total N (Fig. 22b) was less than 0.1% in the Brooklands grassland and adjacent *E. grandis* plantations. Soil total N ranged between 0.26 and 0.40% in the 13 year old *P. patula* plantation while it ranged between 0.19 and 0.27% in the 2 and 30 year old *P. patula* plantations. Soil total N

concentrations ranged between 0.03 and 0.10% in the 2 and 8 year old *E. grandis* plantations and ranged between 0.14 and 0.63% in the 13 year old *E. grandis* plantation.

Figure 22. Soil total N (%) concentration in a) the Driekop grassland and the adjacent 2, 13 and 30 year old *P. patula* plantations and b) the Brooklands grassland and the 2, 8 and 13 year old *E. grandis* plantations.

Soil total P concentrations ranged between 0.02 and 0.04% in the Driekop grassland while it ranged between 0.05 and 0.06% in the adjacent *P. patula* plantations. Soil total P concentrations ranged between 0.01 and 0.02% in the Brooklands grassland and ranged between 0.02 and 0.04% in the adjacent *E. grandis* plantations.

Soil total C concentrations ranged between 2.5 and 3.3% in the Driekop grassland while it ranged between 2.5 and 3.5% in the adjacent *P. patula* plantations. Soil total C concentrations ranged between 1.1 and 1.5% in the Brooklands grassland while it ranged between 1.5 and 2.2% in the adjacent *E. grandis* plantations. Soil total C concentrations were higher in winter in the grasslands and plantations, except for the 2 and 13 year old *P. patula* plantations. In summer, soil total C concentrations decreased with increasing *P. patula* plantation age.

4.1.9. C:N ratios

Soil C:N ratios (Table 6) in the Driekop grassland, the 2 and 30 year old *P. patula* plantations ranged between 12 and 16, except for the 13 year old *P. patula* plantation, which had soil C:N ratios, which ranged between 8 and 10. In winter, soil C:N ratios (Table 7) of the Brooklands grassland and the 8 year old *E. grandis* plantation were 56 and 43, respectively, which were higher than the rest. However, the summer soil C:N ratios of the Brooklands grassland and the 8 year old *E. grandis* plantation were similar to the soil C:N ratios of the 2 and 13 year old *E. grandis* plantations in both seasons, which ranged between 14 and 25. Soil C:N ratios were lower in the Driekop grassland and adjacent *P. patula* plantations when compared with the Brooklands grassland and adjacent *E. grandis* plantations.

4.1.10. Anaerobic Nitrogen (N) mineralisation index

In winter, the anaerobic N mineralisation indices (Table 6) in the Driekop grassland and the adjacent *P. patula* plantations ranged between 15.0 and 18.8 μgNg^{-1}dry soil day^{-1}. However, in summer, the anaerobic N mineralisation index was 2.4 μgNg^{-1}dry soil day^{-1} in the Driekop grassland while it ranged between 7.8 and 9.5 μgNg^{-1}dry soil day^{-1} in the *P. patula* plantations. In both seasons, the soil anaerobic N mineralisation

index was highest in the 13 year old *P. patula* plantation and lowest in the 30 year old *P. patula* plantation.

The anaerobic N mineralisation indices (Table 7) ranged between 1.8 and 10.6 μgNg^{-1}dry soil day^{-1} in the Brooklands grassland, the 2 and 13 year old *E. grandis* plantations, while the 8 year old *E. grandis* plantation had an anaerobic N mineralisation index of 17.2 μgNg^{-1}dry soil day^{-1}.

In winter, the anaerobic N mineralisation index was higher in the Driekop grassland when compared with the Brooklands grassland, while in summer, it was higher in the Brooklands grassland. The 2 and 30 year old *P. patula* plantations had anaerobic N mineralisation indices which were higher when compared with the 2 and 13 year old *E. grandis* plantations, in both seasons. In winter, the 13 year old *P. patula* and the 8 year old *E. grandis* had similar values, whilst in summer, the 13 year old *P. patula* plantation had a lower anaerobic N mineralisation index compared with the 8 year old *E. grandis* plantation.

4.2.Litter

4.2.1. Total basic cations

Litter total base cation concentrations were generally lower in the grasslands when compared with the plantations (Tables 8 & 9), except for litter total K^+ concentrations in the Driekop grassland, which were higher when compared with the adjacent *P. patula* plantations. Litter total Ca^{2+} concentrations (Fig. 23a) increased with *P. patula* plantation age.

Litter total Mg^{2+} and K^+ concentrations in the Brooklands grassland were similar to that of the *E. grandis* plantations. In summer, the litter total Ca^{2+} concentration (Fig. 23b) decreased with increased *E. grandis* plantation age.

In winter, litter total basic cation concentrations in the Driekop grassland were similar to that found in the Brooklands grassland. However, in summer, litter total basic cation concentrations were higher in the Brooklands grassland. Litter total basic cation concentrations were lower in the *P. patula* plantations when compared with the *E. grandis* plantations, except for the litter total Na^+ concentration of the 2 year old *P. patula* in winter, and the litter total Ca^{2+} concentration of the 30 year old *P. patula* in summer, which were higher in the *P. patula* plantations.

Insert table 8

insert table 9

Fig 23 litter total Ca

4.2.2. Total acidic cations

Generally, litter total Al^{3+} and Fe^{3+} (Fig 24) concentrations were higher, while litter total Mn^{2+} concentrations were lower, in the grasslands when compared with the adjacent plantations (Tables 8 & 9).

Litter total Al^{3+}, Fe^{3+} and Mn^{2+} concentrations were higher in the Driekop grassland when compared with the Brooklands grassland, except for the litter total Fe^{3+} of the Brooklands grassland in winter. Litter total Al^{3+}, Fe^{3+} and Mn^{2+}concentrations were higher in the *P. patula* plantations when compared with the *E. grandis* plantations. However, in summer, litter total Fe^{3+} concentrations of the 2, 8 and 13 year old *E. grandis* plantations were higher when compared with the 2, 13 and 30 year old *P. patula* plantations, respectively.

Insert litter total fe Fig 24

4.2.3. Total N, P and C

Litter total N concentrations (Fig. 25a) ranged between 0.18 and 0.43% in the Driekop grassland, while it ranged between 0.12 and 0.89% in the adjacent *P. patula* plantations. In summer, the litter total N concentration of 0.70% found in the 2 year old *P. patula* plantation was significantly higher ($p<0.01$) when compared with 0.12 and 0.36% found in the 13 and 30 year old *P. patula* plantations, respectively.

Litter total N concentrations (Fig. 25b) ranged between 0.04 and 0.31% in the Brooklands grassland while it ranged between 0.19 and 0.81% in the adjacent *E. grandis* plantations. In winter, the litter total N concentration of 0.31% found in the Brooklands grassland was significantly lower ($p<0.05$) when compared with litter total N concentrations found in the *E. grandis* plantations. The litter total N concentration, in winter, of 0.58% found in the 2 year old *E. grandis* plantation was significantly lower ($p<0.05$) when compared with 0.81% found in the 13 year old *E. grandis* plantation.

Litter total N concentrations were higher in the Driekop grassland and adjacent *P. patula* plantations when compared with the Brooklands grassland and adjacent *E. grandis* plantation, except the litter total N concentration of the 8 year old *E. grandis* plantation, in summer, which was higher when compared with the 13 year old *P. patula* in summer. The winter litter total N concentrations of the *P. patula* and *E. grandis* plantations increased with increased plantation age.

The litter total P and C concentrations (Tables 8 & 9) in the grasslands and the plantations were similar, except for the litter total P concentration of 0.15% found, in summer, of the 2 year old *P. patula* plantation, which was significantly higher ($p<0.01$) when compared with the Driekop grassland, 13 and 30 year old *P. patula* plantations.

Insert fig 25. Litter total N.

Figure 25. Litter total N (%) in a) the Driekop grassland and the adjacent 2, 13 and 30 year old *P. patula* plantations and b) the Brooklands grassland and the 2, 8 and 13 year old *E. grandis* plantations.

4.2.4. C:N ratios

The litter C:N ratios (Table 8) in the Driekop grassland, which ranged between 114 and 296, were higher when compared with the adjacent *P. patula* plantations which ranged between 55 and 277, except for the 13 year old *P. patula* plantation, which had a C:N ratio of 345. The litter C:N ratios (Table 9) in the Brooklands grassland, which ranged between 152 and 1120, were higher when compared with the litter C:N ratios of the adjacent *E. grandis* plantations, which ranged between 50 and 307. Litter C:N ratios were lower in the Driekop grassland when compared with the Brooklands grassland, while litter C:N ratios of the *P. patula* plantations were similar to the litter C:N ratios of the *E. grandis* plantations. In winter, the litter C:N ratios decreased with increased age in the plantations.

4.3.Foliage

4.3.1. Total basic cations

In winter, foliar total K^+ and Mg^{2+} (Fig. 26a) concentrations (Table 10) were lower in the Driekop grassland when compared with the adjacent *P. patula* plantations, while in summer, the reverse pattern prevailed. The foliar total Ca^{2+} concentrations ranged between 4961 and 4846 mg kg^{-1} in the Driekop grassland, while it ranged between 2573 and 9423 mg kg^{-1} in the *P. patula* plantations and increased with increased *P. patula* plantation age.

Generally, foliar total Mg^{2+} (Fig. 26b), Ca^{2+} and K^+ concentrations (Table 11) were significantly lower ($p<0.05$) in the Brooklands grassland when compared with the adjacent *E. grandis* plantations. Foliar total Na^+ concentrations were significantly lower ($p<0.05$) in the Brooklands grassland and the 2 year old *E. grandis* plantation when compared with the 8 and 13 year old *E. grandis* plantations.

The Driekop grassland had higher foliar total basic cation concentrations when compared with the Brooklands grassland, except for the winter foliar total Mg^{2+} and K^+ concentrations, which were higher in the Brooklands grassland. The *E. grandis* plantations had higher foliar total basic cation concentrations when compared with the *P. patula* plantations.

Insert table 10

Insert table 11

Insert fig 26. Foliar total Mg.

4.3.2. Total acidic cations

Foliar total Al^{3+} and Mn^{2+} concentrations (Table 10) were lower in the Driekop grassland when compared with the adjacent *P. patula* plantations. In contrast, foliar total Fe^{3+} concentrations in the Driekop grassland, which ranged between 561 and 1218 mg kg^{-1}, were significantly higher ($p<0.05$) when compared with the range of 93 and 332 mg kg^{-1} found in the *P. patula* plantations.

Foliar total Al^{3+} concentrations (Table 11) were similar in the Brooklands grassland and the adjacent *E. grandis* plantations. However, foliar total Mn^{2+} concentrations were lower while foliar total Fe^{3+} concentrations were higher in the Brooklands grassland when compared with the adjacent *E. grandis* plantations.

Foliar total Al^{3+} concentrations were similar in the grasslands while foliar total Mn^{2+} and Fe^{3+} concentrations were higher in the Driekop grassland when compared with the Brooklands grassland. Foliar total acidic concentrations were higher in the *P. patula* plantations when compared with the *E. grandis* plantations, except the foliar total Fe^{3+} concentration of the 8 year old *E. grandis* plantations, in winter, which was higher than the foliar total Fe^{3+} concentration of the 13 year old *P. patula* in winter.

4.3.3. Total N, P and C

Foliar total N (Fig. 27 & 28) and the upper canopy foliar total P concentrations (Tables 10 & 11), in winter, were significantly lower ($p<0.05$) in the grasslands when compared with the adjacent plantations. Foliar total N and P concentrations in the grasslands ranged between 0.46-0.59% and 0.05-0.15% respectively, while the foliar total N and P concentrations in the plantations ranged between 0.70-2.46% and 0.10-0.22%, respectively. In summer, the 2 year old *P. patula* plantation had a significantly higher ($p<0.01$) foliar total N concentration (1.52%) (Fig 27) in the upper canopy when compared with that of the lower canopy (0.86%). In winter, the 2 year old *E. grandis* plantation had a significantly higher ($p<0.01$) foliar total N concentration (1.69%) (Fig 28), in the upper canopy, when compared with that of the lower canopy (1.37%).

Foliar total C concentrations (Table 10) in the Driekop grassland were similar to that of the adjacent *P. patula* plantations. In contrast, foliar total C concentrations (Table 11) in the Brooklands grassland, which ranged between 38 and 52%, were significantly higher ($p<0.05$) when compared with the adjacent *E. grandis* plantations, which ranged between 32 and 46%. Foliar total C concentrations in the Driekop grassland were similar to that of the Brooklands grassland while the *P. patula* plantations had higher foliar total C concentrations compared with the *E. grandis* plantations.

Insert foliar total N fig 27 PINES

FOLIAR TOTAL N EUCS FIG 28

4.3.4. Ratios

In winter, the foliar C:N ratio (Tables 10 & 11), which was 115 in the grasslands, was significantly higher ($p<0.01$) when compared with the adjacent plantations, which ranged between 21 and 49. Foliar C:N ratios in the Driekop grassland were similar to that of the Brooklands grassland. Foliar C:N ratios in the *P. patula* plantations were similar to that of the *E. grandis* plantations.

In winter, the P:N ratios (Tables 10 & 11) in the older *P. patula* and older *E. grandis* plantations ranged between 7 and 9, which were below the optimal range of 10-15, as calculated by Linder (1995) and decreased with increased age in both plantations. However, in summer, the P:N ratios in all the *P. patula* plantations and the 8 year old *E. grandis* plantation were within the optimal range, while the 2 and 13 year old *E. grandis* plantations had P:N ratios above the optimal range.

The K:N ratios (Tables 10 & 11) in the upper canopies of the *P. patula* plantations ranged between 23-33, which were below the optimal range of 35-45 (Linder 1995). The K:N ratios in the *E. grandis* plantations ranged between 46-150, which were above the optimal range, but the K:N ratios decreased with increased plantation age.

4.3.5. Amino acids

The amino acids (Table 12) were significantly lower ($p<0.01$) in the grasslands when compared with the plantations. The Driekop and Brooklands grasslands had amino acid values, which ranged between 0.01 (methionine) to 0.12% (glutamic acid). The *P. patula* and *E. grandis* plantations had amino acid values, which ranged between 0.4 and 0.6%. In the *P. patula* plantations, the amino acids ranged from 0.04 (HO proline) to 1.19% (glutamic acid). The following amino acids increased with increased age in the *P. patula* plantations: alanine, arginine, glycine, histidine, isoleucine, leucine, phenylalanine, serine, threonine and valine. Concentrations of arginine in the 2, 13 and 30 year old *P. patula* plantations were 0.61 ± 0.16, 0.65 ± 0.16, 0.73 ± 0.02

percent, respectively. In the *E. grandis* plantations the amino acids ranged from 0.05 (HO proline) to 0.82% (leucine). The following amino acids increased with increased age in *E. grandis* plantations: arginine, isoleucine, leucine, phenylalanine and proline. Concentrations of arginine in the 2, 8 and 13 year old *E. grandis* plantations were 0.61 ± 0.24, 0.68 ± 0.14, 0.75 ± 0.02 percent, respectively.

Arginine concentrations were found at slightly higher concentrations relative to the other amino acids in plantation foliage. In the grasslands, the arginine concentration was found in the 0.08-0.119% range, in the same range as majority of the other amino acids. In contrast, the arginine concentration in the plantations, was found in the 0.60-0.79% range, while majority of the other amino acids were found in the 0.40-0.59% range.

Table 12. Winter, foliar amino acid (%) means and distribution between the i) Driekop and Brooklands grasslands and ii) averaged values of the age classes within the *P. patula* and *E. grandis* plantations.

i) Driekop & Brooklands grasslands				
Driekop grassland				
0.000-0.039%	**0.040-0.079%**	**0.080-0.119%**	**0.120-0.159%**	**0.160-0.200%**
Histidine HO proline Methionine	Isoleucine Lysine Serine Threonine Tyrosine Glycine	Alanine Arginine Leucine Phenylalanine Proline Valine Aspartic acid	Glutamic acid	
Brooklands Grassland				
0.000-0.039%	**0.040-0.079%**	**0.080-0.119%**	**0.120-0.159%**	**0.160-0.200%**
Histidine HO proline Methionine	Isoleucine Lysine Serine Threonine Tyrosine Aspartic acid	Alanine Arginine Leucine Phenylalanine Proline Valine Glutamic acid Glycine		
ii) averaged *P. patula* & *E. grandis* plantations				
***P. patula* plantations**				
0.000-0.190%	**0.200-0.390%**	**0.400-0.590%**	**0.600-0.790%**	**0.800-1.000%**
HO Proline Methionine	Histidine	Glycine Serine Threonine Tyrosine Proline Valine Isoleucine Alanine	Arginine Leucine Phenylalanine Aspartic acid Lysine	Glutamic acid
***E. grandis* plantations**				
0.000-0.190%	**0.200-0.390%**	**0.400-0.590%**	**0.600-0.790%**	**0.800-1.000%**
HO-proline Methionine	Histidine	Glycine Serine Threonine Tyrosine Proline Valine Isoleucine Alanine Aspartic acid Lysine	Arginine Phenylalanine Glutamic acid	Leucine

The categorisation of values in the above table does not account for standard deviations.

4.3.6. Protein

The foliar protein contents were significantly lower ($p<0.01$) in the grasslands when compared with that of the plantations. The foliar protein content was 2.58 ± 0.72% in the Driekop grassland while it was 9.42 ± 1.37, 10.19 ± 0.72 and 11.16 ± 0.36% in the adjacent 2, 13 and 30 year old *P. patula* plantations, respectively. The foliar protein contents was 2.32 ± 0.12% in the Brooklands grassland while it was 9.04 ± 2.02, 9.79 ± 0.83 and 11.01 ± 0.04% in the adjacent 2, 8 and 13 year old *E. grandis* plantations, respectively. The protein content in Driekop grassland was similar to that of the Brooklands grasslands, while the foliar protein contents in the *P. patula* plantations were similar to that of the *E. grandis* plantations. The foliar protein content increased with increased plantation age.

5. DISCUSSION

5.1. Introduction

The following discussion is based on comparisons made between (i) the Driekop grassland and adjacent *P. patula* plantations (ii) the Brooklands grassland and adjacent *E. grandis* plantations (iii) the Driekop and Brooklands grasslands and (iv) the *P. patula* and *E. grandis* plantations. Discussions on soil moisture and rates of N mineralisation are linked with litter dynamics. It is important to note that the sites used and compared, in this study, differ in many respects. The 13 year old *P. patula* plantation and the 8 year old *E. grandis* plantation had higher soil clay contents compared with the other sites. Standard silvicultural practices such as pruning and thinning of the 2 and 13 year old *P. patula* plantations, respectively, as well as burning of the 8 year old *E. grandis* plantation, prior to planting, increased the complexity of comparing the soil nutrients status using a confounded time series. Furthermore, the unfertilized *P. patula* plantations are compared with fertilized *E. grandis* plantations, which contributed to the uncertainties associated with comparing different species, located on different geologies, at different altitudes and with uncertain site specific histories. Seasonal trends are distinguished and discussed, but it rained during the winter sampling, and thus the results were not a true reflection of the physical conditions prevalent during winter. Foliar nutrients between the lower and upper canopies, within the *P. patula* and *E. grandis* plantations are briefly addressed.

5.2. Grasslands versus plantations

5.2.1. Soil pH

The soils under the *P. patula* and *E. grandis* plantations were more acidic than the soils under adjacent grasslands. The lower soil pH values observed in the soils under the *P. patula* plantations (pH 4.8-5.2) compared with pH 5.3 found in soil of the Driekop grassland, confirmed earlier work of Ndala (2001), Echeverria (2000) and Nowicki (1997), who found that the soil pH in grasslands ranged between 4.55-5.78, while values ranged between 3.26-4.98 in adjacent *P. patula* plantations. The lower

soil pH under the *P. patula* plantations could be a result of the continual deposition of litter containing acidic compounds onto the soil surface, the accumulation of basic cations in the litter layers, ammonium nutrition of plantations and the exportation of basic cations through successive harvesting of biomass.

The soil pH under the *E. grandis* plantations ranged between 4.6 and 5.3, while it ranged between 5.5 and 5.6 in the Brooklands grassland. Louw (1997) found a soil pH of 4.93 under *E. grandis* sites, underlain by granite in Mpumalanga, which was in agreement with the results of this study. Higher concentrations of H^+ ions in plantations were possibly a result of higher cumulative productivity and uptake of NH_4^+ and other cations in the plantations relative to the grasslands. The uptake of ammonium is associated with the release of H^+ ions, from the plant into the soil. Plantation canopies also intercept higher levels of atmospheric pollutants, which may contribute to soil acidification processes because of the acidic nature of atmospheric compounds, but atmospheric compounds also contain basic cations (Olbrich 1995), which would buffer soil acidity. Lower soil pH in the soil under plantations may be a result of the continual removal of cations through successive harvesting and the resultant exportation of basic cations from the system. After several rotations, the exportation of nutrient cations through harvesting and rapid oxidation of litter through clearfelling significantly intensifies soil acidification processes (Scholes & Nowicki 1998). The higher soil acidity observed in the soils under plantations in this study, as compared to adjacent grasslands, is therefore compatible with previous studies and was a result of a combination of factors.

The soil pH values of the older *P. patula* plantations, underlain by dolomite, were higher when compared with the older *E .grandis* plantations, underlain by granite. The lower pH in the soils under the older *E. grandis* plantations, were probably because of previous *E. grandis* plantations, planted on the same sites. *Eucalyptus* plantations have shorter rotation times, which means that the periods of rapid growth rates during the early stages of stand development and the exportation of nutrients occurred more frequently compared with that of the *Pinus* plantations. Thus, the rotations of previous *E. grandis* plantations, planted on the same site, probably influenced the current status of the soil pH.

Louw & Scholes (2002) found higher soil pH values in soils underlain by dolomite compared with soils underlain by granite. The soil pH of the Driekop grassland, underlain by dolomite, was lower when compared with the Brooklands grassland, underlain by granite, which contradicted the findings of Louw & Scholes (2002). However, the Driekop grassland was burnt 15–20 months prior to sampling, whereas the Brooklands grassland was burnt 3-8 months prior to sampling. The relatively recent ash inputs into the soil of the Brooklands grassland, would have raised the soil pH (Tainton 1984), resulting in the relatively higher soil pH values in the soil underlain by granite.

5.2.2. Soil basic and acidic cations

There is evidence for soil acidification under the *P. patula* plantations through reduced soil pH and decreased soil total and exchangeable basic cation concentrations, compared with the adjacent Driekop grassland. Decreased basic cation concentrations in the soil under *P. patula* plantations corresponded with higher concentrations of soil exchangeable aluminium, soil exchangeable acidity in the older *P. patula* plantations and higher aluminium saturation compared with the adjacent Driekop grassland. High concentrations of H^+ ions impact the composition of cations on the soil exchange complex. Soil total, exchangeable Mg^{2+}, K^+ and Ca^{2+} concentrations and the sum of soil exchangeable cations, which ranged between 204 and 300 mg kg^{-1} in the soils under the *P. patula* plantations, were lower when compared with the adjacent Driekop grassland, which had a sum of soil exchangeable cations ranging between 452 and 645 mg kg^{-1}. The results in this study show at least a 220 mg kg^{-1} reduction in base cations between the Driekop grassland and the adjacent, 2^{nd} rotation, 13 year old *P. patula* plantation. When the soil pH is below 5, H^+ ions react with silicate clays thereby releasing exchangeable aluminium (Jordan 1985) into the soil solution and inducing the replacement of basic cations on the exchange complex. Low soil pH under *P. patula* plantations resulted in the solubilisation of acidic cations such as aluminium, which replaced the basic cations on the exchange complex. The basic cations may have leached into soil layers deeper than the upper 20 cm, sampled in this study. Furthermore, the sum of exchangeable cations decreased with increased age in *P. patula* plantations, which suggested a trend of declining concentrations of basic cations with increased plantation biomass and litter accumulation on the soil surface. *P. patula*

needles have longer longevity and the litter decomposes slowly, which results in the accumulation of nutrients contained in the live foliage and the litter layer.

Aluminium liberated by mineral dissolution, dissociation of Al-organic matter complexes and the replacement of basic cations by acidic cations on the cation exchange complex, resulted in enhanced soil exchangeable acidity and a higher aluminium saturation on the cation exchange complex. Jordan (1985) found that aluminium was the dominant cation associated with soil acidity in tropical regions. South African soils with low soil pH values have high soil exchangeable aluminium (Tainton 1984). The aluminium saturation in the *P. patula* plantations ranged between 39.7 and 63.3%, while it ranged between 17.7 and 35.7% in the adjacent Driekop grassland. Echevierra (2000) found acid saturation values which ranged between 67 and 93% in *P. patula* plantations. The soil exchangeable acidity found under *P. patula* plantations ranged between 0.95 and 1.55 cmol(+)kg^{-1}, which was within the range of 0.34 to 3.12 cmol(+)kg^{-1} observed in the dolomitic sites studied by Louw & Scholes (2002).

In contrast, the soil total and exchangeable basic cations concentrations in the *E. grandis* plantations showed no clear trends when compared with the adjacent Brooklands grassland. The sum of soil exchangeable basic cation concentrations in the 2 and 13 year old *E. grandis* plantations ranged between 484 and 653 mg kg^{-1}, while it ranged between 397 and 545 mg kg^{-1} in the Brooklands grassland. The soil exchangeable basic cation concentrations found in the Brooklands grassland were similar to that found in the 2 and 13 year old *E. grandis* plantations, in spite of successive harvesting of the *E. grandis* plantations. *E. grandis* plantations can extract nutrients from deeper soil horizons relative to the *P. patula* plantations and therefore have less of an impact on the uppermost soil horizons, relative to the *P. patula* plantations. *P. patula* locate most of their roots near the soil surface, while *Eucalyptus* roots systems exploit both shallow and very deep soils (Schönau & Fitzpatrick 1981). *E. grandis* plantations enrich the surface soil layers by extracting nutrients from deeper soil horizons and returning the nutrients through rapid litterfall and decomposition. The leaves of *E. grandis* are also shorter lived compared with *Pinus* needles and nutrient cycling is more rapid in the *E. grandis* plantations, whereas the *Pinus* plantations extract nutrients from the upper soil horizons, retain its leaves on the tree for a longer

period of time and the litterfall is slowly decomposed and returned to the plant through direct uptake from the litter layer and the nutrients are not returned to the soil as in the *E. grandis* plantations.

However, the 8 year old *E. grandis* plantation showed soil nutrient characteristics similar to that of the *P. patula* plantations. The 8 year old *E. grandis* plantation had a lower sum of soil exchangeable basic cation concentrations, which ranged between 267 and 291 mg kg^{-1}, a corresponding higher soil exchangeable aluminium concentration of 513 mg kg^{-1}, a higher soil exchangeable acidity of approximately 2.0 cmol(+)kg^{-1}, and a higher aluminium saturation of 66.7-75.7% when compared with the adjacent Brooklands grassland, 2 and 13 year old *E. grandis* plantations. A possible explanation for the variation in nutrient status found in the soil under the 8 year old *E. grandis* plantation, will be dealt with in section 5.3.1.

The *E. grandis* plantations upper soil total base cation reserves were greater than those of the *P. patula* plantations, irrespective of inherent geological differences. The sum of soil exchangeable basic cation concentrations in the *E. grandis* plantations ranged between 267 and 653 mg kg^{-1}, while it ranged between 204 and 300 mg kg^{-1} in the *P. patula* plantations. Thus, the sum of soil exchangeable basic cation concentrations was higher in the *E. grandis* plantations, underlain by granite, when compared with the *P. patula* plantations, underlain by dolomite. However, the sum of soil exchangeable basic cation concentrations in the Brooklands grassland ranged between 397 and 545 mg kg^{-1}, while it ranged between 452 and 645 mg kg^{-1} in the Driekop grassland. The range of the sum of soil exchangeable basic cations was lower in the Brooklands grassland, underlain by granite, when compared with the Driekop grassland, underlain by dolomite. According to Louw (1997) the granite derived soils on the escarpment were relatively low in basic cations, compared with the dolomitic soils, which supports the findings of the comparison made between the Driekop and Brooklands grasslands. However, it is in contrast to the findings of this study, when comparing the plantations, which implies that *P. patula* and *E. grandis* plantations have altered the soil nutrient status of the upper 20 cm of soil when compared with the soil found under adjacent grasslands. The differences in the soil exchangeable basic cation concentrations, when comparing the *P. patula* and *E. grandis* plantations, were possibly a result of rates of litter decomposition, nutrient uptake mechanisms and

different rooting depths. The slow rate of *Pinus* litter decomposition and the uptake of nutrients from the litter layer, directly into the *Pinus* roots, have resulted in reduced soil exchangeable basic cation concentrations in the upper soil layers. In contrast, the deeper rooting *Eucalyptus* and the associated transfer of nutrients from deeper soil horizons, relatively rapid litterfall and decomposition resulted in an enrichment of the upper soil horizons under *E. grandis* plantations. The upper 20 cm of soil may reflect the impacts of *P. patula* on the upper soils horizons, but cannot be directly compared with *E. grandis* because of different rooting strategies and rates of nutrient transformations.

In addition to the different rooting and nutrient uptake strategies of *P. patula* and *E. grandis* plantations, the nutrient allocation patterns between the plantations differ. *E. grandis* sequesters higher quantities of Ca^{2+} than *P. patula*, which leads to rapid soil depletion through harvesting (Scholes & Scholes 1999). Higher quantities of nutrients are removed through the harvesting of *E. grandis* plantations relative to *P. patula* plantations. *E. grandis* plantations should therefore have a greater impact on the soil base cation concentrations as a result of the relative quantities of nutrients stored within the tree biomass. Furthermore, *E. grandis* plantations have shorter rotations times, which leads to higher quantities of base cation removal more frequently compared with the harvesting of *P. patula* plantations. However, Scholes & Scholes (1999) calculated an approximate input and output analysis for a landscape afforested with *P. patula* and *E. grandis* plantations in Mpumalanga underlain by granitic bedrock. They found that the *P. patula* plantations were losing 42.9 N, 3.68 P, 2.52 K^+, 1.87 Ca^{2+}, 11.23 Mg^{2+} (kg ha^{-1} yr^{-1}) whereas *E. grandis* plantations were losing 15.3 N, 0.68 P, 1.12 K^+, 1.57 Ca^{2+} and 4.13 Mg^{2+} (kg ha^{-1} yr^{-1}). The soil under *P. patula* plantations was losing more nutrients as a result of the accumulation of nutrients in the litter layers.

5.2.3. Soil Ca:Al ratios

The soil Ca:Al ratio is a commonly used index in determining forest vitality, although the ratio has not been useful in determining forest vitality in Swedish forests (Binkley & Högberg 1997). According to Sugarman (1999), on the eastern escarpment of South

Africa, Ca:Al ratios above the value of 1, indicate forest vitality, whereas values below 1 indicate potential adverse effects of aluminium on plant growth. The Ca:Al ratio ranged between 1.0 and 2.5 in the Driekop grassland, which was higher when compared with the range between 0.5 and 0.9 in the adjacent *P. patula* plantations. The soil Ca:Al ratios, has in other studies, indicated adverse effects on plant growth in the *P. patula* plantations, while the potential for risk of aluminium toxicity in the Driekop grassland was low. The Ca:Al ratios in the Brooklands grassland and the 2 year old *E. grandis* plantations were similar to and above the value of 1. However, the 8 and 13 year *E. grandis* plantations had Ca:Al ratios of 0.3 and 0.7 respectively, which indicated that the aluminium concentrations were high relative to calcium and were potentially having adverse effects on plant growth.

5.2.4. The influence of site histories on the soil nutrients status of the plantations

The sites on which the *P. patula* plantations were planted, were converted from grasslands to plantations around the year 1920 while the sites on which the *E. grandis* plantations were planted, were converted to plantations around the year 1937. The 2 and the 13 year old *P. patula* sites had *Eucalyptus* plantations planted prior to that of *Pinus*. Two rotations of *E. grandis* and two rotations of *P. patula* planted on the 2 year old *P. patula* site, may explain the higher soil exchangeable acidity and exchangeable aluminium concentration found in the soil under the 2 year old *P. patula* plantation compared with the older plantations. However, the soil pH in the 2 year old *P. patula* plantation was higher compared with the other *P. patula* plantations but Jordan (1985) found that most acidic soils of tropical systems were characterized by higher aluminium concentrations rather than H^+ concentrations.

The cumulative physiological effects of consecutive *E. grandis* and *P. patula* plantations on the 2 and 13 year old *P. patula* sites may have rendered the *P. patula* sites relatively more impacted by afforestation compared with the *E. grandis* sites, which possibly only had *Eucalyptus* plantations planted on the sites. However, uncertainty pertaining to the history of the *E. grandis* sites, geological differences as well as physiological differences between the *P. patula* and *E. grandis* plantations render it difficult to compare the relative effects of *P. patula* and *E. grandis*

plantations on the soil nutrient status. Therefore, the findings of this study cannot be used to infer direct comparative effects of *P. patula* and *E. grandis* plantations on the nutrient status of the soil.

5.2.5. Litter and foliar basic and acidic cations

Generally, litter and foliar total basic cation concentrations were higher, whilst litter and foliar total acidic cation concentrations were lower in the plantations when compared with the adjacent grasslands. However, litter total K^+ and foliar total Fe^{3+} concentrations were higher in the Driekop grassland when compared with the *P. patula* plantations. Magnesium and Ca^{2+} form cell wall components and are therefore contained in the litter material accumulated under the *P. patula* plantations, whereas K^+ was either retranslocated prior to abscision of the *P. patula* needles, leached or rapidly remobilised by plant roots and taken up for growth. Litter total Ca^{2+} concentrations of the older *P. patula* plantations were higher compared with the Driekop grassland because Ca^{2+} accumulates with age and the needles of the *P. patula* were older than that of the grassland foliage.

Higher litter total basic cation concentrations found in the *P. patula* plantations, did not correspond with higher soil exchangeable basic cation concentrations in the *P. patula* plantations, probably because the nutrients were accumulated in the litter layer and nutrient uptake can take place directly from the litter layer, without the nutrients passing through the soil (Scholes & Nowicki 1998). In contrast, higher litter total basic cation concentrations corresponded with a higher range of the sum of soil exchangeable basic cation concentrations found in the soil under the *E. grandis* plantations, when compared with the Brooklands grassland, which corresponds with the deeper rooting strategy of *E. grandis* and litterfall induced enrichment of surface soil layers, as previously discussed in section 5.2.2. In addition, the plantation canopy volumes and relatively large surface areas serve as receptors to atmospheric compounds, which can contain basic cations (Olbrich 1995) and could have resulted in enhanced basic cation concentrations in litter and foliage of the plantations, relative to the soil. Foliar leaching of basic cations could also have enhanced litter nutrient concentrations.

The plantations had higher soil acidic cation concentrations compared with the adjacent grasslands, in spite of higher litter total acidic cation concentrations found in the grasslands. Exudates from extensive mycorrhizal associations in the *P. patula* and *E. grandis* plantations may have chelated metals and thereby prevented their uptake by the plantations rendering plantations more tolerant of acidic soils.

The Driekop grassland, underlain by dolomite, had higher litter and foliar total basic cation concentrations and corresponding higher soil exchangeable basic cation concentrations compared with the Brooklands grassland, underlain by granite, which supports generally higher nutrient concentrations in soil underlain by dolomite, compared with granite (Louw & Scholes 2002). However, the *E. grandis* plantations, underlain by granite, had higher litter and foliar total basic cation concentrations and corresponding high soil total and exchangeable basic cation concentrations when compared with the *P. patula* plantations, underlain by dolomite. *Pinus* generally has larger quantities of foliar biomass compared with *Eucalyptus* and thus *Pinus* foliage is a more significant form of nutrient storage compared with *Eucalyptus* foliage, even though the concentrations were lower in the *Pinus* foliage. According to Nambiar & Fife (1991) *Pinus* foliage represents a small proportion of the biomass of older trees but contains a major proportion of the total nutrients whereas *Eucalyptus* foliage is a relatively less significant nutrient storage. *Pinus* foliage has greater longevity than *Eucalyptus* foliage and is therefore a sink for nutrients and a major source of nutrients for new shoot growth (Nambiar & Fife 1991).

Litter and foliar total acidic cation concentrations were higher in the *P. patula* plantations when compared with the *E. grandis* plantations, except for litter total iron concentrations of the 2, 8 and 13 year old *E. grandis* plantations, which were higher when compared with the 2, 13 and 30 year old *P. patula* plantations, respectively. The *P. patula* plantations had corresponding higher soil exchangeable aluminium concentrations and soil aluminium saturation on the cation exchange complex compared with the *E. grandis* plantations. The *P. patula* plantations were therefore taking up more aluminium compared with the *E. grandis* plantations, probably because the accumulation of basic cations in the *Pinus* litter layer resulted in the

replacement of base cations by acidic cations on the exchange complex while the *E. grandis* plantations were enriching the upper 20 cm of soil with base cations.

Rainfall may have induced lower soil pH through higher leaching rates of exchangeable basic cations (Louw 1997). The *P. patula* plantations and the adjacent Driekop grassland were located approximately 400 m higher up on the escarpment and received at least an additional 400 mm of total annual rainfall relative to the *E. grandis* plantations and the adjacent Brooklands grassland. The litter layer accumulated under the *P. patula* plantations allowed for increased surface area and time of contact between litter material and moisture, thereby allowing for greater rates of nutrient leaching compared with the poorly developed litter layer in the *E. grandis* plantations. Higher rates of leaching in the *P. patula* plantations corresponded with lower total basic cation concentrations contained in the litter layer accumulated under *P. patula* plantations compared with that of *E. grandis* litter. However, the total volume of the litter layer under *P. patula* plantations accounted for higher total nutrient quantities contained in the litter layer. Comparisons between species were further compounded by varying degrees of nutrient allocation and retranslocation patterns, prior to abscission of the leaves.

5.2.6. Soil moisture

Higher soil moisture contents under the *P. patula* plantations (29-39%) compared with the adjacent Driekop grassland (16-25%) were probably influenced by the accumulation of litter under the *P. patula* plantations. Litter on the ground surface tends to retain more water than bare soil, improves conditions for infiltration into the soil (Le Maitre *et al.* 1999; O'Connor 1985) and reduces evaporation. The litter layer under *E. grandis* plantations are generally poorly developed and the canopy cover's capacity to intercept rainfall is also believed to be low (Dye & Mostert 1994). The potential for evaporation from the soil surface is lowered in plantations, especially in plantations with closed canopies, compared with the relatively open grasslands. The forest canopy cover reduces ventilation and light penetration and thereby lowers temperatures under the canopy. The soils below the *P. patula* plantations were wetter

than below the Driekop grassland and wetter during winter than summer, which suggests the capture of drifting mist, by the high canopies, at high altitudes.

In contrast, the soils below the *E. grandis* plantations were drier (moisture content, 5-14%) than below the Brooklands grassland (12-28%), except for the 8 year old *E. grandis* plantation during winter (12%). Beard (1962) measured the amount of interception lost by plant canopies and found that grasslands lost 12.7% of precipitation while measurements and models showed that *P. patula* lost 10% (Dye 1996a cited in Le Maitre *et al.* 1999). A four year old *E. grandis* compartment on the eastern escarpment lost 4% of rainfall through canopy and litter interception (Dye 1993). *P. patula* plantations had higher leaf surface areas when compared with *E. grandis* plantations and lost higher levels of precipitation through rainfall interception. However, the *E. grandis* plantations had lower soil water contents when compared with the *P. patula* plantations. This was probably because *Eucalyptus* plantations extract more water at higher rates compared with *Pinus* (Louw 1997). Dye *et al.* (1997) demonstrated that three year old *E. grandis* trees can tap into sub-soil water reserves, reaching 8 metres below the soil surface. Furthermore, *Pinus* are relatively dormant during the winter whilst *Eucalyptus* continue to be physiologically active throughout the dry season (Dye *et al.* 1995) and *Eucalyptus* has higher rates of transpiration compared with *Pinus*.

5.2.7. Anaerobic N mineralization index

Higher rates of soil N mineralisation in the Driekop grassland and the adjacent *P. patula* plantations were found in winter, which was possibly a result of the high soil moisture contents and carbon accumulated through litterfall at the end of the previous growing season. Soil moisture is required to sustain microbiological activities (Vanlauwe *et al.* 1995) and the higher soil moisture contents of the *P. patula* plantations, in winter, were possibly a result of rainfall, which occurred a few days prior to sampling. The carbon and nitrogen stores in the soil were rapidly mobilized by microbial activities. It is possible that the C stores may have been utilized in the late winter and early spring, resulting in lower rates of anaerobic N mineralization found in mid summer. Scholes & Louw (2002) found that rates of N mineralisation

were higher during the dormant season while immobilisation was higher during the growing season, which is in agreement with the findings of this study, when comparing the Driekop grassland and the *P. patula* plantations. In summer, the rates of N mineralisation in the Driekop grassland, ranged below zero, which indicated that the microbes were utilizing N primarily for their own sustenance, while the *P. patula* plantations had positive N mineralisation rates and thus higher N availability for plant uptake. The 13 year old *P. patula* had the highest N mineralisation rate in both seasons. This was possibly because of the thinning of the 13 year old *P. patula*, which may have resulted in higher temperatures, root mortality and increased decomposition as well as reduced competitive interactions between plant and microbial immobilisation, rendering both N and C more available. However, there were no differences in the rates of N mineralisation when comparing the Brooklands grassland and the adjacent *E. grandis* plantations, except for the higher rates of N mineralisation in the 8 year old *E. grandis* plantation, which were possibly a result of higher annual rainfall and soil clay contents compared with the other *E. grandis* plantations.

Significantly lower soil pH values were accompanied by relatively higher soil exchangeable acidities and anaerobic N mineralisation indices in the *P. patula* plantations relative to the adjacent Driekop grassland. In contrast, Hart *et al.* (1994) predicted lower N mineralisation rates in forests because of rapid plant immobilisation of nitrate and ammonium N, lower soil pH and lower cation exchange capacity (Giddens *et al.* 1997) and lower temperatures in plantation soil. The higher rates of N mineralisation found in the *P. patula* plantations, compared with the adjacent Driekop grassland, may have been induced by higher soil moisture contents and higher N availability through atmospheric inputs. Furthermore, ammonium is thought to dominate acid soils typical of most coniferous forests while nitrate is thought to be the predominant N form in well aerated soils with neutral or close to neutral pH (Näsholm *et al.* 1998). The lower soil pH found under the *P. patula* plantations, would therefore have favoured the dominance of ammonium, whereas the grasslands may have had higher rates of nitrification.

The *P. patula* plantations had higher rates of N mineralisation compared with the *E. grandis* plantations, except the 8 year old *E. grandis* plantation. The Driekop grassland had higher rates of N mineralisation compared with the Brooklands

grassland. Louw & Scholes (2002) found significantly higher levels of N mineralisation in soils underlain by dolomite compared with those underlain with granite, which is in agreement with the findings of this study.

The *E. grandis* plantations did not have less organic C availability despite higher temperatures associated with its location lower down on the escarpment, associated higher rates of decomposition and higher rates of C turnover. However, the soil total carbon concentrations found between the *P. patula* and *E. grandis* plantations, did not differentiate between the labile, intermediate and passive soil carbon pools. Thus, the *E. grandis* plantations may have had a larger labile soil carbon pool when compared with the *P. patula* plantations as a result of rapid decomposition and mineralisation of *Eucalypt* leaves. Wood & Raison (1983) found that *Eucalyptus* leaves lose 30 to 50% of its weight during the first year, despite its sclerophyllous nature, provided that the soil moisture content is favourable for microbial activity (Ericsson *et al.* 1993). The higher soil moisture content found in the soil under the *P. patula* plantations may have resulted in higher rates of N mineralisation compared with that of the *E. grandis* plantations. According to Carlyle *et al.* (1990) soil P levels are also a factor influencing N mineralisation rates and the dolomitic sites had higher soil total P concentrations relative to the granitic sites but the differences in soil total N and P concentrations were not significant and were therefore probably not a contributing factor to higher rates of N mineralisation found in the *P. patula* plantations and Driekop grassland when compared with the *E. grandis* plantations and Brooklands grassland.

5.2.8. Total N, P and C

Soil total N and P concentrations were similar when comparing the grasslands and plantations. In contrast, foliar total N and P concentrations, foliar amino acid and protein contents were higher in the plantations relative to the grasslands. Higher rates of N mineralisation in the soil under the *P. patula* plantations corresponded with higher litter and foliar total N concentrations relative to the adjacent Driekop grassland. In contrast, the soil total N concentrations were not significantly different when comparing the Driekop grassland and the adjacent *P. patula* plantations. Higher

litter and foliar total N concentrations may have been a result of higher atmospheric N deposition onto plantations and higher N uptake through higher rates of N mineralisation. The higher surface area of the plantation canopies allow for higher interception of atmospheric compounds. According to Louw & Scholes (2002), sites with a positive balance in N mineralisation were unlikely to produce any significant reaction to additional N inputs whereas sites experiencing N immobilisation were more likely to produce significant responses in tree growth. Thus, atmospheric N deposition, which is generally higher in summer, is bound to have a positive effect on tree growth because N is most limiting in summer, during times of most active microbial and plant immobilisation. N deposition will also have the most significant effects during the stages of canopy closure, when nutrients are in highest demand.

According to Scholes & Nowicki (1998), it is expected that the introduction of pines causes a shift in dominant available nitrogen from nitrate to ammonium and from mineral N to predominantly organic N. The results of this study suggest that ammonium was the dominant N form in the soil under *P. patula* plantations because of higher rates of N mineralisation found in soil under *P. patula* plantations, but similar soil total N concentrations in the soil under the Driekop grassland and adjacent *P. patula* plantations. Ammonium may therefore have been the dominant N form in the soils under *P. patula* plantations. According to Geiger *et al.* (1999) ammonium grown plants have greater concentrations of free foliar amino acids than nitrate grown plants. The concentration of foliar amino acids and protein contents were significantly higher ($p<0.01$) in the *P. patula* plantations, when compared with the adjacent Driekop grassland, which is in agreement with the relatively high rates of N mineralisation found in the soil under the *P. patula* plantations. According to Miflin & Lea (1980), ammonium taken up from the environment or produced within the tissues, is rapidly assimilated into amino acids, which ensures that NH_4^+ does not accumulate to toxic levels in tissues (Ireland 1990). However, the *E. grandis* plantations also had significantly higher foliar amino acid and protein contents compared with the adjacent Brooklands grassland, but there were no clear trends with respect to comparative rates of N mineralisation. Martin *et al.* (1998) suggested that species with well developed sclerophylly have well developed metabolic activities to assimilate and store N when available and then use N effectively to cope with drought. The plantation foliage had slightly higher concentrations of arginine, relative to the other amino acids, which

corresponded with foliar N concentrations ranging beyond the physiological optimum of 2%, as calculated by Linder (1995) and low P and K concentrations relative to N. Nitrogen may have been stored as arginine in plantation foliage in response to relatively low P and K concentrations. Studies by Näsholm & Ericsson (1990) on *P. sylvestris* and Adams *et al.* (1995) on *Eucalyptus* species have suggested that arginine is accumulated in species adapted to nutrient poor habitats.

The Driekop grassland and adjacent *P. patula* plantations, underlain by dolomite, had higher soil total N and P concentrations compared with the Brooklands grassland and adjacent *E. grandis* plantations, underlain by granite. Louw & Scholes (2002) found that soils underlain by dolomite had higher soil total P concentrations compared with granite soils, which was in agreement with the findings of this study. Higher soil total N and P concentrations corresponded with higher foliar total N and P concentrations found in the *P. patula* plantations when compared with the *E. grandis* plantations. According to Richardson & Rundel (1998) *P. patula* needles contain a major proportion of the total nutrients whereas *Eucalyptus* foliage is a relatively less significant nutrient storage supply. The results of this study confirmed that *P. patula* needles were more important as N stores compared with the leaves of *E. grandis,* while the foliage of the *E. grandis* plantations had higher basic cation concentrations, as previously discussed in section 5.2.5.

The Driekop grassland had higher litter total N concentrations but lower foliar total N concentrations compared with the Brooklands grassland. The Brooklands grassland was burnt three months prior to sampling, which may have resulted in the higher foliar total N concentrations. Burning generally leads to higher foliar nutrient concentrations in the following seasons' growth because the nutrients contained in the previous seasons biomass are returned to the soil via ash inputs and are rapidly taken up by plants, except for those nutrients lost to the atmosphere through volatilization during fires of extremely high temperatures.

A litter C:N ratio greater than 30 indicates a N limited system with low potential for nitrification and thus low risk of N leaching. The litter C:N ratios, which ranged between 50 and 1120, suggested that N was limiting in both seasons and that it was more limiting in summer, in both grasslands and plantations. Furthermore, the ratios

were lower in the plantations when compared with the grasslands, suggesting that N was more limiting in the grasslands, with the exception of the 2 year old *P. patula* and the 13 year old *E. grandis*, which are dealt with in section 5.3.1. This was possibly because the litter collected was a combination of new and old litter. The C:N ratios in this study reflected an average C:N of the entire litter layer, consisting of previously decomposed litter as well as fresh litter on the soil surface. The litter C:N ratios were lower in the Driekop grassland compared with the Brooklands grassland implying that N was more limiting in the Brooklands grassland, possibly because it was recently burnt, which may have resulted in N losses through volatilisation.

Soil total C concentrations were similar when comparing the grasslands and plantations. Scott *et al.* (1999) and Giddens *et al.* (1997) found similar soil carbon concentrations under pastures and plantations. Scott *et al.* (1999) attributed the result to strong interactions between clay minerals and organic matter. Thus, similar soil total N and C concentrations found in grasslands and plantations were probably because of the similar clay contents, which protected the soil organic matter. However, the higher soil clay contents in the 13 year old *P. patula* plantation may be attributed to the higher soil total N concentrations in the 13 year old *P. patula* plantation, while higher clay contents in the 8 year old *E. grandis* plantation did not correspond with any differences in the soil total N of the 8 year old *E. grandis* plantation. The comparison made between the grasslands and plantations has shown that there was no evidence to suggest a decrease in soil total N, P and C in the upper 20 cm of soil under plantations, in spite of the conversion from grasslands to plantations and the impacts of successive harvesting. However, the results of this study provided a snap shot of the nutrient status across grasslands and adjacent plantations and therefore do not reflect long-term trends associated with afforestation.

5.3.Age related trends

Age related trends were obscured as a result of higher soil clay contents found in the 13 year old *P. patula* plantation and the 8 year old *E. grandis* plantation as well as the implementation of various silvicultural practises on the plantations. Nevertheless, trends with increased plantation age were observed and are discussed below.

The soil pH decreased in the older *P. patula* and *E. grandis* plantations. Decreased soil pH, with increased plantation age, was more pronounced in the *E. grandis* plantations. Decreased soil pH corresponded with decreased sum of soil exchangeable cation concentrations with increased *P. patula* age. The cumulative effects of the continual uptake of positively charged cations and its associated release of H^+ ions as the plantations age, probably resulted in lower soil pH and decreased sum of soil exchangeable basic cation concentrations with increased *P. patula* plantation age. Concurrently, the litter total Ca^{2+} concentrations increased with increased *P. patula* age, which was probably because Ca^{2+} is relatively immobile in plant material because it is stored as oxalates in and between cells in leaves. In summer, the soil total C concentrations decreased with increased *P. patula* plantation age possibly because the litter layer thickened with increased plantation age, and any leached soluble carbohydrates were rapidly immobilised or mineralised directly from the litter layer, without initially having reached the soil.

In winter, litter total N concentrations increased with increased *P. patula* and *E. grandis* plantation age. Morris (1986) found that older *P. patula* plantations dropped fewer needles but increasing amounts of cones and branches. Younger stands retranslocated higher amounts of nutrients relative to the older stands and the litter quality, in terms of C:N ratios, increased as the plantations aged. Dames (1996) also found increased litter quality with stand age, where the C:N ratios of the younger stands ranged from 40:1 and older stands ranged from 18:1. Litter from younger stands would therefore decompose more slowly than that of older stands because litter in older plantations had higher N concentrations and lower soluble carbohydrates, associated with lower growth rates in older plantations. In contrast, the soil C:N ratios decreased with increased *E. grandis* plantation age, which may have implied a potential accumulation of N relative to carbon in the soil under the *E. grandis* plantations.

According to Linder (1995), the physiological optimal nutrient concentrations relative to nitrogen for leaves is fairly stable between species and thus can be used as an index for nutrient deficiency. Nitrogen concentrations, during winter, in the upper canopy of the *P. patula* plantations, increased with plantation age from 1.85% in the 2 year old

P. patula plantation, to 2.46% in the 30 year old *P. patula* plantation. According to Linder (1995), the optimal N concentration was 2%, which implied that the *P. patula* plantations were well supplied with N and that the older plantations had N concentrations in excess of the physiological optimal value, possibly as a result of reduced growth rates associated with ageing and low P and K concentrations relative to N. The nitrogen concentrations of the *E. grandis* plantations were lower, compared with the *P. patula* plantations, but increased with increased plantation age from 1.69% in the 2 year old *E. grandis* plantation to 2.12% in the 13 year old *E. grandis* plantation, which according to Herbert (1996) was above the minimum of 1.25% but below the optimum value of 2.98%. Increased foliar total N concentrations in the *P. patula* and *E. grandis* plantations corresponded with increased foliar arginine and glutamic acid relative to other amino acids, together with increased foliar protein contents with increased plantation age.

The winter P:N ratios were below the optimal range of 10-15 (Linder 1995) in the upper canopies of the older *P. patula* and the older *E. grandis* plantations, and the P:N ratios decreased with increased plantation age. The K:N ratios in the upper canopies of the *P. patula* plantations were below an optimal range of 35-45 (Linder 1995). The K:N ratios in the *E. grandis* plantations were above the optimal range, but decreased with increased plantation age. The ratios for all the other measured elements were above the respective target values and thus P and K^+ were the two nutrients most limiting growth in both the *P. patula* and *E. grandis* plantations, at the current N concentration. Foliar N, P and K^+ concentrations found in the *E. grandis* plantations were in agreement with the findings of Carlson *et al.* (2001) who found that *E. grandis* plantations located on the eastern escarpment, underlain by granite, were low in foliar N, P and K^+, when compared with foliar concentrations found under optimal conditions as stipulated by Herbert (1996).

5.3.1. Factors affecting the time series in the plantations

In terms of the observed trends associated with plantation age, both the *P. patula* and *E. grandis* plantations had site factors that confounded the time series. The Driekop grassland and the 2 year old *P. patula* plantation occurred on a western aspect while

the 13 and 30 year old *P. patula* plantation occurred on an eastern aspect, although the sites were physically adjacent to one another and the difference in aspect was not pronounced. Furthermore, the 2 year old *P. patula* plantation was pruned a few weeks prior to the summer sampling event in January 2003. The fresh, pruned foliage was broadcasted over the soil surface. Pruning may have resulted in the significantly higher ($p<0.05$) litter total N and P concentrations found in the 2 year old *P. patula* plantation when compared with litter total N and P concentrations found in the 13 and 30 year old *P. patula* plantations.

The 13 year old *P. patula* and the 8 year old *E. grandis* plantations, had soil clay contents which were significantly higher ($p<0.01$) than the other plantations and the grasslands. Higher clay contents would have rendered the rates of soil chemical and biological processes higher than that of soil with lower soil clay contents. The 13 year old *P. patula* plantation was thinned in the year 2000, but increased soil total carbon concentrations through root mortality and decomposition from the harvested trees was not found. The light fraction of the carbon pool, which was not analysed, may have detected an increase in soil carbon. The thinning would have allowed for increased light penetration, increased soil temperature and possibly increased microbial activity, which was not apparent in the results of this study.

The 8 year old *E. grandis* plantation was located approximately 200 m north west of the Brooklands grassland, while the Brooklands grassland, the 2 and 13 year old *E. grandis* plantations were located adjacent to one another. The 8 year old *E. grandis* plantation had the lowest sum of soil exchangeable basic cation concentrations, highest soil exchangeable aluminium concentration and the highest aluminium saturation relative to the other *E. grandis* and *P. patula* plantations. It also had the highest soil clay content and anaerobic N mineralization index, in spite of low soil pH. The soil nutrient status may have been a result of the cumulative impacts of the site history. Furthermore, the 8 year old *E. grandis* plantation was burnt less than a year prior to the planting, but the effects of burning would have waned in the first few years after planting and would therefore not have influenced the results of this study.

5.4.Seasonal related trends

The following seasonal trends were based on too short a time frame for any confident deductions. It is recommended that the seasonal patterns are investigated over numerous, successive seasons. Nevertheless, the following trends were distinguished. Soil C:N ratios were generally higher in winter, because of the build up of carbon over the dry season through litter inputs and limited microbial activity in winter. Foliar C:N ratios were higher during summer, compared with winter, in both the *P. patula* and *E. grandis* plantations. Linder (1995) found that there was an accumulation of starch in Norway Spruce foliage in summer. The higher C:N ratios were probably a result of starch accumulation and higher rates of nitrogen use during the growing season. However, both grasslands had higher foliar C:N ratios in winter, compared with summer. This was possibly because the grasses were relatively dormant in winter and thus the nitrogen was retranslocated to underground storage organs.

Litter total base cations, total N and C concentrations were generally higher in winter, compared with summer in both grasslands and plantations. Foliage was dropped at the end of the most active growing season and were relatively high in nutrient concentrations. Thereafter, nutrients were leached and/or reabsorbed most actively during the next growing season. Furthermore, a rainfall event occurred one or two days, prior to the winter sampling. Thus, atmospheric deposition associated with the late August rains, may have contributed to higher litter nutrient concentrations found in winter. Seasonally induced leaching was previously discussed in section 5.2.6.

5.5.Inter-canopy variations in the *P. patula* and *E. grandis* plantations

Generally, the foliar total N concentrations, protein and amino acid contents of the lower and upper canopies were not significantly different. However, the total N concentrations in the upper canopy foliage of the 2 year old *E. grandis* plantation, in winter, and the 2 year old *P. patula* plantation, in summer, were significantly higher ($p<0.01$) when compared with the lower canopies. This was probably because of higher growth rates in the younger leaves, located at the crown of the canopy. Evidence from field and laboratory studies showed that N concentrations were lowest

in shade-adapted leaves and highest in leaves exposed to high levels of sunlight, thereby distributing N so as to maximise canopy assimilation (Leuning *et al.* 1991). Inter canopy variations were expected to occur in the older plantations, subjected to higher levels of light limitations imposed on the lower canopies by adjacent trees. However, the 13 year old *P. patula* plantation was thinned and the *E. grandis* plantations undergo self pruning and therefore light limitations, associated with increased height and plantation age, were minimised. Similarly, foliar base and acid cation concentrations in the lower and upper canopies of the *P. patula* and *E. grandis* plantations were generally similar with no clear trends.

5.6. Indicators of nutrient status

The soil and foliage were the more indicative of the nutrient status of the grasslands and plantations than that of the litter. The relatively low base cation concentrations in the soil corresponded with relatively low base cation concentrations in the foliage of the *P. patula* plantations while relatively higher base cation concentrations in the soil corresponded with relatively higher base cation concentrations in the foliage of the *E. grandis* plantations. However, the relatively high acid cation concentrations in the soil did not correspond with higher acid cation concentrations in the foliage of the plantations probably because exudates form mycorrhizal associations chelated acidic compounds, thereby preventing their uptake into plantation foliage and allowing plantations to tolerate relatively low soil pH. In contrast, the acidic cation concentrations were low in the soil under grasslands, whilst the foliar acidic cation concentrations were higher compared with that of the adjacent plantations. In both the grasslands and the plantations, foliar total N, P and C concentrations were higher compared with the soil, but the foliar P:N and K:N ratios indicated that P and K concentrations were low relative to N concentrations and were more sensitive indicators of the nutrient status of the actual tree. In the *P. patula* plantations, high rates of soil N mineralisation corresponded with high litter and foliar total N concentrations, while in the *E. grandis* plantations high litter and foliar total N concentrations did not correspond with higher rates of N mineralisation. Generally, the nutrient concentrations of the lower and upper canopies were not significantly

different and the sub division of the lower and upper canopies for further foliar nutrient analyses is not recommended.

6. CONCLUSIONS

The overall conclusion is that afforestation of grasslands by plantations has altered nutrient cycling. *P. patula* plantations have possibly reduced base cation concentrations in the upper 20 cm of soil, while *E. grandis* plantations have enriched base cation concentrations in the upper 20 cm of soil, through a deeper rooting strategy. Both plantation species showed lower soil pH values and higher acidic cation concentrations compared with adjacent grasslands while soil total N, P and C concentrations in the upper 20 cm of the plantations were similar to that of the adjacent grasslands. In contrast, foliar total N, amino acids and protein contents were higher in the plantations, compared with the adjacent grasslands. Foliar P and K concentrations were low relative to N and appeared to be the nutrients most limiting for growth in plantations.

The following answers each of the originally proposed key questions:

1. How do selected nutrients in grasslands and *P. patula* and *E. grandis* plantations differ?

The plantations had significantly lower soil pH ($p<0.05$) values when compared with the adjacent grasslands. Higher concentrations of H^+ ions in plantations were possibly a result of higher uptake of cations and the associated release of H^+ ions into the soil, and the continual exportation of basic cations through successive biomass harvesting. Lower soil pH in the upper 20 cm of the soil under the *P. patula* plantations, compared with the Driekop grassland, resulted in the replacement of basic cations with acidic cations on the cation exchange complex. Lower soil pH was found in the soils under the older *E. grandis* plantations compared with the older *P. patula* plantations, probably because of differing site histories and more frequent biomass removal through harvesting of *E. grandis* plantations at shorter intervals.

The soil total, soil exchangeable and the sum of soil exchangeable basic cation concentrations in the *E. grandis* plantations were similar to those found in the adjacent

Brooklands grassland, in spite of the harvesting of the *E. grandis* plantations. *E. grandis* plantations are deeper rooted than *P. patula* plantations, thereby enriching the surface soil layers by extracting nutrients from deeper soil horizons and returning the nutrients to the soil through litterfall and decomposition. The soil Ca:Al ratios found in the *P. patula* plantations and the 8 and 13 year old *E. grandis* plantations has, in other studies indicated adverse effects on plant growth. The differences in the soil exchangeable basic cation concentrations, when comparing the *P. patula* and *E. grandis* plantations, were possibly a culmination of the different geologies, rainfall, site histories, rooting depths and associated nutrient uptake mechanisms, rates of litter decomposition, rainfall induced foliar leaching and the collection and interception of atmospheric compounds.

Generally, litter and foliar total basic cation concentrations were higher, whilst litter and foliar total acidic cation concentrations were lower, in the plantations when compared with the adjacent grasslands. The plantations had higher soil acidic cation concentrations compared with the adjacent grasslands, while the litter total acidic cation concentrations were higher in the grasslands. Exudates from mycorrhizal associations may have chelated the metals and thereby prevented their uptake into plantation foliage. Higher litter total basic cation concentrations found in the *P. patula* plantations, did not correspond with higher soil exchangeable basic cation concentrations in the *P. patula* plantations, probably because the nutrients were accumulated in the litter layer. In contrast, higher litter total basic cation concentrations corresponded with a higher range of the sum of soil exchangeable basic cation concentrations found under the *E. grandis* plantations, compared with the Brooklands grassland and corresponded with the deeper rooting strategy of *E. grandis* and litterfall induced enrichment of surface soil layers.

The *E. grandis* plantations, underlain by granite, had higher litter and foliar total basic cation concentrations and corresponding higher soil total and exchangeable basic cation concentrations relative to the *P. patula* plantations, underlain by dolomite. In contrast, the soil, litter and foliage of the Driekop grassland, underlain by dolomite, were relatively nutrient rich compared with the Brooklands grassland, underlain by granite. Litter and foliar total acidic cation concentrations were higher in the *P. patula* plantations when compared with the *E. grandis* plantations, except for litter total iron concentrations. The *P. patula* plantations had correspondingly higher soil

exchangeable aluminium and soil aluminium saturation on the cation exchange complex and were therefore taking up more aluminium compared with the *E. grandis* plantations. The *P. patula* plantations have decreased the base cation concentrations in the upper 20 cm of soil, compared with the adjacent Driekop grassland, while the *E. grandis* plantations have increased the base cation concentrations of the upper 20 cm of soil, compared with the adjacent Brooklands grassland.

Soil total N, P and C concentrations were similar when comparing the grasslands and plantations, while foliar total N, amino acids and protein contents were higher in the plantations. The results of this study confirmed that *P. patula* needles were more important as N stores compared with the leaves of *E. grandis,* while the foliage of the *E. grandis* plantations had higher total basic cation concentrations. However, relative to nitrogen, foliar ratios indicated that phosphorus and potassium were the most limiting nutrients for the plantations and corresponded with higher concentrations of arginine relative to other amino acids and protein concentrations in plantations.

The Driekop grassland and adjacent *P. patula* plantations, underlain by dolomite, had higher soil total N, rates of N mineralisation and total P concentrations compared with the Brooklands grassland and adjacent *E. grandis* plantations, underlain by granite. Higher soil total N and P concentrations corresponded with higher foliar total N and P concentrations found in the *P. patula* plantations, compared with the *E. grandis* plantations. The comparison made between the grasslands and plantations has shown that there was no evidence to suggest a change in soil total N, P and C in the plantations, in spite of the conversion from grasslands to plantations and the successive exportation of nutrients through harvesting. However, the upper 20 cm of the soil found under *P. patula* plantations indicated relatively low base cation concentrations and high acid cation concentrations compared with the adjacent grassland.

The soil moisture contents were higher in the soil found under *P. patula* plantations and the adjacent Driekop grassland, compared with the *E. grandis* plantations and the adjacent Brooklands grassland because of higher altitude of the former, together with higher rainfall and lower rates of evaporation. The *P. patula* plantation had higher soil moisture contents compared with the adjacent Driekop grassland, possibly because the

litter layer under the *P. patula* plantations retains more water than bare soil and reduces soil evaporation from the mineral soil. In contrast, the soil moisture contents under the *E. grandis* plantations were lower when compared with the adjacent Brooklands grassland because *Eucalyptus* plantations have higher rates of water use and transpiration and a poorly developed litter layer compared with *Pinus*.

The rates of N mineralisation were higher in the soil under *P. patula* plantations compared with the adjacent Driekop grassland. In summer, the rates of N mineralisation in the Driekop grassland, ranged below zero, which indicated that the microbes were utilizing N primarily for their own sustenance, while the *P. patula* plantations had positive rates of N mineralisation and therefore higher N availability for plant uptake. Higher rates of N mineralisation in the *P. patula* plantations corresponded with higher litter and foliar total N concentrations relative to the adjacent Driekop grassland. In contrast, there were no clear trends when comparing the rates of N mineralisation between the Brooklands grassland and adjacent *E. grandis* plantations.

2. How do the soil, litter and lower and upper canopy foliar nutrients differ with plantation age and season?

Age related trends were obscured as a result of higher soil clay contents found in the 13 year old *P. patula* plantation and the 8 year old *E. grandis* plantation as well as the various silvicultural practices implemented. Nevertheless, the following age related trends were noted. The cumulative effects of the continual uptake of cations and its associated release of H^+ ions and the continual uptake of base cations for growth as the plantation ages, resulted in the lower soil pH with increased plantation age. The sum of soil exchangeable basic cation concentrations decreased with increased *P. patula* plantation age, while this trend was not apparent in the soil found under the *E. grandis* plantations. The ratio of P:N and K:N decreased in the older plantations, while foliar protein and amino acid, arginine, concentrations increased in older plantations. Low P and K concentrations possibly resulted in reduced growth rates and hence, N storage as protein and arginine.

High plantation foliar C:N ratios, in summer, were probably a result of starch accumulation and higher rates of nitrogen use during the growing season. However, the grasslands had higher foliar C:N ratios in winter, compared with summer because N was retranslocated to underground storage organs. Litter total base cations, total N and C concentrations were generally higher, in winter, compared with summer in both grasslands and plantations because of lower rainfall, lower rates of decomposition, lower growth rates and the litterfall during the previous autumn.

3. What are the relationships between soil, litter and foliar variables?

The soil and foliage were more indicative of the nutrient status of the grasslands and plantations. Base cation concentrations in the soil and foliage corresponded while acidic cation concentrations in the soil and foliage did not correspond probably because exudates from mycorrhizal associations chelated acidic compounds, thereby preventing its uptake into plantation foliage, allowing plantations to tolerate relatively low soil pH. In both the grasslands and the plantations, foliar total N, P and C concentrations were higher compared with the soil, but the foliar P:N and K:N ratios indicated that P and K were low relative to foliar N concentrations and were more sensitive indicators of the nutrient status of the plantations than that of the litter.

7. RECOMMENDATIONS

The P:N and K:N ratios found in the plantations indicated that P and K are possibly limiting growth, resulting in the accumulation of foliar N. Relatively high foliar N concentrations may render plantations relatively less frost resistant and increasingly susceptible to insect infestations. In addition, low base cation concentrations coupled with high acid cation concentrations found in the soil under plantations, compared with that of the grasslands, may impact on the long-term sustainability of the *Pinus* plantations located on the eastern escarpment of South Africa. The following is recommended for further studies:

1. Based on the findings that P and K were the nutrients most limiting plantation growth in relation to N, it is recommended that multi-factorial N, P and K trials be implemented which will allow for the testing of long-term residual fertiliser effects. These trials would build on the knowledge gained in the 1970s and 1980s and allow for a much better predictive understanding of the constraints limiting plant growth.
2. The P and K limitations relative to N should be tested using the permanent sampling plots in the Mpumalanga Province across a gradient of altitude and rainfall. Soil and foliar sampling should be conducted from as many sites as possible.
3. In terms of sampling for the determination of foliar nutrient analyses, one should sample at least six trees per plantation, every second year. The same trees should be sampled in order to investigate changes in the nutrient status over time. No major trends were found when comparing the lower and upper canopy foliar samples and thus the sub division of the lower and upper canopies is not recommended for further foliar nutrient analyses.

8. APPENDICES

9. REFERENCES

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